Spatial patterns of seagrasses and salinity regimes interact to structure marine faunal assemblages in a subtropical bay

Rolando O. Santos[1,5,*], Diego Lirman[1], Simon J. Pittman[2,3], Joseph E. Serafy[1,4]

[1]Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, FL 33149, USA
[2]Biogeography Branch, Marine Spatial Ecology Division, National Centers for Coastal Ocean Science,
U.S. National Oceanic & Atmospheric Administration, 1305 East-West Highway, Silver Spring, MD 20910, USA
[3]Marine Conservation & Policy Research, Marine Institute, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK
[4]NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149, USA

[5]*Present address:* Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA

ABSTRACT: Anthropogenic disturbances in coastal and marine environments have resulted in the transformation of vegetated benthic habitat spatial patterns, which is thought to influence the distribution, community composition, and behavior of marine fauna. In Biscayne Bay, Florida, USA, freshwater discharges into nearshore areas have resulted in the fragmentation of the spatial patterning of submerged aquatic vegetation (SAV). To understand the ecological consequences of the freshwater-induced SAV seascape fragmentation, fish and crustaceans were sampled using seine nets across seascapes with continuous and highly fragmented SAV spatial configurations and across salinity regimes. Fragmented SAV seascapes supported significantly higher species diversity of fish and crustaceans, especially in areas influenced by freshwater discharges. Also, fragmented seascapes supported a higher abundance of the pink shrimp *Farfantepenaeus duorarum* and the goby *Gobiosoma robustum,* and higher biomass of generalist predatory fishes than seascapes with continuous SAV. In contrast, pinfish *Lagodon rhomboides* was more abundant in seascapes with continuous SAV. Faunal assemblage composition differed between zones of contrasting salinity regimes, and the contribution of species occurrence and abundance to the differentiation of assemblage composition between seascape types was associated with the salinity regimes of the seascapes. Thus, water salinity and spatial properties of SAV seascapes are factors that interact to influence faunal community structure in Biscayne Bay. These findings highlight the importance of understanding how environmental context (e.g. salinity regimes) can modulate the influence of benthic spatial patterning on the abundance and biodiversity of nekton communities.

KEY WORDS: Seascape ecology · Seagrasses · Submerged aquatic vegetation · Habitat fragmentation · Species diversity

INTRODUCTION

Submerged aquatic vegetation (SAV), such as seagrasses and macroalgae, is distributed across time and space in a variety of configurations. The spatial configuration, or spatial pattern, of vegetated seafloor habitats influences the distribution and abundance of many associated marine species (Pittman et al. 2004, Boström et al. 2011). The study of the ecological consequences of spatial pattern is the core theme of landscape ecology, with the key underlying premise that both the composition and spatial arrangement of a landscape mosaic affect ecosystem structure and function in ways that are different

where spatial patterns differ (Wiens et al. 1993, Turner et al. 2001).

Considerable research in terrestrial landscape ecology has focused on the process and consequences of habitat fragmentation. Habitat fragmentation is a landscape process that breaks apart large, continuous patches into smaller units, changing the amount of habitat available for associated organisms, the ratio between the edge and core habitat, patch size, and connectivity (Fahrig 2003, Lindenmayer & Fischer 2007, Didham et al. 2012). According to the static island biogeographic model, the spatial transformation through fragmentation and habitat loss can progress through several phases of spatial patterns (i.e. perforation, dissection, subdivision, shrinkage, and attrition), all ultimately resulting in the creation of fragmented or patchy landscape patterns (Forman 1995, McGarigal et al. 2005). Species respond to landscape patterns resulting from habitat fragmentation in different ways (i.e. negative and/or positive effects) and at different spatial scales depending on their ecological needs (Betts et al. 2007, Villard & Metzger 2014). Here, we explore the relationship between spatial patterning and the community structure of diverse nektonic organisms associated with SAV.

Seascape ecology, the marine counterpart of landscape ecology, has focused predominantly on SAV seascapes (i.e. mosaics of seagrass/algae patches within a sediment matrix) revealing dynamic spatial patterning and associated ecological consequences (Boström et al. 2011). The dynamics of SAV patches are influenced by a range of internal organismal and external factors. Internal factors encompass a species' ability to resist and recover from disturbance (recolonization ability, growth rates, and other life history traits). External factors include physical and biological disturbances (Fonseca & Bell 1998, Gillanders 2007, Jackson et al. 2017). For example, SAV patches can become fragmented by wave action and other hydrodynamic forces (Fonseca & Bell 1998), sedimentation events (Frederiksen et al. 2004), 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 (Waycott et al. 2009, Santos et al. 2011), as well as direct physical removal by dredging, vessel groundings, and propeller scarring (Orth et al. 2006).

Seascape ecology studies have provided important insights into how spatial patterns of SAV habitats influence faunal assemblages (Turner et al. 1999,

Pittman et al. 2004, Boström et al. 2011, Hensgen et al. 2014). Field studies and simulation modeling indicate that both the composition (i.e. habitat amount and types) and spatial configuration (i.e. spatial arrangement, connectivity) of seascapes influence key ecological processes such as faunal recruitment, dispersal, and survivorship (Irlandi & Crawford 1997, Pittman et al. 2004, Hovel & Regan 2008).

While habitat fragmentation and habitat loss are typically reported as undesirable endpoints, some degree of habitat fragmentation can, in fact, increase species diversity and the abundance and growth of certain species through positive edge effects and increased spatial heterogeneity (Fahrig 2003, Ries & Sisk 2004). Edges are boundaries or transition zones between adjacent habitat patches that exhibit abrupt changes in physical structure, biomass, and assemblage composition (Ries & Sisk 2004, Porensky & Young 2013). Edge effects in vegetated seascapes are associated with higher fish and epifaunal abundance (Bologna & Heck 2002, Macreadie et al. 2010b, Boström et al. 2011, Pierri-Daunt & Tanaka 2014). SAV habitat edges may positively affect faunal abundance by increasing movement between patches, increasing the accumulation of food resources, and modifying predation (Ries & Sisk 2004, Macreadie et al. 2010b). In fragmented or patchy habitats, edge effects can permeate the entire seascape (Porensky & Young 2013). Fragmentation increases the proportion of edge-to-interior habitat, which may influence prey–predator interactions, and the proportion of specialist and generalist species (Bell et al. 2001, Ries & Sisk 2004). Habitat fragmentation can also increase spatial heterogeneity by increasing the amount and diversity of microhabitats that could be utilized by different species (Horinouchi et al. 2009). Furthermore, fragmented SAV seascapes can influence prey accessibility and predation success, which affect assemblage structure and function of the nekton community (Hovel et al. 2002, Connolly & Hindell 2006, Boström et al. 2011).

Previous studies on the influences of SAV habitat structure on faunal composition have often provided contradictory results (Connolly & Hindell 2006, Bell et al. 2007, Boström et al. 2011, 2017). Part of the difficulty encountered when examining faunal–habitat relationships relates directly to the often limited spatial scale of previous studies that have examined the effects of fragmentation at the scale of individual patches rather than the broader context of the seascape (Boström et al. 2011). Habitat fragmentation, however, is a process that occurs across mosaics of

patches, where the size of patches, distances between patches, and composition of the matrix (e.g. unvegetated sediments) influence organisms and ecological processes (McGarigal & Cushman 2002, Boström et al. 2011, Driscoll et al. 2013). Thus, a seascape approach is needed to fully understand key faunal–habitat relationships.

We examined the influence of the spatial configuration of SAV seascapes on spatial patterns of marine faunal diversity, abundance, and distribution, and evaluated both increases and decreases of faunal responses in seascapes with differing spatial configurations. We assessed habitat–faunal relationships using a field sampling design that takes into account spatial variability in seascape patterning using a binary patch-matrix model (Fig. A1 in the Appendix), whereby patches are classified as either dominated by seagrasses or unvegetated (i.e. dominated by sediments). We also explored the interaction between habitat patterning and salinity environments in nearshore SAV habitats of Biscayne Bay (Florida, USA). Biscayne Bay has been altered by water management practices that release fresh water seasonally from drainage canals. The pulsed release of fresh water into littoral habitats has been linked directly to the fragmentation of SAV seascapes in this coastal lagoon (Santos et al. 2011, 2016). Concomitantly with seascape transformation, changes in salinity regimes across Biscayne Bay nearshore areas have been linked to the reduction of estuarine fish abundance and biomass, increased dominance of euryhaline species (i.e. organisms that can tolerate a wide range of salinity levels), and spatial changes in diversity patterns (Serafy et al. 1997, 2003, Browder et al. 2005). 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. Thus, the objective of this study was to determine the effects of changes in SAV seascape patterns induced by freshwater discharges on marine fish and crustacean assemblages. We combined field surveys with analytical tools from landscape ecology to test the hypotheses that:

(1) Fish and crustacean abundance, biomass, and diversity in more patchy, fragmented seascapes will be higher than in continuous vegetated seascapes (i.e. positive edge effects).

(2) Differences between seascapes would be accentuated in areas with a salinity regime characterized by wider ranges of salinity by providing a more spatially and temporally heterogeneous biophysical environment which promotes coexistence of different species.

MATERIALS AND METHODS

Study area

Biscayne Bay is a shallow-water subtropical lagoon (i.e. <3 m in depth) 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 SAV seascapes (<500 m from shore) in western Biscayne Bay, where seagrasses are the dominant benthic macrophyte (Lirman et al. 2008, 2014). SAV patches are mostly composed of the seagrass *Thalassia testudinum*, with some patches mixed with the seagrass *Halodule wrightii* and rhyzophitic and drift macroalgae (Lirman et al. 2014). SAV communities have been stable over the last 5 yr (Lirman et al. 2016). These vegetated communities, as well as the fringing mangroves, provide habitat for a large number of commercially and recreationally valuable species, including pink shrimp *Farfantepenaeus duorarum*, gray snapper *Lutjanus griseus*, hogfish *Lachnolaimus maximus*, and spotted seatrout *Cynoscion nebulosus* (Serafy et al. 1997, 2003, Faunce & Serafy 2008, Browder et al. 2012).

Seascape mapping

To quantify the spatial patterning of seascapes and to classify the study region into seascapes characterized by more continuous SAV and those with patchy, more fragmented SAV configurations, the seafloor (Fig. 1b) was mapped first using a *K* nearest neighbor supervised classification applied to high-resolution multispectral satellite images (Quickbird-2 satellite images, 2.4 m pixel size) of the study region acquired in November 2009 (ITT Visual Information Solutions 2008, Xie et al. 2008). The statistical classification technique was based on an object-based (ENVI v4.5 Feature Extraction module, ITT Visual Information Solutions 2008) approach that identified and delineated patches with moderate to high macrophyte cover (>40% of the bottom occupied by SAV). We used >40% bottom cover as a threshold to define a dense patch because studies have defined diffuse or sparse SAV classes to areas with <40% SAV cover, and moderate and dense SAV classes to areas with
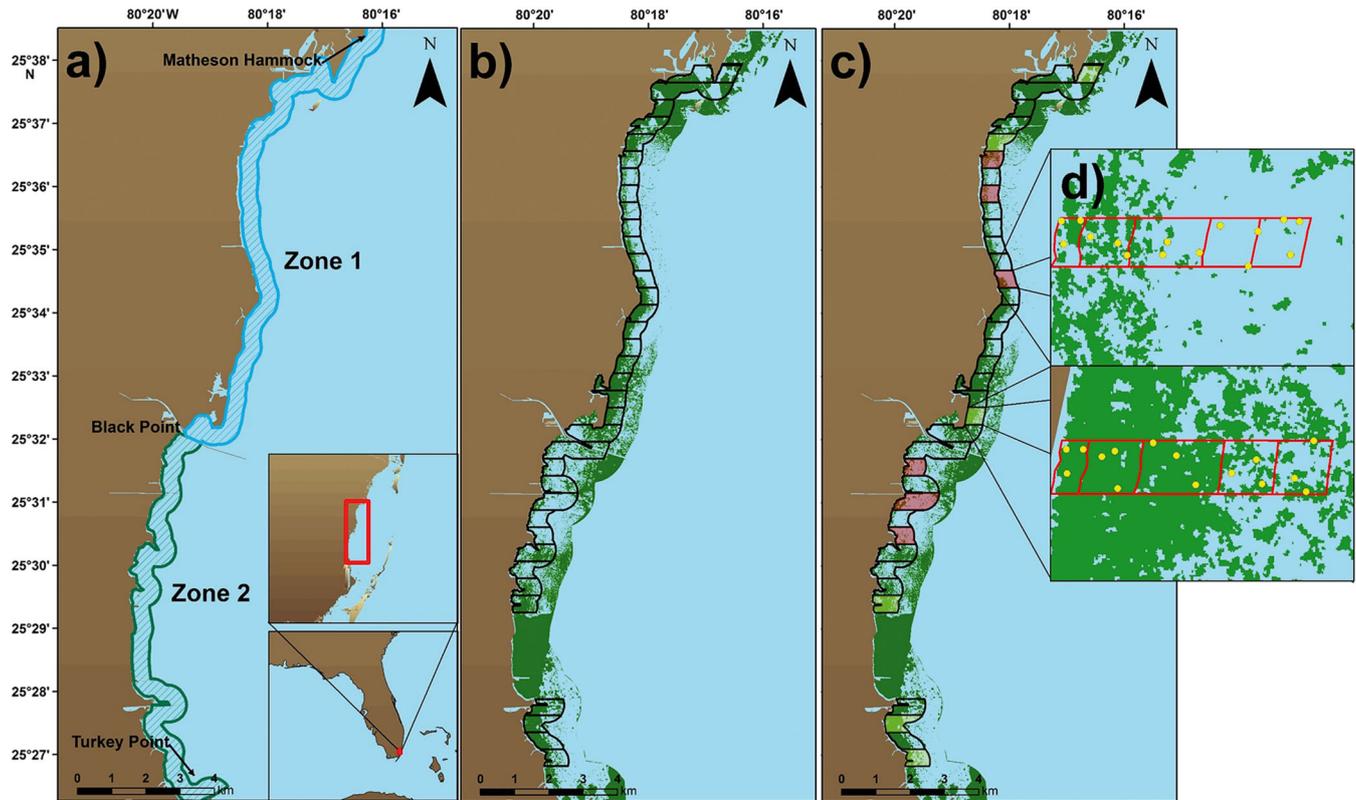
Fig. 1. (a) Study area and sampling design. The study area was divided into 2 zones based on salinity regimes: Zone 1 (high and stable salinity, blue) and Zone 2 (low and variable salinity, green). (b) Submerged aquatic vegetation (SAV) seascape map (dark green patches) with superimposed 500 × 500 m grid cells (i.e. seascape sampling unit; black line grid); some grid cells in the south were excluded due to cloud cover interference with the image classification process. (c) Seascape sampling units randomly selected and classified as continuous (light green) and fragmented (red) SAV seascapes. (d) Within each selected grid cell, a 100 × 500 m plot was centered. Each plot was divided into 5 distance-to-shore strata (100 × 100 m) where 3 sampling replicates (yellow points) were randomly placed

~≥40% SAV cover (Mumby & Edwards 2002, André-fouët et al. 2003).

Object-based image classification optimized the delineation of exterior and internal patch boundaries (e.g. gaps, perforations) and provided better discrimination between highly vegetated and sparse patch classes under varying water depth and image quality conditions than per-pixel based image classification methods (Santos et al. 2011). Because objects (i.e. image segments with distinct 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).

The average percent cover of SAV from 153 georeferenced locations was used to inform the statistical classification algorithm and estimate the accuracy of the seascape map produced. Approximately 20 benthic photos were taken at each of the 153 georeferenced locations for SAV community characterization, following the methods of Lirman et al. (2014).

The delineation of the vegetated patches resulted in an overall accuracy of 65%, and user accuracy of 64% (i.e. the probability that a pixel classified into a given category represents that category on the ground). Even though this accuracy demonstrated only a moderate degree of agreement between the maps and reference locations (Lathrop et al. 2006, Lyons et al. 2010), maps were accepted as an accurate representation of the seagrass seascape in Biscayne Bay for the following reasons. (1) The accuracy estimate of the maps may have been compromised due to the horizontal disagreement between the satellite images and the true position of the location used for the accuracy assessment. (2) The values assigned to the locations used for this assessment were average percent cover estimates of SAV using a series of benthic photos taken around the assigned reference location, thus increasing the probability of spatial mismatch values between the reference location and the habitat representation at the map scale (Xie et al. 2008).

Table 1. Spatial pattern metrics used to quantify composition and configuration of submerged aquatic vegetation (SAV) seascape patterns in Biscayne Bay, Florida (USA). Metrics were used in multivariate analysis to identify continuous and fragmented SAV seascapes. Variables in formulas: A: total landscape area (m^2); a_{ij}: area (m^2) of patch type (class) i; n_i: total number of patches of type (class) i; e_{ik}: total length (m) of edge in landscape involving patch type (class) i; p_{ij}: perimeter (m) of patch ij

Metric	Abbreviation	Category	Aspect	Description	Formula
Percentage of landscape	PLAND	Composition	Area/density	Percentage of the total landscape made up of the corresponding class	$PLAND = \dfrac{\sum_{j=1}^{n} a_{ij}}{A}(100)$
Mean patch size (ha)	MPS	Composition/ configuration	Area/density	Average size of a particular class	$MPS = \dfrac{\sum_{j=1}^{n} a_{ij}}{n_i}$
Patch size coefficient of variation (ha)	PSCV	Configuration	Area/density	Variability in patch measures	$PSCV = \dfrac{\sqrt{\dfrac{\sum_{j=1}^{n}\left(a_{ij}-MPS\right)^2}{n_i}}}{MPS}$
Patch density (patches ha^{-1})	PDENS	Configuration	Area/density	Number of patches of a certain class divided by the total landscape area	$PDENS = \dfrac{n_i}{A}$
Total edge (m)	TE	Configuration	Edge	Sum of the lengths of all edges	$TE = \sum_{k=1}^{m} e_{ik}$
Area-weighted mean patch fractal dimension	AWMPFD	Configuration	Shape	Measure of patch shape complexity	$AWMPFD = \sum_{j=1}^{n}\left[\dfrac{2\ln(0.25\,p_{ij})}{\ln a_{ij}}\left(\dfrac{a_{ij}}{\sum_{j=1}^{n} a_{ij}}\right)\right]$

Spatial patterns of SAV seascapes

To assess the influence of seascape spatial patterning (i.e. seascape effects) on fish and crustacean assemblages, various spatial pattern metrics were used to classify the survey sites (n = 12 sites) into different SAV seascape categories: fragmented (FS) and continuous seascape (CS). First, using a geographical information system (GIS), a grid with 500 × 500 m cells was superimposed over the seascape maps delineating seascape sample units (SSUs) (i.e. 250 000 m^2 SSUs; Fig. 1b,c). The 500 m × 500 m grid cells were identified as SSUs because this spatial extent encompasses most of the seascape heterogeneity, and because SAV habitats <500 m from shore have been identified as the most heterogeneous SAV habitats where seascape differences can be observed along the mainland coast of Biscayne Bay (Santos et al. 2011). In addition, the area up to 500 m from shore has been identified as the area most likely to be influenced by freshwater management decisions and watershed restoration projects (Lirman et al. 2008).

The seascape characteristics within each grid cell were evaluated using spatial-pattern metrics that quantify structural attributes of seascape composition (variety and amount of patch types) and spatial configuration (spatial arrangement of patches). The 6 metrics calculated 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) (Table 1). These metrics have been widely used in landscape ecology to investigate faunal–landscape associations in terrestrial (Tischendorf 2001, Turner et al. 2001, McGarigal et al. 2005) and marine environments (Pittman et al. 2004, Sleeman et al. 2005, Santos et al. 2011), and are robust and stable across multiple spatial scales (Wu 2004). Each cell or SSU was classified as either FS or CS (Fig. 1c) using principal component analysis (PCA) and hierarchical cluster analysis as described by Santos et al. (2011) based on the seascape pattern metrics described above (Fig. 2). The 500 m × 500 m cells classified as CS had a higher proportion of the benthos covered by larger SAV patches with lower shape complexity. In contrast, FS cells had a higher density of
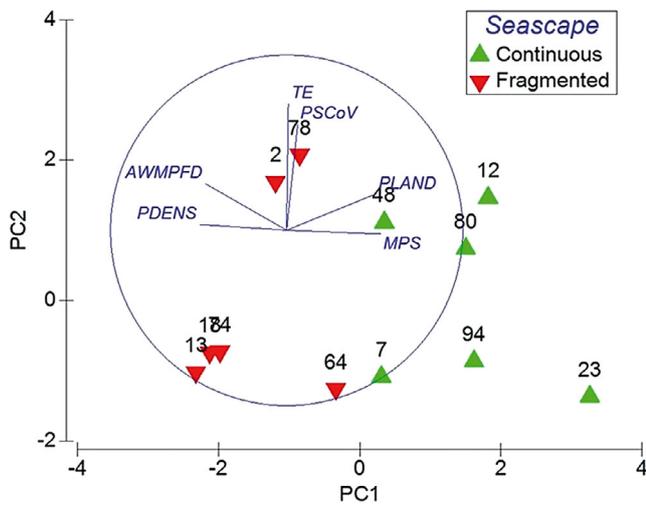
Fig. 2. Principal component analysis (PCA) based on the spatial pattern metrics (see Table 1) and performed to assess distinct seascape types. Based on this analysis, grid cells or seascape sampling units were grouped into 2 seascape types: continuous (green) and fragmented (red). The separation occurred across the first axis (PC1) which explained 49.7% of the variation. The second axis (PC2) explained 31.4% of the variation and illustrated heterogeneity in seascape patterns among seascape types
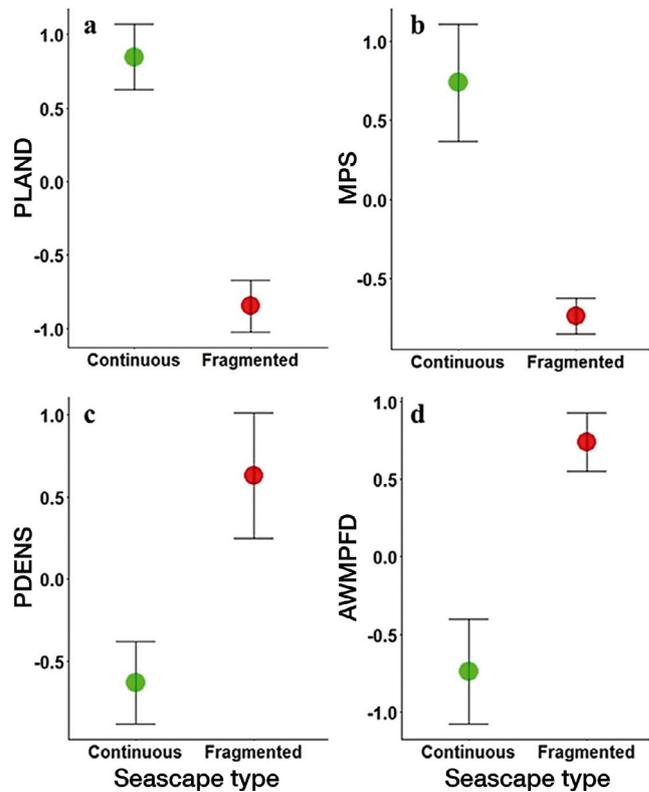

Fig. 3. (a) Proportion of the seascape occupied by submerged aquatic vegetation (SAV) patches (PLAND), (b) mean patch size (MPS), (c) patch density (PDENS), and (d) area-weighted mean patch fractal dimension (AWMPFD) between seascape types (error bars: SE). Values are expressed as the standardized distance from the mean (value subtracted by the mean and divided by the standard deviation). Grid cells classified as continuous SAV seascapes (green) tended to have a higher proportion of the bottom covered by larger SAV patches with lower shape complexity. In contrast, cells classified as fragmented SAV seascape had a higher density of smaller SAV patches with complex shapes and a lower proportion of the substrate covered by SAV. All spatial pattern metrics were significantly different between seascape types (see Table A1 in the Appendix)

smaller SAV patches with complex shapes and a lower proportion of the substrate covered by SAV patches (Fig. 3, Table A1 in the Appendix). A total of 12 cells was selected (6 in each of the salinity zones described below) at random, with 6 cells classified as FS and 6 as CS.

Due to the difference in salinity environments created by the release of fresh water from canals in Biscayne Bay (Caccia & Boyer 2005), sampling in this study was also replicated within 2 zones with distinct salinity regimes that have been previously described by Lirman et al. (2008, 2014) (Zones 1 and 2, Fig. 1a). Zone 1, an area with limited input of fresh water from canal structures, was characterized by higher and more stable salinity (wet season mean ± SD salinity: 26.6 ± 4.6 ppt, min−max: 13–36 ppt). In contrast, Zone 2 is influenced by pulsed freshwater flows from canals that create a nearshore environment with low and variable salinity (wet season mean salinity: 17.1 ± 8.2, min−max: 2–33) (Lirman et al. 2008, 2014, Santos et al. 2011). This sampling design allowed us to assess the influence of seascape spatial patterns on fish and crustaceans under different salinity environments. Three habitat grid cell replicates for each seascape type (CS and FS) were randomly selected within salinity Zones 1 and 2 (Fig. 1c,d). We were able to select different seascape types within each salinity zone due to different factors. For example, FS and CS in Zone 2 were

identified adjacent and distant to canals, respectively, thus enabling evaluation of the notion that freshwater pulses are a major driver of seascape structuring in Biscayne Bay. However, in Zone 1, seascapes classified as FS were identified close to natural creeks, but also in a portion of the bay characterized by shallow sediments and adjacent to exposed carbonate hardbottom (Lirman et al. 2003, 2008, Browder et al. 2005).

Fish and crustacean sampling

For the faunal sampling, a 100 m × 500 m plot or transect starting at the shore was randomly placed

within each SSU (average depth = 1.1 m, average depth range = 0.8 m; Fig. 1d). To document fish and crustacean assemblage composition, abundance, biomass, and diversity across the heterogeneous seascape, each plot within the SSU was divided into 5 distance-to-shore strata (100 × 100 m), and 3 seine sampling locations were randomly positioned within each of these distance-to-shore strata (n = 15 points plot^{-1}, 3 deployment sites stratum^{-1}; Fig. 1d). The fish and crustacean sampling was conducted in 2012 during the wet season (July–October). To maximize the probability of capture, the sampling was performed at night when many faunal species were actively foraging over seagrasses (Luo et al. 2009, Hammerschlag et al. 2010). In summary, the survey design included: 2 seascape types (FS and CS), 2 salinity zones (1 and 2), 3 replicates of each seascape type per salinity zone, 5 distance-to-shore strata within each plot, and 3 randomly located seine locations within each distance-to-shore stratum, for a total number of 180 seine locations.

Organisms were collected with a center-bag seine net (21.3 m long, 1.8 m deep, 3 mm mesh) following the Florida Marine Research Institute Fisheries-Independent Monitoring Program Procedure Manual (Florida Marine Research Institute 2007). The seine was deployed and retrieved by motorboat, and each seine haul swept a bottom area of approximately 210 m^2, including both SAV patches and the matrix (i.e. unvegetated or patches with low SAV cover) within the hauling area. In addition, we randomized the order of the seining hauls to promote the independence of replicates across the 100 × 500 m sampling plot and homogenize the distribution of environmental conditions (e.g. tides, moonlight, temperature).

Sample and data processing

The fish and crustaceans collected were identified to the lowest possible taxonomic level, counted, and measured (total length, mm). Several metrics were calculated to quantify species assemblages, including species diversity indices (see below), occurrence (presence/absence), and abundance (count of ind. seine^{-1}). Biomass (g seine^{-1}) was estimated using published length–weight relationships. Peer-reviewed scientific publications and reports were used to obtain allometric relationships to estimate biomass. The delta approach was used to account for positively skewed data and for zero-inflation (Serafy et al. 2007). The data were thus separated into a binary species occurrence matrix

(present = 1, absent = 0), and a species abundance and biomass matrix when present (Clarke & Warwick 2001, Serafy et al. 2007).

Different indices were used to assess the species diversity between seascape types to minimize any bias associated with any of the diversity indices (Clarke & Warwick 1998, Izsák & Papp 2000). The diversity indices considered were: number of species per sample (species richness), Shannon-Wiener index, Simpson diversity, and variation in taxonomic distinctness. Variation in taxonomic distinctness is a measure of 'biological diversity' that accounts for the taxonomic differences in 'relatedness' among the species rather than abundance. It is less biased by site-to-site differences in sample size and has been considered a proxy for functional diversity (Clarke & Warwick 1998, Izsák & Papp 2000).

There was a difference of over 2 yr between the date of capture of the imagery used to develop the SAV seascape map (November 2009) and the seine sampling (July–October 2012). While SAV abundance changes (i.e. growth and/or dieback) may have influenced some of the spatial pattern metric estimates due to changes in patch area, total edge, and perimeter:area ratios (Frederiksen et al. 2004, Cunha & Santos 2009), no significant changes in the SAV species composition or abundance across Biscayne Bay were recorded over the time span between the collection of the 2 data sources (Lirman et al. 2014, 2016). In addition to the consistent levels of SAV cover recorded in the area over the past 7–10 yr, SAV seascape fragmentation in Biscayne Bay is mostly a slow process that causes significant changes in spatial characteristics over decadal scales (Santos et al. 2016). Also, no major storms or hurricanes occurred during this period (Lirman et al. 2016; https://coast.noaa.gov/hurricanes/). Thus, we believe that seascape characteristics remained relatively constant between the habitat classification and the collection of fish and crustaceans.

Statistical analyses

Faunal responses (i.e. occurrence, abundance, biomass) sampled from the 3 seine hauls per distance-to-shore stratum were averaged. The averaged values per distance stratum were used as replicates within each seascape sampling unit to capture the species assemblage variability between the seascape type and salinity zone treatments.

To examine if the assemblage composition differed across seascape types and salinity zones, we used a

2-way crossed permutational multivariate analysis of variance (PERMANOVA, type model I) with 1000 residual permutations. PERMANOVA allows the use of dissimilarity measures to test for significance of specific effects (i.e. similar to a multivariate ANOVA) using a permutation test that does not require the data to follow a particular distribution, and therefore is more robust than parametric alternatives (Anderson et al. 2008). We evaluated a habitat effect (seascape types) and salinity effect (salinity zones) (both as fixed effects), as well as their interaction. We used the square-root of the estimated component of variation ($\sqrt{ECV}$) as a measure of the relative importance between the fixed factors (seascape types and salinity zones) and their interaction (Anderson et al. 2008). Next, constrained ordinations (with Seascape × Zone as a constrained factor) using a canonical analysis of principal coordinates (CAP; Anderson & Willis 2003, Anderson et al. 2008) were used to evaluate the differences in faunal assemblage composition within and among seascape types (CS and FS) and salinity zones (Zones 1 and 2). The correlations of individual species (i.e. species occurrence, abundance, biomass) with CAP axes were used to characterize the multivariate effect by determining which species were driving the assemblage composition differences between the seascape types and salinity zones (Anderson & Willis 2003).

The means of the diversity indices were compared among the seascape types and salinity zones using a full-factorial 2-way ANOVA. Post hoc multiple comparisons were made using the Tukey multiple comparisons of means.

All ordination procedures (PERMANOVA, CAP) were performed in PRIMER v6 with the add-on software PERMANOVA+ (Anderson et al. 2008). ANOVA and post hoc analysis were performed in R (R Core Development Team 2010). We used α = 0.05 on all tests to determine significant effects. Ordination multivariate procedures were based on a Bray-Curtis dissimilarity matrix excluding the top 3 species (i.e. *Eucinostromus* spp., *Atherinomorus stipes*, *Lucania parva*). These very abundant species were dominant across all seascape and zone treatments and were removed from subsequent analyses because they masked subtler differences in the faunal assemblage (their removal increased dissimilarity between seascape types by 11%). The abundance and biomass data were log-transformed to approach a normal distribution and augment the contribution of rare species (i.e. buffer the dominance of abundant species on the species structure; Clarke & Warwick 2001). This transformation was also applied to diversity indices to validate statistical assumptions for ANOVA.

RESULTS

Assemblage composition in continuous vs. fragmented SAV seascapes

The species occurrence, abundance, and biomass of the SAV-associated faunal assemblages differed as a function of both seascape type and salinity environment (Table 2). Significant interactions between seascape type and salinity environment were found for faunal occurrence and abundance based on the PERMANOVA (pseudo-$F_{1,56}$, p < 0.05), but were not significant for biomass at p < 0.05 (Table 2). For occurrence and abundance, the interaction between seascape and salinity environment was evident in the CAP plots that showed the largest assemblage dissimilarity between seascape types in Zone 2 (low and variable salinity; Fig. 4a,b). In contrast, based on biomass, the largest assemblage dissimilarity between seascape types was in Zone 1 (Fig. 4c). Seascape types showed a higher effect size (see higher $\sqrt{ECV}$ in Table 2) than salinity zones across all tests, indicating that seascape types have a relatively higher importance in explaining the assemblage composition.

Distinct seascape/salinity zone associations were observed for fish and crustacean species. Based on the correlations with both canonical axes (Fig. 4,

Table 2. Results of the permutational multivariate analysis of variance (PERMANOVA) conducted to assess the faunal response to seascape type and salinity zone based on occurrence, abundance (number haul^{-1}), and biomass. $\sqrt{ECV}$: square-root of estimated component of variation; pseudo-F with associated p-values estimated from Monte Carlo permutation (MC). Variables with p-values that are significant at α = 0.05 are shown in **bold**

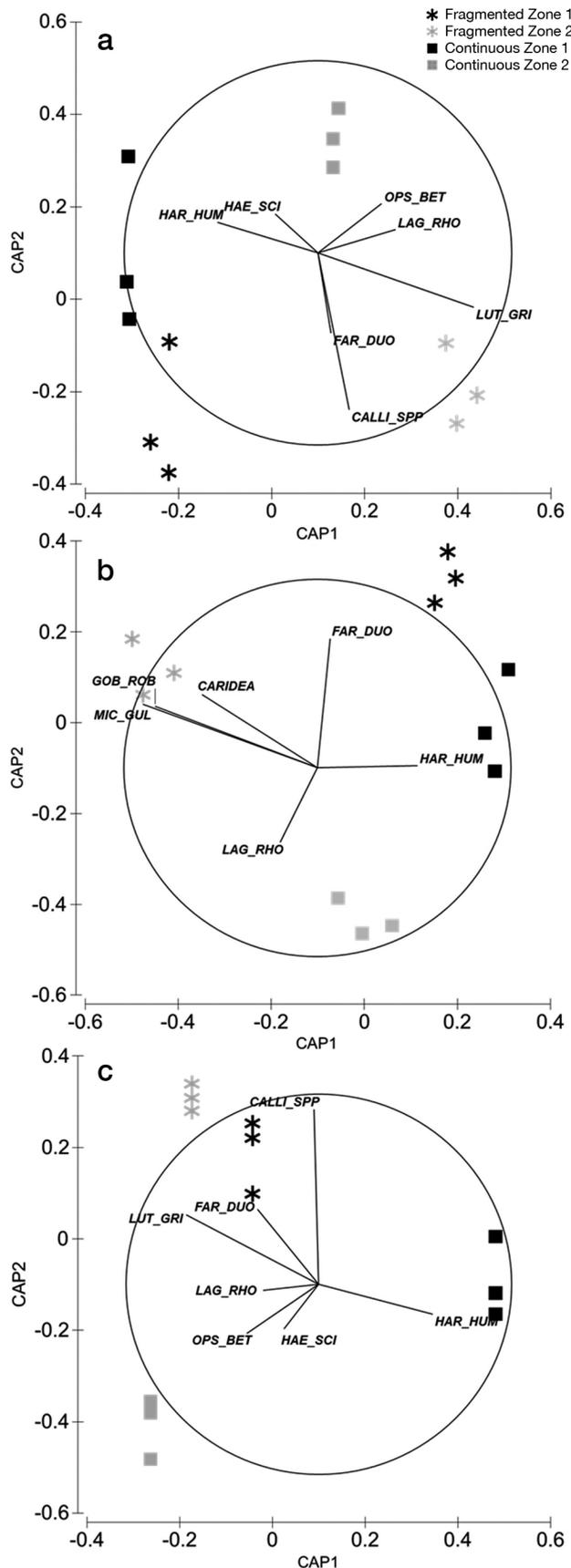| Source	df	$\sqrt{ECV}$	Pseudo-F	p (MC)
Occurrence				
Seascape	1	11.05	7.42	**<0.001**
Zone	1	8.41	4.71	**<0.001**
Seascape × Zone	1	7.51	2.48	**<0.05**
Residual	56	23.91		
Abundance				
Seascape	1	18.96	11.95	**<0.001**
Zone	1	11.73	5.19	**<0.001**
Seascape × Zone	1	15.07	4.46	**<0.001**
Residual	56	31.38		
Biomass				
Seascape	1	10.59	4.25	**<0.001**
Zone	1	8.02	2.86	**<0.001**
Seascape×Zone	1	6.83	1.67	0.106
Residual	56	32.19		

Table 3), species such as *Lagodon rhomboides*, *Opsanus beta*, and *Harengula humeralis* were associated with CS, especially in Zone 2, except for *H. humeralis* which was highly associated with CS only in Zone 1 (high and constant salinity; Fig. 4, Table 3). Conversely, *Lutjanus griseus*, *Farfantepenaeus duorarum*, and *Callinectes* spp. were associated with FS. Species such as *Gobiosoma robustum* and *Microgobius gulosus*, and *L. griseus* were highly associated with FS in Zone 2.

Faunal diversity

Total number of species and number of unique species (i.e. only observed in 1 of the seascape categories) differed between the seascape types and salinity zones in western Biscayne Bay. FS seascapes had a higher number of total and unique species compared to CS habitats (i.e. 53 total species in FS vs. 44 in CS). Eight species were only found in CS and 15 species were only found in FS. A total of 45 and 43 species were identified in Zone 1 and Zone 2, respectively, with 12 species unique to Zone 1 and 10 to Zone 2.

Faunal assemblages in FS were significantly more diverse than in CS, according to all of the diversity indices (Fig. 5, Table 4, Table A2). While significantly higher values were observed for all 4 metrics tested in FS in Zone 2 (low and variable salinity), the Simpson and Shannon-Wiener diversity metrics did not differ significantly between seascapes in salinity Zone 1 (high and constant salinity).

Fig. 4. Plots of canonical analysis of principal coordinates (CAP) for the: (a) occurrence, (b) abundance, and (c) biomass of species assemblages in fragmented (stars) and continuous (squares) submerged aquatic vegetation (SAV) seascapes. To illustrate the interactive effect of SAV seascapes and salinity regimes, species assemblages were placed in ordination space based on seascape types within Zone 1 (high/stable salinity; black symbols) and Zone 2 (low/variable salinity, grey symbols). Vectors illustrate the strength and direction of individual fish and crustacean species showing absolute correlation ρ > 0.20 that contributed to the separation in species assemblages between seascape types and zones. CALLI_SPP: *Callinectes* sp.; CARIDEA: caridean shrimps; FAR_DUO: *Farfantepenaeus duorarum*; GOB_ROB: *Gobiosoma robustum*; HAE_SCI: *Haemulon sciurus*; HAR_HUM: *Harengula humeralis*; LAG_RHO: *Lagodon rhomboides*; LUT_GRI: *Lutjanus griseus*; MIC_GUL: *Microgobius gulosus*; OPS_BET: *Opsanus beta*

Table 3. Correlations of species occurrence, abundance, and biomass with canonical axes 1 and 2 (ρ_{axis1} and ρ_{axis2}) obtained from canonical analyses of principal coordinates (CAP, see Fig. 4a–c). Only correlations of $|r| \geq 0.20$ are shown. The last 4 columns present the average ($\bar{y}$) occurrence, abundance (number haul^{-1}), and biomass (g) of these species within each combination of seascape type and salinity zone. Averages are used to illustrate how each species contributed to the separation of the species assemblages between the seascape type and salinity zone

| Species	ρ_{axis1}	ρ_{axis2}	$\bar{y}_{Fragmented-Zone1}$	$\bar{y}_{Continuous-Zone1}$	$\bar{y}_{Fragmented-Zone2}$	$\bar{y}_{Continuous-Zone2}$
Occurrence						
Lutjanus griseus	0.80	−0.28	0.73	0.47	0.87	0.80
Harengula humeralis	−0.52	0.16	0.73	0.80	0.47	0.40
Lagodon rhomboides	0.40	0.12	0.93	0.93	1	0.93
Opsanus beta	0.33	0.26	0.53	0.4	0.80	0.73
Haemulon sciurus	−0.22	0.20	0.93	0.67	0.47	0.87
Callinectes sp.	0.16	−0.82	0.87	0.60	1	0.87
Farfantepenaeus duorarum	0.01	−0.42	1	1	1	1
Abundance						
Microgobius gulosus	−0.90	0.34	0.40	0.01	4.44	0.12
Gobiosoma robustum	−0.84	0.33	0.51	0.18	6.26	1.23
Caridean shrimps	−0.60	0.39	5.13	5.60	19.67	1.53
Lagodon rhomboides	−0.19	−0.39	5.49	5.00	6.49	13.28
Farfantepenaeus duorarum	0.01	0.68	45.22	31.63	25.79	19.67
Biomass						
Lutjanus griseus	−0.69	0.37	27.53	15.44	100.25	43.10
Harengula humeralis	0.59	−0.16	3.17	14.50	1.31	4.31
Opsanus beta	−0.37	−0.26	10.96	11.77	15.41	34.28
Farfantepenaeus duorarum	−0.32	0.40	56.08	36.66	40.64	36.49
Lagodon rhomboides	−0.29	<0.1	100.84	109.52	153.73	222.77
Haemulon sciurus	−0.18	−0.23	27.92	13.74	17.34	32.36
Callinectes sp.	<0.1	0.92	15.32	21.64	19.87	8.07
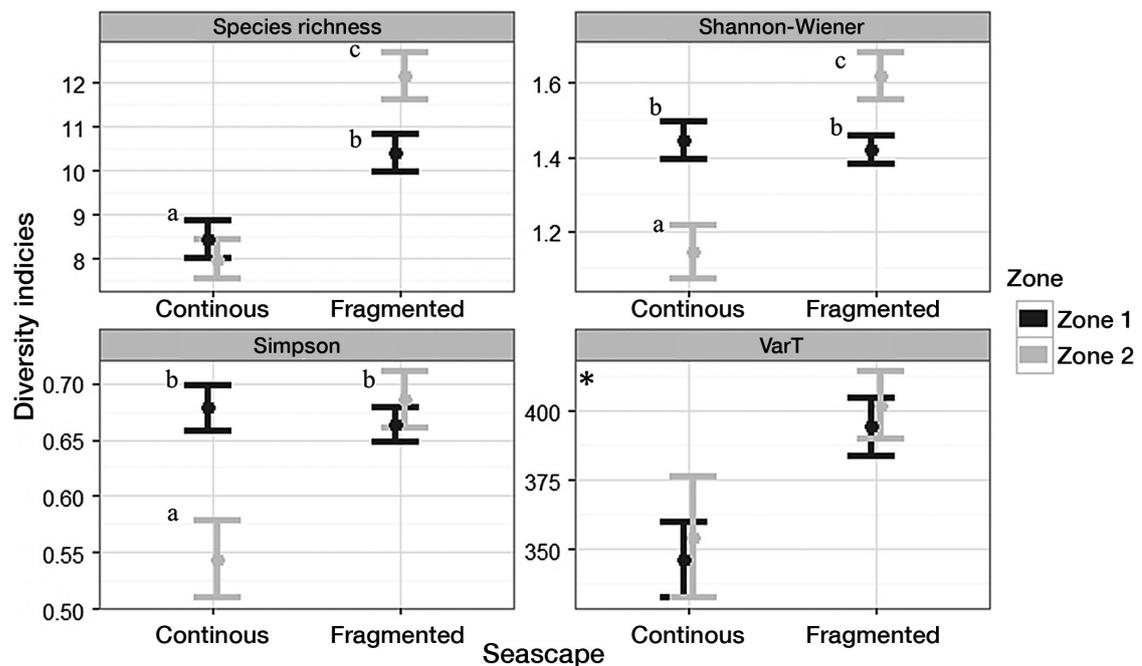
Fig. 5. Mean of species diversity indices (error bars: SE): species richness, Shannon-Wiener, Simpson diversity, and variation in taxonomic distinctness (VarT) compared between continuous and fragmented submerged aquatic vegetation (SAV) seascapes and salinity Zones 1 and 2. If interaction effects were significant, groups (letters) were identified using the Tukey multiple comparisons of means (see Table A2). Asterisks (∗) identify significant seascape type effects only (2-way ANOVA, $F_{1,159}$, p < 0.05)

Table 4. Two-way ANOVA testing for differences of diversity indices among the submerged aquatic vegetation (SAV) seascape types, salinity zones, and their interaction. The results present the *F*-statistic with associated degrees of freedom and estimated p-values for the null hypothesis. **Bold** p-values ($\alpha = 0.05$) identify significant treatment effects. If interaction effects were significant, groups were identified using the Tukey multiple comparisons of means (see Table A2 in the Appendix). VarT: variation in taxonomic distinctness

Biodiversity index	Factor	$F_{1,159}$	p
Species richness	Seascape	44.541	**<0.001**
	Zone	1.983	0.161
	Seascape × Zone	5.584	**0.019**
Shannon-Wiener	Seascape	15.705	**<0.001**
	Zone	0.748	0.388
	Seascape × Zone	18.703	**<0.001**
Simpson diversity	Seascape	6.726	**0.010**
	Zone	5.002	**0.027**
	Seascape × Zone	9.880	**0.002**
VarT	Seascape	0.900	**0.002**
	Zone	0.110	0.600
	Seascape × Zone	1.820	0.992

DISCUSSION

SAV habitats and nekton communities have been monitored in Biscayne Bay for over a decade to understand the ecological impacts of freshwater management on coastal habitats (Browder et al. 2012, Lirman et al. 2014). Understanding the influence of spatial patterns of SAV seascapes on associated fauna is of growing importance due to increased seagrass fragmentation and habitat loss, and the degradation of SAV ecosystem services associated with changes in freshwater regimes (Orth et al. 2006, Waycott et al. 2009, Boström et al. 2011). Here, we show that higher relative abundance and biomass for several species and higher diversity of fish and crustacean species (based on species richness and variation in taxonomic distinctness) in seagrass habitats were associated with fragmented and patchy SAV seascapes. At the spatial scale of this study of SAV seascapes (500 × 500 m SSU), the fragmentation state observed in nearshore Biscayne Bay revealed positive effects, interacting with salinity regimes (i.e. positive effects predominantly in Zone 2 and not Zone 1), on the diversity of the faunal community and the abundance and biomass of certain trophic groups.

Seascape transformation (i.e. changes in the spatial patterning of marine habitat patches) is a continuous process driven by a series of disturbance/succession events occurring at different scales (Cunha & Santos 2009, Santos et al. 2016, Jackson et al. 2017). Thus,

the positive fragmentation effects observed in this study may not be static, and possible ecological thresholds likely exist with respect to fragmentation gradients that, when exceeded, can result in drastic reductions in habitat value and provisioning (Fonseca & Bell 1998, Mizerek et al. 2011, Yeager et al. 2016). If SAV seascape fragmentation and habitat loss proceed, most seagrass associated fishes could disappear and the nekton assemblages may become more similar to those over unvegetated sediments (Horinouchi 2007, Boström et al. 2011). With the continuing decline in SAV extent, increased urbanization, and the realized and projected global impacts of climate change, the detection and characterization of such thresholds based on a patch-mosaic model should be a priority of SAV research.

Faunal assemblages in continuous vs. fragmented seascapes

As expected, there were differences in assemblage composition between seascape types, driven by the higher abundance of *Lagodon rhomboides* and biomass of *Haemulon sciurus* in continuous SAV seascapes, and by higher abundance and larger individuals of *Lutjanus griseus* and *Farfantepenaeus duorarum* in fragmented SAV seascapes. Ecological traits and trophic interactions of these species suggest that tradeoffs between food availability and predation risk may be the mechanisms behind the faunal responses to seascape patterns (Connolly & Hindell 2006, Boström et al. 2011). For example, *L. rhomboides*, an estuarine seagrass-dependent fish (Levin et al. 1997, Potthoff & Allen 2003), uses continuous SAV seascapes to avoid predation (Jordan et al. 1997) and enhance the tradeoff between growth and foraging efficiency (Levin et al. 1997). Larger individuals of *L. griseus*, a generalist benthivore that forages at night (Luo et al. 2009), 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 & Orth 2006). In Australia, King George whiting *Silliginodes punctatus* consumed more prey in areas within mosaics of seagrass seascapes and unvegetated patches (Jenkins et al. 2011), indicating increased foraging efficiency within patchy or fragmented SAV seascapes. Lastly, similar to Syngnathidae and crustacean studies (Browder et al. 1989, Macreadie et al. 2010b), *F. duorarum* tended

to be more abundant and larger in FS with smaller patches with complex shapes (i.e. small patches with high number of small edges) where its prey tend to accumulate (Bologna & Heck 1999, 2002, Eggleston et al. 1999, Healey & Hovel 2004).

The differences in assemblage composition between seascape types were also driven by the higher abundance of small mobile species such as the carideans and Gobiidae species in FS. Higher abundances of shrimp and other small crustacean species in fragmented SAV seascapes have been linked to (1) the formation of isolated patches and seascapes with small patches and higher edge density (Bologna & Heck 1999, 2002, Healey & Hovel 2004); (2) concentration of individuals and species into remnant patches after surrounding areas experienced habitat loss or fragmentation (i.e. crowding effects) (Macreadie et al. 2010a,b); and (3) increased mobility along edges and connectivity between patches (Eggleston et al. 1998).

Faunal diversity

Manipulative studies have shown that sometimes habitat fragmentation and edge effects can have a positive influence on mobile marine fauna (Bologna & Heck 2002, Pierri-Daunt & Tanaka 2014), whereas some fauna appear unaffected by changes in patchiness (Lefcheck et al. 2016) and others were only affected when seagrass area was very low (<25% cover; Yeager et al. 2016). In Biscayne Bay, 2 diversity indices indicated that faunal species diversity was significantly higher in fragmented than in CS. This study explored habitat–faunal characteristics based on a patch-mosaic model; thus, the field sampling design, on average, in FS sampled proportionally more substrate types (i.e. seagrass patches and the matrix composed of barren substrates or substrates with low SAV cover) than in CS, potentially influencing the number of species caught between both seascape types. However, other studies using either a patch or a patch-mosaic approach have also described higher species diversity in fragmented versus continuous marine habitats (Healey & Hovel 2004, 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 2 competing species can be promoted when the habitat is fragmented (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 2 species prefer seagrass habitats over unvegetated sediment, but, when competing directly for the same patch, *G. robustum* can displace *M. gulosus* onto patches of unvegetated sediment (Schofield 2003). In addition, in the presence of the predator fish *Opsanus beta*, both species prefer bare substrate to seagrass patches (Schofield 2003).

FS may provide more niche space due to juxtaposed microhabitat patches that generalist and transient predators could exploit (Ryall & Fahrig 2006). For example, higher occurrence and abundance of omnivore and generalist predators such as *Floridicthys carpio*, *F. duorarum*, *L. griseus*, *C. sapidus*, *G. robustum*, and *M. gulosus* were observed in FS versus CS. 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), which may also partly explain the enhanced diversity in FS. Thus, in accordance with the habitat heterogeneity hypothesis (MacArthur & MacArthur 1961), intermediate levels of fragmentation may increase the diversity within the seascape by increasing the number of microhabitats and species interactions in contrasting habitats (Tscharntke et al. 2012).

Seascape and salinity interactions

We observed that the seascape patterns significantly interacted with the salinity zones to modulate differences in faunal assemblage composition and diversity, highlighting the complexity and challenges faced when trying to understand the response of faunal assemblages to changes in their natural habitat. Our study included salinity regimes as an explanatory factor because salinity can influence both spatial attributes of SAV habitats (Santos et al. 2011) and faunal responses in Biscayne Bay (Serafy et al. 2003, Serrano et al. 2010, Browder et al. 2012). Salinity preferences and osmoregulation requirements can spatially limit animals to remain within specific salinity ranges and influence energy allocation (i.e. tradeoffs between growth, reproduction, motility, and habitat use; Hurst & Conover 2002, Serrano et al. 2010, McManus et al. 2014). Results from a salinity laboratory experiment using the most abundant nearshore fish species in Biscayne Bay suggested that the dif-

ferential osmoregulatory abilities explain some, but not all, of the differences in distribution and abundance of fish assemblages in different salinity environments (Serafy et al. 1997). In agreement with our findings, this suggests that faunal composition and distribution in nearshore Biscayne Bay are modulated by both distinct combinations of seascape characteristics and salinity environments.

The interaction between seascape types and salinity regimes suggested that the largest contrast in abundance and biomass between seascape types occurred when the salinity regime was optimal for different species. Patterns of species composition, abundance, and diversity can be a result of a spatial hierarchy of interacting processes operating across multiple ecological scales — for example, physiological processes influenced by salinity, species interaction, and movement dynamics (Pittman & McAlpine 2003, Howey et al. 2017). Salinity requirements may primarily drive species distribution as well as the species assemblage in a patchy or suboptimal salinity environment. However, when salinity conditions are favorable, biotic interactions and demographic processes operating at the scale of the seascape may influence structure, diversity, and distribution patterns. This hierarchy of drivers was evidenced in our study for species such as *F. duorarum, L. griseus*, and *L. rhomboides* that have a wide salinity tolerance and were ubiquitous across our study area (Serafy et al. 1997, Santos 2010, Serrano et al. 2010). For these species, the highest contrast in abundance and biomass was observed between the seascape types (and not between salinity zones), especially within their optimal salinity regimes. For *F. duorarum,* the largest contrast in abundance between the seascape types was observed in Zone 1, which exhibited stable polyhaline regime optimal for this invertebrate species (Browder et al. 2005, Zink et al. 2017). At the spatial scale of this study, seascape types tended to outweigh the salinity regime effects, as demonstrated by the response variance attributable to each factor (i.e. $\sqrt{ECV}$ values in Table 2).

Our findings suggest that in Biscayne Bay, the combination of seascapes with fragmented properties and variable salinity may support a better habitat for some SAV-associated species. Within the context of the intermediate disturbance hypothesis (Connell 1978), the right combination of seascape fragmentation and variable salinity appear to be fostering the co-existence of a diverse and productive faunal community not recorded in continuous or more stable adjacent habitats. In addition, the interactive effects of seascape types and salinity regimes on diversity (species richness and Shannon-Wiener; Fig. 5) could be attributed to an increase in facilitative interactions associated with moderate-stress environments (Bruno et al. 2003, Holmgren & Scheffer 2010), and the expected increased presence of generalist and euryhaline species in FS (Fahrig 2003, Ryall & Fahrig 2006, Villard & Metzger 2014).

Further studies of fragmentation as a continuous variable, and more detailed analyses of salinity (and correlated variables like nutrients), are needed to explore and predict potential thresholds in the interaction between seascape patterns and environmental variables to determine when and under what conditions habitat value decreases with increasing fragmentation (e.g. Yeager et al. 2016). Using a seascape approach that combines statistical models, computer simulations, fine-scale (10s of m) manipulations, and broad-scale (100s of m to ha) inter-annual surveys may provide the necessary information to identify such 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 SAV seascapes and their associated nekton communities.

Urban coastal ecosystems are dynamic in disturbance regimes, and our findings show the relevance of spatial patterning in the context of resource management and restoration strategies to evaluate essential fish habitats and spatial distribution of marine resources. Based on our study, 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. Forecasted increases of extreme disturbance events associated with climate change will likely expose seascapes to a series of fragmentation/recovery events overlapping with other environmental changes occurring at broad scales (i.e. freshwater discharges, nutrient loads, wave or current exposure), highlighting the importance of incorporating landscape ecology concepts to understanding habitat pattern–process relationships at relevant ecological scales.

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Appendix. Comparison of the spatial pattern metrics between the seascape types and the post-hoc analysis for the diversity indices observed between the seascape types and salinity zone interaction terms. A conceptual diagram illustrating the patch-matrix approach considered in the study is also included

Table A1. One-way ANOVA testing for differences in spatial pattern metrics among the submerged aquatic vegetation (SAV) seascape types: fragmented (FS) vs. continuous seascapes (CS). The results present F with associated degrees of freedom and estimated p-values for the null hypothesis. These results illustrate that both FS and CS have different spatial structure of SAV habitat patches. All p-values were significant ($p < 0.05$). PLAND: proportion of the seascape occupied by SAV patches; MPS: mean patch size; PDENS: patch density; AWMPFD: area-weighted mean patch fractal dimension

Diversity index	$F_{1,8}$	p
PLAND	36.054	**<0.001**
MPS	14.466	**0.003**
PDENS	7.577	**0.02**
AWMPFD	14.736	**0.003**

Table A2. Table of computed Tukey HSD pairwise comparisons for the diversity indices observed between the Seascape × Zone interaction terms. A **bold** $p_{adjusted}$ value indicates significant differences between a distinct combination of Seascape × Zone factor levels. Results were used to identify significant groups in Fig. 3. VarT: variation in taxonomic distinctness

| Diversity index	Interaction term comparison	Difference of means	$p_{adjusted}$
Species richness	Continuous:Zone 1–Continuous:Zone 2	0.449	0.903
	Fragmented:Zone 1–Continuous:Zone 2	2.424	**0.002**
	Fragmented:Zone 2–Continuous:Zone 2	4.167	**0.000**
	Fragmented:Zone 1–Continuous:Zone 1	1.975	**0.017**
	Fragmented:Zone 2–Continuous:Zone 1	3.718	**0.000**
	Fragmented:Zone 2–Fragmented:Zone 1	1.743	0.042
Shannon-Wiener	Fragmented:Zone 1–Continuous:Zone 2	0.276	**0.005**
	Continuous:Zone 1–Continuous:Zone 2	0.302	**0.002**
	Fragmented:Zone 2–Continuous:Zone 2	0.475	**0.000**
	Continuous:Zone 1–Fragmented:Zone 1	0.025	0.990
	Fragmented:Zone 2–Fragmented:Zone 1	0.199	0.075
	Fragmented:Zone 2–Continuous:Zone 1	0.173	0.149
Simpson	Fragmented:Zone 1–Continuous:Zone 2	0.119	**0.005**
	Continuous:Zone 1–Continuous:Zone 2	0.134	**0.001**
	Fragmented:Zone 2–Continuous:Zone 2	0.142	**0.000**
	Continuous:Zone 1–Fragmented:Zone 1	0.015	0.976
	Fragmented:Zone 2–Fragmented:Zone 1	0.022	0.922
	Fragmented:Zone 2–Continuous:Zone 1	0.007	0.997
VarT	Continuous:Zone 2–Continuous:Zone 1	8.179	0.981
	Fragmented:Zone 1–Continuous:Zone 1	48.101	0.124
	Fragmented:Zone 2–Continuous:Zone 1	55.959	0.049
	Fragmented:Zone 1–Continuous:Zone 2	39.922	0.255
	Fragmented:Zone 2–Continuous:Zone 2	47.780	0.117
	Fragmented:Zone 2–Fragmented:Zone 1	7.857	0.983
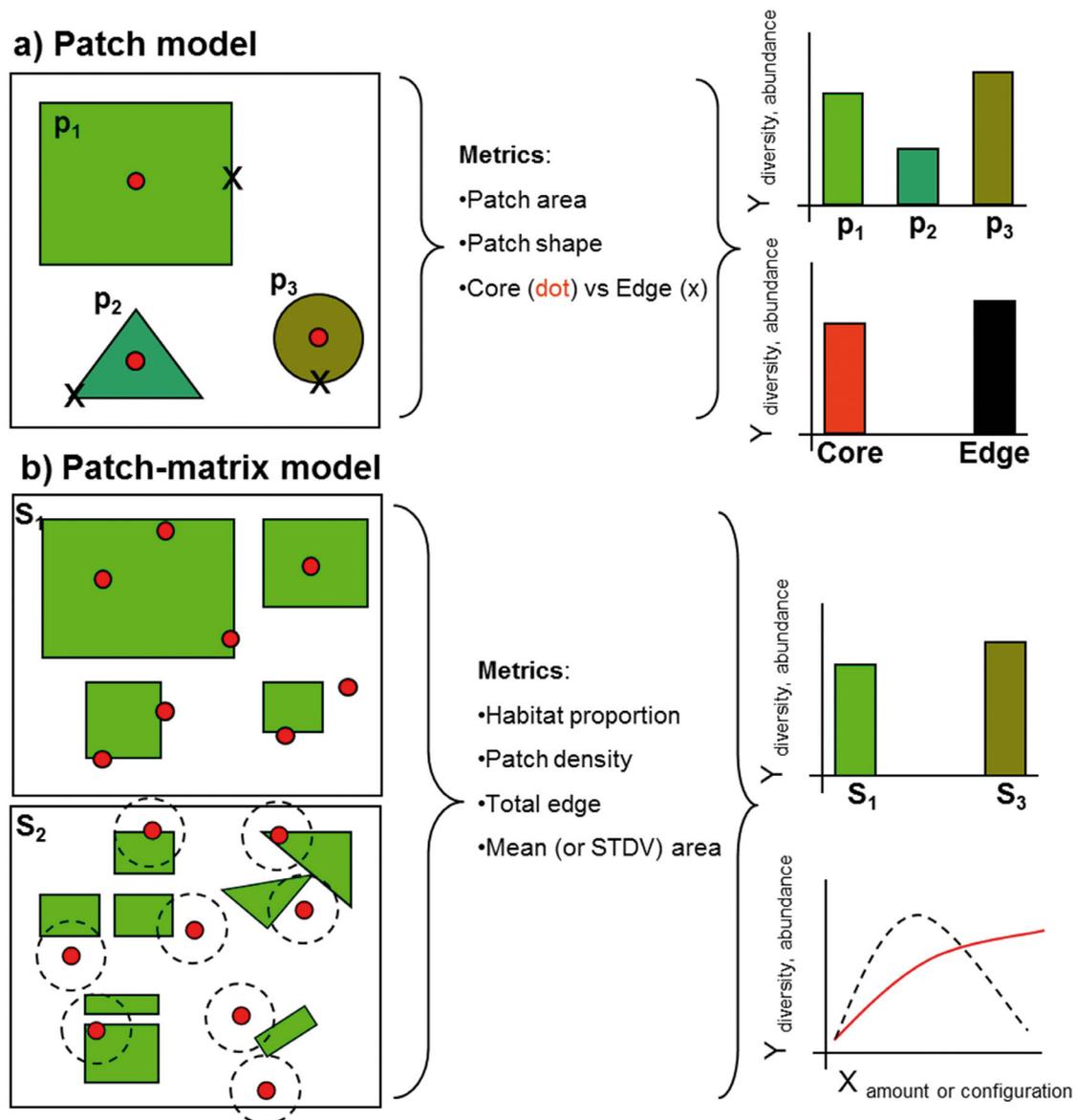
Fig. A1. Illustration of a seascape analysis with (a) patch model and (b) patch-matrix approach. Red dots and black X illustrate sampling points. In a patch model seascape analysis, faunal responses (Y_i) are compared between patches (p_i) with different characteristics (e.g. area, shape, perimeter:area ratio) or between habitat core (dot) and edge (X) (right panel). In a seascape analysis with a patch-matrix approach, faunal responses (Y_i) are explored between different seascapes (S_i) with distinct amount and arrangement of patches or within an organism's home range (dashed circles), thus incorporating faunal responses across the entire mosaic of patches