



## Seagrass fragmentation impacts recruitment dynamics of estuarine-dependent fish



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### ABSTRACT

Seagrass beds are a key component of the estuarine landscape supporting high productivity, abundant marine life, and serve as nursery areas for many estuarine-dependent species. With increasing anthropogenic activity, there is concern about overall habitat loss via fragmentation and what effects this may have on local biotas relying on seagrasses for persistence. To examine these effects, fragmented seagrass beds (*Halodule wrightii*, Ascherson 1868) in two different bay systems, Corpus Christi and Aransas Bay, Texas, were delineated, quantified, and mapped, and red drum (*Sciaenops ocellatus*, Linnaeus 1766) was used as a model species to test for impacts of fragmentation on this common estuarine-dependent species. Red drum density, growth, and movement were measured in response to varying levels of fragmentation (i.e., High, Medium, and Low). No difference in initial recruitment of red drum density was observed among fragmentation levels for newly settled arrivals. However, there was a significant size effect; larger fish were found in non-fragmented areas. Growth rates were also compared among fragmented habitats using both RNA:DNA ratios and otolith microstructure, and no significant effect of growth among fragmentation levels was found. Migration potential was measured at the landscape-level within and among fragmented seagrass meadows by tagging and releasing 200 juvenile red drum into three separate replicated fragmented networks. Within 24 h, only one fish was recaptured within the original fragmented network. The vast majority of recaptured fish were found in the nearest continuous non-fragmented seagrass bed over 50 m from their release point. These results suggest a temporal transition of small newly recruited red drum, where individuals settle ubiquitously among varying levels of fragmentation but over time migrate toward more continuous beds. This study provides evidence that there may be a fragmentation “threshold” for red drum, whereby once a habitat becomes too fragmented; individuals either suffer higher mortality or more likely move to more continuous landscapes. Overall, this study suggests that habitat fragmentation and loss of more continuous seagrass meadows may have negative impacts on estuarine-dependent species using these areas as their primary recruitment habitat.

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### 1. Introduction

On a global scale, both terrestrial and marine environments are experiencing stressors such as overexploitation, physical modification, nutrient and sediment pollution, introduction of nonnative species, and climate change (Waycott et al., 2009). Often, a result of much of these impacts is habitat loss (Pandolfi et al., 2003; Rapport et al., 1998; Skole and Tucker, 1993; Vitousek et al., 1997; Waycott et al., 2009). When environments experience degradation or loss, they typically go through phases of fragmentation (Jaeger, 2000). Often, widely-separated patches appear and will continue to shrink in size and eventually disappear (Forman, 1995). In the past, attention has centered on more obvious and well-known environments such as tropical

rain forests, coral reefs, and mangrove forests. However, recent attention has focused on seagrass ecosystems that are characterized by overall loss rates comparable to those of more charismatic ecosystems (Waycott et al., 2009). Seagrass habitats support abundant and diverse communities and provide nursery habitat for many estuarine species (Beck et al., 2001; Chambers, 1991) and availability of nursery and juvenile habitat is essential when determining the dynamics and structure of marine fish populations (Connell and Jones, 1991). Therefore, understanding fragmentation's effect on these systems is timely and important for the maintenance of many marine ecosystems.

Examining the relationship between fish recruitment and nursery availability at the landscape-scale provides a better understanding of spatial and temporal requirements for population persistence, and the impacts of fragmentation on these processes. An important link exists between fish recruitment and the quality of available nursery habitat (Minello, 1999). Ultimately, survival rates of new recruits may be

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lowered if they settle into compromised environments (Levin and Stunz, 2005). Thus, selection for viable nursery habitat is paramount, as they must provide for some level of growth and protection from predation (Stunz and Minello, 2001; Stunz et al., 2002a). Rapid growth to adult stages often confers lower prey vulnerability and ultimate contribution to adult populations. Thus, growth rate is a useful proxy for assessing the health of nursery habitats and survival into adulthood (Houde, 1987). The use of RNA:DNA ratios and otolith microstructure has become a well-accepted method for determining both age and growth rates in juvenile fish (Caldarone et al., 2006; Hovenkamp and Witte, 1991; Rooker and Holt, 1996) among various habitat types. However, each has its own advantage and utility. For example, DNA is species-specific and relatively constant throughout an organism's life while RNA levels increase with somatic growth. Hence, higher RNA:DNA ratios represent faster growth while lower RNA:DNA ratios reflect slower growth (Buckley et al., 1999). Similarly, patterns recorded in otolith microstructure are useful for measuring fish growth rates at various life history stages (Campana and Neilson, 1985; Secor et al., 1991) and can also be used as a proxy for recent fish growth and habitat quality (Stunz et al., 2002b).

Understanding animal movement patterns within the environment is fundamental to the study of animal ecology and to resource management strategies (Pittman and McAlpine, 2003). When areas become more fragmented, distances between individual patches increase, possibly causing density dependent processes to influence survival through local interactions. As a patch shrinks in size, these effects may become magnified unless migration to a more suitable habitat occurs. The well-known "Settle-and-Stay Hypothesis" (Bell and Westoby, 1986) predicts that fish remain in the seagrass beds they first arrive in, as predation risks are too great and outweigh benefits of moving to new areas. Red drum movement within large seagrass beds has been suggested (Rooker et al., 1998a, 1998b), and directly observed by Bushon et al. (2007). Fragmented seagrass meadows present an opportunity to empirically test the "Settle-and-Stay Hypothesis" under varying levels of patchiness. Mark-and-recapture experiments are effective ways to monitor animal movements (Etnier, 1972; Turchin and Thoeny, 1993; White and Burnham, 1999), and a study by Bushon et al. (2007) tagged red drum (<50 mm TL) using visible implant elastomer (VIE; Northwest Marine Technology, Inc.) to track movement patterns within large continuous seagrass meadows. Bushon et al. (2007) recaptured a marked red drum three days after release, 200 m from its original release point, suggesting that red drum are capable of covering relatively large distances in short periods of time. Here, this work is expanded upon by incorporating inter-patch movement of juvenile red drum within a fragmented network of seagrass beds in a replicated experimental design.

Red drum are an economically important, estuarine-dependent species whose habitat requirements and recruitment are well-understood (Holt, 1993; Pattillo et al., 1997; Rooker and Holt, 1997; Stunz and Minello, 2001) making them an ideal study species. Their transition from juvenile into adulthood is critical and relative changes in daily growth can have important consequences for recruitment (Houde, 1987) and regulating their year-class strength (Scharf, 2000). Juvenile red drum can enhance survival by selecting environments that maximize energy intake and minimize predator interactions (Sogard, 1997). Additionally, well-established models for both otolith microstructure and RNA:DNA ratios in red drum have been developed (Rooker and Holt, 1996; Stunz et al., 2002b) for this species making them an excellent model to assess distribution, habitat selection, and growth rates within different levels of seagrass fragmentation.

The overall goal of the study was to experimentally test the response of an estuarine-dependent species to variability in fragmentation of seagrass meadows in terms of distribution, growth, and movement. Specifically, the objectives of this study were to: (1) map patchy networks of seagrass beds within Corpus Christi Bay and Aransas Bay that represent varying levels of fragmentation; (2) describe the effect of

seagrass bed fragmentation on red drum density and size distribution; (3) examine whether growth rates of red drum are influenced by levels of fragmentation; (4) and observe fine-scale movement of juvenile red drum within a fragmented seagrass system.

## 2. Materials and methods

### 2.1. Study site

Two bay systems along the northwestern Gulf of Mexico, Aransas Bay and Corpus Christi Bay, Texas were chosen to test impacts of fragmentation level on an estuarine fish. The system is separated from the Gulf of Mexico by Mustang Island and Padre Island, and major exchange with Gulf water occurs through Aransas Pass and Packery Channel (Fig. 1). The Environmental Protection Agency (1999) has recognized Aransas and Corpus Christi bay systems as containing habitats of significant importance, as more than 490 species of birds and 234 species of fish are found in these bays. Much of this diversity is driven by several species of seagrass that cover over 138 km<sup>2</sup>. These species include: *Thalassia testudinum* Banks ex König 1805, *Halophila engelmannii* Ascherson 1868, *Syringodium filiforme* Kützinger 1860, and *Ruppia maritima* Linnaeus 1753, but the dominant species is *Halodule wrightii*. According to Wilson and Dunton (2012), the estimated seagrass coverage mentioned above is most likely in decline.

### 2.2. Mapping

In each bay system, nine adjacent study plots (50 m × 100 m) were selected representing varying levels of patchiness from continuous *H. wrightii* seagrass meadows to highly fragmented beds. Plots were initially chosen haphazardly from each bay system based upon a visual approximation of cover, taking into account the size, number, and proximity of patches within each plot. Thus, a highly fragmented site was characterized by having small seagrass patches far apart (>2 m), while a medium fragmented site consisted of larger patches closer together (<2 m; Fernandez et al., 2005). Low or no fragmentation was represented by large continuous seagrass meadows (≥1000 m<sup>2</sup>). Study sites had both fragmented plots and continuous meadows within close proximity to minimize differences in hydrodynamic conditions (Fig. 2).

Fragmentation was further mapped and characterized for each individual seagrass patch within every study plot using a sub-meter GPS (Trimble® GeoXT™ GeoExplorer® 2008 series). High-resolution shapefiles were created in the field and later quantified in ArcMap software, version 9.3 (Arc View, ESRI, Redmond, CA, USA). All maps and measurements made within ArcMap were done so using a WGS 1984 UTM Zone 14 N projection. Plots were mapped within a maximum of three weeks prior to sampling events to minimize change in cover and spatial arrangement of patches through growth or degradation. Percent seagrass cover was used as an approximation for fragmentation *per se* (Fernandez et al., 2005; Robinson et al., 1995) and verified using ArcMap. Substrate was classified as either seagrass or bare substrate. Mean and standard error (SE) for percent cover within a standardized sampling grid (50 m × 50 m) was calculated for each fragmented plot. Within each bay, three low cover plots (≤20% seagrass), three medium cover plots (25–55% seagrass), and three continuous plots (≥75% cover) were selected (Fig. 3). In an associated study, these same sites are described in much greater detail including 23 landscape pattern indices (Hensgen et al., 2014).

### 2.3. Sampling (densities and size distribution)

Samples for density estimates were collected during two sampling events for each plot during red drum peak recruitment in fall 2009 (Oct. 21–Nov. 2), (Rooker and Holt, 1997). Suitable patches within mapped plots were randomly selected and sampled using an epibenthic

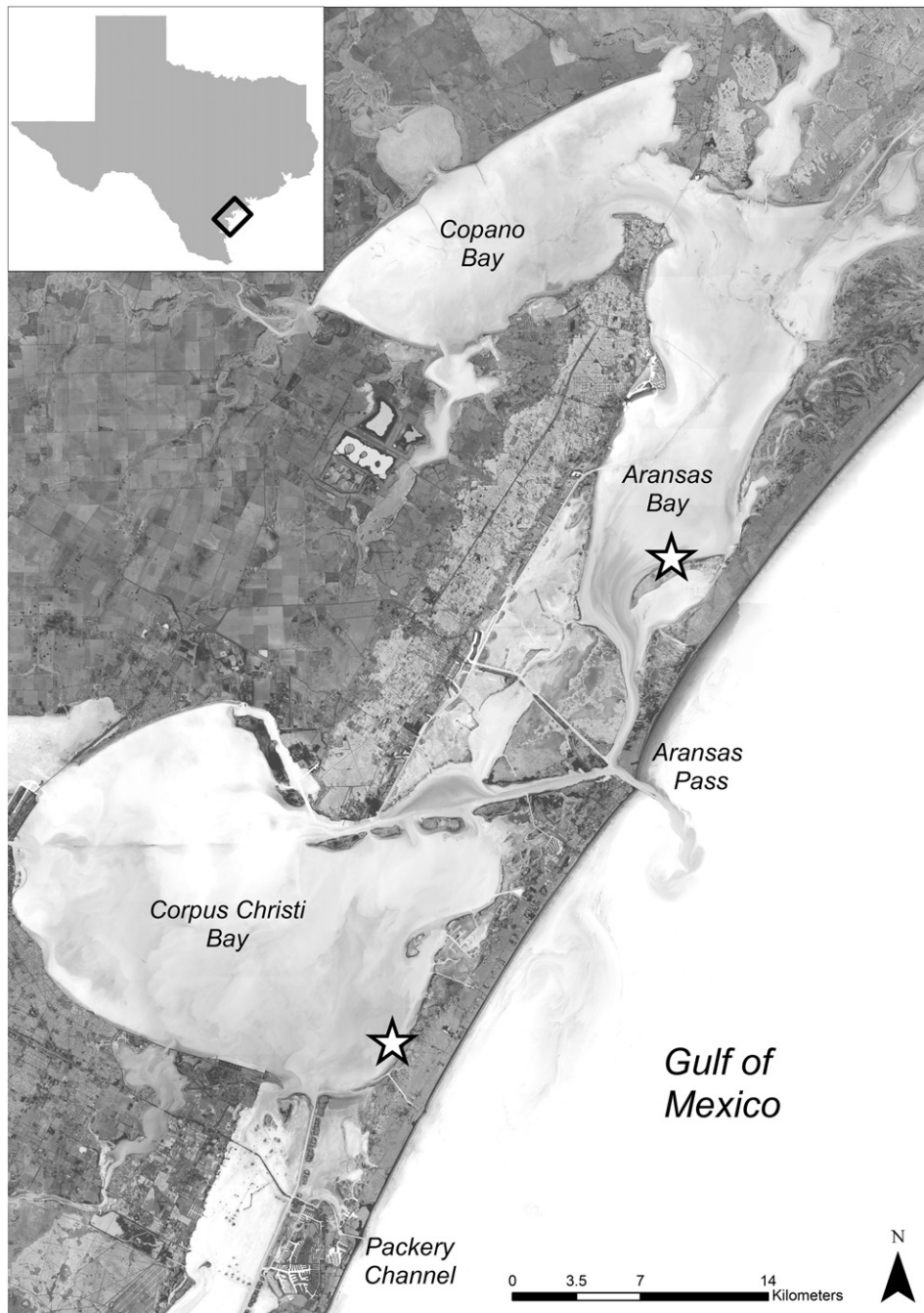


Fig. 1. Map of study sites along the Texas coast. Stars represent the location of fragmented study sites in Corpus Christi Bay and Aransas Bay.

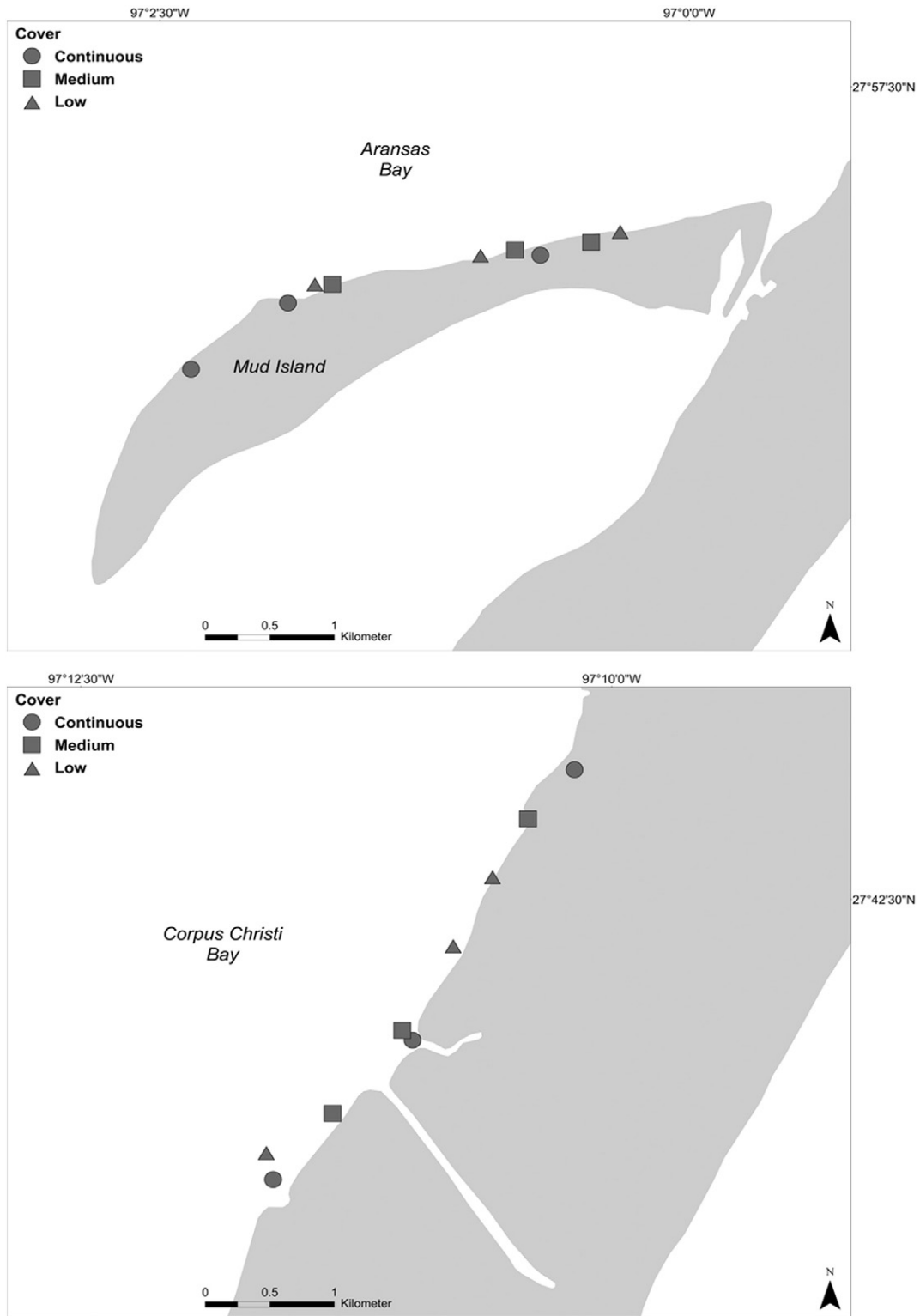
sled; see Stunz et al., 2002a for detailed description. This device has been well-established in the literature as an effective and efficient gear for sampling small nekton, including red drum, (Stunz et al., 2002a; Robillard et al., 2010; Neahr et al., 2010) in seagrasses and other estuarine habitat types. In medium and low cover plots, three separate patches were sampled, and three replicates were taken at each plot yielding a total of 30 m<sup>2</sup> seagrass sampled per plot. Tows were only performed in seagrass, and each tow length and position was mapped using the GEOXT Trimble unit, allowing for patch identification and calculation of total nekton density (number m<sup>-2</sup>). During each sampling event, dissolved oxygen (DO) and temperature was measured using a YSI model DO 200. Salinity was measured using a refractometer. All samples were rough-sorted in the field and preserved using 10% formalin.

Densities and standard length (SL) of newly settled red drum among different levels of seagrass cover within Corpus Christi Bay and Aransas

Bay were analyzed using a two-way ANOVA ( $\alpha = 0.05$ ), where bay and cover were the independent variables. All data were ( $\log_{10}[x + 1]$ ) transformed. *A priori* linear contrasts were performed to test for significant differences in densities and size distribution of red drum among different cover plots within each bay ( $\alpha = 0.05$ ). This analysis was used because comparisons among varying levels of fragmentation between bays in terms of biological response were determined *a priori*. Red drum settle from the plankton into seagrass habitat between 6 and 8 mm standard length (SL) (Holt et al., 1983), for this reason only fish  $\geq 6$  mm standard length were used for these analyses.

#### 2.4. Growth

To measure age and growth rates within fragmented sites, newly settled red drum were collected 2 weeks from the original epibenthic



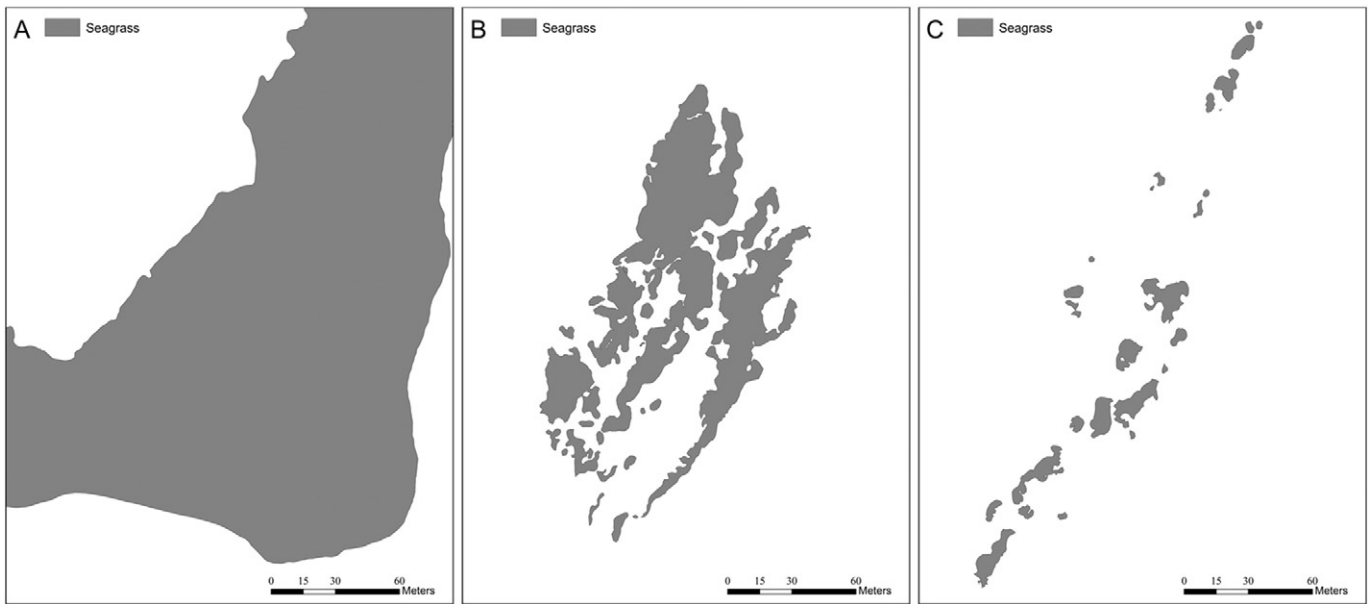
**Fig. 2.** Map of Aransas Bay and Corpus Christi Bay study plots; where (●) represents continuous seagrass bed (no fragmentation), (▲) low cover (high fragmentation) and, (■) medium cover plots (medium fragmentation).

sled tows for recruitment and abundance studies. This time lag was intentional to allow fish to recruit to these areas and be influenced by the local characteristic of the habitat, and it was a necessary assumption that the fish had been using these areas prior to collection. In November 2009, each level of cover (low, medium, and continuous) from both Aransas and Corpus Christi Bays was sampled with a bag seine (6 m long with 5-mm mesh wings and a 3-mm mesh bag). Fish of similar

sizes were used for growth analyses using two techniques: RNA:DNA ratios and otolith microstructure.

Juvenile red drum were measured in the field to the nearest 0.1 mm SL. The heads were removed using a scalpel and were preserved in 70% ethanol for otolith analyses, and the trunks were temporarily preserved on dry ice and then stored in a  $-80^{\circ}\text{C}$  freezer for RNA:DNA analyses. The RNA:DNA ratios were determined using ethidium-bromide





**Fig. 3.** Examples of (A) continuous cover (no fragmentation), (B) medium cover (medium fragmentation), and (C) low cover (high fragmentation) seagrass plots mapped using a GeoXT Trimble coupled with ArcMap software.

fluorometric techniques (Caldarone et al., 2006). Using a spectrophotometer, RNA:DNA ratios were compared between fragmentation levels and integrated over the fish's life. An ANCOVA model was used to test for the assumption of no significant interaction between the treatment (fragmentation) and the effect of the covariant (age) on the dependent variable (RNA:DNA ratio) ( $\alpha = 0.05$ ). ANCOVA tested for differences in  $y$  intercepts and if no significant interaction was found then the model was re-rerun without the interaction.

Lapillar otoliths were removed under a Leica S4E dissecting microscope and used for growth analysis. Otoliths were placed concave up on a slide and fixed in Flo-Texx®. Left and right lapilli were used for age determination based upon ring count and otolith microstructure (David et al., 1994; Rooker and Holt, 1997; Stunz et al., 2002b). Counts were made using an Olympus CX41 compound microscope under  $40\times$  magnification. Left and right lapilli were photographed using an Olympus QColor-3 camera and the Qcapture® program. Otolith radii were measured to the nearest  $0.01 \mu\text{m}$ . All measurements were made from the inner primordium (origin) to the longest edge of the otolith. Age was determined by taking an average between left and right lapillar otolith ring counts. A linear relationship was established between fish SL and otolith radii. Ring counts were performed on left and right lapilli using the image program GIMP 2.6.2©. Often, the inner core rings were difficult to read, in which case a regression established by Rooker and Holt (1997) was used to supplement inner ring counts. A measurement was taken from the primordium to the inner most observable ring and put into the equation:

$$\text{Age in days} = 34.46 + 15.94 \log(\text{radius mm}).$$

Growth rates for individual fish were based upon incremental widths of individual rings (Hovenkamp and Witte, 1991; Stunz et al., 2002b). Growth rates between fragmented and non-fragmented habitats integrated over the life of the fish were compared using analysis of covariance (ANCOVA). A regression model was used to test for the assumption of no interaction between the treatment (Fragmentation) and the effect of the covariate (Age) on the dependent variable (Fish Length). ANCOVA tested for differences in  $y$  intercepts. Outer rings were used to establish recent growth rates (Stunz et al., 2002b). Measurements of the outer seven, ten, and fourteen rings were used to derive a daily incremental growth rate ( $\mu\text{d}^{-1}$ ). This assumes that the fish

captured had been using the habitat during the previous two weeks. A one-way ANOVA was used to test for significant differences in growth rates between fragmented and non-fragmented habitats for the last seven, ten, and fourteen days.

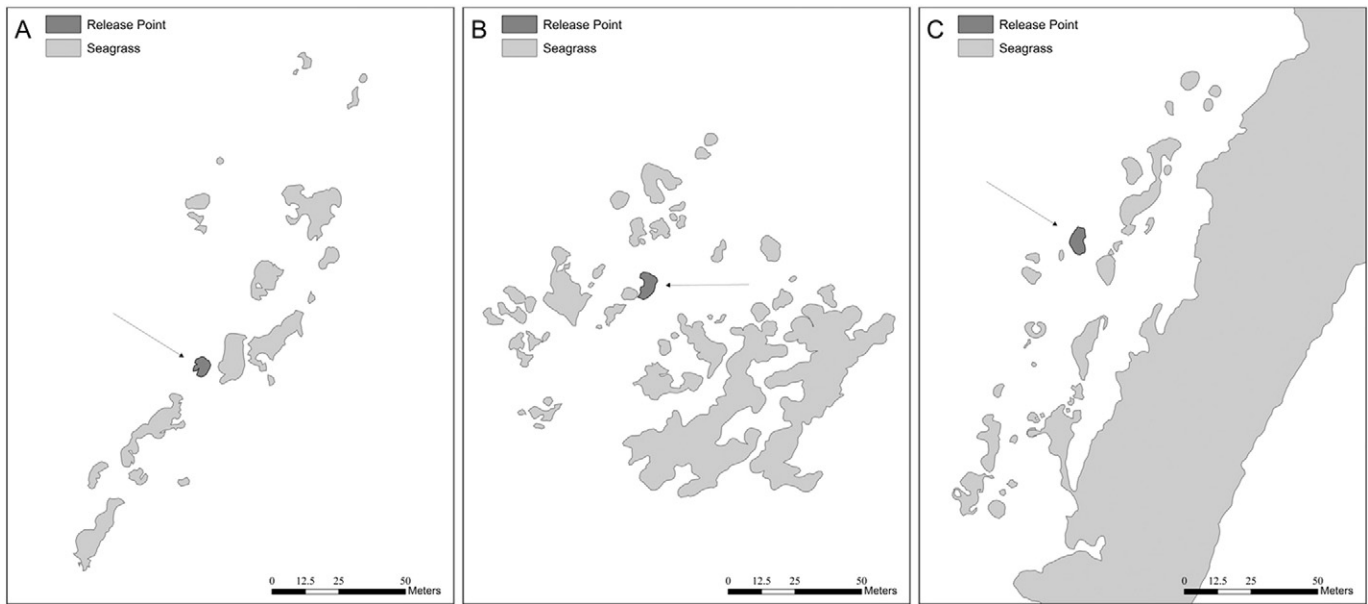
### 2.5. Experimental movement trials

Live juvenile red drum were collected from continuous seagrass meadows within Aransas Bay using a 6-m length bag seine with 5-mm mesh and returned to the laboratory, where they were injected with a Visible Implant Elastomer (VIE) tag below and parallel to the dorsal fin (Bushon et al., 2007). It was logistically infeasible to collect large numbers of red drum for movement experiments from the study's fragmented seagrass beds. Thus, fish were collected from other nearby locations that had high densities. Once tagged, fish were observed for an additional 24 h to ensure there were no residual effects on health from the capturing and tagging processes. On November 26th, 2009, 200 VIE-marked red drum were released into three previously mapped, highly fragmented patch networks within Corpus Christi Bay at naturally high densities ( $1.5 \text{ fish per m}^2$ ) (Stunz et al., 2002a) (Table 1; Fig. 4). Recapture events occurred 24, 48, and 72 h post-release using the same bag seine used to originally capture the fish. Each patch within the fragmented network was seined at least twice or until no additional red drum were collected. All other nekton collected were placed back into the sampled patch. If a marked fish was recaptured it was

**Table 1**

Summary of red drum mark and recapture study where marked fish ( $n = 200$ ) were released into three highly fragmented sites in Corpus Christi Bay. Events were number of hours from release to recovery attempts, and numbers represent either marked or unmarked "wild" fish that were captured.

Site	Fish released	Distance from continuous meadow	Recapture events					
			24 h		48 h		72 h	
			Marked	Wild	Marked	Wild	Marked	Wild
1	50	400 m	1	0	0	0	1	0
2	75	120 m	0	0	0	0	0	0
3	75	50 m	5	25	0	0	1	19



**Fig. 4.** Map of highly fragmented seagrass networks located in Corpus Christi Bay for movement experiment. 50 marked red drum were released at Site 1 (A), 75 marked red drum were released at Site 2 (B), and 75 marked red drum were released at Site 3 (C) on November 26th, 2009. Arrows indicate release points.

measured, enumerated, and released into the patch. Total distance traveled of recaptured fish was measured using ArcMap. Additionally, any unmarked red drum collected were enumerated, measured (SL), and released.

### 3. Results

#### 3.1. Mapping

The Trimble GeoXT unit allowed for highly accurate measurements of percent cover within all study plots. Mean seagrass among three levels of cover was significantly different ( $F_{2,13} = 95.79$ ;  $p < 0.001$ ) and *a priori* linear contrasts showed that low ( $945.15 \text{ m}^2 \pm 113.65$ ), medium ( $2719.91 \text{ m}^2 \pm 245.58$ ), and continuous ( $4776.17 \text{ m}^2 \pm 146.79$ ) cover plots were significantly different from one another.

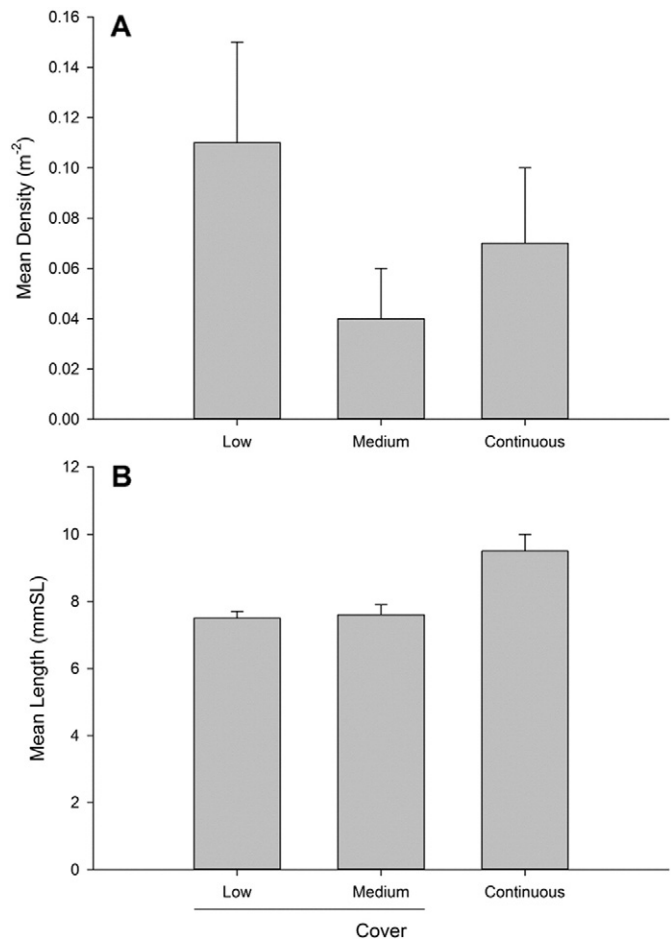
#### 3.2. Sampling (densities and size distribution)

One hundred twenty-three red drum were collected during fall epibenthic sampling ranging in size from 6.0 mm to 14.4 mm SL (mean =  $7.8 \text{ mm} \pm 0.2 \text{ SE}$ ). Red drum densities were not significantly different among continuous (mean =  $0.07 \text{ m}^{-2} \pm 0.03 \text{ SE}$ ), medium (mean =  $0.04 \text{ m}^{-2} \pm 0.02 \text{ SE}$ ), or low cover (mean =  $0.11 \text{ m}^{-2} \pm 0.04 \text{ SE}$ ) ( $F_{2,29} = 1.99$ ;  $p = 0.154$ ) (Fig. 5A); however, the mean size of red drum was significantly different ( $F_{5,117} = 5.83$ ;  $p < 0.001$ ). *A priori* linear contrasts indicate that red drum lengths are significantly larger in continuous (mean =  $9.5 \text{ mm} \pm 0.5 \text{ SE}$ ) than both medium (mean =  $7.6 \text{ mm} \pm 0.3 \text{ SE}$ ) and low (mean =  $7.5 \text{ mm} \pm 0.2 \text{ SE}$ ) cover plots. Red drum lengths from medium and low cover plots did not differ significantly from each other (Fig. 5B).

#### 3.3. Growth analysis

Subsequent to these recruitment and abundance studies, seagrass patches within all eighteen plots were re-sampled to collect fish for growth analysis. However, red drum were not found at every fragmentation level most likely due to fish migration from heavily fragmented areas (see migration study results and discussion below). Consequently, the total number of fish collected for growth analyses in this study was 100 fish (64 from Corpus Christi Bay and 36 from Aransas Bay). Growth

analysis was only performed on the 64 red drum collected from Corpus Christi Bay (28 from continuous and 36 from medium cover sites). Aransas bay was removed from the analysis due to a low sample size



**Fig. 5.** (A) Mean red drum densities (number  $\text{m}^{-2} \pm \text{SE}$ ) and (B) standard length (mm  $\pm \text{SE}$ ) for three levels of cover in Corpus Christi Bay and Aransas Bay during fall, 2009.

(3 fish) collected from fragmented beds; the only fish remaining were located in continuous meadows (see movement studies below). Fish of similar sizes were used for growth analyses for both RNA:DNA ratio studies and otolith microchemistry. An ANCOVA analysis performed on RNA:DNA ratios showed there was no significant interaction (ANCOVA;  $F_{1,60} = 0.00$ ;  $p = 0.971$ ) between fish size and age (days). The ANCOVA also showed that growth rates of fish were not influenced by fish size and found no difference in growth rates between fragmentation levels. There was a significant overall age–length relationship ( $F_{1,60} = 224.93$ ;  $p < 0.001$ ). Results also showed no significant difference in size-at-age of red drum found in continuous and medium cover habitats ( $F_{1,60} = 0.02$ ;  $p = 0.887$ ). The ANCOVA model showed no significant interaction between fragmentation and age ( $F_{1,60} = 0.00$ ;  $p = 0.9832$ ); thus the model was run without the interaction. Results indicate no significant difference in RNA:DNA ratios between fish taken from continuous and medium cover beds ( $F_{1,61} = 1.36$ ;  $p = 0.2489$ ).

There was a strong correlation between otolith radius and fish length (radius  $\mu\text{m} = 11.476x + 55.258$ ;  $r^2 = 0.96$ ), enabling us to use otolith growth as a proxy for fish growth. There was no significant difference in age of red drum between medium ( $51.83 \text{ d} \pm 1.36$ ) and continuous cover ( $54.89 \text{ d} \pm 1.88$ ) plots ( $F_{1,62} = 1.82$ ;  $p = 0.182$ ). There was also no significant difference in mean growth ( $\text{mm d}^{-1}$ ) of red drum between medium ( $0.41 \text{ mm d}^{-1} \pm 0.01$ ) and continuous ( $0.43 \text{ mm d}^{-1} \pm 0.01$ ) habitats ( $F_{1,62} = 1.15$ ;  $p = 0.287$ ). A one-way ANOVA indicated no significant difference in growth rates between medium and continuous habitats for the last seven ( $F_{1,62} = 1.75$ ;  $p = 0.191$ ), ten ( $F_{1,62} = 0.72$ ;  $p = 0.4$ ), and 14 ( $F_{1,62} = 0.72$ ;  $p = 0.4$ ) days.

#### 3.4. Movement

Red drum, marked by VIE, were released into three previously mapped, highly fragmented patch networks within Corpus Christi Bay. Patches were intensively sampled by seining 24, 48, and 72 h after release. After 24 h, almost all marked fish were absent from the original fragmented patches where they were released. Only one fish was recaptured within the original fragmented network. The fish was recaptured at the first highly-fragmented site, 40 m from its release point, which involved crossing two bare, sand bottom expanses approximately 2 and 3 m wide. No “wild” (unmarked), red drum were collected within these three highly fragmented sites, and no marked red drum were recaptured at the second and third sites. However, 5 marked red drum were recaptured within the neighboring continuous network 50 m away from the release point in fragmented network 3. In addition, 25 wild red drum were also collected in the same continuous seagrass meadow. 48 h after release, no marked or wild red drum were captured at any of the sites. 72 h after release, 1 marked red drum was recaptured within site 1 in the same patch it was found two days prior. Likely this was the same fish due to its growth from 18.6 mm to 20.1 mm in three days, resulting in an empirical growth rate ( $0.5 \text{ mm d}^{-1}$ ). No marked or wild red drum were found at the second or third highly fragmented sites. One marked red drum and 19 wild red drum were found in the neighboring continuous seagrass meadow near the third site 72 h after release (Table 1).

## 4. Discussion

These natural experiments coupled with empirical migration studies suggest a temporal transition of small newly recruited red drum, initially settling ubiquitously among varying levels of fragmentation, toward more continuous seagrass beds. Combining both traditional sampling and experimental approaches provided insight to how estuarine-dependent species are impacted by seagrass fragmentation, and specifically indicate that this impairment of habitat may influence the population dynamics for estuarine-dependent fishes by affecting their abundance and migrations patterns.

### 4.1. Densities and size distributions

Although no significant difference in density among fragmentation levels was observed, larger fish were found in continuous seagrass beds. Because red drum are visual predators, they likely select for environments which increase foraging success. Stoner (1982) suggests that fish are more successful at capturing prey in less vegetated areas. Thus, one might expect more red drum to be found in fragmented areas with increased edge; this trend was not observed. Previous research has yielded varied results of fragmentation's effect on density and size distribution of nekton, whereby some species are affected by patch size and connectivity while other species are not (Jelbart et al., 2006; Macreadie et al., 2009; Hensgen et al., 2014). The present research indicates that red drum are affected by fragmentation since the size differences were so large among fragmentation levels; however, density and size alone do not fully explain these differences and may be related to growth.

### 4.2. Growth analysis

Both RNA:DNA ratios and otolith microstructure indicated no significant differences in growth rates between the fragmented study sites, suggesting there was no difference in recent food availability as a function of habitat fragmentation. These results are consistent with previous studies, where no significant difference in RNA:DNA growth assessment or growth rates, as determined through otolith microstructure, was found among seagrass beds and other habitat types (Rooker and Holt, 1997; Stunz et al., 2002b). Slower growth rates of red drum have been observed in lab and field caging experiments but not for “wild” fish under natural collections (Hoff and Fuiman, 1993; Holt, 1993; Reese et al., 2008; Rooker and Holt, 1997; Stunz et al., 2002b). The plausible explanations for not observing differences in growth patterns among varying levels of fragmentation are two-fold. First, slow-growing fish are selected from the population through predation independent of habitat type. Second, larger size fish distributions in continuous meadows suggest that the fragmented habitat only supports newly recruited fish for a short period while the larger (*i.e.*, older) individuals either suffer higher mortality or migrate to other more desirable areas. Researchers have shown that undernourished red drum have slower growth rates prolonging the critical phase of fish development, thus lowering chances for survival (Rice et al., 1993). Fuiman (1994) also found that red drum survival increased substantially once they reached 20 mm SL. Fish greater than 20 mm SL in size would have lower predation risks and could more easily select habitats that maximized growth rates and increased predator avoidance. However, no differences in growth rates were observed. Based on these observations and growth analyses, these data suggest that differences in fish size among fragmented areas are best explained by larger fish migrating to areas with more continuous seagrass cover. Certainly, there is a need for future studies to address differences in food availability and potential competition for resources associated with different levels of fragmentation and how they might affect demographic parameters for red drum.

### 4.3. Movement

For this study, fish movement *via* habitat selection for more continuous cover best explains why weeks after initial sampling event, in which fish were found in all three levels of fragmentation, none were collected from the lower cover (more fragmented) sites. The ecological trade-off for red drum to move from highly fragmented seagrass networks to more continuous habitats increases risk of predation through exposure over large expanses of non-vegetated bottom (Bell and Westoby, 1986; Sogard, 1989). Previous research has shown that at least from a predation risk perspective, it would be most beneficial for the fish to remain in the area they first settle (Bell and Westoby, 1986; Boesch and Turner, 1984; Dresser and Kneib, 2007; Holt et al., 1983;

Rooker and Holt, 1997; Stunz and Minello, 2001). Evidence by Bushon et al. (2007) however, shows that small red drum have a very high capacity for movement within seagrass meadows. Sampling only during red drum peak recruitment did not allow a full examination of fragmentation impacts because the potential for movement was not anticipated as predicted by the “Settle and Stay” hypothesis. Thus, future studies should focus on not only the time of peak recruitment, but also on periods of lower fish density several weeks after initial settlement.

Movement of juvenile red drum and estuarine nekton in general among these putative nursery habitats is not well-documented. The results from this movement experiment provide the best explanation for the observed density, size, and growth findings. Except for one fish, no marked or unmarked red drum were found in highly fragmented sites. All other marked red drum were recaptured in continuous beds in the presence of wild, “unmarked” red drum. This migration required crossing at least 50 m of bare substrate. The gaps between beds are typically sand bottom, which exposes the fish to large expanses of bare substrate and presumably a higher predation rate while emigrating to larger, more ‘suitable’ areas of seagrass cover. As fragmentation increases the distance from one patch to another, it also decreases the actual size of individual patches (Bender et al., 1998). It is plausible that an individual patch could become too small, effectively removing an inner core of predation refuge for smaller, more vulnerable fish (<20 mm SL) or restricted food supplies within the patch force migration. At this point, the patch is no longer suitable as a viable habitat for newly-settled fish, providing little protection from predators, or perhaps no more shelter than bare substrate; thus, the observation of movements across large expanses of non-vegetated bottoms. At a landscape level, proximity of fragmented seagrass meadows to large continuous areas of habitat may be important to the survival of newly recruited red drum. The distance between fragmented and non-fragmented areas is essential in terms of isolating newly settled juvenile red drum, thereby potentially increasing predation mortality. Movement, in fact, may be the result of local predator pressure, and in this case, may be more so than food availability, since no differences in growth rates were found, and other studies have shown that predation risk can influence red drum habitat selection patterns.

Collectively, these results suggest that early juvenile red drum settle ubiquitously into varying levels of fragmented habitats but preferentially select for continuous habitat over fragmented areas relatively quickly post-recruitment. Then fish either actively move to more continuous beds through relatively long migrations over bare bottom, or they are removed by predation or starvation. Growth rates indicate seagrass areas that are fragmented are not food limited and are at least providing enough resources for growth rates similar to areas of more continuous cover. However, the movement experiment along with observations from field collections, shows that highly fragmented beds may have a lower habitat value based on lack of long-term use and persistence of larger juvenile red drum. Thus, based on these findings, future conservation and management of these crucial nursery habitats needs to understand that continuous seagrass meadows are valuable for supporting newly recruiting estuarine-dependent species, particularly when they are near fragmented habitats as the loss of more continuous seagrass meadows may have negative impacts on estuarine-dependent species using these areas as their primary recruitment habitat.

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