

Landscape pattern influences nekton diversity and abundance in seagrass meadows

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ABSTRACT: We studied how spatial qualities and configuration of seagrass patches influence the diversity and abundance of resident nekton. Shallow landscapes of equal area (4225 m²) in 2 bays were mapped and sampled in the summer and fall to identify different qualities of landscape structure and the abundance and diversity of nekton. Two suites of characteristics were found to describe the natural landscape structure: (1) habitat area, connectivity, patch proximity and patch density; and (2) patch shape complexity and edge length. These were used to quantitatively distinguish between 3 naturally occurring seagrass landscape patterns: (1) small, isolated patches; (2) reticulated edge patches; and (3) continuous cover. Species evenness (Pielou's *J'*) was significantly lower in small, isolated patches and reticulated edge patches compared to continuous cover. This pattern was temporally consistent despite significant seasonal differences in total nekton density and seasonal shifts in the distribution of individual species among landscape patterns. Nekton species density (no. of species per 61.2 m² of seagrass) and species richness (no. of species per 1683 ind. sampled) did not differ significantly among landscape patterns; however, a landscape structure threshold may exist for species evenness between 45 and 85% cover. High densities of shrimp in small, isolated patches and reticulated edge patches during summer drove species evenness levels lower and overall nekton density levels higher than in continuous cover. Large expanses of continuous seagrass harbor more stable nekton communities across time. They may provide enough space for different species to feed and reproduce without depleting food resources to the point that nekton populations become unstable.

KEY WORDS: Biodiversity · Seagrass · Landscape structure · Habitat fragmentation

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INTRODUCTION

Seagrasses form biologically productive systems throughout the world (Boström et al. 2006), providing essential habitat for important marine species such as fish (Rooker et al. 1998, Stunz et al. 2002, Horinouchi 2007), shrimps (Tolan et al. 1997, Pittman et al. 2004, Johnson & Heck 2006a) and crabs (Hovel & Lipcius 2001). Seagrass meadows harbor larger numbers of nekton (Smith et al. 2008), nekton species (Horinouchi 2007) and compositionally distinct communities com-

pared to bare substrate (Turner et al. 1999). Landscape structure is a critical factor influencing species distribution and abundance in seagrass meadows (Pittman et al. 2004). Although landscape structure and composition have been studied extensively in terrestrial settings (Hanski & Gaggiotti 2004), less is known about how they influence nekton communities that use seagrass as their primary habitat (Boström et al. 2006).

Seagrass meadows are disappearing worldwide (Short & Wyllie-Echeverria 2000). Many of the factors that have been implicated in their global decline

have also been cited as influencing their geometry and spatial qualities. These landscapes exhibit a variety of patch patterns (Connolly & Hindell 2006) ranging from continuous cover to convoluted, interconnected patch cover and small, isolated patches. These patterns can be produced by seasonal growth (Robbins & Bell 2000) and dieback as well as by disturbances such as fragmentation from habitat destruction, changes in water turbidity, pollution, hydrodynamic regime and storm activity (Short & Wyllie-Echeverria 1996, Hovel et al. 2002).

To understand the implications of both natural and human-caused alterations to seagrass landscapes, we need to know how the spatial qualities and configuration of patches influence the diversity and abundance of nekton that reside within them (Pittman et al. 2004). Biodiversity, a component supporting ecosystem functionality and services (Koellner et al. 2013), has been assessed through measures such as species richness (Colwell 2009) and species evenness (Mulder et al. 2004).

Community diversity depends on the motility, food requirements, reproductive strategies and trophic interactions of individual species (Irlandi & Crawford 1997, Johnson & Heck 2006b). A decrease in the percentage of seagrass (habitat area) and an increase in patchy or 'fragmented' landscape patterns create species-specific constraints on movement, energetics and survival and, in turn, influence patterns of spatial distribution and abundance of animals (Pittman et al. 2004). Habitats with relatively little seagrass cover can support high numbers of taxa; however, different thresholds in seagrass cover may exist for species richness and animal abundance (Andren 1994, With & Crist 1995, Fahrig 1997, Pittman et al. 2004). In some cases, no habitat area threshold is detected for species richness in fishes (Salita et al. 2003), invertebrates (Eggleston et al. 1999) or communities containing both taxa (Bell et al. 2001, Arponen & Boström 2012) at small spatial scales ($\leq 100 \text{ m}^2$). Arponen & Boström (2012) found that community diversity (quantified by Shannon's H') was lower in isolated artificial seagrass units (ASUs) than in ASUs that were close together, or in continuous cover. Patch proximity is positively related to fish abundance (Johnson & Heck 2006a) and can enhance their predation on shrimp by facilitating fish movement between habitats (Irlandi & Crawford 1997).

Benthic macrofauna species richness and diversity (Shannon's H') differ between patch core and edge positions (Turner et al. 1999), and thus patch shape complexity and edge length are important (McGarigal et al. 2002). Differences in fish densities between

edge and core areas of patches are often species-specific and typically disappear at small patch sizes (Jelbart et al. 2006, Macreadie et al. 2010, Smith et al. 2010). Thus, the net effects of patch edges on diversity are often variable and may also depend on the spatial scale of focal patches (Moore & Hovel 2010).

Quantitative estimates of habitat connectivity are rare (Gillanders et al. 2003); however, reduced habitat connectivity has been implicated as a threat to fish dispersal between coral reefs (Munday et al. 2009). Fernandez et al. (2008) found higher reef fish density in artificial structures established in seagrass meadows with high connectivity but highest evenness in meadows with low connectivity. Small species with limited mobility were associated with areas of high connectivity, and more motile medium-sized animals were associated with isolated patches, again suggesting that the influence of this landscape pattern on nekton is species-specific.

The degree to which estuarine species associate with seagrass habitats can vary significantly across their life cycles (Wenner & Beatty 1993, Tolan et al. 1997), resulting in seasonal differences in species abundance (Johnson & Heck 2006a), composition (Turner et al. 1999) and community structure (Hironouchi et al. 2009). Landscapes change in patch area and configuration over time (With 2004), necessitating approaches that compare the response of nekton to landscape pattern as they simultaneously change between seasons.

This study had 3 objectives: (1) to assess the *in situ* characteristics of landscape pattern in a range of seagrass habitats, (2) to compare the abundance and diversity of nekton that reside in different landscape configurations while accounting for geographical and seasonal variability in species abundance and landscape pattern and (3) to understand how landscape pattern might impact different groups of nekton based on their biological and ecological characteristics. To achieve these objectives, shallow landscapes of equal area in 2 bays were mapped in the summer and fall to identify and quantify different qualities of landscape pattern. Measures of community diversity and nekton abundance were then assessed as a function of these landscape qualities.

MATERIALS AND METHODS

Study sites

Monospecific meadows of shoalgrass *Halodule wrightii* in Aransas Bay and Corpus Christi Bay, Texas,

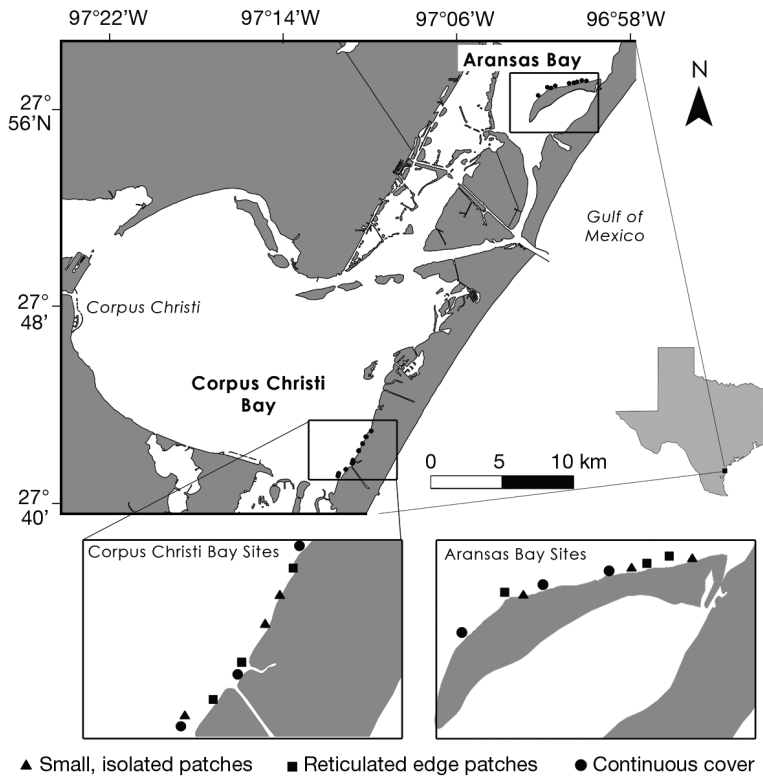


Fig. 1. Sampling sites in Aransas and Corpus Christi bays. See Fig. S1 in the Supplement for illustration of patch types

USA (Fig. 1), were mapped using visual estimates of landscape pattern (percent seagrass cover, patch size and proximity). These shallow (0.5 to 1.5 m water depth) habitats were mapped *in situ* from data obtained by Trimble GeoXT GPS receivers (Trimble Navigation), which are capable of sub-meter accuracy. The GPS unit recorded the geoposition (once every second) of the operator, who walked the exact perimeter of each patch in a meadow to capture its spatial features. Mapping was performed from 1 to 4 wk preceding sampling in both the summer and fall of 2009. ArcGIS 9.3 (ESRI 2008) was used to process receiver data and create georeferenced, vector-based maps of each seagrass meadow, each approximately 200 × 100 m. Within each meadow, 65 × 65 m landscapes were chosen as sampling plots to approximate 3 levels of naturally occurring 'patchiness' landscape patterns (see Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m507p139_supp.pdf). This sampling plot size was selected because it consistently captured the geometry of most of the patches where nekton sampling occurred.

Each bay had 3 sampling plots representing each of the 3 patchiness levels, and each plot was studied during summer and fall (9 plots per bay, 18 per sea-

son, 36 total). They were evenly dispersed across approximately 4 km of bay shoreline in areas with similar hydrodynamic conditions, and were separated by at least 30 m of bare substrate of sand/mud (Fig. 1).

Landscape pattern analysis

GIS vector map data for each sampling plot were converted to raster grids with 10 cm cell size. This size best preserved patch geometry during data conversion. Measures of landscape pattern in each of the plots were computed with FRAGSTATS software (McGarigal et al. 2002).

A total of 23 indices previously used to evaluate terrestrial (Kumar et al. 2006, 2009) and marine (Sleeman et al. 2005) landscapes were calculated for each plot. A Pearson correlation matrix was used to eliminate metrics that were highly correlated with each other ($r \geq 0.800$), to reduce the number of redundant measures in the principal components analysis (PCA). Mean patch area and percent cover were retained despite being correlated with other metrics because they are direct measures of relative habitat area and among the most important landscape qualities influencing animals in seagrass systems (Boström et al. 2006, Connolly & Hindell 2006).

A PCA of the 12 remaining indices (Table 1) was performed using SYSTAT 12 (SYSTAT 2007) to identify the major qualities that differed among the 36 study plots (Sleeman et al. 2005). Landscape data obtained during both seasons were used in the PCA and are summarized in Table S1 in the Supplement. Landscape pattern indices vary in their possible range of values (McGarigal et al. 2002), so index values were transformed [e.g. logarithmic, $\log(x + 1)$] where appropriate to achieve data normality and adjust values to a common, positive scale (see Table S1) in preparation for the PCA (Baxter 1995). To test for differences in landscape qualities among patchiness levels, a 3-way ANOVA ($\alpha = 0.05$) was performed in SYSTAT on principal component factor scores that plots from each patchiness level received in the PCA. Patchiness level (3), Season (2) and Bay (2) were fixed factors, and Bay was treated as a geographical blocking variable. This design was also used for all subsequent community structure analyses. Significant ($\alpha = 0.05$) main effects of Patchiness level were further evaluated in post hoc pairwise comparisons

($\alpha = 0.05$) using Tukey's HSD (Pittman et al. 2004).

Nekton sampling

During the summer (June 16 to 25) and fall (October 21 to November 2) of 2009, nekton samples were obtained from each plot in both bays on 2 separate dates approximately 7 d apart. Seagrass was sampled within each plot by towing a 0.6 m wide by 0.75 m high epibenthic sled equipped with a 1 mm mesh conical plankton net over the bed surface. This device is designed for collecting epibenthic nekton 4 to 50 mm in length including larval and small juvenile fish, small shrimp and other decapods and provides a reliable and efficient nekton density estimate over the habitat types encountered in this study (Stunz et al. 2002).

Sampling paths were planned *a priori* in ArcGIS within each plot to obtain a minimum sample size of 51 linear meters (30.6 m²) within each plot per sampling event. Variable patch size and configuration within each plot often required that multiple tows be taken to obtain the minimum total sample size, but no plots were sampled with fewer than 3 (10.2 m²) tows. Individual tows varied in length from 4 to 17 m, depending on patch size. Samples were collected inside seagrass beds only.

Each sample was sorted in the field to remove extraneous macroalgae and vegetation, and the remainder was preserved in 10% formalin. The *in situ* tow length for each sample was recorded on a Trimble GPS unit while following the sled and converted to square meters to calculate sample size based on seagrass area. In the laboratory, fish, shrimp and crabs were identified to the lowest possible taxon, counted and measured.

Community structure analyses

To assess abundance as a function of patchiness level within or between seasons, a 3-way ANOVA ($\alpha = 0.05$) was performed on overall animal density (ind. m⁻²) in each plot. To explore relationships between the abundance of individual species and measures of community diversity, 3-way ANOVAs

Table 1. Principal component analysis (PCA) eigenvalues and variable loadings for 12 metrics used to quantify seagrass landscape patterns. Strong variable loadings are in **bold**. See McGarigal et al. (2002) or Sleeman et al. (2005) for metric definitions and calculations

		Principal component		
		1	2	3
Eigenvalue		4.221	3.142	1.965
Percentage		35.18	26.18	16.38
Cumulative percentage		35.18	61.36	77.74
PCA variable description	FRAGSTATS name	Loading		
Landscape connectivity	COHESION	-0.965	0.020	0.060
Percent cover	PLAND	-0.945	-0.173	0.093
Mean patch proximity	PROX_MN	-0.879	-0.099	0.091
Mean patch area	AREA_MN	-0.863	-0.393	0.228
Number of patches	NP	0.644	0.520	0.314
Mean patch shape complexity	SHAPE_MN	0.061	0.853	0.170
Mean patch elongation	CIRCLE_MN	0.478	0.759	0.283
Landscape contiguity	CONTAG	0.153	-0.741	0.562
Edge length	TE	0.358	0.635	-0.576
Mean Euclidean patch complexity	FRAC_MN	0.214	0.632	0.241
Landscape compactness	NLSI	-0.150	-0.150	0.713
Patch aggregation	CLUMPY	0.111	0.015	-0.686

were also performed on densities of the 25 most abundant taxa. This encompassed the largest value (24.8 species per 61.2 m² of seagrass) calculated for a sampling plot in the species density analysis. Data from the 2 sampling events within each season were pooled within each plot for the analyses, and log transformation was necessary to meet assumptions of data normality and homogeneity of variance. P-values of tests that returned $\alpha \leq 0.05$ for individual taxon densities were evaluated using a false discovery rate (FDR) procedure (Pike 2011) with a maximum adjusted FDR value of 0.05, which helps protect against Type I errors in multiple comparisons (Benjamini & Hochberg 1995, Shaffer 1995) while simultaneously retaining statistical power suitable for non-independent statistical tests (Abdi 2010). Significant (FDR value ≤ 0.05) main effects of landscape pattern were further evaluated in post hoc pairwise comparisons ($\alpha = 0.05$) using Tukey's HSD.

Biodiversity across habitat patchiness levels was quantified in 3 ways.

Species density

The number of species observed in 61.2 m² of seagrass allowed comparisons among habitats based on equal amounts of habitat area (m²). Sample sizes

were occasionally larger in plots within highly fragmented habitats because the entire length of several small patches was sampled, causing pooled sample sizes larger than the 30.6 m² of habitat targeted per plot in each sampling event.

To account for potential biases in species number estimates from these variations in sample size, species accumulation data (Tables S2 & S3 in the Supplement) were used to estimate the number of species from a standardized sample size from each plot. Species accumulation curves were constructed for each plot based on 6 to 13 samples, depending on the degree of patchiness (and thus the number of tows required) in each plot. PRIMER v6 (Clarke & Gorley 2006) was used to estimate species accumulation as a function of increasing number of samples, based on 999 permutations in sample order. Mean number of species and 95% confidence intervals as a function of increasing sample number were computed for each plot. The total tow area in each plot was divided by the total number of samples to derive species accumulation curves as a function of increasing sampling area.

The R² values for mean species accumulation curves ranged from 0.979 to 0.999. Confidence intervals were inspected for equality above and below the mean of each data point on the accumulation curves to ensure the sample size selected for comparison across plots was unbiased by the re-sampling algorithm used to compute species accumulation (Walker et al. 2008). An area of 61.2 m² was identified as the largest universal sample size on which to estimate species density across plots. Species accumulation equations for each plot were used to interpolate the number of species found in 61.2 m² of sampled seagrass area to provide an estimate of species density. Using these data, a 3-way ANOVA ($\alpha = 0.05$) was performed on species density in each plot. Data were log transformed where necessary to meet assumptions of data normality and homogeneity of variance.

Table 2. Three-way ANOVAs and Tukey's post hoc comparison of factor scores that sampling plots from each landscape category received in the principal components analysis (PCA). Landscape categories are (1) small, isolated patches; (2) reticulated edge patches; and (3) continuous cover. MSE: mean square error

Dependent variable	df	Mean square	F	p
PCA Factor 1: Habitat area, habitat connectivity, patch proximity, patch density				
Season	1	1.261	12.675	0.001
Bay	1	0.069	0.696	0.411
Landscape category	2	3.441	34.576	0.000
Landscape category × Season	2	0.447	4.496	0.020
Residual	29	0.100		
Summer				
Bay	1	0.122	0.914	0.355
Landscape category	2	10.269	77.212	0.000
Residual	14	0.133		
Pairwise comparison				
		MSE		
1:2	14	0.133		0.000
1:3	14	0.133		0.000
2:3	14	0.133		0.002
Fall				
Bay	1	0.001	0.008	0.930
Landscape category	2	5.123	73.834	0.000
Residual	14	0.069		
Pairwise comparison				
		MSE		
1:2	14	0.069		0.000
1:3	14	0.069		0.000
2:3	14	0.069		0.005
PCA Factor 2: Patch shape and edge length				
Season	1	0.038	0.104	0.749
Bay	1	0.309	0.841	0.367
Landscape category	2	11.849	32.216	0.000
Landscape category × Season	2	0.144	0.391	0.680
Residual	29	0.368		
Pairwise comparison				
		MSE		
1:2	29	0.368		0.000
1:3	29	0.368		0.078
2:3	29	0.368		0.000
PCA Factor 3: Patch aggregation and compactness				
Season	1	1.080	1.127	0.297
Bay	1	2.108	2.200	0.149
Landscape category	2	1.156	1.207	0.314
Landscape category × Season	2	0.862	0.900	0.418
Residual	29	0.958		

Species richness

There was potential for differences in animal abundance between patchiness levels to bias richness estimates based on habitat area during summer and to bias overall diversity estimates between summer and fall (Table 2). Therefore, species richness based on standardized animal abundance was calculated for each sampling plot using rarefaction. This method

uses probability theory to estimate the number of species at smaller animal abundances from a larger population sample (Sanders 1968, Gotelli & Colwell 2001), thereby permitting direct comparison between samples at a smaller, common animal abundance level.

Sampling paths were haphazardly placed in multiple patches and locations in each plot to obtain a sample that was extensive and spatially heterogeneous. Data collected from each set of samples within the plots were pooled to perform individual-based rarefaction analyses on the animal community in each plot. A computer program, EcoSim (Gotelli & Entsminger 2001), was used to estimate species richness. A 3-way ANOVA ($\alpha = 0.05$) was performed on rarefied animal diversity estimates.

To provide this analysis with rarefied sample data, the plot containing the smallest number of total animals from both sampling events (1683 ind.) was selected as the universal abundance level with which to compute diversity estimates in the other sampling plots. The actual number of species observed in the smallest sample was used in the ANOVA; however, mean diversity values in samples with larger animal abundances were rarefied using EcoSim based on 1000 simulations. The confidence intervals for mean diversity estimates based on 1683 ind. was inspected and verified to be approximately normal in each plot, thereby ensuring that the estimate was a valid data point in the statistical analysis (Walker et al. 2008).

Species evenness

We calculated Pielou's J' , ranging from 0 (minimum evenness) to 1 (maximum evenness) that quantifies how equally represented different species are within a given sample. Pielou's J' was computed using PRIMER v6 (Clarke & Gorley 2006), and a 3-way ANOVA ($\alpha = 0.05$) compared mean Pielou's J' among plots as a function of patchiness.

RESULTS

Landscape pattern

Summary data and frequency distributions were calculated for mean patch size, percent cover and

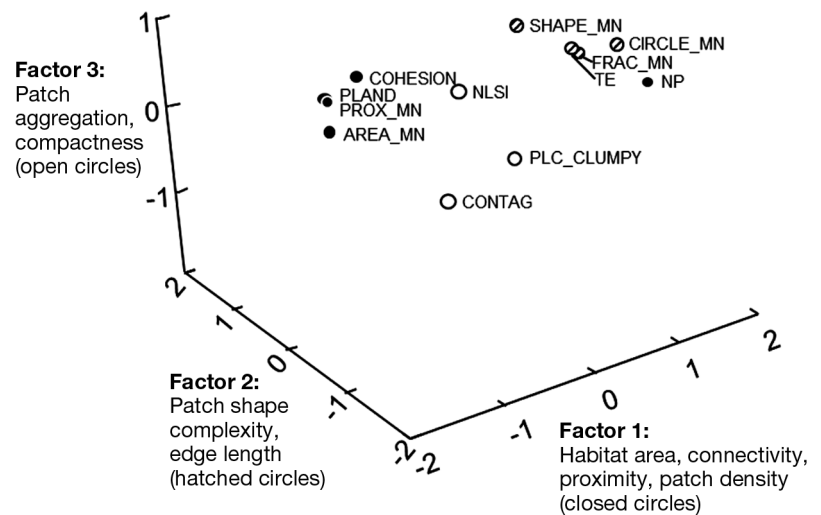


Fig. 2. Principal components analysis of habitat fragmentation metrics in sampling plots. See Table 1 for descriptions of variables

edge length in each patchiness level (Fig. S1 & S2 in the Supplement). In both summer and fall, values for most of the 12 landscape pattern metrics used in the PCA differed between 2 or all 3 of the patchiness levels to which sampling plots were assigned (Table S1, Fig. S3 in the Supplement). Landscape pattern metrics that loaded strongly (≥ 0.600 or ≤ -0.600) in the PCA were used to describe 3 principal component factors (Table 1, Fig. 2). Factor 1 was comprised of measures of decreasing habitat connectivity, habitat area, patch proximity and increasing number of patches. This aspect of landscape pattern accounted for over 35% of the variability across sampling plots. Factor 2 encompassed measures of increasing patch shape complexity and edge length (i.e. patch perimeter created from the sand–edge interface) and explained over 26% of the variance observed in habitat measures across plots. Factor 3 described patch aggregation or ‘clumpiness’ in the spatial arrangement of patches within the landscape. It accounted for approximately 16% of variability across sampling plots.

The Factor 1 ANOVA results show significant differences between Seasons ($F_{1,29} = 12.675$, $p = 0.001$) and among Patchiness levels ($F_{2,29} = 34.576$, $p = 0.000$). A significant interaction ($F_{2,29} = 4.496$, $p = 0.02$) between Season and Patchiness level was also observed (Table 3). Therefore, Factor 1 scores were analyzed separately as a function of Patchiness level for each Season (Mulder et al. 2004), with adjusted alpha level ($\alpha = 0.025$) calculated by dividing the original alpha level by the number of simple effects tests (2). Separate analyses of summer ($F_{2,14} = 77.212$,

$p < 0.001$) and fall ($F_{2,14} = 73.834$, $p < 0.001$) data showed that PCA Factor 1 scores differed significantly among all Patchiness levels for both Seasons (Table 3, $p < 0.001$ for all post hoc orthogonal comparisons), indicating that habitat area, connectivity and proximity declined monotonically from the most patchy to the least patchy plots. The significant Patchiness level \times Season interaction term occurred because the difference in Factor 1 scores between patchy and continuous landscapes was significantly larger in the summer than in the fall (Fig. 3).

The 3-way ANOVA ($\alpha = 0.05$) of Factor 2 scores for each Patchiness level showed significant differences among Patchiness levels ($F_{2,29} = 32.216$, $p = 0.000$) but not between Seasons ($F_{1,29} = 0.749$, $p = 0.749$), and there was no significant interaction between Season and Patchiness level ($F_{2,29} = 0.391$, $p = 0.680$). Post hoc analysis of Factor 2 scores among Patchiness levels showed that patch shape complexity and edge length was significantly higher in reticulated edge patches than in either small, isolated patches or continuous cover (Fig. 4) in both Seasons ($F_{2,29} = 32.216$, $p < 0.001$; $p < 0.01$ for post hoc orthogonal comparisons; Table 3), indicating that reticulated edge patches had more complex patch shapes and longer edges than either continuous cover or small, isolated patches. No significant differences in Factor 3 scores were observed across the 3 Patchiness levels, so no further analysis was conducted. The results of the PCA and ANOVAs of Factor 1 and 2 scores enabled each level of patchiness to be described as a distinct landscape category: (1) continuous cover (large expanse of seagrass); (2) reticulated edge patches (large, close patches with complex shapes); and (3) small, isolated patches.

Animal density

Patterns of overall animal abundance as a function of landscape pattern differed between summer and fall. A significant interaction between season and landscape category on animal density was observed ($F_{2,29} = 7.061$, $p = 0.003$). Separate analysis by season

Table 3. Three-way ANOVA comparing animal density from sampling plots in each landscape category. Landscape categories are (1) small, isolated patches; (2) reticulated edge patches; and (3) continuous cover. MSE: mean square error

Dependent variable	df	Mean square	F	p
Animal density (ind. m ⁻²)				
Season	1	1.504	27.332	0.000
Bay	1	0.160	2.899	0.099
Landscape category	2	0.032	0.587	0.562
Landscape category \times Season	2	0.389	7.061	0.003
Residual	29	0.055		
Summer				
Bay	1	0.005	0.086	0.774
Landscape category	2	0.317	5.977	0.013
Residual	14	0.053		
Pairwise comparison				
		MSE		
1:2	14	0.053		0.778
1:3	14	0.053		0.014
2:3	14	0.053		0.052
Fall				
Bay	1	0.247	4.556	0.051
Landscape category	2	0.104	1.908	0.185
Residual	14	0.054		
Pairwise comparison				
		MSE		
1:2	14	0.054		1.000
1:3	14	0.054		0.239
2:3	14	0.054		0.247

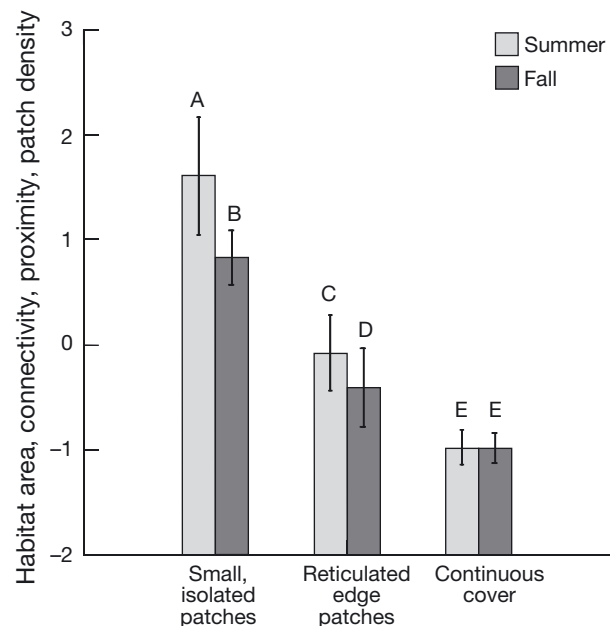


Fig. 3. Higher scores in PCA Factor 1 indicate reduction in habitat area, connectivity, proximity and patch density. Error bars represent 95% confidence intervals. Different letters indicate highly significant differences in scores using Tukey's test ($p < 0.01$)

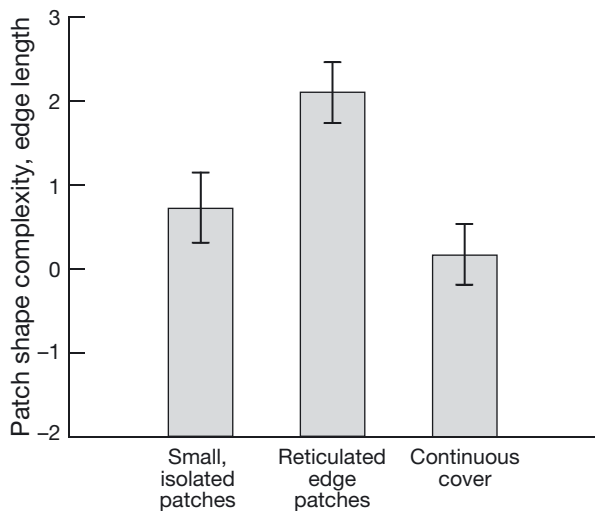


Fig. 4. Higher scores in PCA Factor 2 indicate reduction in habitat area, proximity and connectivity. Error bars represent 95% confidence intervals. Different letters indicate highly significant differences in scores using Tukey's test ($p < 0.01$)

(Mulder et al. 2004) with adjusted alpha level ($\alpha = 0.025$) showed that in the summer, animal densities were significantly different across landscape categories ($F_{2,14} = 5.977$, $p = 0.013$, Table 2), but no difference in densities was observed in the fall. A post hoc comparison using Tukey's test ($\alpha = 0.025$) showed that in summer, animal densities were significantly greater in small, isolated patches than in continuous cover ($p = 0.014$). During this season, animal densities within reticulated edge patches were highly variable (Fig. 5). This variability may explain why animal density in reticulated edge patches only approached significance ($p = 0.052$) compared to continuous cover in a post hoc comparison. In the fall, densities were less variable and not significantly different across landscape categories.

Over 460 000 nekton organisms and benthic crustaceans were collected in this study (Table 4). The size of animals included in the analysis ranged from approximately 4.5 mm for grass shrimp and newly settled red drum to 160 mm for adult chain pipefish and are summarized in Table S5 in the Supplement. The nekton assemblage was dominated by arrow shrimp, especially in the summer (Table 4). On average, they accounted for approximately 56% of the community across all landscape categories in the summer and 67% in the fall. Across both seasons, they dominated the assemblage in isolated patches (82% total abundance) and reticulated edge patches (75% total abundance) (Fig. 6). Densities of the 25 most abundant fish and decapods were highly vari-

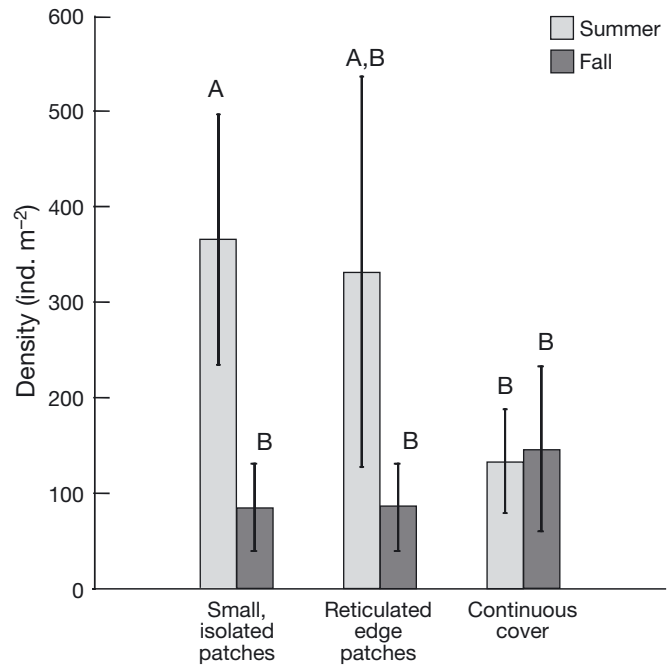


Fig. 5. Animal densities as a function of landscape pattern. Error bars represent 95% confidence intervals. Different letters indicate levels where densities were significantly different in post hoc comparisons using Tukey's test

able as a function of landscape pattern (Figs. S3 & S4 in the Supplement). Despite this variability, several taxa showed significant differences in abundance among landscape categories within each season (see Table S4 in the Supplement).

Taxa with significant differences in density among landscape categories showed a variety of response patterns (Figs. S4 & S5 in the Supplement). Snapping shrimp and code gobies showed greater abundance in small, isolated patches and reticulated edge patches than in continuous cover in both seasons, whereas grass shrimp showed the exact opposite abundance pattern. In the summer, arrow shrimp densities did not differ significantly between small, isolated patches and reticulated edge patches; however, densities in both of these categories were significantly higher than in continuous cover. Black-cheek tonguefishes were significantly more abundant in small, isolated patches than in reticulated edge patches and continuous cover, whereas the dusky pipefish was significantly more abundant in reticulated edge than in either small, isolated patches or continuous cover.

Densities of broken-back and arrow shrimp declined from summer to fall within small, isolated patches and reticulated edge patches but increased in continuous cover. Consequently, during fall, arrow

Table 4. Captured species in decreasing order of total number of individuals

Taxon	Common name	Small, isolated patches	Reticulated edge patches	Continuous cover	Total
Decapoda					
<i>Tozeuma carolinense</i>	Arrow shrimp	162 948	127 265	32 568	322 781
<i>Hippolyte pleuracantha</i>	Broken-back shrimp	26 004	21 024	44 529	91 557
<i>Palaemonetes</i> sp.	Grass shrimp	6 793	6 849	17 646	31 288
<i>Farfantepenaeus</i> sp.	Brown/pink penaeid shrimp	1 795	1 759	3 364	6 918
<i>Litopenaeus setiferus</i>	White penaeid shrimp	98	73	73	244
<i>Latreutes parvulus</i>	Sargassum shrimp	18	18	8	44
<i>Leptochela serratorbita</i>	Combclaw shrimp	10	2	10	22
<i>Alpheus heterochaelis</i>	Snapping shrimp	2	3	14	19
<i>Callinectes</i> sp.	Blue crab	204	208	525	937
Perciformes					
<i>Ctenogobius boleosoma</i>	Darter goby	473	310	1328	2111
<i>Gobiosoma robustum</i>	Code goby	216	245	515	976
<i>Syngnathus scovelli</i>	Gulf pipefish	330	260	335	925
<i>Eucinostomus argenteus</i>	Spotfin mojarra	333	59	262	654
<i>Syngnathus floridae</i>	Dusky pipefish	209	286	89	584
<i>Bairdiella chrysoura</i>	Silver perch	132	138	40	310
<i>Cynoscion nebulosus</i>	Spotted seatrout	152	93	53	298
<i>Sciaenops ocellatus</i>	Red drum	95	60	39	194
<i>Lagodon rhomboides</i>	Pinfish	16	22	39	77
<i>Symphurus plagiusa</i>	Blackcheek tonguefish	49	16	8	73
<i>Gobiosoma bosci</i>	Naked goby	9	12	49	70
<i>Hippocampus zosterae</i>	Dwarf seahorse	16	22	24	62
<i>Syngnathus louisianae</i>	Chain pipefish	20	11	6	37
<i>Anchoa mitchilli</i>	Bay anchovy	15	18		33
<i>Hypsoblennius hentz</i>	Feather blenny	11	7	6	24
<i>Orthopristis chrysoptera</i>	Pigfish	12	3	2	17
<i>Chasmodes bosquianus</i>	Striped blenny	4	4	3	11
<i>Chilomycterus schoepfi</i>	Striped burrfish	2	2	3	7
<i>Opsanus beta</i>	Gulf toadfish	1	1	3	5
<i>Ophichthus gomesii</i>	Shrimp eel		1	4	5
<i>Synodus foetens</i>	Inshore lizardfish	3	1		4
<i>Gobiesox strumosus</i>	Skilletfish	1	2		3
<i>Leiostomus xanthurus</i>	Spot	1	1		2
<i>Menticirrhus americanus</i>	Southern kingfish	2			2
<i>Archosargus probatocephalus</i>	Sheepshead			2	2
<i>Trinectes maculatus</i>	Hogchocker		2		2
<i>Chaetodipterus faber</i>	Spadefish	1			1
<i>Bathygobius soporator</i>	Frillfin goby		1		1
<i>Citharichthys spilopterus</i>	Bay whiff		1		1
<i>Pomatomus saltatrix</i>	Bluefish	1			1
<i>Fundulus similis</i>	Longnose killifish			1	1
<i>Adinia xenica</i>	Diamond killifish			1	1
<i>Lucania parva</i>	Rainwater killifish			1	1
<i>Menidia beryllina</i>	Inland silverside		1		1

shrimp showed comparable densities across landscape categories, and broken-back shrimp and brown/pink shrimp showed significantly higher densities in continuous cover than in the other 2 landscape categories.

Flatfish and pipefish species that showed significantly higher densities in small, isolated patches and reticulated edge patches, respectively, than in continuous cover during summer showed no significant differences in fall. In contrast, Gulf pipefish showed

significantly higher densities in small, isolated patches than in continuous cover in fall.

Community diversity

A total of 34 fish species, 8 shrimp species, and blue crabs were included in the diversity analysis (Table 4). No significant differences in species den-

sity were observed as a function of landscape category ($F_{2,29} = 0.393$, $p = 0.679$; Table 5). Species density was significantly higher in summer than in fall ($F_{1,29} = 48.811$, $p < 0.001$). No significant differences in rarefied species richness were detected as a function of landscape category ($F_{2,29} = 1.298$, $p = 0.288$) or season ($F_{1,29} = 0.078$, $p = 0.783$).

Species evenness was significantly lower in small, isolated patches and reticulated edge patches compared to continuous cover ($F_{2,29} = 21.343$, $p < 0.001$; $p < 0.01$ for both significant pairwise comparisons; Table 5). A trend for species evenness to decrease as a function of landscape category may exist; however, evenness was not significantly different between small, isolated patches and reticulated edge patches (Fig. 6). This pattern among landscape categories was consistent during both summer and fall.

DISCUSSION

Landscape structure and species evenness

Our approach used precise mapping technology to capture the *in situ* geometry and spatial configuration of patches within 4225 m² landscapes. Seagrass meadows are often categorized as simply fragmented or continuous using subjective visual criteria (Barbera-Cebrian et al. 2002, Horinouchi et al. 2009, Macreadie et al. 2009). We identified 2 suites of characteristics that describe natural landscape structure: (1) habitat area, habitat connectivity, patch proximity and patch density; and (2) patch shape complexity and edge length. These characteristics were subsequently used to quantitatively distinguish between 3 different landscape patterns: small, isolated patches, reticulated patches, and continuous cover.

Habitat area, connectivity and proximity were positively related to the degree to which individual species were equally represented in the community. Species evenness was lower in small, isolated patches and reticulated edge patches than in continuous cover. This pattern was temporally consistent despite seasonal differences in total nekton density and seasonal shifts in the distribution of individual species among landscape categories.

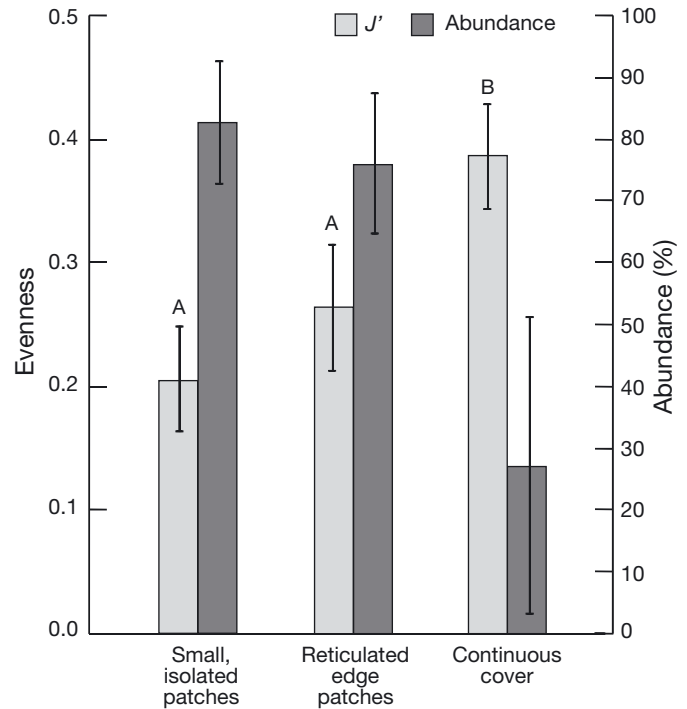


Fig. 6. Relative abundance of arrow shrimp *Tozeuma carolinense* expressed as percentage of total animal abundance, and species evenness (Pielou's J') as a function of landscape pattern. Error bars represent 95% confidence intervals

Table 5. Three-way ANOVA analyses comparing diversity in sampling plots representing 3 landscape categories: (1) small, isolated patches; (2) reticulated edge patches; and (3) continuous cover. MSE: mean square error

Dependent variable	df	Mean square	F	p
Species density (no. of species in 61.2 m²)				
Season	1	174.052	48.811	0.000
Bay	1	2.066	0.579	0.453
Landscape category	2	1.401	0.393	0.679
Landscape category × Season	2	4.647	1.303	0.287
Residual	29	3.566		
Rarefied species richness (Mean no. of species in 1683 ind.)				
Season	1	0.171	0.078	0.783
Bay	1	9.861	4.478	0.043
Landscape category	2	2.858	1.298	0.288
Landscape category × Season	2	6.217	2.823	0.076
Residual	29	2.202		
Species evenness (Pielou's J')				
Season	1	0.015	3.113	0.088
Bay	1	0.003	0.622	0.437
Landscape category	2	0.101	21.343	0.000
Landscape category × Season	2	0.003	0.585	0.563
Residual	29	0.005		
Pairwise comparison				
		MSE		
1:2	29	0.005		0.117
1:3	29	0.005		0.000
2:3	29	0.005		0.000

Species abundance and evenness

The significant difference in overall animal abundance between continuous cover and small, isolated patches (and near-significant difference with reticulated edge patches) in summer was driven by the distribution pattern of a few highly abundant shrimp species. In summer, arrow shrimp densities dominated small, isolated patches and reticulated edge patches, driving species evenness levels lower and overall nekton density levels higher, compared to continuous cover. Broken-back shrimp were common in all 3 habitat types, and grass shrimp were most abundant in continuous cover, suggesting that a degree of spatial partitioning may have occurred among caridean shrimp species (Alon & Stancyk 1982, Tayasu et al. 1996). Arrow shrimp often attach themselves high up on seagrass blades (Cournoyer & Cohen 2011), making use of a third (i.e. vertical) dimension in the meadows. This ability to use vertical space (Cournoyer & Cohen 2011) conveys a competitive advantage in habitats with restricted size, proximity and connectivity.

In fall, species evenness was also positively related to habitat area, proximity and connectivity. Several taxa, however, exhibited seasonal shifts in abundance in favor of landscapes with continuous cover such that overall nekton abundance did not differ among landscape categories during this season. Abundance of arrow shrimp declined in both small, isolated patches and reticulated edge patches but not in continuous cover, and they were thus distributed evenly among all landscapes. Although densities of arrow shrimp were greatly reduced from summer, they still dominated the assemblages in small, isolated patch and reticulated patch edge habitats because broken-back shrimp and penaeid shrimp underwent large seasonal density reductions in these landscapes as well, resulting in greater densities in continuous cover.

Landscape structure, nekton feeding ecology, and life history

High densities of arrow shrimp in small, isolated patches and reticulated edge patches during summer may have resulted in intense grazing pressure on epiphytic algae on seagrass blades in these landscapes. Caridean shrimp can significantly reduce epiphyte load on blades (McCall & Rakocinski 2007); a single adult arrow shrimp can denude the epiphytic algae from 40 to 50 seagrass blades in 2 to 3 d (Ewald 1969). Densities of epiphyte-grazing shrimp averaged 357 m⁻² in small, isolated patches, 324 m⁻² in reticu-

lated edge patches and 120 m⁻² during summer. Consequently, food resources in these crowded habitats were likely depleted in fall, causing nekton to emigrate to habitats (Edgar 1990) that experienced less intense grazing pressure such as large, continuous meadows.

A bimodal size distribution of the 3 most dominant shrimp (arrow, broken-back, grass; Fig. S6 in the Supplement) was commonly observed in all 3 landscape categories, indicating that both juvenile and adult shrimp use these habitats for food. Similarly, size measurements (Table S5 in the Supplement) and size distributions (Fig. S7 in the Supplement) of pipefishes and gobies show that both juveniles and mature adults were commonly captured in this study, corroborating the findings of other research (Diaz-Ruiz et al. 2000, Ross & Rhode 2004) that these fishes spend their entire lives feeding within seagrass meadows. Seasonal differences in the distribution of medium-sized to large pipefishes and gobies between landscape categories, however, suggest that these fishes become sensitive to space and food resources as they mature in seagrass meadows. The size distributions of Gulf pipefish show a shift in medium-sized to large fishes out of small, isolated patches from summer to fall. The darter goby's seasonal shift in abundance also involves adults, which were abundant in both small, isolated patches and reticulated edge patches during summer but comparatively scarce in those habitats during fall.

Several fishes such as silver perch, spotted sea-trout, red drum, spotfin mojarra and pinfish showed no significant differences in abundance as a function of landscape pattern. These transient fish species (Rooker et al. 1998, Meyer & Posey 2009) consisted mostly of post-settlement juveniles (Table S5), indicating that they were using these landscapes as nursery areas (Tolan et al. 1997, Rooker et al. 1998). Transient fish species inhabit various structurally complex estuarine habitats as well as bare substrate across their life span. The observed size of these species may be related to the capture efficiency of the epibenthic sled used to sample nekton, because larger juvenile or adult stages use these habitats as well.

Landscape structure, and species density and richness

There were clear differences in species evenness and total animal abundances among landscape patterns; however, there were no significant differences in species density or rarefied species richness in this study. Processes such as species dispersal are influ-

enced by landscape qualities such as connectivity, which influences movement of individuals (With & Crist 1995, With 2004). However, the wide size distributions of common taxa observed within each landscape category in this study corroborate other research (Sogard 1989, Darcy & Eggleston 2005) showing that adults and juvenile nekton can colonize and use patches by crossing bare substrate through larval dispersal and adult migration. Therefore, habitat connectivity, patch proximity and patch density do not appear to significantly affect animal movement in these landscapes and are not as important as habitat area in influencing species evenness.

Habitat area has been implicated as the most important quality influencing nekton in other research (McNeill & Fairweather 1993, Jelbart et al. 2006, Mills & Berkenbusch 2009), and an abrupt decline in density and diversity within landscapes that contained less than 20 (Pittman et al. 2004) to 30% (Andren 1994) seagrass cover has been reported. Pittman et al.'s (2004) study assessed landscape structure at a much larger scale than the one used here (approximately 280 000 vs. 4225 m² in our study). We saw no significant reduction in species density or rarefied species richness even though mean percent cover in landscapes with small, isolated patches was lower than 20% in our study (Figs. S1 & S2). Pittman et al.'s (2004) data, however, suggest that the amount of seagrass in the area surrounding our sampling plots played an important role in supporting the diversity levels we observed.

Our study did not find distinct patterns in species density or rarefied species richness or in nekton density and evenness between small, isolated patches and reticulated edge patches, indicating that these measures of diversity and abundance are not related to edge length or patch shape complexity. Thus, patch size is more important than edge length in small patches. Other studies have shown no edge effect on species richness in small patches but do find effects in large patches (Jelbart et al. 2006, Macreadie et al. 2010, Smith et al. 2010). Since evenness was significantly higher in continuous patches than in small, isolated patches or reticulated edge patches, we suggest that a landscape structure threshold exists for community evenness between approximately 45 and 85% cover. This differs from the 20 to 30% cover reported as a threshold for species density (Andren 1994, Pittman et al. 2004), suggesting that the spatial distribution of dominant nekton species among habitats or the relative abundance of species within habitats is the first aspect of community structure affected by differences in landscape structure in seagrass meadows.

Conclusions

The spatial characteristics of seagrass meadows influenced species evenness despite seasonal differences in nekton abundance and shifts in distribution of individual species between landscapes. Habitats with low habitat area, connectivity and proximity harbored the highest total nekton abundance and lowest evenness in summer, a pattern driven by the numerically dominant arrow shrimp. These habitats subsequently exhibited shifts in the distribution of several shrimp species in favor of continuous cover during fall, resulting in comparable overall nekton abundance across landscape types in that season. Differences in species evenness persisted in fall, even when arrow shrimp densities were similar across landscape types.

Our study highlights the need for future research that confirms whether landscape pattern influences the linkage between primary producers (such as epiphytic algae), herbivorous invertebrates and the fishes that feed on them. Epiphytic algae can limit the growth of seagrasses (Hays 2005); therefore, research that clarifies the influence of landscape pattern on grazing intensity and epiphyte depletion in these estuarine habitats will improve our understanding of how these habitats support different nekton taxa as well as the implications of fragmentation and declines in habitat area for both nekton diversity and top-down or bottom-up control (Hays 2005, McCall & Rakocinski 2007, Whalen et al. 2013) of seagrass growth.

Our data indicate that the life history traits and feeding ecology of individual species play important roles in how habitat area, connectivity and proximity influence nekton density within seagrass landscapes across time. Large expanses of continuous cover, therefore, appear to harbor more stable nekton communities and provide sufficient space for different species to coexist without depleting food resources to the point that nekton populations become unstable.

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