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**The effects of habitat fragmentation on the diversity of nekton  
inhabiting subtropical seagrass meadows**

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**The effects of habitat fragmentation on the diversity and community  
structure of nekton inhabiting subtropical seagrass meadows**

**by**

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## **Dedication**

This thesis is dedicated to two housecats: Dolemite and Scatter. 5 years ago, they gave up everything they had so I could pursue a career in science and conservation.

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## **Abstract**

### **The effects of habitat fragmentation on the diversity and community structure of nekton inhabiting subtropical seagrass meadows**

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Habitat fragmentation is often regarded as a biodiversity threat associated with habitat degradation; however, research has also revealed beneficial effects on biodiversity as well, depending on the ecosystem and species community. This study examined the biodiversity of small nekton residing in seagrass meadows characterized by three levels of habitat fragmentation, and as a habitat gradient comprised of measures such as habitat amount, connectivity, patch shape, and proximity. Landscapes were mapped using recent advances in GPS and GIS technology, and analyzed using established methods from research in terrestrial ecosystems. Species richness was not significantly different as a function of fragmentation regardless of season, suggesting that the amount of habitat and configuration of several patches in fragmented habitats is sufficient to support comparable numbers of species in several patches compared to communities in large,

continuous seagrass meadows. Species evenness declined significantly in fragmented habitats versus continuous ones in both seasons. Within fragmented landscapes, evenness progressively declined as habitat amount and connectivity decreased and patch isolation and density increased, suggesting that changes in landscape qualities can differentially impact processes supporting metapopulations such as dispersal and reproduction in certain species, thereby influencing community structure. Analyses that included measures of habitat connectivity, proximity, and patch density in addition to habitat amount accounted for more variability in species evenness than those just containing percent cover, and showed that fragmentation's impacts can differ geographically. These data suggest that community resilience to fragmentation can differ between similar animal communities residing in separate locations, and that landscape configuration plays an important role in determining how communities respond to fragmentation after a threshold of change in habitat amount has been exceeded.

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# **Chapter 1: The diversity of nekton within three levels of seagrass meadow fragmentation**

## **INTRODUCTION**

Habitat fragmentation is often regarded as a biodiversity threat associated with habitat degradation (Haila 2002) however research has revealed beneficial effects on biodiversity as well, depending on the ecosystem and species community (Barbera-Cebrian, Sanchez-Jerez et al. 2002; Jelbart, Ross et al. 2006; Horinouchi, Tongnunui et al. 2009). Fragmentation is typically defined as an increase in the proportion of habitat edge and distance between patches, thereby causing the breaking apart of habitat, and can be considered separate from habitat loss (Boström et al., 2006). Compared with a continuous habitat expanse such as that found in a dense forest, fragmented landscapes typically have a “matrix” of dissimilar habitat (such as bare ground or human development) that often separates and invaginates patches of original habitat structure to various degrees. This matrix habitat is usually observed to be neutral or less favorable for the species or community of concern (Hanski 2004).

Fragmentation reduces habitat connectivity and may alter processes of community formation (Jelbart, Ross et al. 2006), trophic interactions (MacArthur 1967; Johnson and Heck 2006), and abundance levels (Salita, Ekau et al. 2003). The matrix of dissimilar habitat between isolated patches can impede or prevent movement of organisms across a given spatial range, or between critical habitats. In many cases, habitat fragments can be regarded as individual “islands” that harbor separate communities that comprise metapopulations of various organisms (McNeill and Fairweather 1993). Theories addressing metapopulation dynamics in fragmented habitats typically focus a single species over ecological time scales, whereas the theory of island biogeography

(MacArthur 1967) focuses on communities comprised of several species over longer time scales (Hanski 2004) that may influence evolutionary trajectories.

For individual species, the effects of fragmentation have been observed on several life history traits including insect dispersal and mortality (Schtickzelle, Mennechez et al. 2006), mammal, bird, and fish dispersal (Newmark 1987; Munday 2009; Robertson and Radford 2009), and the habitat architects themselves such as vegetation density (Horinouchi 2007) and coral distribution (Munday 2009). Patterns of faunal response to fragmentation have not been observed to be consistently positive or negative (Haila 2002). Beyond a certain threshold of habitat loss, however, empirical models of metapopulations of animals predict deterministic extinction because of impacts to the processes of dispersal and colonization supporting animal populations, and in highly fragmented landscapes, qualities of landscape configuration separate from habitat amount play an important role in determining extinction thresholds (Ovaskainen 2004).

Extinction or reduction in abundance of one or more species can alter the diversity and structure of the community in a given system. In recent years, considerable attention has been given to the fact that seagrass habitat has undergone significant change and degradation due to natural and anthropogenic causes. Seagrass meadows have been demonstrated to serve as nursery habitats for commercially and ecologically vital fish species (Rooker, Holt et al. 1998) and for a variety of shrimps and crabs across their lifespan. Evidence suggests that not all seagrass habitats function equally (Heck 2003) and there is concern that the ecological role seagrass habitat plays may be impaired by fragmentation (Bell, Brooks et al. 2001).

Studies on seagrass habitat alterations have increased in number over the last two decades, however less is known about fragmentation's effects on seagrass inhabitants compared to terrestrial systems. Studies that focus exclusively on animal communities

observed within seagrass beds permit direct comparisons of diversity within seagrass habitats and some have found positive impacts in habitats with characteristics associated with fragmentation. Species richness was higher in metacommunities comprised of two smaller patches versus a single community within a large patch (McNeill and Fairweather 1993). Studies involving benthic macroinvertebrates have observed reduced species richness in metacommunities from small, fragmented patches versus continuous landscapes (Mills and Berkenbusch 2009), however this effect was not always significant across study sites. Other studies have found no difference in species richness in macroinvertebrate metacommunities from fragmented landscapes versus communities from continuous seagrass at multiple spatial scales (Borg, Rowden et al. 2010)

Empirical studies of metapopulations in fragmented terrestrial landscapes point towards the need to understand the impact that landscape patterns have on processes supporting species persistence and community diversity over time (Hanski 2004). In seagrass systems, the degree to which estuarine species associate with seagrass habitats can vary significantly across their lifecycle (Wenner and Beatty 1993; Tolan 1997). Differences in the way animals utilize seagrass along with changes in habitat structure itself over time may account for why overall diversity has been observed to differ between seasons (Turner, Hewitt et al. 1999; Horinouchi, Tongnunui et al. 2009). Further research is needed to investigate whether patterns of diversity as a function of different levels of fragmentation are temporally consistent in lieu of any potential changes in species composition or utilization of seagrass habitats.

This study concerns itself with three questions. The first is whether diversity of small nekton inhabiting seagrass differs among fragmented and continuous seagrass landscapes in a Gulf of Mexico estuarine system. Seagrass meadows with intermediate levels of fragmentation, compared to those with either minimal or high levels, were

predicted to have the highest biodiversity. The second question is whether diversity patterns observed in fragmented and continuous landscapes are consistent across seasons. Fragmentation's effects on animals has been observed to differ across small geographical distances (Johnson & Heck, 2006), and so the present study compared its effects in two separate locations (bays). Here, the central concern was not whether the effects of fragmentation on diversity were different in each bay; rather the focus was placed on whether net impacts to biodiversity were consistent in two seasons (summer and fall) despite the potential existence of any geographical differences in effects.

The final question was which spatial qualities of landscape patterns produced by fragmentation are associated with changes in community diversity at a landscape scale. This question was focused on describing changes in specific qualities of landscape pattern apart from just habitat loss that are associated with biodiversity impacts, including aspects such as differences in patch shape complexity, edge amount, and spatial arrangement within a landscape. Communities within meadows with intermediate fragmentation may be diverse due to the heterogeneous nature of the habitat that is available, including abundant levels of both seagrass and edge-sand interface. Seagrass meadows with continuous cover were hypothesized to have lower biodiversity which may be partly due to the lack of habitat heterogeneity. Highly fragmented habitats were predicted to have intermediate levels of species richness because of the relatively high proportion of edge contained within patches, yet patch isolation may increase the risk of predation and decrease rates of dispersal-related immigration of nekton to individual patches, thereby counteracting to some degree against potential benefits of habitat heterogeneity. To answer these questions, shallow landscapes of equal area were mapped and assessed to determine the level of seagrass fragmentation, and measures of

community diversity found within high fragmentation, intermediate fragmentation, and continuous cover were compared.

## **METHODS**

### **Habitat Mapping**

Monospecific meadows of shoalgrass, *Halodule wrightii*, were surveyed visually and selected for mapping in Aransas Bay and Corpus Christi Bay, TX (Figures 1, 2 & 3) to determine levels of fragmentation. These shallow (0.5m – 1.5m water depth) landscapes were mapped *in situ* from data obtained by Trimble GPS receivers (GeoXT Handheld, Trimble Navigation Limited, 2008) which were tested in trials to be capable of sub-meter accuracy. The GPS recorded the geolocation of the operator every second, who slowly walked the exact perimeter of every seagrass patch in a landscape to capture its spatial features. Mapping was performed in one to four weeks preceding sampling both in the summer and fall of 2009. ArcGIS 9.3.1 (ESRI Software, 2008) was used to process receiver data and create geo-referenced, vector-based maps of these shoreline landscapes, which were approximately 200m long and 100m wide. Within each landscape, locations for sampling plots were chosen using visual criteria (percent cover, patch size and proximity) to approximate 3 levels of naturally occurring habitat fragmentation:

1. Continuous Cover (no fragmentation)
2. Intermediate Fragmentation (large, close patches, and reticulated cover)
3. High Fragmentation (small, isolated, or thin patches)

In Corpus Christi Bay and Aransas Bay, three replicates of each fragmentation level (9 plots per Bay, 18 per season) were selected for study during summer and fall. Plots representing each fragmentation level were evenly dispersed across approximately 4

km of bay shoreline in areas with similar hydrodynamic conditions, and were separated by at least 30m of bare sand and mud bottom (Figure 1).

### **Habitat Fragmentation Analysis**

The landscapes analyzed in this study were defined by an extensive and equal area (4225m<sup>2</sup>) within the larger meadow in which a spatially broad and thorough sampling effort could be applied. Habitat fragmentation metrics change as a function of the geographical scale at which they are quantified (Pinto and Keitt 2008). These sampling plots contained patches with a wide range of sizes and shapes, so the general landscape characteristics directly within the sampled area were captured. Vector map data for each sampling plot was converted to raster grids with 10 cm cell size. This size was chosen after evaluating several options to see which best preserved patch geometry during data conversion. Measures of habitat fragmentation in each of the plots were computed with FRAGSTATS software (McGarigal 2002). Twenty-three habitat fragmentation indices used to evaluate terrestrial landscapes (Kumar, Stohlgren et al. 2006; Kumar, Simonson et al. 2009) and marine landscapes (Sleeman, Kendrick et al. 2005) were calculated for each plot. A Pearson correlation matrix was used to identify metrics that were highly correlated with one another ( $\geq \pm 0.800$ ). One measure was retained, and correlated measures were eliminated from further analysis to prevent inclusion of redundant measures. Mean Patch Area (MA) and Percent Cover (PA), were included despite being correlated with other metrics because they are critical measures of relative habitat amount. Index values were log-transformed where necessary to minimize heteroskedasticity in data and plotted on a common scale. A principal components analysis (PCA) involving 12 remaining indices (Table 1) was performed using SYSTAT 12 (2007) to identify the major qualities that differed in the 36 study plots (Figure 4),

similar to the approach used in other studies of fragmented seagrass landscapes (Sleeman, Kendrick et al. 2005).

### **Nekton Sampling**

During early summer (June 16-25) and late fall (Oct 21- Nov 2) of 2009, nekton samples were obtained from each plot in both bays on two separate dates, approximately 7 days apart. During each sampling event, a minimum of approximately 38.25 m<sup>2</sup> of seagrass was sampled by towing an epibenthic sled which had a metal frame opening of 0.6 m (length) X 0.75 m (height) equipped with a 1-mm mesh conical plankton net over the seagrass bed surface. This device is designed for collecting epibenthic nekton 4-50mm in length, including small/juvenile fish, larval fish, shrimps, and decapods (Stunz, Minello et al. 2002).

Multiple sampling paths were planned *a priori* in ArcGIS within each plot to obtain minimum sample requirements of 51 linear m within each plot. Individual tow samples varied in length from 4 - 17m depending on patch size. Samples were collected inside seagrass beds only. Tow transects were placed in beds haphazardly, however in small patches, tows were started by placing the sled at the patch edge and ending on the other side of the patch. Additional samples within patches were obtained from the plots approximately 7-10 days later, and efforts were made to avoid directly overlapping previous tow paths during the second sampling event.

The *in situ* tow length for each sample was recorded on Trimble GPS units by carefully following the sled with a GPS in order to calculate sample size based on seagrass area (m<sup>2</sup>). Three depth measurements were recorded along equidistant points for each tow path. Salinity, temperature, and dissolved oxygen levels were recorded at each sampling plot. Macroalgae and seagrass were carefully rough-sorted in the field, and the

remaining nekton preserved in 10% formalin. In the laboratory, shrimp, fish, and decapods were identified and counted to species level and preserved in 70% ethanol.

## **Community Structure Analyses**

### ***Animal Density***

To assess overall animal abundance as a function of fragmentation level within or between seasons, a three-way ANOVA ( $\alpha = 0.05$ ) was performed on animal densities (calculated as the number of animals  $m^{-2}$  seagrass sampled) in each plot. Fragmentation Level (3), Season (2) and Bay (2) were fixed factors in the analyses, with Bay treated as a blocking variable. Data from both sampling events were pooled within each plot for the analysis, and log-transformation was necessary to meet assumptions of data normality and homogeneity of variance. Significant main effects of fragmentation level were further evaluated in post-hoc pair-wise comparisons using Tukey's test.

### ***Community Diversity***

Biodiversity across habitat fragmentation levels was quantified by three measures. The first measure was species density, defined by the number of species observed in a given area of seagrass. This measure allowed comparisons between habitats that were based on equal amounts of seagrass area ( $m^2$ ) sampled in each plot. Although a minimum of  $38.25 m^2$  of seagrass per plot was targeted for sampling during each event, actual sample sizes were often larger in plots within highly fragmented habitats. Several small patches in these areas were sampled in order to obtain the minimum sample size. Since the entire length of small patches was sampled, overages in total plot sample size occasionally resulted. To account for potential biases in species number estimates from these variations in sample size, species accumulation curves were used to estimate the number of species from a standardized sample size from each plot.

Samples from both events were used to construct species accumulation curves for each plot. This ranged from 6-13 samples, depending on the degree of fragmentation in each plot. PRIMER V6 (Clarke 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 ( $\text{m}^2$  seagrass sampled) in each plot was divided by the total number of samples to derive species accumulation curves as a function of increasing tow area.  $R^2$  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, Poos et al. 2008). Sixty-one  $\text{m}^2$  was identified as the largest universal sample size upon which to estimate species density across plots. Species accumulation equations for each plot were used to interpolate the number of species found in  $61\text{m}^2$  of sampled seagrass area (species density). Using these data, a three-way ANOVA ( $\alpha = 0.05$ ) was performed on species density in each plot. Fragmentation Level (3), Season (2) and Bay (2) were fixed factors in the analyses, with Bay treated as a blocking variable (interaction terms involving Bay were not included). Data were log-transformed where necessary to meet assumptions of data normality and homogeneity of variance.

The second measure was species richness based on standardized animal abundance. There was potential for differences in animal abundance between fragmentation levels to bias richness estimates based on habitat area during summer, and for bias in overall diversity estimates between summer and fall (Table 2). Rarefaction is a method of estimating species richness that accounts for potential biases that may exist

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

Animals were sampled using transects that were haphazardly placed in multiple patches or patch locations in each plot in order to obtain an estimate of animals that was extensive and spatially heterogeneous, which satisfied important assumptions in the use of rarefaction. The data collected from each set of samples within the plots were pooled in order to perform individual-based rarefaction analyses on the animal community in each plot. ECOSIM (Gotelli 2001) was used to estimate species richness on rarefied animal abundance levels. This program has been used for rarefaction in biodiversity studies of insect fauna (Ahrne, Bengtsson et al. 2009; Quintero, Morales et al. 2010) and birds (Estrada, Cammarano et al. 2000). A three-way ANOVA ( $\alpha = 0.05$ ) was performed on rarefied animal diversity estimates with Fragmentation Level (3), Season (2) and Bay (2) as fixed factors in the analyses, and Bay treated as a blocking variable (interaction terms involving Bay were not included).

To provide this analysis with rarefied sample data, the plot containing the smallest number of total animals from both sampling events (1683 individuals) was identified and selected as the universal abundance level with which to compute and compare 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 individuals 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, Poos et al. 2008). Data met the assumptions of normality and homogeneity of variance.

The third and final diversity measure in this study was species evenness. Using PRIMER V6 (Clarke 2006), evenness was measured using Pielou's  $J'$ , which is a bounded index ranging from 0 (minimum evenness) to 1 (maximum evenness) that quantifies how equally represented different species are within a given sample. Pielou's  $J'$  has been used in other biodiversity studies in seagrass (Turner, Hewitt et al. 1999; Cardoso, Pardal et al. 2004; Gil, Armitage et al. 2006). A three-way ANOVA ( $\alpha = 0.05$ ) comparing mean Pielou's  $J'$  among plots as a function of fragmentation in the study. Fragmentation Level (3), Season (2) and Bay (2) were fixed factors in the analyses, with Bay treated as a blocking variable (interaction terms involving Bay were not included). Similar to other analyses, samples from both events were pooled within each plot in a given season for the analysis. Data met the assumptions of normality and homogeneity of variance.

## **RESULTS**

### **Habitat Fragmentation**

Fragmentation metrics that loaded strongly ( $\geq 0.60$  or  $\leq -0.60$ ) in each principal component factor were used to describe principal component factors (Table 1). Factor 1 was comprised of measures of habitat connectivity, habitat amount, patch proximity, and number of patches. This aspect of "habitat continuity" accounted for over 35% of the variability across sampling plots. In the summer, mean patch sizes as quantified within the plot boundaries ranged from 32 - 88m<sup>2</sup> in high fragmentation, 89 - 315m<sup>2</sup> in intermediate fragmentation, and 1736 - 4225m<sup>2</sup> in continuous cover (Figure 2). Percent seagrass cover in the plots during this season ranged from 5 - 10% in high fragmentation

and 20 - 42% within intermediate fragmentation. One continuous plot contained 40% cover but consisted of a large patch; the rest of the continuous plots ranged from 85 - 100% cover.

During the fall, mean patch sizes ranged from 31 - 181m<sup>2</sup> in high fragmentation, 153 - 697m<sup>2</sup> in intermediate fragmentation, and 1376 - 4225m<sup>2</sup> in continuous cover (Figure 3). Percent seagrass cover in the plots during this season ranged from 12 - 21% in high fragmentation, 27 - 65% within intermediate fragmentation, and 61 - 100% for continuous cover. All plots representing continuous cover were comprised of seagrass patches that extended well beyond the plot boundaries, and this was often also the case for plots representing intermediate fragmentation. However, measurements of patch size and other metrics were restricted to the landscape that was quantified within the plot boundaries for this study.

Factor 2 encompassed measures of patch shape complexity and edge amount (i.e. patch perimeter created from the sand-edge interface), and explained over 26% of the variance observed in habitat measures across plots. In the summer, total plot edge amount varied from 245 - 255m in high fragmentation, 478 - 1013m in intermediate fragmentation, and 0 - 183m in continuous cover. In the fall, total edge in plots varied from 260 - 602m in high fragmentation, 600 - 1023m in intermediate fragmentation, and 0 - 166m in continuous cover. Factor 3 described patch aggregation or “clumpiness” in the spatial arrangement of patches, and how compact shapes were within the landscape. It accounted for approximately 16% of variability across sampling plots.

A three-way ANOVA ( $\alpha = 0.05$ ) was performed in SYSTAT on Factor 1, 2 and 3 scores that plots from each fragmentation level received in the principal components analysis (Table 2). Fragmentation Level (3), Season (2), and Bay (2) were fixed factors, and Bay was treated as a blocking variable in the ANOVA (interaction terms involving

Bay were not included). Potential differences in the blocking variable were not analyzed in this study.

Factor 1 scores increased as habitat amount, connectivity, and proximity declined. A significant interaction ( $F_{2,29} = 4.496$ ,  $p = 0.020$ ) between Season and Fragmentation Level was observed so seasons were analyzed separately. 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 between all fragmentation levels within each season (Table 2, Figure 5). The significant interaction term occurred because Factor 1 scores in High and Intermediate Fragmentation Levels were significantly higher than continuous cover in the spring than in fall.

Factor 2 scores increased as patch shapes in each plot became more complex and edge amount increased. A three-way ANOVA ( $\alpha = 0.05$ ) of Factor 2 scores for each fragmentation level showed no interaction between season and fragmentation ( $F_{2,29} = 0.391$ ,  $p = 0.680$ ), and that intermediate fragmentation had more complex patch shapes and edge amount than both high fragmentation and continuous cover in both seasons ( $F_{2,29} = 32.216$ ,  $p < 0.001$ ;  $p < 0.01$  for both post-hoc orthogonal comparisons; Table 2, Figure 6). No significant differences in Factor 3 scores were observed across the three fragmentation levels, and so the role of patch aggregation in determining animal density and community diversity could not be further evaluated at this scale.

### **Animal Density**

Over 460,000 nekton and benthic crustaceans were collected (Table 3). Animal sizes in the analysis ranged from approximately 4.5mm for American prawns, (*Palaemonetes sp.*), and newly settled red drum (*Sciaenops ocellatus*) to 160mm adult chain pipefish (*Syngnathus louisianae*). A significant interaction between season and

fragmentation on animal density was observed ( $F_{2,29} = 7.061$ ,  $p = 0.003$ ; Table 4), which showed that in the summer, animal densities were significantly different across fragmentation levels ( $F_{2,14} = 5.977$ ,  $p = 0.013$ ) but no difference in densities was observed in the fall. A post-hoc comparison using Tukey's test showed that animal densities were significantly greater in highly fragmented habitats than continuous cover habitats ( $p = 0.014$ ) in the summer. During this season, animal densities within intermediate fragmentation were highly variable (Figure 7) and differences compared to continuous cover approached significance ( $p = 0.052$ ). In the fall, densities were less variable and not significantly different across fragmentation levels. Arrow shrimp, *Tozeuma carolinense*, were the most abundant animal in the assemblage (Table 4). They accounted for a very large proportion of the community across fragmentation levels in both seasons, and dominated the assemblage in fragmented habitats during both seasons (Figure 8).

### **Community Diversity**

Thirty four fish species, 8 shrimp species, and blue crabs (identified to genus level) were included in the diversity analysis (Table 3). No significant differences in species density were observed as a function of fragmentation level ( $F_{2,29} = 0.393$ ,  $p = 0.679$ ; Table 5, Figure 9). Species density was significantly higher in summer than fall ( $F_{1,29} = 48.811$ ,  $p < 0.001$ ; Figure 10). No significant differences in rarefied species richness were detected as a function of fragmentation level. Seasonal differences in rarefied species richness were not detected ( $F_{1,29} = 0.023$ ,  $p = 0.879$ ; Figure 11). Diversity in fragmented landscapes should be treated with caution due to the fact that species density and rarefied species richness measures in each plot were based on samples from multiple patches, which may harbor separate communities that do not share the same species.

Species evenness was significantly lower in high and intermediate fragmentation levels compared to continuous cover ( $F_{2,29} = 21.343$ ,  $p < 0.001$ ;  $p < 0.01$  for both significant pair-wise comparisons; Table 5). A trend for species evenness to decrease as a function of fragmentation level may exist; however evenness was not significantly different between intermediate and high fragmentation levels (Figure 12). This pattern among fragmentation levels was consistent both during summer and fall.

## DISCUSSION

This study showed that fragmented seagrass landscapes have enough habitat and suitable configuration of patches to sustain comparable numbers of species as continuous cover, however differences in these characteristics influence the degree to which individual species are represented in the community. In both seasons, species evenness was lower in landscapes containing intermediate and high levels of fragmentation than in continuous cover. Consistent with predictions of theoretical studies (With and Crist 1995; With 2004), differences in landscape connectivity and habitat amount appear to negatively impact demographic rates of many species in this study while others remain unaffected, thereby affecting community structure.

The approach used here is unique because it describes the *in situ* geometry and spatial configuration of seagrass patches within a given area, identifying several important qualities that differentiate a large number of landscapes which are often categorized as fragmented or continuous using visual criteria (Barbera-Cebrian, Sanchez-Jerez et al. 2002; Horinouchi, Tongnunui et al. 2009; Macreadie, Hindell et al. 2009). Highly fragmented habitats were characterized by small isolated patches that had simple shapes. Habitats with intermediate fragmentation contained larger patches with complex shapes and high amounts of edge, whereas continuous landscapes contained expanses of

seagrass that were uninterrupted by any bare sand, and had very little edge amount. The impact that differences in these landscape qualities had on diversity may reflect how both the process (With 2004) and resulting landscape pattern (Ovaskainen 2004) of habitat fragmentation operate together to influence the population dynamics supporting animal communities in this study area.

Seagrass landscapes appear to undergo constant change across seasons and years. Annual patterns of natural seagrass fragmentation occur as a result of die-back and re-growth. Landscape patterns are likely governed by environmental conditions such as sedimentation and wave energy (Turner, Hewitt et al. 1999; Barbera-Cebrian, Sanchez-Jerez et al. 2002), light, and nutrient levels. As a result, animal communities may form and change along with ongoing processes within these dynamic landscapes. Because changes in landscape pattern in the present study area did not happen instantaneously, the communities in these landscapes may have had time to organize themselves as a function of the landscape pattern in the immediate area. Comparable numbers of species had colonized fragmented and continuous habitats in both seasons.

Local population extinctions are generally predicted to occur more frequently in dynamic landscapes than static ones, where patch demographics such as size drive dynamics of metapopulations in fragmented systems (With 2004). The complete history of fragmentation within the landscapes examined in this study is not fully known, however patch area and degree of proximity increased in the sampling plots from summer to fall. Thus, the trajectory of fragmentation was not consistent with conditions that would necessarily cause species to disappear in highly fragmented landscapes, and the temporally stable patterns of species richness across fragmentation levels support this observation. Metacommunities comprised of several fragmented patches harbored comparable numbers of species to communities in continuous landscapes. It is still

possible that communities within individual patches in fragmented landscapes do not share all of the same species, and could therefore have lower species richness than large, continuous landscapes. Metapopulation dynamics are supported by landscape connectivity, which influences individual species movement (With 2004). Within landscapes of comparable size in this study area, the degree of habitat connectivity and amount do not appear to have surpassed dispersal thresholds when considering the total number of species across multiple patches.

Seasonal differences in seagrass structural complexity, animal density, and assemblage composition are common in Gulf of Mexico seagrasses (Tolan 1997). In this study, several fish species (e.g., pigfish, *Orthopristis chrysoptera*, striped blennies, *Chasmodes bosquianus*, and Gulf toadfish, *Opsanus beta*) were only found in summer, where species richness was highest. Conversely, species such as red drum (*Sciaenops ocellatus*) were only found in fall. Despite seasonal differences in species composition and significantly higher species richness in summer, no significant differences were found in species richness as a function of fragmentation level. These observations are generally consistent with other research that found no effect of seagrass patch characteristics on species richness of benthic infauna despite significant seasonal differences in richness (Turner, Hewitt et al. 1999). Similarly, other studies of seagrass-associated fauna have found no difference in species richness as a function of individual patch size in epifaunal invertebrates (Eggleston, Elis et al. 1999) and for small fish, shrimps, and gastropods (Johnson 2008) when they colonized Artificial Seagrass Units (ASUs). Considering the results from other studies, it appears that fragmentation's effects on species richness are temporally consistent even if the direction of impact or overall level of diversity varies across time. The results of this study support this

observation. The role of habitat patterns in structuring animal communities appears to operate the same way across two seasons.

Although fragmentation was not observed to impact species richness, species evenness was significantly lower in fragmented landscapes than continuous ones. Arrow shrimp are likely to be a major force driving differences in evenness by dominating animal communities in fragmented habitats versus continuous ones in the summer and fall. They represented over 70% of the total catch across both seasons, and played a major role in total animal abundance in each fragmentation level. There was a trend for arrow shrimp to dominate highly fragmented habitats more than intermediate fragmentation, suggesting that these animals can thrive in habitats that are very limited in space and degree of connectivity with each other.

Because arrow shrimp were still a significant part of the community in continuous seagrass, there is no evidence that they prefer fragmented habitats over continuous *per se*. Patch shape complexity and edge amount do not appear to be important habitat qualities for arrow shrimp, because intermediate fragmentation had greater amounts of edge and more complex patch shapes than highly fragmented habitats, yet arrow shrimp dominated both of these habitat types. However, their food and space requirements may be such that they can grow, reproduce, and persist to a greater degree in small, isolated habitats than other members of the community. Communities with low evenness have been observed to be common in climatically unstable environments (Magurran 1988) and have impaired functionality (Wittebolle, Marzorati et al. 2009) under stress. In the present study area, uneven animal communities may be a reflection of the environmental stressors thought to produce fragmented landscapes, the spatial characteristics of the resulting landscape pattern itself, or both.

The lifespan of fragmented patches in this study may also play a role in observed evenness patterns. Fragmented habitats, especially those containing small isolated patches, were visually noted to have markedly reduced shoot density in the fall, coinciding with seasonal patterns of dieback. The fact that these habitats grew in size and spatial configuration over the summer, yet showed signs of dieback in the fall suggests that these habitats are temporally less stable than large, continuous meadows. Dynamic habitats that have turnover rates that outpace the lifecycles of certain species may not support them to the same degree that more stable habitats do (With 2004). Arrow shrimp have been observed to vigorously reproduce year round in multiple habitats (Ewald 1969), and they may be able to reproduce in fragmented habitats more successfully than other nekton species, thereby influencing community evenness. Some research has found no effect of fragmentation on species evenness in benthic infauna, even when seasonal effects were significant (Turner, Hewitt et al. 1999). Because arrow shrimp are motile and were abundant in both seasons during this study, they are more likely to respond to changes in landscape pattern than benthic infauna over shorter time periods, which could explain differences in findings.

As seen in other studies that examined communities exclusively in seagrass (Eggleston, Elis et al. 1999; Turner, Hewitt et al. 1999; Johnson 2008), the number of species in a given area was not related to habitat characteristics associated with fragmentation in this study. However studies that examine communities residing both within seagrass and bare substrate in fragmented habitats arrive at different conclusions in some cases. From observations both in seagrass and matrix habitat, species richness has often been observed not to differ between fragmented versus continuous landscapes (Fernandez, Milazzo et al. 2005; Jelbart, Ross et al. 2007; Fernandez, D'Anna et al. 2008). Other studies have reported negative impacts of fragmentation to species density

(Jackson, Attrill et al. 2006; Jackson, Attrill et al. 2006; Reed and Hovel 2006; Macreadie, Hindell et al. 2009). Positive impacts from fragmentation have also been observed (Fernandez, Milazzo et al. 2005; Horinouchi, Tongnunui et al. 2009).

These kinds of ecological investigations take into account an additional dimension of habitat heterogeneity (bare substrate) that is not assessed in studies that focus solely on animals residing within seagrass. This may explain why a greater range of impacts (positive, negative, and neutral) have been reported compared to the positive and neutral impacts observed in animal communities sampled only in seagrass. Careful consideration with regards to the different ways that fragmentation and animal communities have been defined is necessary when drawing conclusions about habitat fragmentation's effects on diversity. Animal communities in bare substrate are often different in composition, which may influence observations of overall diversity levels.

In conclusion, fragmented seagrass landscapes in this study area harbored comparable numbers of species in seagrass compared to continuous cover despite significant seasonal differences in overall species richness. Species evenness was consistently lower in fragmented habitats, which suggests that differences in habitat amount and patch configuration can differentially impact demographic rates of several species such as reproductive success, thereby influencing degree to which they are represented in a given community. The unstable environmental conditions and dynamic nature of fragmented seagrass landscapes may play important roles in determining community structure, however this study showed that the size and spatial configuration of seagrass patches have significant effects on community structure despite seasonal changes in habitat configuration, and identified the major landscape qualities that were associated with impacts to diversity.

## **Chapter 2: Geographical and seasonal comparisons of nekton across fragmentation gradients in seagrass meadows**

### **INTRODUCTION**

Studies from a wide range of estuarine systems have shown fragmentation's effects on community structure to differ within estuaries as a function of geographical location (Mills and Berkenbusch 2009), season (Jelbart, Ross et al. 2006) or both (Johnson and Heck 2006). Seasonal differences in seagrass structural complexity, animal density, and assemblage composition are common in seagrasses (Tolan 1997; Horinouchi, Tongnunui et al. 2009). From a research perspective, it is important to understand the degree to which fragmentation's effects can be seen across extended time periods in various landscapes within an estuarine region (Boström 2006), and across a full spectrum of landscape configurations (Connolly and Hindell 2006).

The effect of habitat fragmentation on biodiversity in seagrass meadows is variable (Connolly and Hindell 2006). Researchers have found negative (Jackson, Attrill et al. 2006) and positive (Jelbart, Ross et al. 2007) impacts to fish diversity, while others have found no impact (Johnson and Heck 2006). The variability among findings may be related to whether animal communities in fragmented habitats are sampled only in seagrass or both seagrass and matrix habitat together (e.g., sand). Among studies that make direct comparisons of the diversity of animals living only in seagrass, several approaches to assessing landscape configuration have been taken. Some studies focus on the habitat qualities of individual patches such as their size and shape (McNeill and Fairweather 1993; Johnson and Heck 2006), while others take a broader view of the landscape by examining diversity within multiple patches from fragmented landscapes and make comparisons between metacommunities from fragmented patches versus single communities in continuous seagrass (Mills and Berkenbusch 2009; Borg, Rowden et al.

2010). Natural seagrass fragmentation is generally observed to happen gradually, however few studies have examined changes in biodiversity across a spectrum of landscape pattern that reflect various stages of fragmentation. They have found no impacts to species richness or evenness to benthic infauna (Turner, Hewitt et al. 1999) or to richness in epibenthic macrofauna (Johnson and Heck 2006).

Equally important is the relative importance of differences in habitat amount versus other aspects of habitat fragmentation such as patch isolation and connectivity have in impacting biodiversity in seagrasses. These components have proven difficult to separate in observational studies of a wide variety of landscapes (Fahrig 1997; Fahrig 2003). Researchers have often relied on using small Artificial Seagrass Units to experimentally manipulate patch and landscape qualities while controlling for patch size, with inconclusive results regarding impacts to diversity (McNeill and Fairweather 1993; Johnson and Heck 2006; Johnson 2008). Given these efforts, it is useful to identify whether qualities in landscape configuration beyond habitat amount are important over a spatial scale that captures a broad, naturally observed gradient in habitat fragmentation.

The primary objective of this study is to determine whether impacts to nekton diversity exist as a function of fine scale gradients in landscape qualities resulting from seagrass fragmentation. The majority of studies examining fragmented landscapes have relied on making categorical comparisons between fragmented and continuous landscapes, however seagrass landscapes exhibit a wide range of patch sizes and configurations within a given area. This study also examines whether fragmentation's effects on diversity are geographically and temporally stable, and the degree to which aspects of fragmentation beyond habitat amount account for changes in diversity. Knowing whether quantifiable differences in specific habitat qualities influence community diversity as seagrass meadows become increasingly fragmented will further

scientific understanding of the sensitivity that animal communities have to the resulting landscape produced by the process of fragmentation in different locations and time periods.

This study compares the results of models containing information about habitat amount, to those containing information about habitat amount, proximity, connectivity and patch density in order to determine whether the addition of these variables decreases the variability in observed diversity in animal communities in two bays and seasons. The hypothesis is that the effect of fragmentation in this system will be stable across both seasons and bays, and that models that account for habitat qualities beyond just habitat loss will account for the largest amount of change in observed diversity.

## **METHODS**

### **Habitat Mapping**

Monospecific meadows of shoalgrass, *Halodule wrightii*, were surveyed visually, and selected for mapping in Aransas Bay and Corpus Christi Bay, TX (Figures 1, 2 & 3). These shallow (0.5m – 1.5m water depth) landscapes were mapped *in situ* from data obtained by Trimble GPS receivers (GeoXT Handheld, Trimble Navigation Limited, 2008) which were tested in trials to be capable of sub-meter accuracy. The GPS recorded the geolocation of the operator every second, who slowly walked the exact perimeter of every seagrass patch in a landscape to capture its spatial features. Mapping was performed in one to four weeks preceding sampling both in the summer and fall of 2009. ArcGIS 9.3.1 (ESRI Software, 2008) was used to process receiver data and create georeferenced, vector-based maps of these shoreline landscapes, which were approximately 200m long and 100m wide. Within each landscape, locations for sampling plots were

chosen using visual criteria (percent cover, patch size and proximity) representing a gradient spanning 3 levels of naturally occurring habitat fragmentation:

1. Continuous cover (no fragmentation)
2. Intermediate Fragmentation (large, close patches, and reticulated cover)
3. High Fragmentation (small, isolated, or thin patches)

In two bays, three examples of each fragmentation level (9 plots per Bay, 18 per season) were selected for study during summer and fall. Plots representing each fragmentation level were evenly dispersed across approximately 4 km of bay shoreline in areas with similar hydrodynamic conditions, and were separated by at least 30m of bare sand and mud bottom (Figure 1).

### **Nekton Sampling**

During early summer (June 16-25) and late fall (Oct 21- Nov 2) of 2009, nekton samples were obtained from each plot in both bays on two separate dates, approximately 7 days apart. During each sampling event, a minimum of approximately 38.25 m<sup>2</sup> of seagrass was sampled by towing an epibenthic sled which had a metal frame opening of 0.6 m (length) X 0.75 m (height) equipped with a 1-mm mesh conical plankton net over the seagrass bed surface. This device is designed for collecting epibenthic nekton between 4mm-50mm in length, including small/juvenile fish, larval fish, shrimps, and decapods (Stunz, Minello et al. 2002).

Multiple sampling paths were planned *a priori* in ArcGIS within each plot to obtain minimum sample requirements of 51 linear m within each plot. Individual tow samples varied in length from 4 - 17m depending on patch size. Samples were collected inside seagrass beds only. Tow transects were placed in beds haphazardly, however in small patches, tows were started placing the sled at the patch edge and ending on the

other side of the patch. Additional samples within patches were obtained from the plots approximately 7-10 days later, and efforts were made to avoid directly overlapping previous tow paths during the second sampling event.

Macroalgae and seagrass were carefully sorted in the field, and the remaining nekton preserved in 10% formalin. The *in situ* tow length for each sample was recorded on Trimble GPS units by carefully following the sled with a GPS in order to calculate sample size based on seagrass area (m<sup>2</sup>). Three depth measurements were recorded along equidistant points for each tow path. Salinity, temperature, and dissolved oxygen levels were recorded at each sampling plot. In the laboratory, shrimp, fish, and decapods were identified and counted to species level and preserved in 70% ethanol.

### **Habitat Fragmentation and Community Diversity Analyses**

The landscapes analyzed in this study were defined by an extensive and equal area (4225m<sup>2</sup>) within the larger meadow in which a spatially broad and thorough sampling effort could be applied. Habitat fragmentation metrics change as a function of the geographical scale at which they are quantified (Pinto and Keitt 2008). These sampling plots contained patches with a wide range of sizes and shapes, so the general landscape characteristics directly within the sampled area were captured. Vector map data for each sampling plot was converted to raster grids with 10 cm cell size. This size was chosen after evaluating several options to see which best preserved patch geometry during data conversion. Measures of habitat fragmentation in each of the plots were computed with FRAGSTATS software (McGarigal 2002). Twenty-three habitat fragmentation indices used to evaluate terrestrial landscapes (Kumar, Stohlgren et al. 2006; Kumar, Simonson et al. 2009) and marine landscapes (Sleeman, Kendrick et al. 2005) were calculated for each plot. A Pearson correlation matrix was used to identify

metrics that were highly correlated with each other ( $\geq \pm 0.800$ ). One measure was retained, and correlated measures were eliminated from further analysis to prevent inclusion of redundant measures. Mean Patch Area (MA) and Percent Cover (PA), were included despite being correlated with other metrics because they are critical measures of relative habitat amount. Index values were log-transformed where necessary to minimize heteroskedasticity in data and plotted on a common scale. A principal components analysis (PCA) involving 12 remaining indices (Table 1) was performed using SYSTAT 12 (2007) to identify the major qualities that differed in the 36 study plots (Figure 4), which is a similar approach to that used in other studies of fragmented seagrass landscapes (Sleeman, Kendrick et al. 2005).

Fragmentation was treated as a continuous predictor variable on diversity using regression, and the regression was compared across two categorical factors - season and bay, using ANCOVA as the unifying framework. Emphasis was placed on the statistical test of the overall relationship between fragmentation and diversity, and whether this relationship differed significantly between bays and seasons ( $\alpha = .05$ ). Secondary consideration was given to differences in diversity between bays and seasons. Although this approach is less common than traditional applications of the General Linear Model, ANCOVA has been used successfully in other ecological studies to directly examine the relationship between both continuous and categorical factors on a response variable (Ebert, Hernandez et al. 2011; Hicks and Frost 2011).

A habitat measure (such as percent cover) was the continuous predictor variable, and entered as the covariate of the response variable (a diversity measure such as species richness) in the model. Season (2) and Bay (2) were fixed factors. In this model, the interaction term between the continuous predictor variable, and categorical factors (Season and Bay) on diversity served several important purposes. First, it was used to

verify the validity of the overall ANCOVA (Field 2009) by testing whether the effect of fragmentation on diversity was significantly different between bays or seasons (homogeneity of slopes). If the difference in slopes was not significant, the effect of fragmentation on diversity was directly evaluated, and comparisons of overall diversity between seasons or bays were also possible. If the difference in slopes was significant, the analysis was re-run separately within season (with Bay as a factor) or bay (with Season as a factor). If necessary, the interaction term between the continuous predictor variable and categorical factor was tested within season or bay. If the interaction term was significant, a common slope did not exist for further analysis, and individual linear regression between the continuous predictor and response variables was performed instead (Ebert, Hernandez et al. 2011) for each bay within a given season.

From the Principal Components Analysis of landscape characteristics, Factor 1 (habitat amount, proximity, connectivity, patch density) was selected as a covariate habitat measure in the ANCOVA. An additional ANCOVA that only included percent cover as the habitat measure was also performed. This allowed comparisons of the relative strength of the primary model which included several measures of habitat fragmentation in addition to measures of habitat amount to an analysis that only included habitat amount. Principal Component Factor 2 (patch shape complexity and edge amount) was determined to be unsuitable as an independent variable in the ANCOVA because it was observed to have a non-linear relationship with fragmentation level (Chapter 1).

### ***Animal Abundance***

Differences in animal abundance can potentially bias estimates of species richness in different habitats (Gotelli and Colwell 2001). To investigate whether potential for this

bias existed in this study, a 2-way ANCOVA was performed on animal densities as a function of fragmentation, using PCA Factor 1 (habitat amount, proximity, connectivity, and patch density) as the continuous predictor variable, with Season (2) and Bay (2) as Factors. Data from both sampling events were pooled within each plot for the analysis, and log-transformed where necessary to meet assumptions of data normality and homogeneity of variance.

### ***Community Diversity***

To account for the potential for differences in animal abundances to bias estimates of numbers of species in this study, two complementary measures of species richness were used. Species density was defined as the number of species within a standard area (61m<sup>2</sup>) of seagrass sampled within each plot, and species richness was computed using rarefaction, which estimates the number of species found within a standard subsample of animals (860 individuals). Species evenness was the final diversity measure used, and procedures for quantifying all three are described in Chapter 1. Diversity measures were log-transformed where necessary to meet assumptions of normality and homogeneity of variance.

## **RESULTS**

### **Habitat Fragmentation**

Fragmentation metrics that loaded strongly ( $\geq 0.60$  or  $\leq -0.60$ ) in each principal component factor were used to describe principal component factors (Table 1). Factor 1 (referred to now on as Fragmentation Factor 1) was comprised of measures of habitat connectivity, habitat amount, patch proximity, and number of patches. This aspect of “habitat continuity” accounted for over 35% of the variability across sampling plots. In the summer, mean patch sizes as quantified within the plot boundaries ranged from 32 -

88m<sup>2</sup> in high fragmentation, 89 - 315m<sup>2</sup> in intermediate fragmentation, and 1736 - 4225m<sup>2</sup> in continuous cover (Figure 2). Percent seagrass cover in the plots during this season ranged from 5 - 10% in high fragmentation and 20 - 42% within intermediate fragmentation. One continuous plot contained 40% cover but consisted of a large patch; the rest of the continuous plots ranged from 85 - 100% cover.

During the fall, mean patch sizes ranged from 31 - 181m<sup>2</sup> in high fragmentation, 153 - 697m<sup>2</sup> in intermediate fragmentation, and 1376 - 4225m<sup>2</sup> in continuous cover (Figure 3). Percent seagrass cover in the plots during this season ranged from 12 - 21% in high fragmentation, 27 - 65% within intermediate fragmentation, and 61 - 100% for continuous cover. All plots representing continuous cover were comprised of seagrass patches that extended well beyond the plot boundaries, and this was often also the case for plots representing intermediate fragmentation. However, measurements of patch size and other metrics were restricted to the landscape that was quantified within the plot boundaries for this study.

Factor 2 encompassed measures of patch shape complexity and edge amount (i.e. patch perimeter created from the sand-edge interface), and explained over 26% of the variance observed in habitat measures across plots. In the summer, total plot edge amount varied from 245 - 255m in high fragmentation, 478 - 1013m in intermediate fragmentation, and 0 - 183m in continuous cover. In the fall, total edge in plots varied from 260 - 602m in high fragmentation, 600 - 1023m in intermediate fragmentation, and 0 - 166m in continuous cover. Factor 3 described patch aggregation or “clumpiness” in the spatial arrangement of patches, and how compact shapes were within the landscape. It accounted for approximately 16% of variability across sampling plots.

## **Animal Abundance**

The effect of Fragmentation Factor 1 on animal density differed between seasons ( $F_{1,28} = 7.067$ ,  $p = 0.013$ ; Table 1). Therefore, separate analyses within summer and fall were performed. No significant interactions between bay and fragmentation degree on animal density was observed within summer ( $p = 0.604$ ) or fall ( $p = 0.180$ ), so the interaction terms were removed from subsequent analyses within each season. Animal densities were observed to have a significant positive relationship with fragmentation in the summer ( $F_{1,15} = 6.34$ ,  $p = 0.024$ ), but not in the fall ( $F_{1,15} = 2.82$ ,  $p = 0.114$ ; Figure 13). Arrow shrimp, *Tozeuma carolinense*, were pervasive in all the samples, however they were especially prevalent in samples from highly fragmented areas. When excluded from the community, animal densities decreased as a function of fragmentation in both seasons (Figure 14).

## **Community Diversity**

### ***Species Density***

No effect of Fragmentation Factor 1 on species density (number of species per 61m<sup>2</sup> seagrass) in sampling plots was observed in either bay during summer or fall ( $F_{1,28} = 0.307$ ,  $p = 0.584$ , Table 7). Species density was significantly lower in fall, however a significant season X bay interaction ( $F_{1,28} = 20.125$ ,  $p < 0.001$ ; Figure 15) showed that the seasonal difference in species density was greater in Aransas Bay than Corpus Christi Bay. Similar results were observed for ANCOVA of species density as a function of percent cover, however the overall strength of this model ( $R^2 = 0.804$ ) was stronger than the analysis involving Fragmentation Factor 1 ( $R^2 = 0.789$ ; Table 7).

### ***Species Richness***

The effect of Fragmentation Factor 1 on rarefied species richness (860 individuals per sample) differed between seasons ( $F_{1,28} = 4.836$ ,  $p = 0.036$ ; Table 8) requiring separate analyses within season. In the summer, species richness declined significantly as a function of fragmentation ( $F_{1,15} = 14.229$ ,  $p = 0.002$ ; Figure 16). In the fall, the effect of Fragmentation Factor 1 on diversity was significantly different between bays ( $p = 0.004$ ), requiring separate linear regression analysis of each bay. In Corpus Christi Bay, species richness increased significantly with fragmentation ( $F_{1,7} = 14.918$ ,  $p = 0.006$ ,  $R^2 = 0.681$ ; Figure 17), whereas no effect was observed in Aransas Bay ( $F_{1,7} = 0.790$ ,  $p = 0.404$ ,  $R^2 = 0.101$ ).

Fragmentation's effect on diversity differed between bays ( $F_{1,28} = 7.788$ ,  $p = 0.009$ ; Table 8). In Aransas Bay fragmentation's impact was negative ( $F_{1,15} = 8.134$ ,  $p = 0.012$ ; Figure 18). In Corpus Christi Bay, the effect of fragmentation differed between seasons. Separate linear regression analysis showed no significant effect of fragmentation on diversity ( $F_{1,7} = 2.403$ ,  $p = 0.165$ ,  $R^2 = 0.149$ ) in the summer, however species richness increased significantly with fragmentation in the fall, as shown in the within-season analysis previously mentioned.

The effect of percent cover on species richness differed as a function of season ( $F_{1,28} = 4.824$ ,  $p = 0.037$ ), but not bay ( $F_{1,28} = 2.071$ ,  $p = 0.161$ ; Table 9), which differed from the analysis involving Fragmentation Factor 1. Species richness declined significantly with reduced percent cover in the summer ( $F_{1,15} = 12.534$ ,  $p = 0.003$ ) but not in the fall ( $F_{1,15} = 0.260$ ,  $p = 0.618$ ). The strength of the model involving Fragmentation Factor 1 ( $R^2 = 0.511$ ) was stronger than that involving percent cover alone ( $R^2 = 0.412$ ).

### ***Species Evenness***

Species evenness consistently declined as a function of fragmentation degree in both Corpus Christi Bay ( $F_{1,15} = 4.976$ ,  $p = 0.041$ ) and Aransas Bay ( $F_{1,15} = 39.192$ ,  $p < 0.001$ ). In both seasons, the effect of Fragmentation Factor 1 on species richness was consistently greater in Aransas Bay than Corpus Christi Bay ( $F_{1,28} = 7.548$ ,  $p = 0.010$ ; Table 10). Evenness was significantly higher in summer than fall ( $F_{1,15} = 6.687$ ,  $p = 0.021$ ).

No difference in the relationship between evenness and percent cover was observed between bays ( $F_{1,28} = 3.506$ ,  $p = 0.072$ ). Species evenness declined significantly as a function of decreasing percent cover ( $F_{1,31} = 6.700$ ,  $p = 0.015$ ) in both seasons. Species evenness was significantly higher in summer than fall ( $F_{1,31} = 6.700$ ,  $p = 0.015$ ). The model involving Fragmentation Factor 1 ( $R^2 = 0.599$ ) was stronger than the model only including percent cover ( $R^2 = 0.558$ ).

### **DISCUSSION**

Species evenness consistently and progressively declined in landscapes that were characterized as having decreasing habitat amount, connectivity, proximity, and more patches. This indicates that as seagrasses become fragmented, evenness is sensitive to small changes in the amount and configuration of each landscape, which has not been observed in previous research (Turner, Hewitt et al. 1999). However, our results are consistent with other studies (Turner, Hewitt et al. 1999; Johnson and Heck 2006), in that species density was not significantly different among landscapes despite substantial differences in the overall number and composition of species between seasons. Thus, habitats containing smaller, isolated seagrass patches can potentially hold similar numbers of species over time, but the relative abundance of species is progressively less even than communities inhabiting continuous landscapes. There may be enough seagrass

and suitable patch configuration to sustain comparable numbers of species in a given area, yet subtle differences in these landscape characteristics can influence the degree to which individual species are represented in the community.

In Chapter 1, Evenness was significantly lower in fragmented habitats than continuous ones; however no significant difference was detected in intermediate versus highly fragmented landscapes. The results presented here extend upon those results by showing a progressive decline in evenness across landscapes with increasing degrees of fragmentation, suggesting that animals in this habitat organize themselves more as a function of the landscape pattern resulting from fragmentation than they do from processes driving it. Differences in the shape and size of habitats can affect demographic rates of dispersal and reproduction (With 2004). Differences in the threshold beyond which fragmentation impacts various species may drive the patterns of community evenness observed in this study. Given the broad change observed in evenness across fragmentation gradients, communities appear to be sensitive to progressive differences in patch size and connectivity in fragmented landscapes. Some species may perform better in these habitats than others, and there was a trend for arrow shrimp to dominate more fragmented landscapes. Contrary to the results of this study, no differences in species evenness were reported in benthic infauna in New Zealand (Turner, Hewitt et al. 1999), however the relative lack of mobility of infaunal animals may explain why differences were not seen.

Landscape qualities such as habitat connectivity, proximity, and patch density play a significant role in influencing diversity, and models that included these variables accounted for more variability than ones containing just percent cover. Although landscape qualities such as connectivity can influence species extinction thresholds (Ovaskainen 2004), they were only influential in observed patterns of species evenness in

this study. When strictly taking differences in habitat amount into consideration, the effect of habitat amount on evenness was not different between bays; species evenness was observed to decline in habitats with lower amounts of seagrass. However, when additional landscape qualities such as habitat connectivity, proximity, and patch density were included in the assessment, fragmentation's impact on evenness was observed to be consistently and significantly greater in one bay than the other. The inclusion of these variables strengthened the model's ability to account for variability in response to fragmentation between bays. This suggests that nekton communities in one location may be more sensitive to differences in landscape configuration than in others because the degree to which species evenness declined as a function of fragmentation was significantly different between bays. Consistent with this finding, geographical differences have been observed in studies of the effects of seagrass patch size and proximity on animal density (Johnson and Heck 2006) and diversity (Mills and Berkenbusch 2009) between two bay systems, and theoretical studies suggest that location-specific environmental conditions can amplify fragmentation's impact on metapopulation dynamics (Ovaskainen 2004).

The results in this study build upon those described in Chapter 1 because previously the primary concern was whether fragmentation had a consistent overall effect on diversity. In that analysis, fragmentation's effects on evenness were observed to be consistently negative across seasons. The results described here show that geographical differences observed in fragmentation's effects on evenness were seasonally consistent, in addition to the fact that fragmentation itself negatively impacted evenness. This is noteworthy because both seagrass landscapes and the resident animal communities changed as a function of season. Habitat amount, connectivity, proximity, and patch density in fragmented habitats was observed to increase from summer to fall, however

overall animal density and species richness was observed to be significantly lower. Regardless of these systemic changes over time, the effect of fragmentation on evenness remained temporally and geographically consistent.

Communities with low evenness have been observed to be common in climatically unstable environments (Magurran 1988) and show impaired functionality under stress (Wittebolle, Marzorati et al. 2009). In this study, overall species evenness was not significantly different in animal communities between bays, so aside from potential differences in community resilience to the effects of fragmentation or environmental instability, it may be necessary to look at landscape qualities at larger geographical or time scales in order to understand what is driving compositionally similar animal communities to show different responses to fragmentation in two locations. In this study, the landscape structure and diversity contained within it were quantified in plots that were approximately half the size of a football field, yet the amount and estuarine location of surrounding habitat may strongly influence the evenness of animal communities in these areas, especially as it relates to qualities of habitat connectivity, proximity, and patch density. Alternatively, differences in the life spans of fragmented habitats between bays as expressed by changes in connectivity, proximity, and patch density can account for why the effect of fragmentation was observed to be stronger in one bay than the other (With 2004). Fragmented habitats in one bay may be more developmentally stable than in the other, thereby permitting successful reproduction of a greater number of species with different life histories in fragmented habitats.

The results of this study are consistent with other studies that found no differences in species density as a function of fragmentation exclusively in seagrass across large spatial scales (Turner, Hewitt et al. 1999; Johnson and Heck 2006). The number of species in several patches may be insensitive to differences in landscape configuration

because of high immigration and emigration rates. Studies show that nekton and epibenthic fauna rapidly colonize seagrass (Sogard 1989; Jelbart, Ross et al. 2006; Johnson 2008), and this may explain why studies in seagrass have typically not shown negative impacts to species density, as has been reported in terrestrial systems such as forests or in theoretical studies (Fahrig 2003; With 2004).

When comparing a standard number of individuals in each community using rarefaction, patterns in species richness were temporally inconsistent regardless of whether only habitat amount or the combined effects of all fragmentation variables were considered. In summer, greater diversity was observed in landscapes with more continuous habitats, which may have been driven by movement within abundant seagrass that smaller, isolated habitats did not have. To compare diversity in a universal number of individuals, only a small subsample of animals in each landscape was examined when using rarefaction. This resulted in a sample size of individuals that was numerically equal but much smaller in quantity on average than what was used to assess the number of species in a given area (species density). At this reduced sample size, richness estimates may have been sensitive to differences in habitat amount or landscape configuration. Habitats with abundant, highly connected seagrass may support greater numbers of species from a small population of individuals inhabiting any one area within a large landscape than isolated patch fragments do.

Patterns in rarefied species richness in the fall were different than summer, and they were geographically inconsistent as well. No effect of habitat amount was observed, but measures of habitat amount, connectivity, proximity, and patch density showed geographical differences in fragmentation's effects. The lack of consistent response to fragmentation may point to the possibility that patterns in species evenness observed in this study also influenced rarefied richness estimates. Rarefied species richness has been

observed to be affected by species evenness in other studies (Weibull, Ostman et al. 2003). In this study, differences in evenness were driven by animals like arrow shrimp that dominated fragmented habitats, and abundance of this species was negatively correlated with rarefied species richness, suggesting they may have influenced estimates of species richness based on subsamples of each community. Without arrow shrimp, animal densities decline as a function of fragmentation degree, and analysis of the animal community without them may reveal important differences in richness across the habitat gradient observed in this study that are otherwise obscured by the abundance of highly dominant shrimp species.

Seasonal patterns of natural seagrass fragmentation occur as a result of gradual die-back and re-growth. As a result, comparable numbers of species may have ample time to colonize seagrasses with different landscape configurations. There is a critical threshold of habitat amount beyond which animal populations are expected to go extinct (Ovaskainen 2004) however this was not detected when considering species richness in metacommunities inhabiting several different patches within fragmented landscapes. Caution should be applied here due to the possibility that individual patches within a landscape may not all share the same species, and therefore have lower species richness than communities in continuous seagrass.

Few studies have assessed biodiversity exclusively in seagrass across a gradient of landscape qualities assessed at large spatial scales. The majority of studies examining large-scale changes in landscape structure sampled animal communities residing both within seagrass and the adjacent “matrix” habitat such as bare sand which may contain different species, thereby influencing diversity estimates. Positive impacts (Fernandez, Milazzo et al. 2005) and negative impacts (Jackson, Attrill et al. 2006; Jackson, Attrill et al. 2006) to species richness have been reported, and they are thought to be associated

with the increased heterogeneity provided by landscapes that contain both sand and seagrass.

This study took a unique approach by identifying several habitat qualities related exclusively to the seagrass meadows themselves that changed in relation to habitat fragmentation, and determining the relative role that they played in observed differences in species evenness and species richness of communities exclusively within seagrass. In two seasons, species richness was not observed to differ as a function of fragmentation, however species evenness declined primarily as a function of decreasing habitat amount and this appears to be related to the influence of numerically dominant species in fragmented habitats. Animal communities showed geographical differences in sensitivity to changes in landscape qualities such as habitat connectivity, proximity, and patch density which indicates that compositionally similar animal communities in different locations may differ in resilience within isolated, disconnected seagrass habitats.

The results presented here suggest that the processes supporting community evenness such as dispersal and reproduction appear to be impacted by fragmentation to a degree that is unique to each bay, regardless of seasonal changes in species composition. Thresholds in patch size and connectivity may affect the demographic rates of some species but not others, thereby affecting community structure. Processes determining community evenness appear to be sensitive to differences in landscape qualities that vary extensively across fragmentation gradients, and their impact on species evenness is closely coupled with subtle differences in landscape configuration that are not always detected by categorizing the degree of difference between habitats. This study elucidates which aspects of community structure are most sensitive to habitat fragmentation, and identifies important landscape qualities that affect animal populations after thresholds in habitat amount are exceeded.

## Appendix

Figure 1. Map of sampling regions and study sites in Aransas and Corpus Christi Bay, Texas

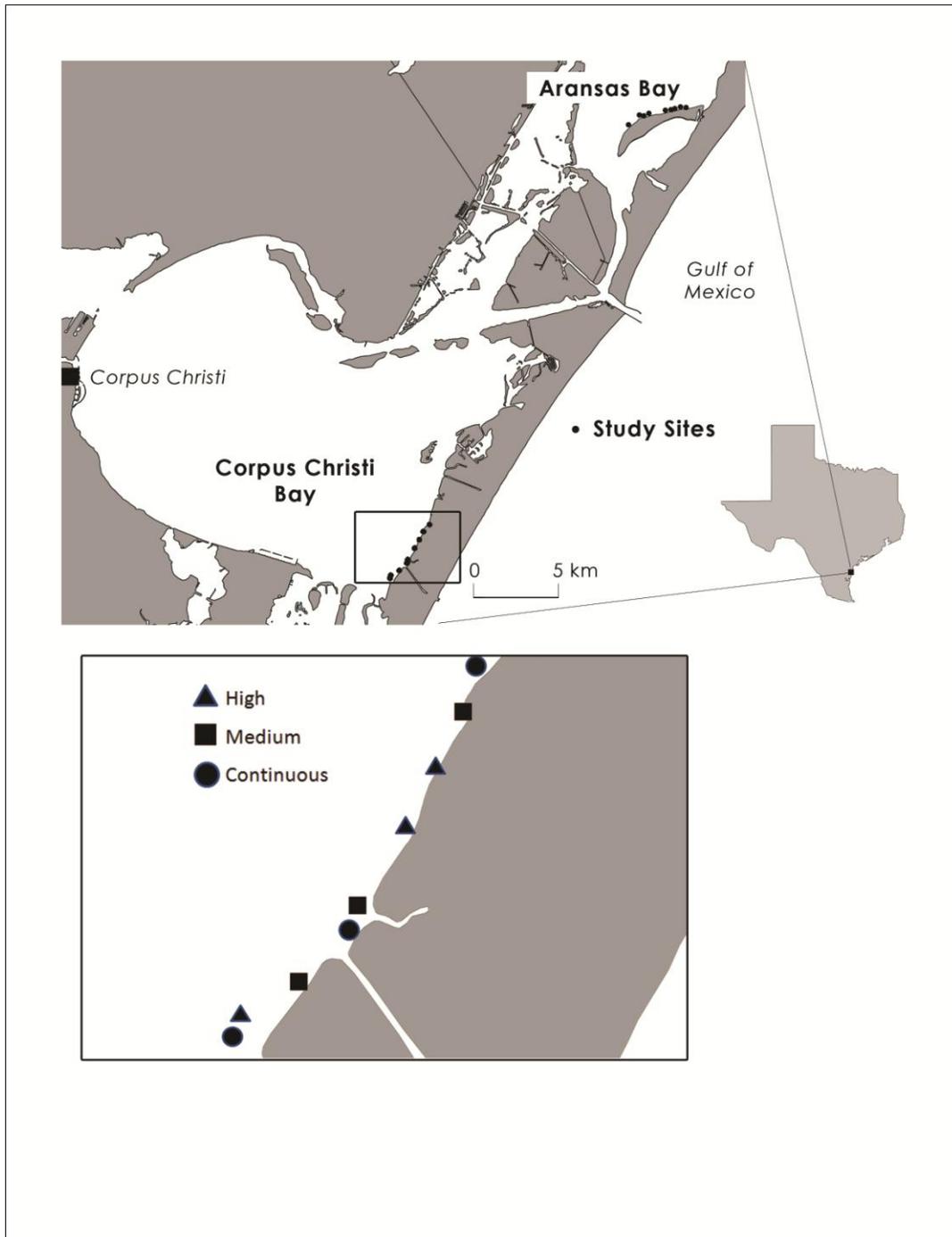


Figure 2. Sampling plots in summer 2009. These shallow landscapes were mapped *in situ* from data obtained by Trimble GPS receivers. Mapping was performed one to four weeks preceding sampling.

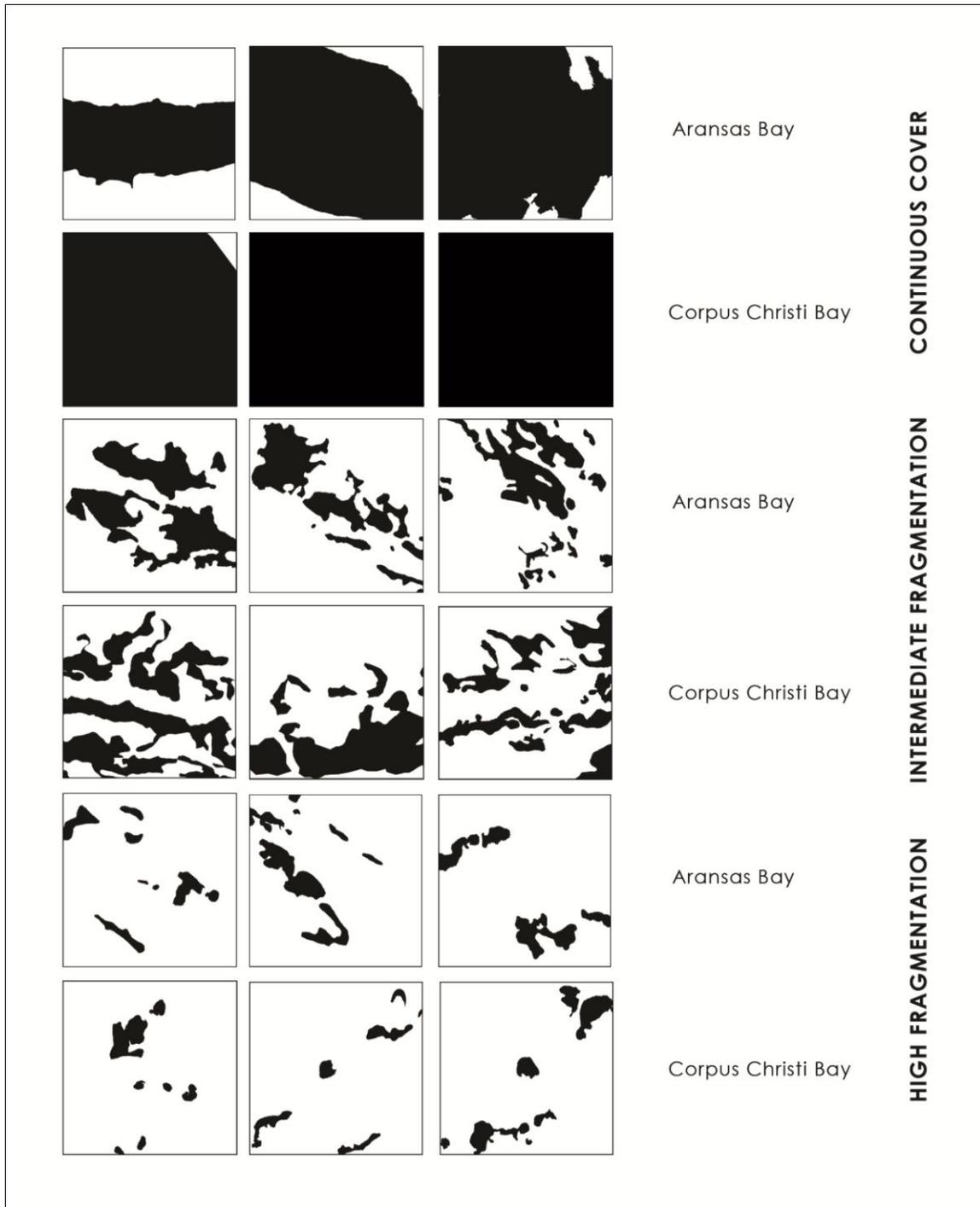


Figure 3. Sampling plots in fall 2009. These shallow landscapes were mapped *in situ* from data obtained by Trimble GPS receivers. Mapping was performed one to four weeks preceding sampling.

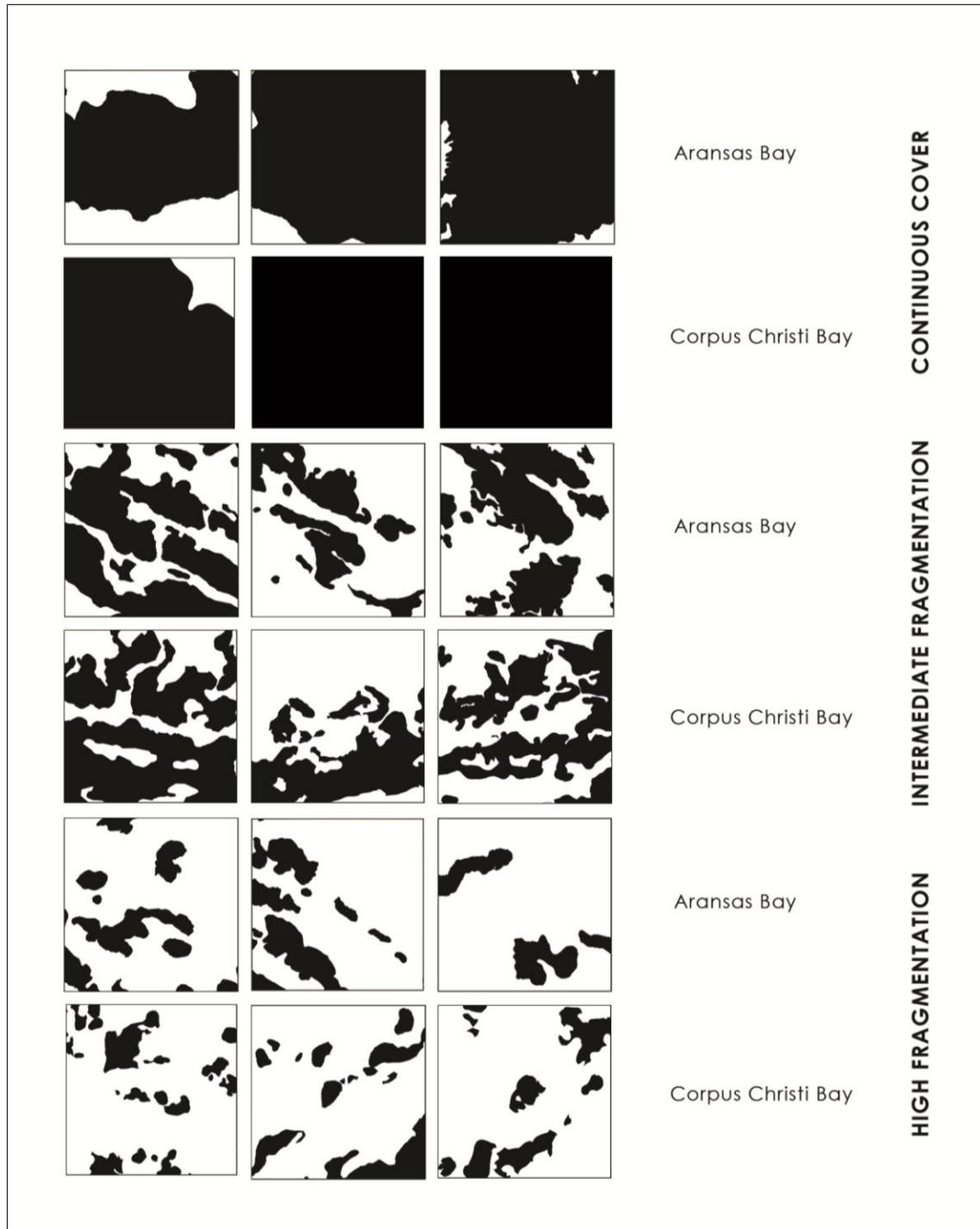


Table 1. Principal components analysis (PCA) eigenvalues and variable loadings for 12 metrics used to quantify seagrass fragmentation. Strong variable loadings ( $\geq .600$  or  $\leq -.600$ ) are bold.

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

Figure 4. Principal components visual depicting seagrass habitat fragmentation metrics in sampling plots. See Table 1 for descriptions of abbreviated variables.

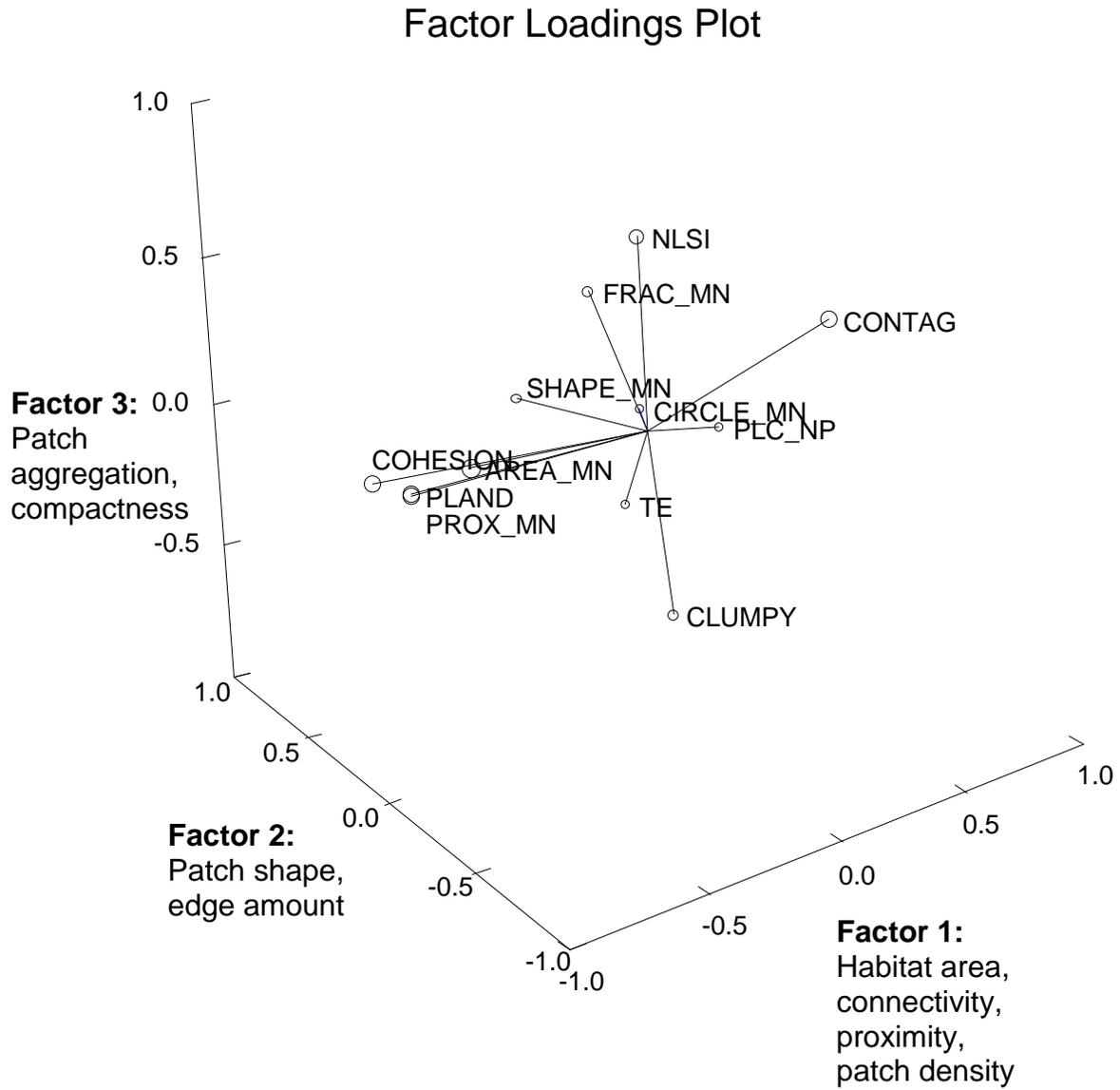


Table 2. Three-way ANOVA analyses comparing animal density from sampling plots in each fragmentation level. Significant ( $p < .05$ ) interactions and main effects are bold. \*Animal density was significantly higher in high fragmentation than continuous cover ( $p = .014$ ) \*\*Individual analyses within each season were performed due to the interaction between season and fragmentation level on species richness.

Dependent Variable	Source	df	Mean square	F-value	P-value
<b>Animal Density</b>	Season	1	1.504	27.332	0.000
<i>(animals m<sup>-2</sup> seagrass sampled)</i>	Bay	1	0.160	2.899	0.099
	Fragmentation Level	2	0.032	0.587	0.562
	Fragmentation Level X Season	2	0.389	7.061	<b>0.003**</b>
	Residual	29	0.055		
Summer	Bay	1	0.005	0.086	0.774
	Fragmentation Level	2	0.317	5.977	<b>0.013*</b>
	Residual	14	0.053		
Fall	Bay	1	0.247	4.556	0.051
	Fragmentation Level	2	0.104	1.908	0.185
	Residual	14	0.054		

Table 3. Three-way ANOVA analyses comparing factor scores that sampling plots from each fragmentation level received in the principal components analysis. Significant values ( $p < .05$ ) are bold. \*Differences between all fragmentation levels are significant ( $p < .01$ ) in all post-hoc comparisons between fragmentation levels for PCA factor 1 using Tukey's test. \*\*Differences between fragmentation levels are significant ( $p < .01$ ) only for post-hoc comparisons between intermediate fragmentation and the other two levels for PCA factor 2 using Tukey's test.

Dependent Variable	Source	df	Mean square	F-value	P-value
<b>PCA Factor 1</b> Habitat connectivity, habitat amount, patch proximity, patch density	Season	1	1.261	12.675	0.001
	Bay	1	0.069	0.696	0.411
	Fragmentation Level	2	3.441	34.576	0.000
	Fragmentation Level X Season	2	0.447	4.496	<b>0.020</b>
	Residual	29	0.100		
Summer	Bay	1	0.122	0.914	0.355
	Fragmentation Level	2	10.269	77.212	<b>0.000**</b>
	Residual	14	0.133		
Fall	Bay	1	0.001	0.008	0.930
	Fragmentation Level	2	5.123	73.834	<b>0.000*</b>
	Residual	14	0.069		
<b>PCA Factor 2:</b> Patch shape and edge amount	Season	1	0.038	0.104	0.749
	Bay	1	0.309	0.841	0.367
	Fragmentation Level	2	11.849	32.216	<b>0.000**</b>
	Fragmentation Level X Season	2	0.144	0.391	0.680
	Residual	29	0.368		
<b>PCA Factor 3:</b> Patch aggregation and compactness	Season	1	1.080	1.127	0.297
	Bay	1	2.108	2.200	0.149
	Fragmentation Level	2	1.156	1.207	0.314
	Fragmentation Level X Season	2	0.862	0.900	0.418
	Residual	29	0.958		

Figure 5. Habitat fragmentation metrics in seagrass sampling plots. Higher scores in Factor 1 indicate reduction in habitat amount, proximity, and connectivity. Error bars represent 95% confidence intervals. Different letters indicate significant differences in scores using Tukey's test ( $p < .01$ ).

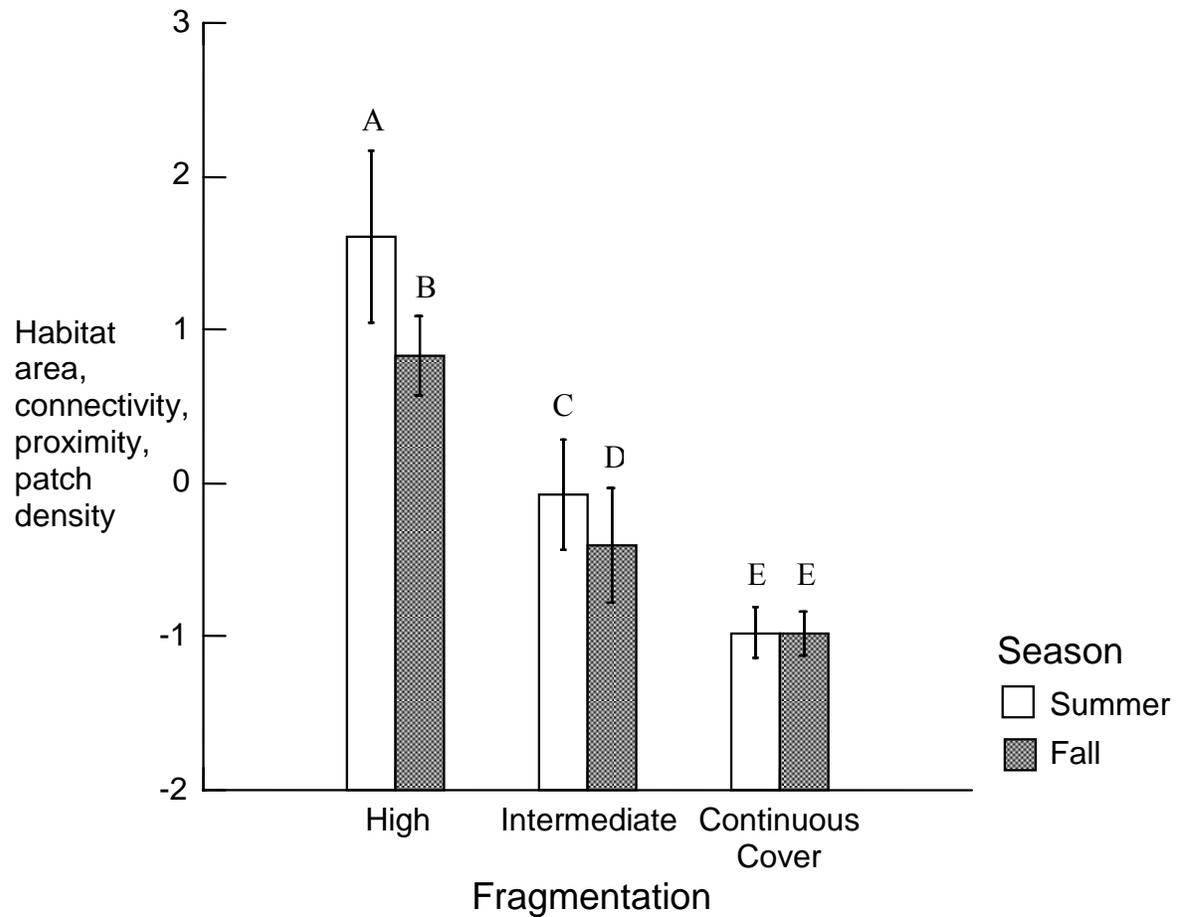


Figure 6. Habitat fragmentation metrics in seagrass sampling plots. Higher scores in Factor 2 indicate increases in patch complexity and edge amount. Different letters indicate where scores were significantly higher in post-hoc comparisons using Tukey's test ( $p < .01$ ).

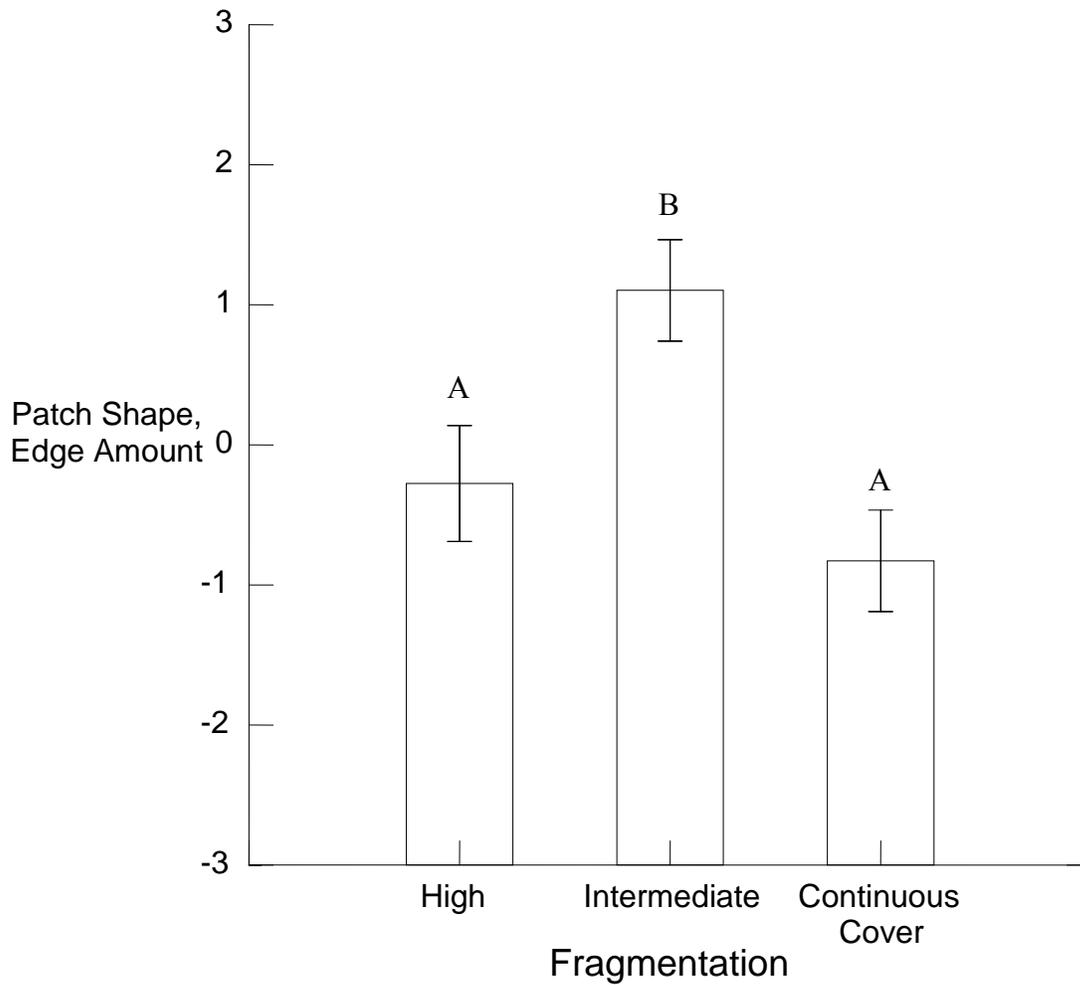


Table 4. Species collected in Aransas Bay and Corpus Christi Bay, in order of decreasing total number of individuals.

Order	Common Name	Scientific Name	Summer	Fall	Total
Decapoda	Arrow shrimp	<i>Tozeuma carolinense</i>	242035	80746	322781
	False zostera shrimp	<i>Hippolyte pleurocantha</i>	59215	32342	91557
	Grass shrimps	<i>Palaemonetes sp.</i>	26876	4412	31288
	Brown / Pink penaeid shrimps	<i>Farfantepenaeus sp.</i>	5466	1452	6918
	White penaeid shrimp	<i>Litopenaeus setiferus</i>	112	132	244
	Sargassum shrimp	<i>Latreutes parvulus</i>	17	27	44
	Combclaw shrimp	<i>Leptochela serratorbita</i>	11	11	22
	Bigclaw snapping shrimp	<i>Alpheus heterochaelis</i>	18	1	19
	Blue crabs	<i>Callinectes sp.</i>	621	316	937
Perciformes	Darter goby	<i>Ctenogobius boleosoma</i>	1883	228	2111
	Code goby	<i>Gobiosoma robustum</i>	858	118	976
	Gulf pipefish	<i>Syngnathus scovelli</i>	538	387	925
	Silver mojarra	<i>Eucinostomus argenteus</i>	643	11	654
	Dusky pipefish	<i>Syngnathus floridae</i>	397	187	584
	Silver perch	<i>Bairdiella chrysoura</i>	294	16	310
	Spotted seatrout	<i>Cynoscion nebulosus</i>	146	152	298
	Red drum	<i>Sciaenops ocellatus</i>		194	194
	Pinfish	<i>Lagodon rhomboides</i>	74	3	77
	Blackcheek tonguefish	<i>Symphurus plagiusa</i>	57	16	73
	Naked goby	<i>Gobiosoma bosc</i>	69	1	70
	Dwarf seahorse	<i>Hippocampus zosterae</i>	52	10	62
	Chain pipefish	<i>Syngnathus louisianae</i>	34	3	37
	Bay anchovy	<i>Anchoa mitchilli</i>	15	18	33
	Feather blenny	<i>Hypsoblennius hentz</i>	12	12	24
	Pigfish	<i>Orthopristis chrysoptera</i>	17		17
	Striped blenny	<i>Chasmodes bosquianus</i>	11		11
	Striped burrfish	<i>Chilomycterus schoepfi</i>	5	2	7
	Gulf toadfish	<i>Opsanus beta</i>	5		5
	Shrimp eel	<i>Ophichthus gomesii</i>	4	1	5
	Inshore lizardfish	<i>Synodus foetens</i>	4		4
	Skilletfish	<i>Gobiesox strumosus</i>	3		3
	Spot croaker	<i>Leiostomus xanthurus</i>	2		2
	Southern kingfish (whiting)	<i>Menticirrhus americanus</i>		2	2
	Sheepshead	<i>Archosargus probatocephalus</i>	2		2
	Hogchocker	<i>Trinectes maculatus</i>	2		2
	Atlantic spadefish	<i>Chaetodipterus faber</i>	1		1
	Frillfin goby	<i>Bathygobius soporator</i>	1		1
	Bay whiff	<i>Citharichthys spilopterus</i>	1		1
	Bluefish	<i>Pomatomus saltatrix</i>	1		1
	Longnose killifish	<i>Fundulus similis</i>	1		1
	Diamond killifish	<i>Adinia xenica</i>	1		1
	Rainwater killifish	<i>Lucania parva</i>		1	1
	Inland silverside	<i>Menidia beryllina</i>		1	1
<b>Total</b>			<b>339504</b>	<b>120803</b>	<b>460307</b>

Figure 7. Animal densities (number of individuals m<sup>-2</sup>) as a function of fragmentation level in seagrass sampling plots during summer and fall 2009. Error bars represent 95% confidence intervals. Different letters indicate levels where densities were significantly different in post-hoc comparisons using Tukey's test.

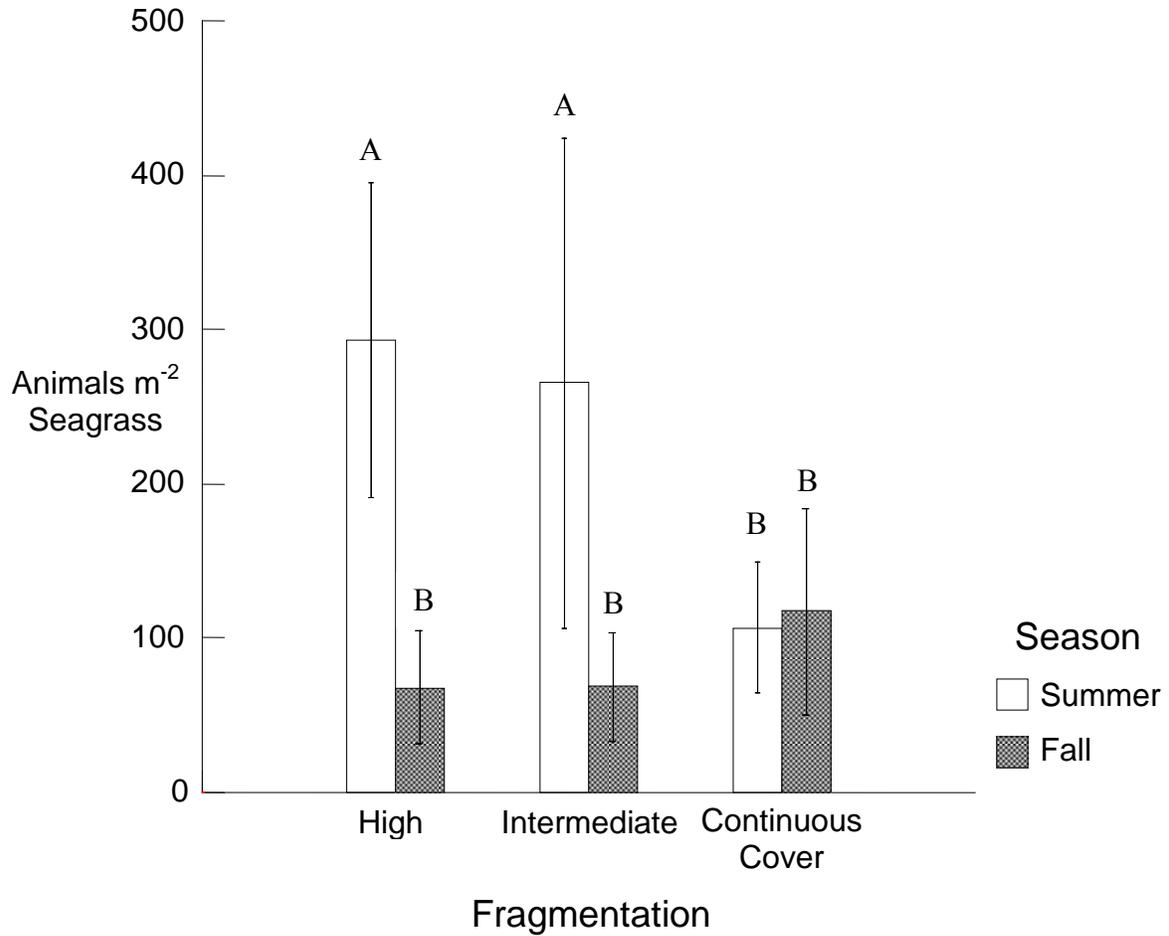


Figure 8. Relative arrow shrimp abundance expressed as a percent to total animal density (number of individuals  $m^{-2}$ ) as a function of fragmentation level in seagrass sampling plots. Error bars represent 95% confidence intervals of mean arrow shrimp abundance.

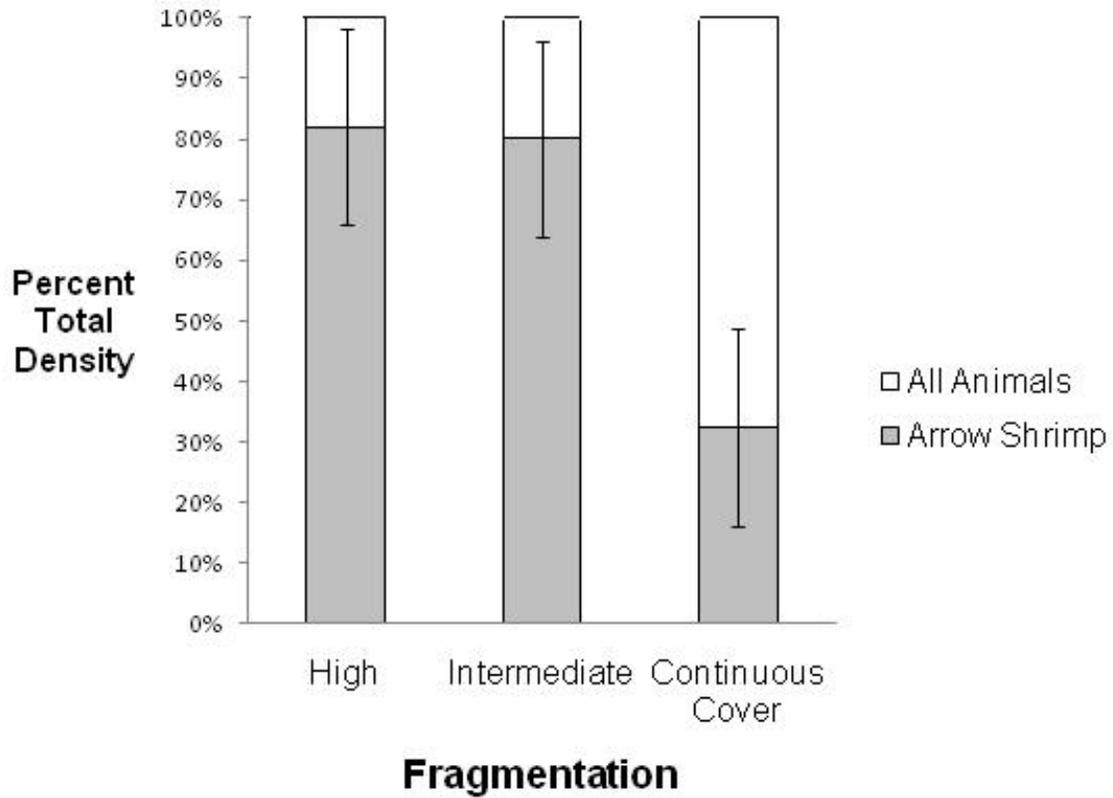


Table 5. Three-way ANOVA analyses comparing diversity in seagrass sampling plots representing three fragmentation levels. Significant ( $p < .05$ ) interactions and main effects evaluated are bold. \* Species evenness was significantly different in pair-wise comparisons between continuous cover and both fragmented habitats using Tukey's test (intermediate and high fragmentation,  $p < .01$ ).

<b>Dependent Variable</b>	<b>Source</b>	<b>df</b>	<b>Mean square</b>	<b>F-value</b>	<b>P-value</b>
<b>Species Density</b>	Season	1	174.052	48.811	<b>0.000</b>
<i>Number Species in 61m<sup>2</sup> of seagrass</i>	Bay	1	2.066	0.579	0.453
	Fragmentation Level	2	1.401	0.393	0.679
	Fragmentation Level X Season	2	4.647	1.303	0.287
	Residual	29	3.566		
<b>Species Richness</b>	Season	1	0.050	0.023	0.879
<i>Mean Number of species in 1683 animals</i>	Bay	1	11.269	5.232	<b>0.030</b>
	Fragmentation Level	2	2.591	1.203	0.315
	Fragmentation Level X Season	2	5.629	2.614	0.090
	Residual	29	2.154		
<b>Species Evenness</b>	Season	1	0.015	3.113	0.088
<i>Pielou's J'</i>	Bay	1	0.003	0.622	0.437
	Fragmentation Level	2	0.101	21.343	<b>0.000*</b>
	Fragmentation Level X Season	2	0.003	0.585	0.563
	Residual	29	0.005		

Figure 9. Estimated species richness in 61m<sup>2</sup> of seagrass sampled in plots during summer and fall 2009. Error bars represent 95% confidence intervals. Species richness was significantly higher in summer than fall ( $p < .01$ )

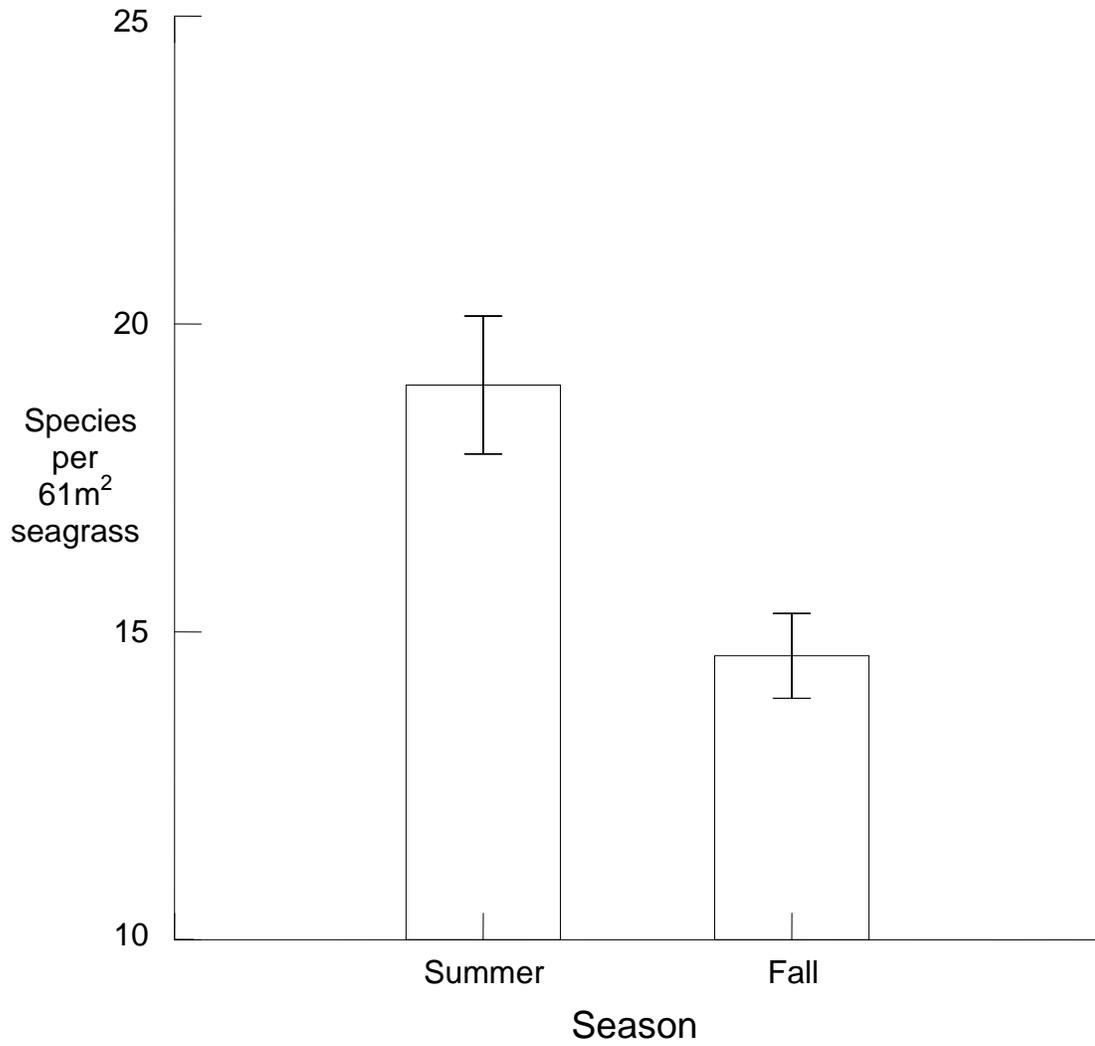


Figure 10. Estimated species richness as a function of fragmentation level in 61m<sup>2</sup> of seagrass sampled in plots. Error bars represent 95% confidence intervals.

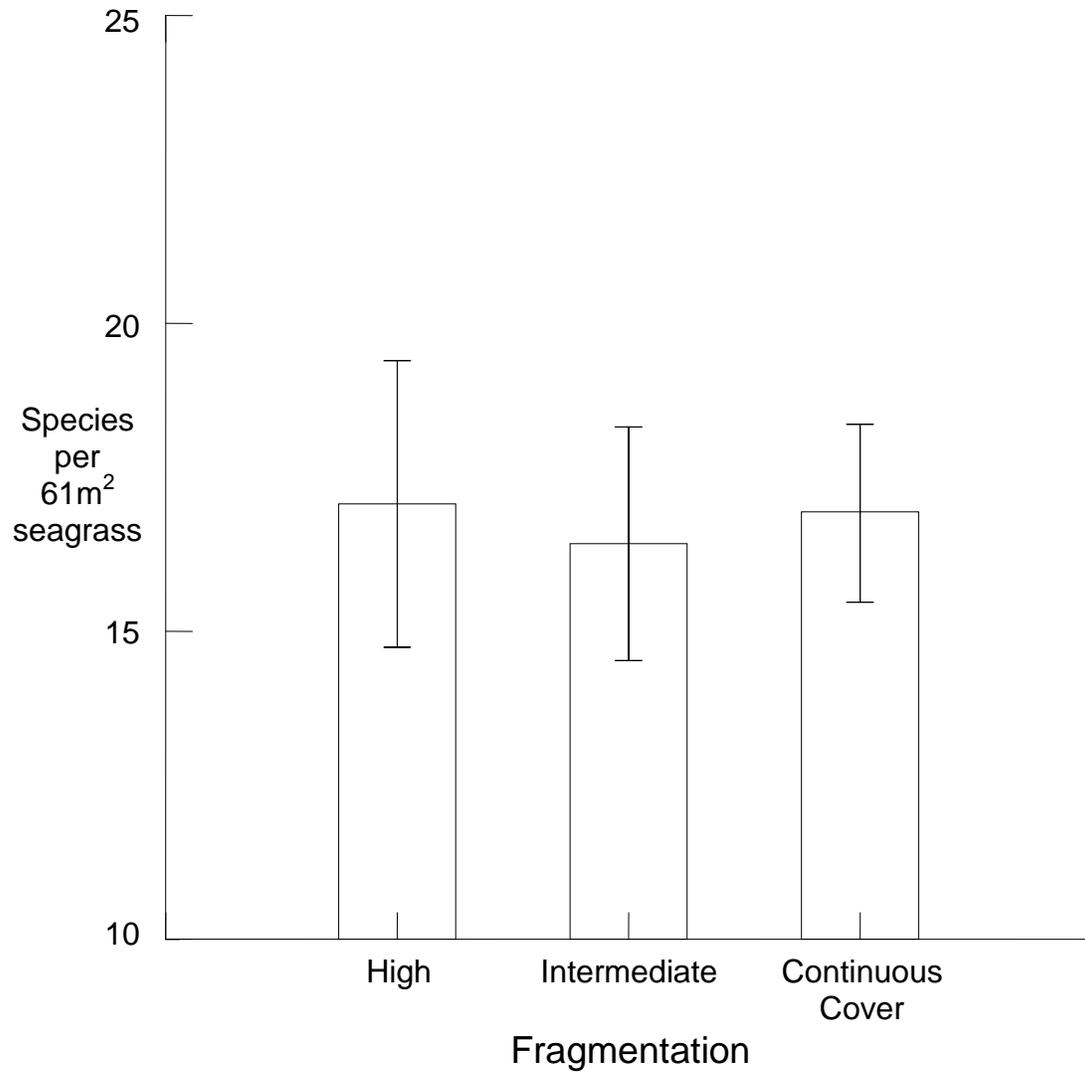


Figure 11. Rarefied species richness (based on 1683 animals) as a function of fragmentation level in seagrass sampling plots. Error bars represent 95% confidence intervals.

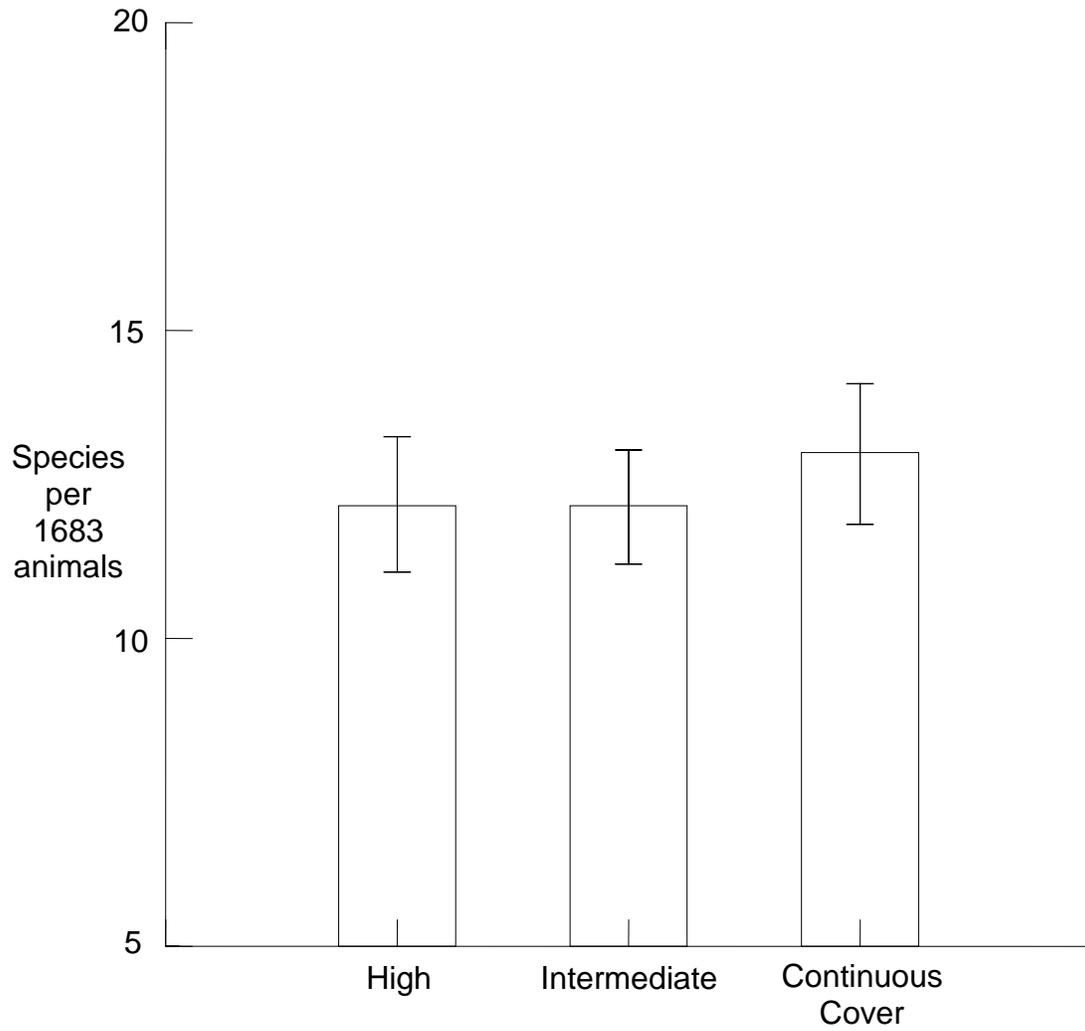


Figure 12. Species evenness as a function of fragmentation level in seagrass sampling plots. Error bars represent 95% confidence intervals. Different letters indicate where species evenness was significantly different using Tukey's test ( $p < .01$ ).

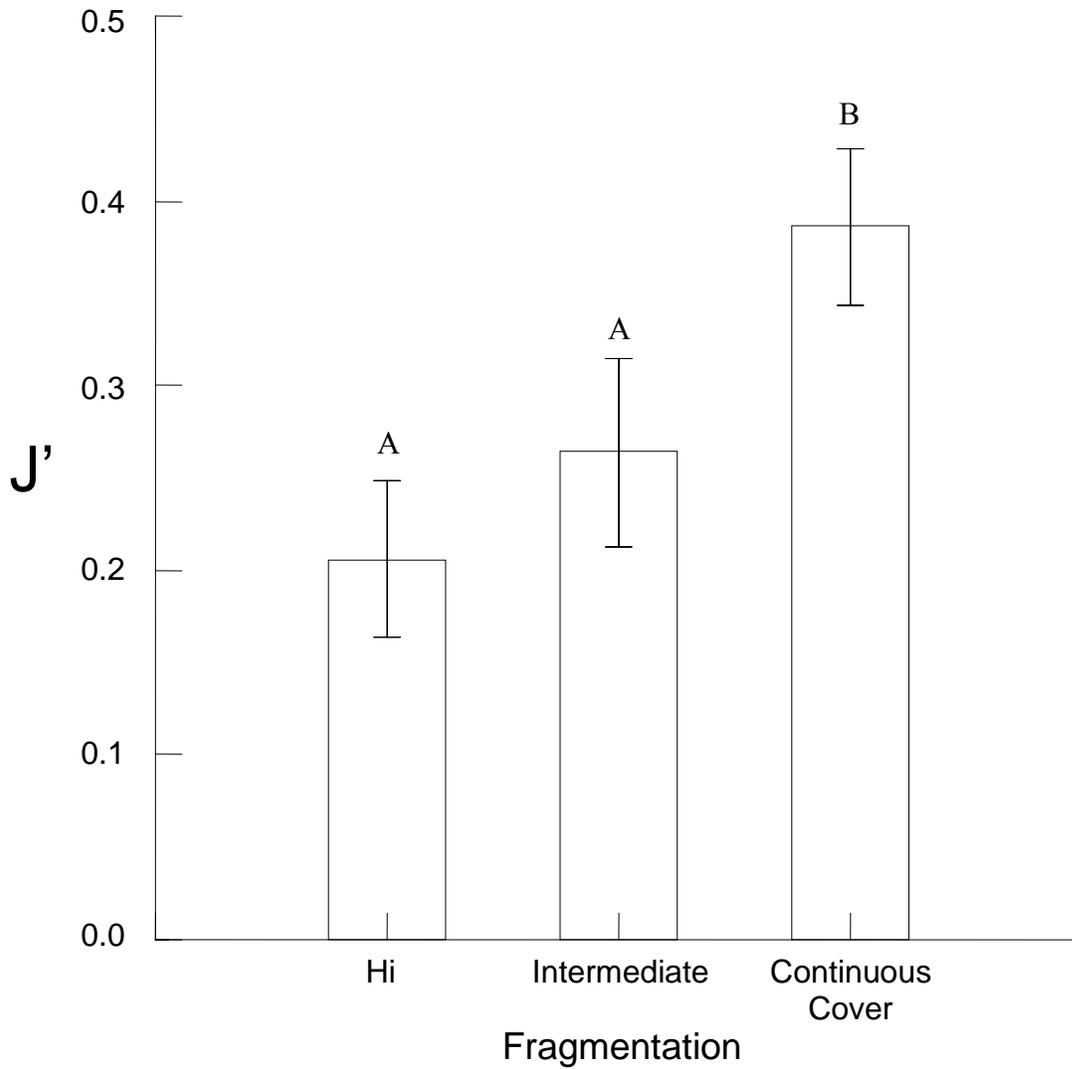


Table 6. ANCOVA analyses examining the relationship between animal density and fragmentation (PCA Factor 1) in two bays and two seasons. Fragmentation was quantified by Principal Component Factor 1 in sampling plots, comprising measures of habitat amount, proximity, connectivity, and patch density. Significant ( $p < .05$ ) interactions and evaluated main effects are bold.

Dependent Variable	Source	df	Mean square	F-value	P-value
	<b>Total Animal Community</b>				
<b>Animal Density</b>	Season	1	1.404	23.645	0.000
<i>(number of individuals/ m<sup>-2</sup> seagrass)</i>	Bay	1	0.104	1.749	0.197
	Fragmentation	1	0.010	0.169	0.684
	Fragmentation X Season	1	0.420	7.067	<b>0.013</b>
	Fragmentation X Bay	1	0.115	1.944	0.174
	Fragmentation X Season X Bay	1	0.033	0.552	0.464
	Season X Bay	1	0.069	1.168	0.289
	Residual	28	0.059		
Summer	Bay	1	0.000	0.006	0.937
	Fragmentation	1	0.409	6.336	<b>0.024</b>
	Residual	15	0.065		
Fall	Bay	1	0.250	4.607	0.049
	Fragmentation	1	0.153	2.818	0.114
	Residual	15	0.054		

Figure 13. Animal Density as a function of fragmentation level in seagrass sampling plots during summer (solid line) and fall (dashed line) 2009.

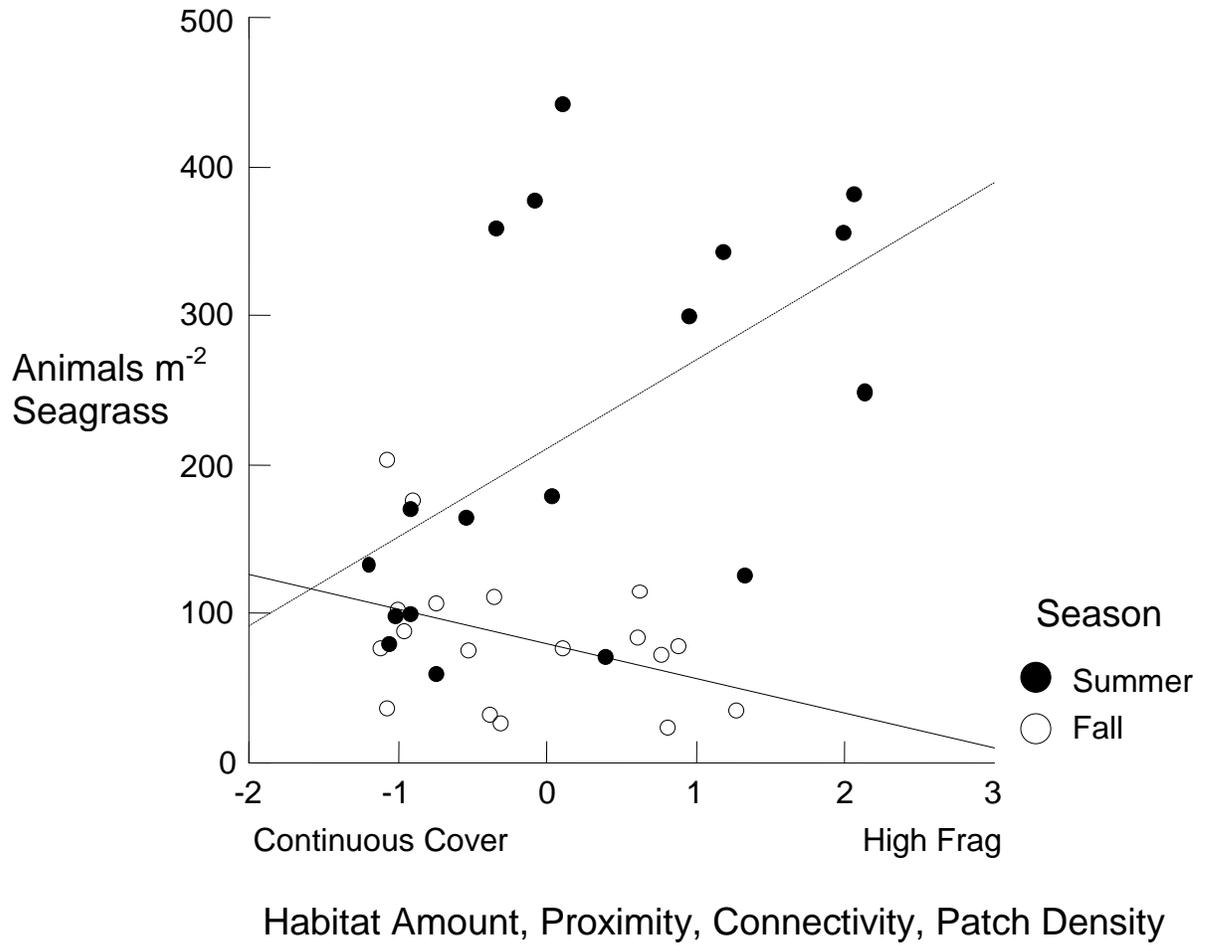


Figure 14. Animal Density as a function of fragmentation level during summer (solid line) and fall (dashed line) 2009, excluding arrow shrimp *Tozeuma carolinense*.

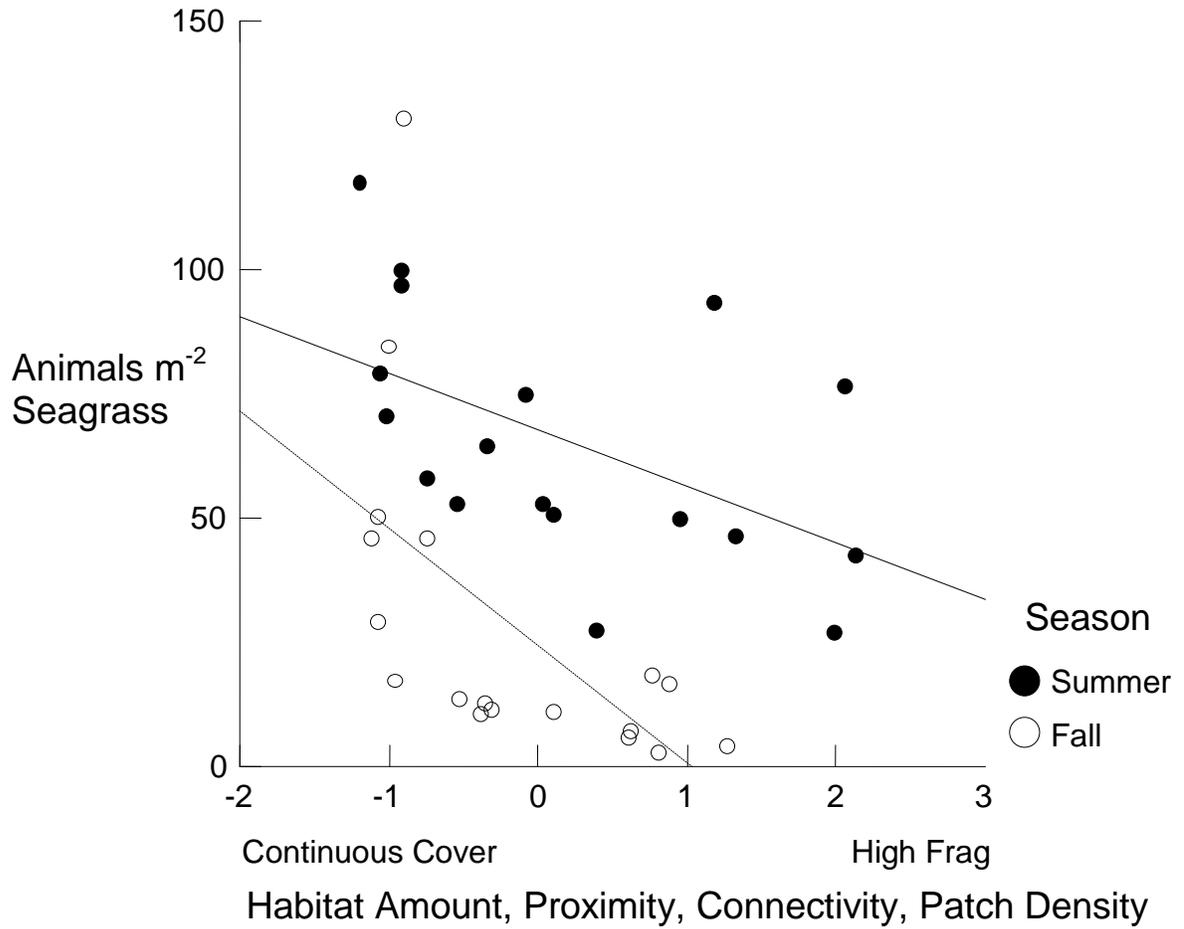


Table 7. ANCOVA analyses examining the relationship between fragmentation and species density in 4225m<sup>2</sup> seagrass sampling plots, in two bays and two seasons. Fragmentation quantified by Principal Component Factor 1 in sampling plots comprised of measures of habitat amount, proximity, connectivity, and patch density. Significant (p < .05) interactions and evaluated main effects are bold. \*A violation of homogeneity of variance (p = .008) was observed using Levene's test despite having log-transformed species density for the analysis.

Dependent Variable	Source	Model R <sup>2</sup>	df	Mean square	F-value	P-value
	<b>PCA Factor 1</b>	.789				
<b>Species Density</b> (number of species/61m <sup>2</sup> seagrass)	Season		1	0.605	81.212	0.000
	Bay		1	0.000	0.012	0.914
	Fragmentation		1	0.002	0.307	0.584
	Fragmentation X Season		1	0.014	1.946	0.174
	Fragmentation X Bay		1	0.004	0.492	0.489
	Fragmentation X Season X Bay		1	0.006	0.853	0.364
	Season X Bay		1	0.150	20.125	<b>0.000</b>
	Residual		28	0.007		
CC Bay	Season		1	0.082	33.223	<b>0.000*</b>
	Residual		16	0.002		
Aransas Bay	Season		1	0.676	57.345	<b>0.000</b>
	Residual		16	0.012		
	<b>Percent Cover</b>	.804				
<b>Species Density</b> (number of species/61m <sup>2</sup> seagrass)	Season		1	0.333	48.300	0.000
	Bay		1	0.000	0.011	0.916
	Fragmentation		1	0.000	0.000	0.989
	Fragmentation X Season		1	0.027	3.965	0.056
	Fragmentation X Bay		1	0.000	0.009	0.923
	Fragmentation X Season X Bay		1	0.013	1.910	0.178
	Season X Bay		1	0.090	12.993	<b>0.001</b>
	Residual		28	0.007		

Figure 15. Species density in sampling plots during summer and fall 2009. Error bars represent 95% confidence intervals.

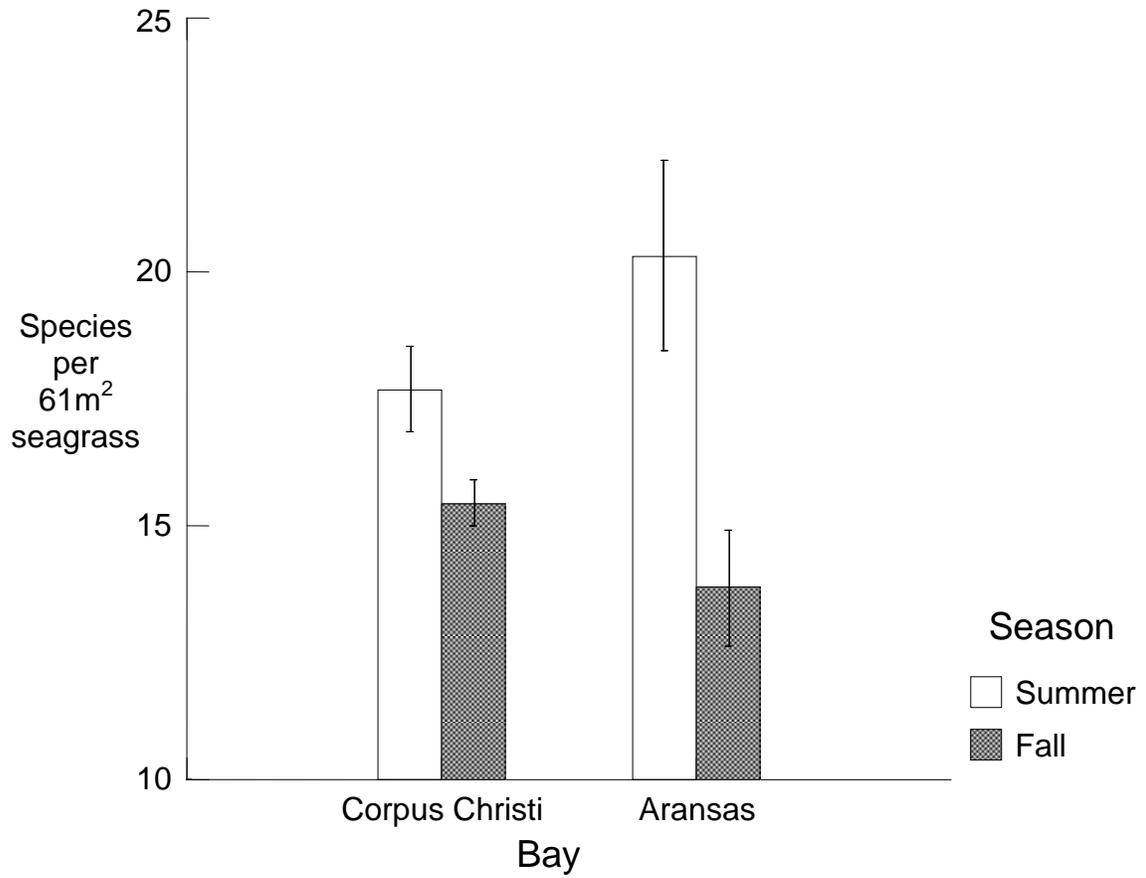


Table 8. ANCOVA analyses and linear regressions examining the relationship between Fragmentation Factor 1 (comprised of measures of habitat amount, proximity, connectivity, and patch density) and rarefied species richness (860 individuals) in 4225m<sup>2</sup> sampling plots, in two bays and two seasons. Significant ( $p < .05$ ) interactions and evaluated main effects are bold. \*In summer, the Bay X Fragmentation interaction term was not significant ( $p = 0.135$ ). \*\* In fall the Bay X Fragmentation interaction term was significant ( $p = .049$ ), requiring separate linear regression analysis of each bay. \*\*\* In Corpus Christi Bay the Bay X Fragmentation interaction term was significant ( $p = .004$ ), requiring separate linear regression analysis of each bay. \*\*\*\*In Aransas bay, the Season X Fragmentation interaction term was not significant ( $p = 0.645$ )

Dependent Variable	Source	Model R <sup>2</sup>	df	Mean square	F-value	P-value
	<b>PCA Factor 1</b>	0.511				
<b>Species Richness</b> (860 individuals)	Season		1	0.116	0.098	0.757
	Bay		1	5.227	4.386	0.045
	Fragmentation		1	2.663	2.235	0.146
	Fragmentation X Season		1	5.763	4.836	<b>0.036</b>
	Fragmentation X Bay		1	9.281	7.788	<b>0.009</b>
	Fragmentation X Season X Bay		1	2.218	1.861	0.183
	Season X Bay		1	6.426	5.393	0.028
	Residual		28	1.192		
<b>Within-Season</b>						
Summer*	Bay	0.664	1	10.615	13.202	0.002
	Fragmentation		1	11.440	14.229	<b>0.002</b>
	Residual		15	0.804		
Fall**	Corpus Christi					
	Fragmentation	0.681	1	6.264	14.918	<b>0.006</b>
Aransas	Residual		7	0.420		
	Fragmentation	0.101	1	2.280	0.790	0.404
Residual	Residual		7	2.886		
<b>Within-Bay</b>						
Corpus Christi †						
Summer	Fragmentation	0.149	1	2.597	2.403	0.165
	Residual		7	1.081		
Fall	Fragmentation	0.681	1	6.264	14.918	0.006
	Residual		7	0.420		
Aransas ††	Season	0.372	1	2.668	1.723	0.209
	Fragmentation		1	12.595	8.134	<b>0.012</b>
Residual	Residual		15	1.548		

Figure 16. The relationship between Fragmentation Factor 1 (comprised of measures of habitat amount, proximity, connectivity, and patch density) and rarefied species richness (860 individuals) in summer (solid line) and fall (dashed line) 2009. Black dots and solid line represent Aransas Bay. Hollow dots and dashed line represent Corpus Christi Bay. The relationship between PCA Factor 1 and rarefied richness differed between seasons ( $p = 0.036$ ). In summer, species richness declined as a function of increasing fragmentation across both bays ( $p = 0.002$ ).

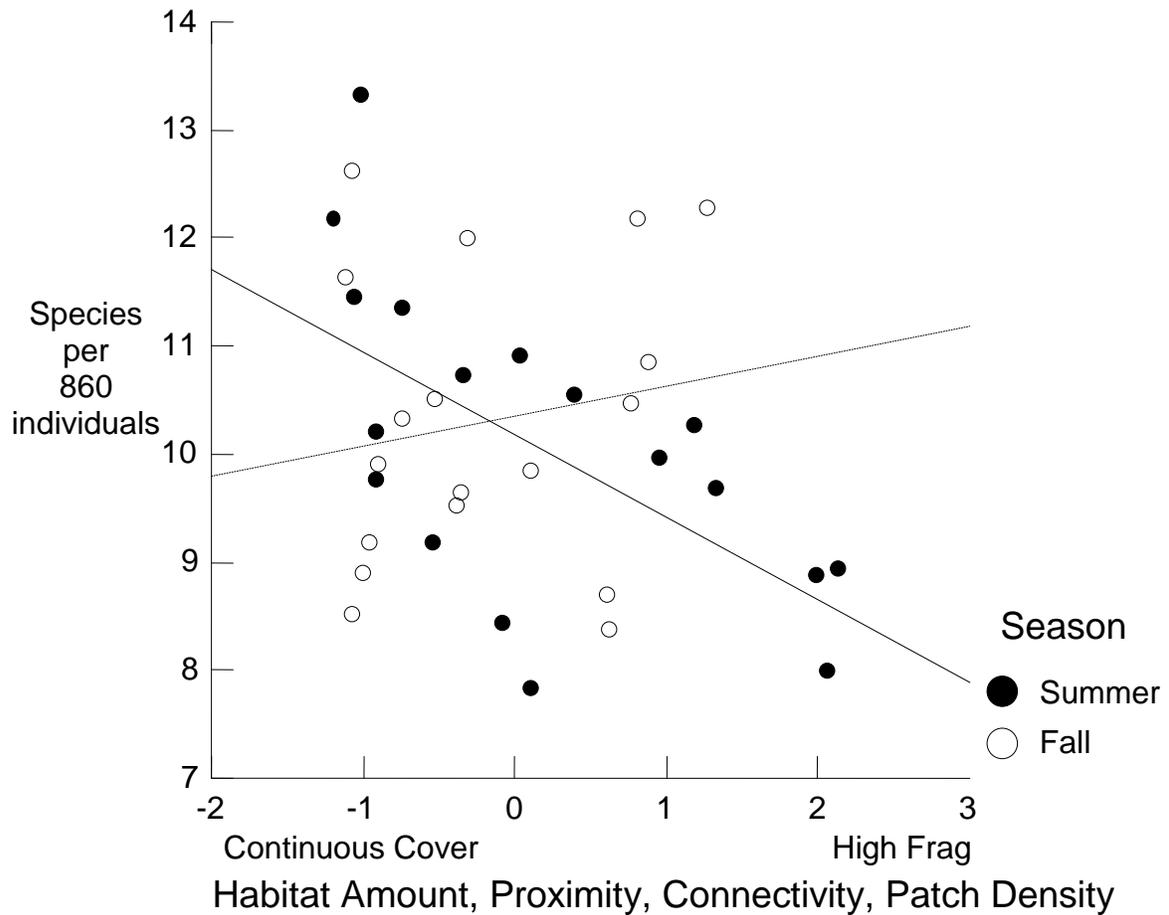


Figure 17. The relationship between Fragmentation Factor 1 (comprised of measures of habitat amount, proximity, connectivity, and patch density) and rarefied species richness (860 individuals) Corpus Christi Bay (solid line) and Aransas Bay (dashed line) in fall. Black dots and solid line represent Corpus Christi Bay. Hollow dots and dashed line represent Aransas Bay. Species richness increased with fragmentation in Corpus Christi bay (0.006); no relationship was detected in Aransas Bay in the fall.

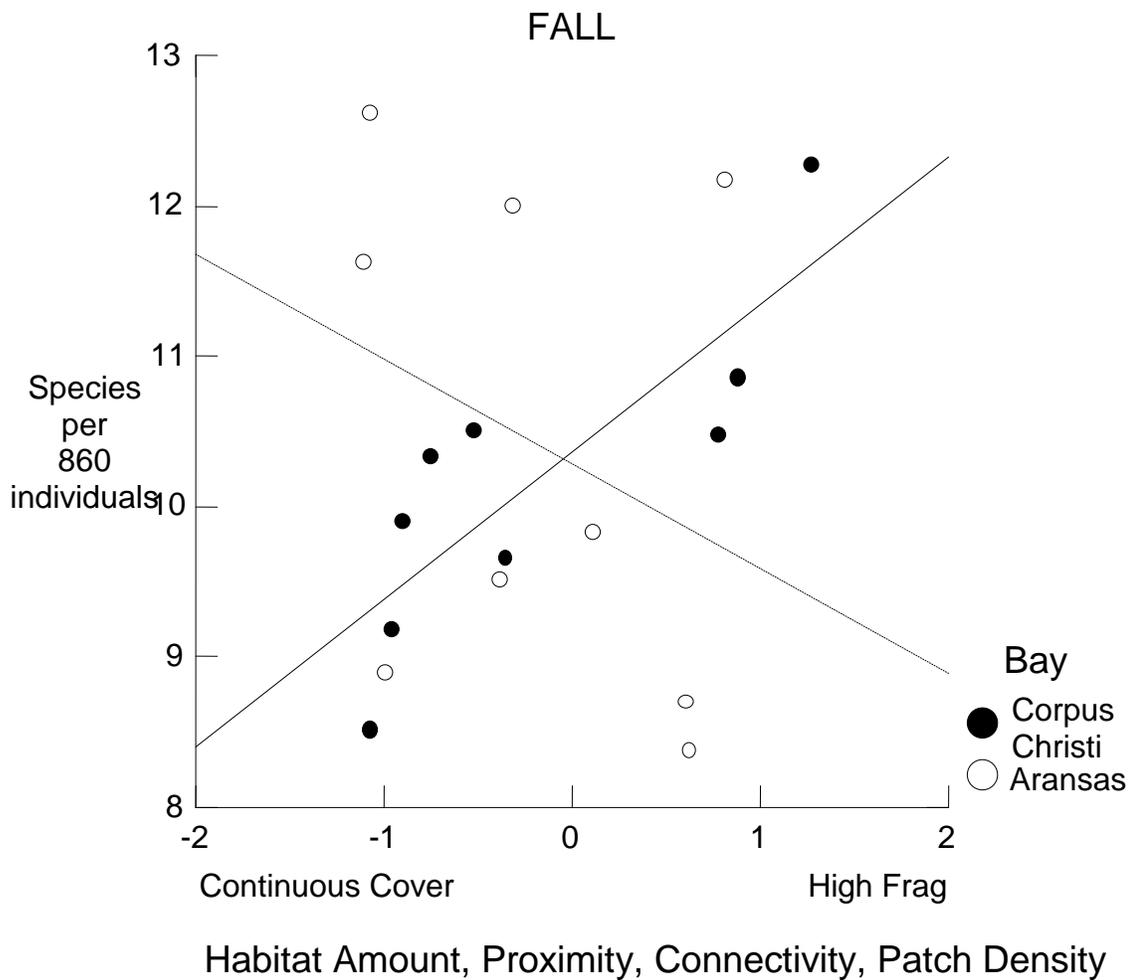


Figure 18. The relationship between Fragmentation Factor 1 (comprised of measures of habitat amount, proximity, connectivity, and patch density) and rarefied species richness (860 individuals) for Corpus Christi Bay (solid line) and Aransas Bay (dashed line). Black dots and solid line represent Aransas Bay. Hollow dots and dashed line represent Corpus Christi Bay. The effect of relationship between PCA Factor 1 and rarefied richness differed between bays ( $p = 0.009$ ). Species richness declined significantly and consistently in fragmented habitats in Aransas Bay ( $p = 0.012$ ).

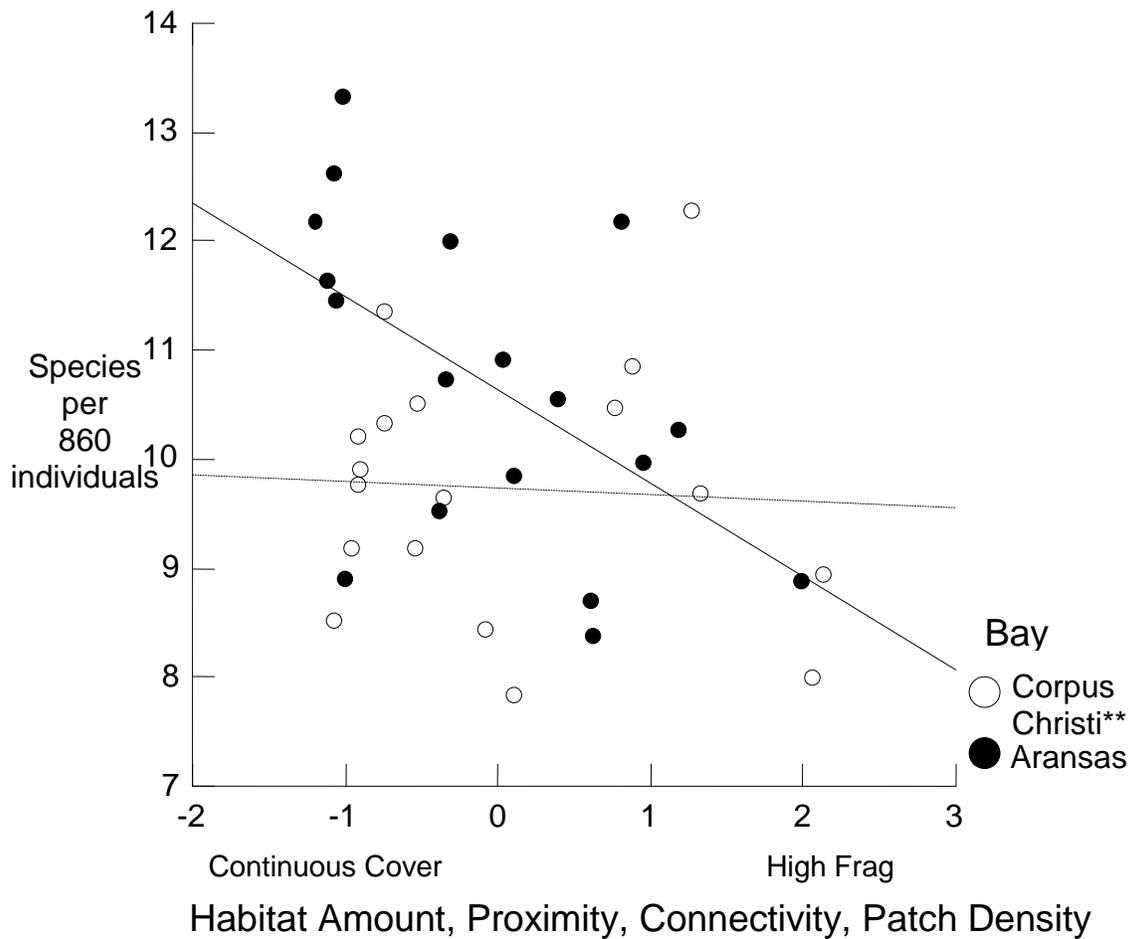


Table 9. ANCOVA analyses examining the relationship between percent cover and rarefied species richness (860 individuals) in 4225m<sup>2</sup> sampling plots, in two bays and two seasons. Significant (p < .05) interactions and evaluated main effects are bold. \*The Bay X Fragmentation interaction term in the overall model was not significant, and removed from within-season analyses. \*\* The relationship between percent cover and rarefied richness differed between seasons, requiring separate analyses.

Dependent Variable	Source	Model R <sup>2</sup>	df	Mean square	F-value	P-value
	<b>Percent Cover</b>		1			
<b>Species Richness</b> (860 individuals)	Season	0.412	1	5.619	3.925	0.057
	Bay		1	0.128	0.089	0.768
	Fragmentation		1	3.426	2.393	0.133
	Fragmentation X Season		1	6.907	4.824	<b>0.037**</b>
	Fragmentation X Bay		1	2.966	2.071	0.161*
	Fragmentation X Season X Bay		1	1.138	0.795	0.380
	Season X Bay		1	6.434	4.494	<b>0.043</b>
	Residual		28	1.432		
Summer	Bay	0.643	1	16.393	19.208	<b>0.001</b>
	Fragmentation		1	10.697	12.534	<b>0.003</b>
	Residual		15	0.853		
Fall	Bay	0.024	1	0.172	0.083	0.777
	Fragmentation		1	0.539	0.260	0.618
	Residual		15	2.077		

Figure 19. The relationship between percent cover and rarefied species richness (860 individuals) in summer (solid line) and fall (dashed line) 2009. Black dots and solid line represent summer. Hollow dots and dashed line represent fall. The effect of fragmentation differed between seasons ( $p = 0.037$ ), and the relationship between fragmentation and rarefied richness in the summer was significant ( $p = 0.003$ ).

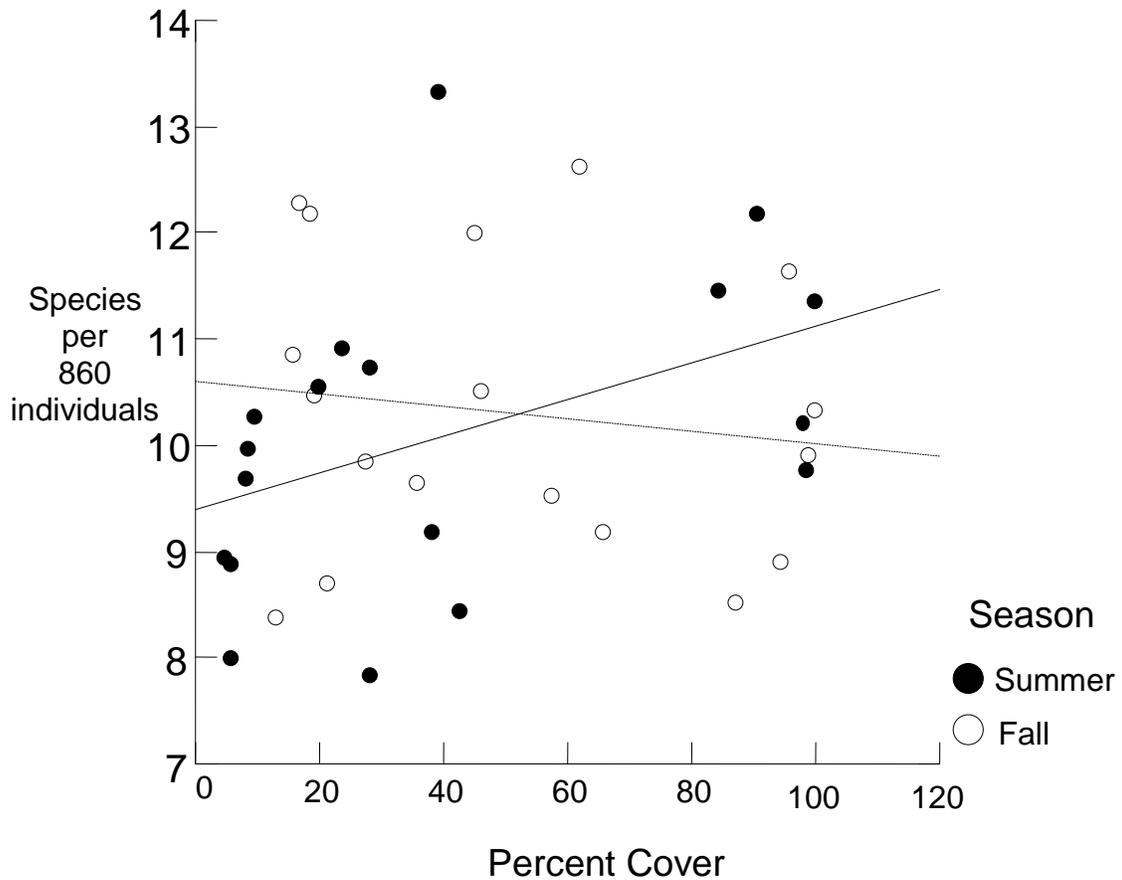


Table 10. ANCOVA analyses examining the relationship between Fragmentation Factor 1 (comprised of measures of habitat amount, proximity, connectivity, and patch density) and species evenness (Pielou's  $J'$ ) in 4225m<sup>2</sup> sampling plots, in two bays and two seasons. Significant ( $p < .05$ ) interactions and evaluated main effects are bold. \*The effect of fragmentation on evenness was significantly stronger in Aransas Bay than Corpus Christi Bay. The Season X Fragmentation interaction term in the overall model was not significant, and removed from within-bay analyses.

Dependent Variable	Source	Model R <sup>2</sup>	df	Mean square	F-value	P-value
	<b>Percent Cover</b>					
<b>Species Evenness</b> (Pielou's $J'$ )	Season	0.599	1	0.038	7.232	0.012
	Bay		1	0.001	0.170	0.683
	Fragmentation		1	0.164	31.424	0.000
	Fragmentation X Season***		1	0.001	0.174	0.680
	Fragmentation X Bay		1	0.039	7.548	<b>0.010*</b>
	Fragmentation X Season X Bay		1	0.001	0.134	0.717
	Season X Bay		1	0.003	0.500	0.485
	Residual			28	0.005	
<b>Within-Bay</b>						
Corpus Christi	Season	0.279	1	0.010	1.863	0.192
	Fragmentation		1	0.027	4.976	<b>0.041</b>
	Residual			15	0.005	
Aransas	Season	0.736	1	0.029	6.687	<b>0.021</b>
	Fragmentation		1	0.171	39.192	<b>0.000</b>
	Residual			15	0.004	

Figure 20. The relationship between Fragmentation Factor 1 (comprised of measures of habitat amount, proximity, connectivity, and patch density) and species evenness in Corpus Christi Bay (dashed line) and Aransas Bay (solid line). Solid circles and line represent evenness in Aransas Bay, hollow circles and dashed line represent Corpus Christi Bay. Across both seasons, species evenness significantly declined as a function of fragmentation degree in Corpus Christi Bay. Evenness was not significantly different in summer versus fall.

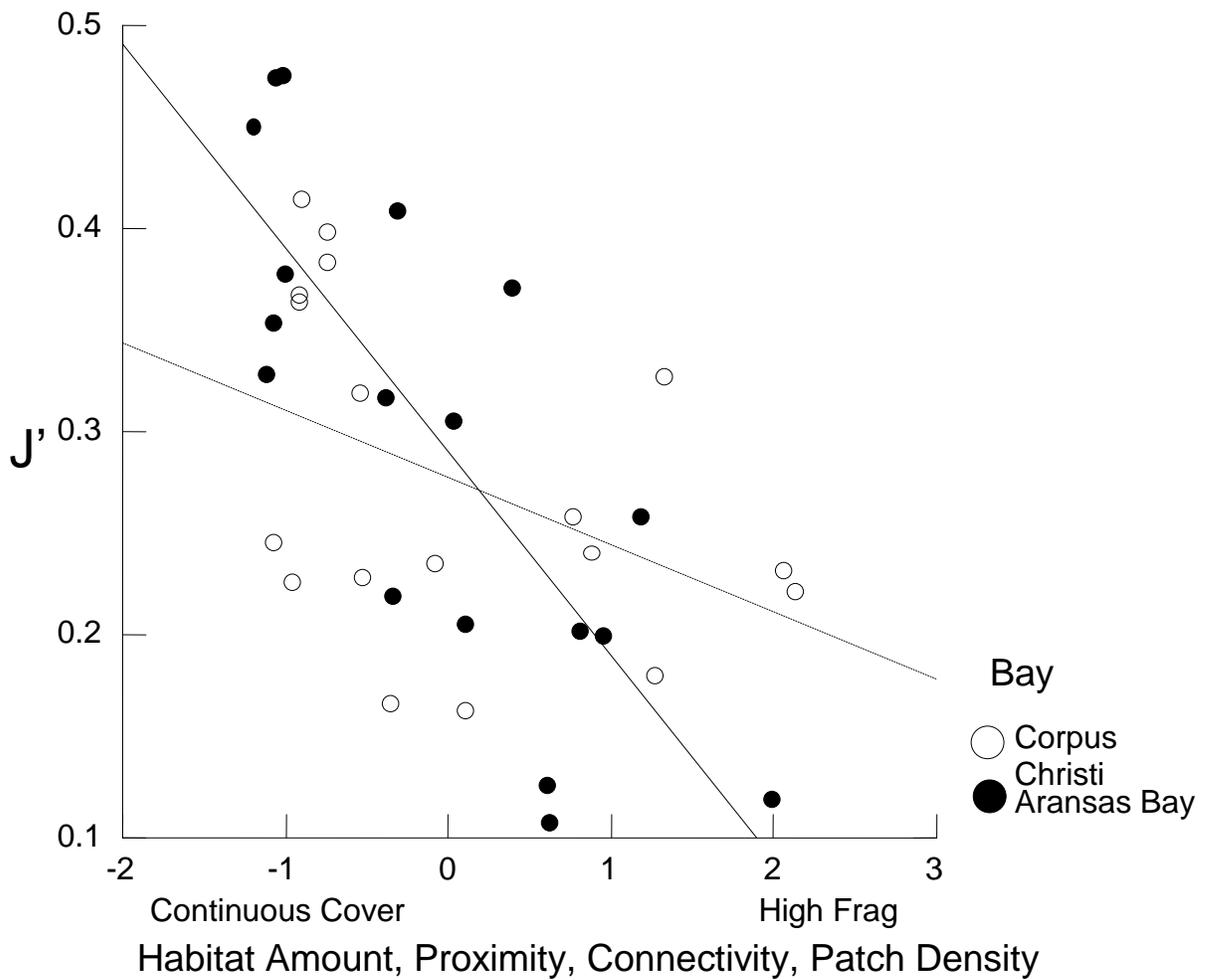
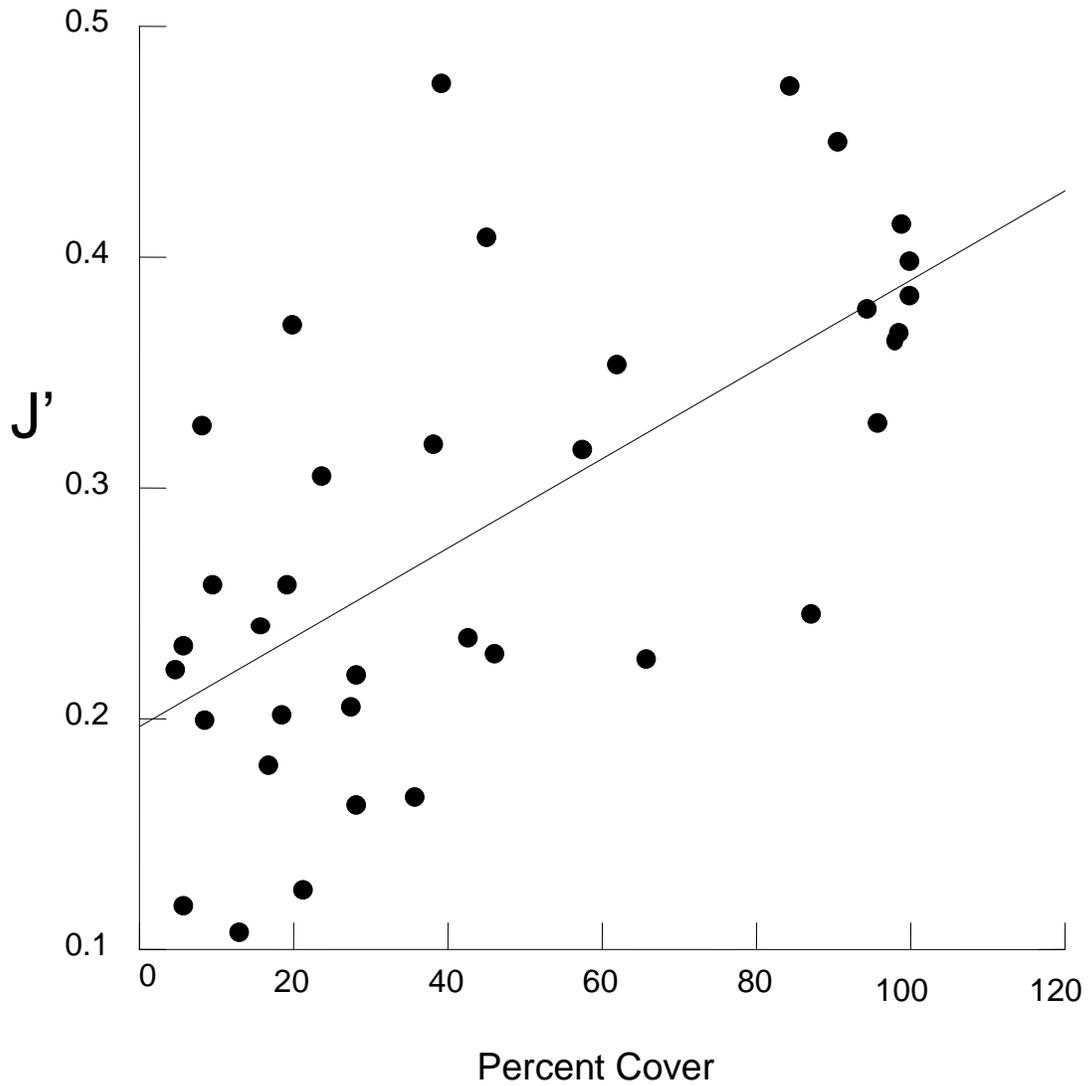


Table 11. ANCOVA analyses examining the relationship between percent cover and species evenness (Pielou's  $J'$ ) in 4225m<sup>2</sup> sampling plots, in two bays and two seasons. Significant ( $p < .05$ ) interactions and evaluated main effects are bold. The season X percent cover interaction term ( $p = 0.912$ ) bay X percent cover ( $p = 0.072$ ) term, and season X bay X percent cover ( $p = 0.587$ ) were not significant, and were excluded from the analysis.

Dependent Variable	Source	Model R <sup>2</sup>	df	Mean square	F-value	P-value
	<b>Percent Cover</b>					
<b>Species Evenness</b> <i>(Pielou's <math>J'</math>)</i>	Season	0.558	1	0.035	6.700	0.015
	Bay		1	0.013	2.455	0.127
	Fragmentation		1	0.184	35.543	<b>0.000</b>
	Season X Bay		1	0.002	0.476	0.495
	Residual		31	0.005		

Figure 21. The relationship between percent cover and species evenness in 4225m<sup>2</sup> sampling plots. Species evenness increased significantly with percent cover ( $p < 0.001$ ).



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