Influence of marsh island size on nekton communities: intermediate optima rather than Single-Large-or-Several-Small (SLOSS)

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ABSTRACT: Habitat extent and configuration are critical drivers of faunal abundance, diversity, and ecosystem functioning. Evidence from terrestrial systems often suggests that large contiguous tracts of habitat generally support more species and individuals than several small patches of equal summed area. However, studies from shallow-water marine systems often suggest the opposite trend or that there are more complex interactions. Since tidal wetlands (e.g. salt marshes and mangrove forests) are at the interface between terrestrial and marine ecosystems and provide essential nursery habitat for a variety of estuarine taxa, it is important to elucidate how the size, configuration, and surrounding matrix of these wetlands influence their role in supporting faunal communities. We sampled 12 isolated marsh islands ranging in size from 300 to 55 000 m^2 within North Carolina, USA, to better understand the influence of marsh size and configuration on overall biodiversity and faunal abundance of estuarine nekton. Field observations indicated that nekton catch rates were directly correlated with marsh area and perimeter; however, species richness did not change with marsh size or configuration. Further analysis indicated that small and medium marsh islands support higher species turnover among islands than large marsh islands. Quantitative simulations using the 'Single-Large-Or-Several-Small' framework and idealized, circular islands showed that intermediate-sized islands support the highest relative abundance of nekton after standardizing for total marsh area. Our findings suggest that focused conservation or restoration efforts for marsh islands ranging in size from 1000 to 10 000 m^2 may help maintain and enhance estuarine nekton communities.

KEY WORDS: Landscape · Conservation · Tidal marshes · Fragmentation · Biodiversity · Faunal abundance

1. INTRODUCTION

Anthropogenic activities resulting in habitat loss, degradation, and/or fragmentation at local, regional, and global scales are directly linked to declines in faunal diversity, abundance, and biomass across diverse ecosystems (Haddad et al. 2015). In coastal systems, the loss of structured shallow-water habitats is believed to directly impact both faunal communities and associated ecosystem services. For example, oyster reefs have been degraded globally to 15–35% of their historic extent (zu Ermgassen et al. 2012), resulting in diminished nursery function, shoreline protection, and water filtration (Grabowski et al. 2012).

Habitat degradation resulting in a transition from structured to relatively unstructured habitat may affect local- and regional-scale species composition, abundance, richness, and broad-scale functional diversity (Dobson et al. 2006, Micheli et al. 2008). However, quantitative information on the relationship between the amount of structured habitat and its value as nursery habitat remains limited, and determining the mechanisms that regulate these faunal–habitat relationships is needed to increase the success of future conservation or restoration efforts (Rose 2000).

Several strategies have been developed to mitigate the impacts of habitat loss or degradation on faunal species, such as preserving, conserving, and restoring critical habitat. Biogenic habitats that are degraded and/or fragmented may become island patches surrounded by relatively unstructured habitat matrices (e.g. unvegetated sandflats and mudflats in coastal systems; Fahrig 2003, Lindenmayer & Fischer 2013, Villard & Metzger 2014). The position of these isolated habitat patches within a landscape and its subsequent effect on functionality for faunal communities has been examined across a breadth of habitat types and geographic locations (Skilleter & Loneragan 2003, Grabowski et al. 2005, Gain et al. 2017, Gittman et al. 2018, Gilby et al. 2019). For example, a recent study in coral reef systems showed that when habitat patch size was held consistent, more isolated patch reefs supported greater abundances and diversity of coral reef fishes (Jones et al. 2020). However, due to variation in environmental, ecological, and human-induced stressors in coastal systems, habitat patch dynamics may vary substantially across both space and time.

Due to spatial variation in anthropogenic impacts, remaining habitat islands resulting from habitat loss may vary in shape, total habitat area, and length of edge or perimeter. Based on principles of island biogeography (MacArthur & Wilson 1967), it is hypothesized that larger habitat islands (with greater area) sustain higher species diversity and densities compared to individual small islands (Wilcove et al. 1986). Additionally, higher edge-to-area ratios (defined as the length of perimeter or edge habitat relative to the total area of an island) may facilitate species interactions at habitat boundaries (Fagan et al. 1999) and promote species that move across landscapes with more edge habitat (Stamps et al. 1987). These hypotheses are based on several ideas: (1) larger islands have higher recruitment (immigration > extinction) rates than small islands, (2) increased habitat heterogeneity on large islands allows for more species to colonize unique habitats and thus

reduces competition and extinction, and (3) populations on large islands can better withstand disturbances (MacArthur & Wilson 1967). A hotly debated topic in terms of designing future conservation areas or reserves built upon principles of island biogeography is whether, when controlling for overall area, single large or several small reserves or habitat patches (referred to as the 'SLOSS' concept) maximize faunal diversity, abundance, and biomass across a landscape (Diamond 1975, Simberloff & Abele 1982).

Reserve design research over the past 50 yr (Williams et al. 2005) demonstrates that the effects of a single large or several small reserves on faunal communities is context dependent (Ovaskainen 2002, Le Roux et al. 2015). In many terrestrial systems, empirical evidence and theoretical models show that large contiguous tracts of habitat typically support more species, individuals, and biomass than several small patches when total area was held constant (Tjørve 2010). Studies from marine systems, by contrast, often show that several small habitat patches can support more species, individuals, and faunal biomass than a single large habitat patch. For example, seagrass meadows comprised of several small patches (with increased edge to area ratio) tend to support higher recruitment, diversity, and abundance of organisms than one large swath (McNeill & Fairweather 1993) until habitat loss reaches a critical threshold (Yeager et al. 2016).

Notably, species richness is often scale-dependent and can be greatly influenced by the spatial or temporal scale of observation (Chase et al. 2018). Both scale-dependence and critical ecological thresholds (for habitat loss) may play a key role in determining faunal–habitat relationships across both terrestrial and marine systems (Boström et al. 2011) in the context of reserve design and with continued habitat fragmentation increasing the number of small habitat patches (Fahrig 2001). This suggests that understanding several small versus single large patch dynamics will provide insight into both reserve design and how species may respond to continued habitat loss. In addition, the variability and strength of edge effects for a given habitat type may dictate SLOSS dynamics across both terrestrial and marine habitats (Laurance et al. 2007).

In particular, tidal wetlands (e.g. salt marshes and mangrove forests) may have unique SLOSS dynamics because they are critical ecotone habitats that lie at the interface between terrestrial and marine systems. Due to the highly complex nature of wetland geomorphology and hydrodynamics, these habitats

may exhibit unique patch and edge dynamics not present in other coastal habitats (Peterson & Turner 1994, Tran & Fischer 2017). A study supporting single large islands found that physical and geographical factors such as wetland island size, degree of isolation, and surrounding ocean currents drove species diversity and abundance through dispersal and recruitment dynamics (Field et al. 1998). Similarly, recent studies by Meyer & Posey (2014, 2019) found that marsh islands (up to 10 000 m^2) supported higher catch rates of marsh resident taxa, although smaller marsh islands (~1000 m^2) and fringing mainland marshes supported higher catch rates of predatory species along the marsh edge. These studies have advanced our understanding of landscape features and habitat patch dynamics affecting nekton in tidal wetlands. However, key knowledge gaps remain in how small (<5000 m^2), medium (5000–10 000 m^2), and large marsh islands (>10 000 m^2) and adjacent habitat structure influence nursery function for nekton in terms of estuarine biodiversity and abundance. Additionally, translating these empirical findings into useful conservation and management strategies remains a challenge.

To address how the size of isolated marsh islands influences species diversity and abundance of estuarine nekton, we conducted monthly sampling on naturally occurring marsh islands ranging from 300 to 55 000 m^2 in size from June to October in 2017 and 2018. We examined how the area, perimeter (edge length), amount of adjacent structured habitat, and fine-scale marsh grass characteristics influenced species richness and faunal catch rates. Using our empirical survey findings, we also conducted quantitative simulations using idealized, circular islands to determine the optimal island size and number (invoking SLOSS) that best maximize the conservation impact vis-à-vis abundance of estuarine nekton utilizing marsh-island habitat. Specifically, we asked whether one large marsh island supports more, fewer, or the same number of individuals than several smaller islands. Based on previous work indicating that the vegetated edge is the most valuable component of a marsh for estuarine species (Minello et al. 1994, Peterson & Turner 1994, Meyer & Posey 2019), we hypothesized that marshes with the highest edge to area ratio (i.e. small to intermediate-sized marsh islands) will best support estuarine nekton abundance and overall species diversity.

2. MATERIALS AND METHODS

2.1. Habitat identification and characterization

We sampled 12 marsh islands across 3 sounds in North Carolina (USA): Back Sound, Bogue Sound, and Core Sound. These sounds are interconnected mixoeuhaline back-barrier embayments with multiple oceanic inlets and contain naturally occurring isolated marsh islands. Within each sound we chose 4 isolated marsh islands ranging from 300 to 55 000 m^2 in area with varying perimeters or edge lengths (Table 1, Fig. 1). To ensure that the entire range of natural marsh islands was encompassed in each sound, we targeted islands across 3 size bins: small (300–1200 m^2), medium (6000–10 000 m^2), and large (30000–55000 m^2). Each isolated island was at least 250 m from the nearest marsh, and each site was dominated by salt marsh cordgrass *Spartina alterniflora*. Within a 250 m buffer surrounding each marsh

Table 1. Information for each site including site ID, sound, assigned marsh type, latitude, longitude, area, perimeter, perimeter to area ratio, and proportion of seagrass within 250 m buffer surrounding the marsh island

| Site ID	Sound	Marsh type	Latitude (°N)	Longitude (°W)	Area (m^2)	Perimeter (m)	Perimeter: area ratio	Proportion of adjacent seagrass
BA1	Back	Large	34.7197	76.5853	37 005	2105	0.0569	0.137
BA2	Back	Small	34.7069	76.6000	430	88	0.2047	0.055
BA3	Back	Medium	34.6969	76.6319	6610	500	0.0756	0.077
BA6	Back	Medium	34.7248	76.6199	8053	506	0.0628	0.250
BO1	Bogue	Large	34.6831	76.9997	31950	963	0.0301	0.305
BO2	Bogue	Medium	34.6789	76.9967	6553	543	0.0829	0.119
BO3	Bogue	Small	34.6761	76.9964	863	135	0.1564	0.030
BO6	Bogue	Small	34.6758	77.0000	1119	151	0.1349	0.128
CS1	Core	Large	34.6792	76.4997	30181	947	0.0314	0.594
CS2	Core	Medium	34.6628	76.5118	9338	623	0.0667	0.110
CS3	Core	Small	34.6667	76.5097	317	82	0.2587	0.210
CS6	Core	Large	34.6817	76.4947	55042	1106	0.0201	0.586
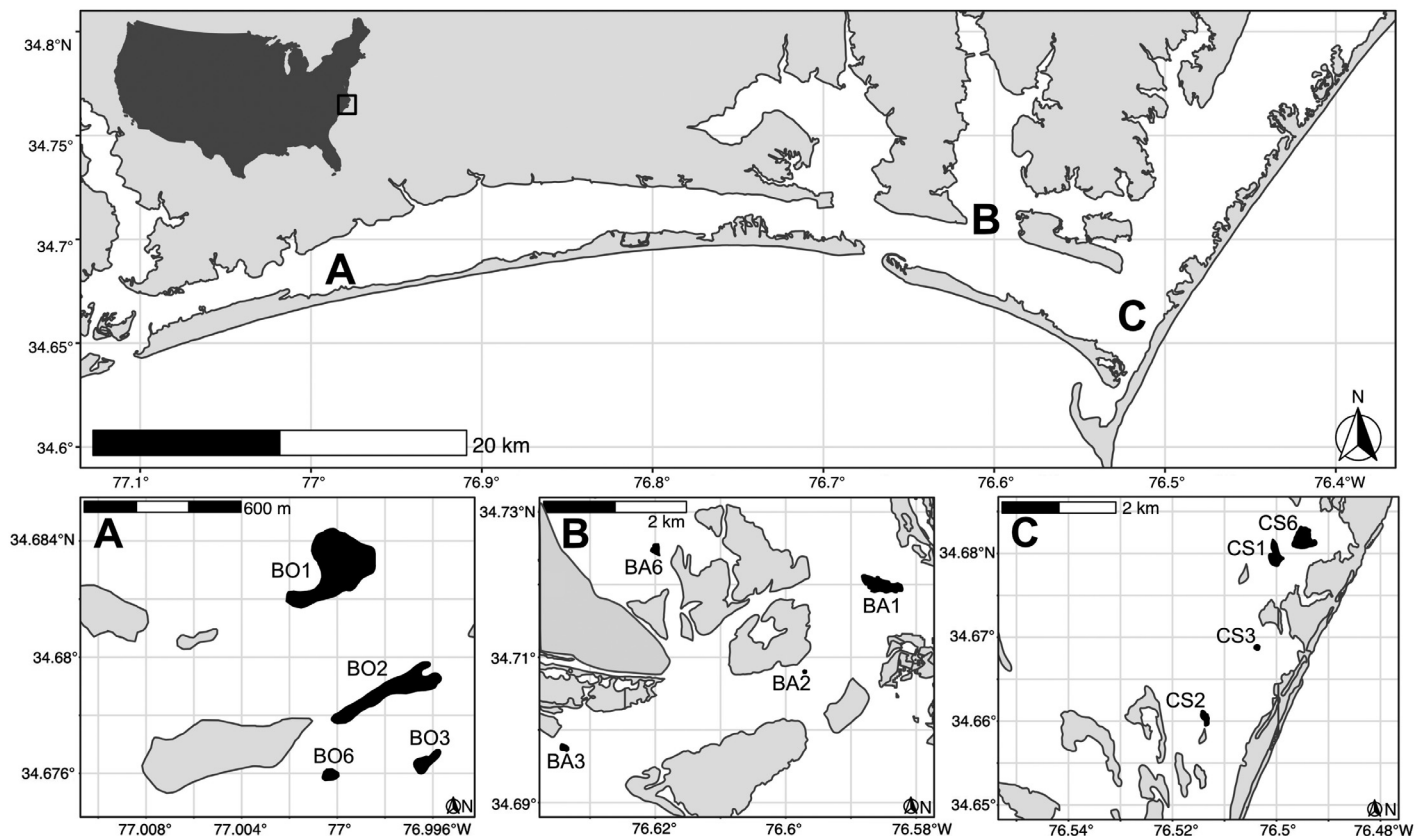
Fig. 1. Marsh island study sites with corresponding labels along the North Carolina (USA) coast in (A) Bogue Sound, (B) Back Sound, and (C) Core Sound

island, the coverage of bare sandflat habitat and vegetated habitat (i.e. mixed eelgrass *Zostera marina* and shoalgrass *Halodule wrightii* meadows) was evaluated using Google Earth Engine (Gorelick et al. 2017). Using Landsat-8 imagery, we trained the program to identify areas of seagrass using the classification and regression trees approach with the 'classifier' package in Google Earth Engine (Breiman et al. 1984). At each site, we measured fine-scale marsh grass characteristics during bi-monthly surveys from June to October in 2017 and 2018. Along the seaward edge of the marsh, 4 quadrats (0.25 m²) were placed at least 25 m apart during each sampling event. Within each quadrat, we assessed the plant species composition and enumerated edge shoot density for the dominant plant species (*S. alterniflora*).

2.2. Characterization of the nekton community

We sampled the fish and crustacean (nekton) community at each site with a combination of 2 fyke nets, 2 gill nets, and 12 Gee-style minnow traps once a month at night from June to September (2017) or October (2018) across a total of 48 nights. Nets and traps were set within 1 h of nighttime high tide and left to soak through one-half tidal cycle (~6 h) during spring tides to capture nekton being flushed off the marsh surface or predators foraging along the marsh edge. Fyke nets were comprised of a 0.9 × 0.9 × 5.1 m central mesh bag (3.2 mm mesh) with 2 wings of 0.9 × 5.1 m extending from either side, and were placed along the vegetated, seaward edge of the marsh with a total wing-span measuring 8 m (i.e. in the water facing the marsh). Gill nets were 15 m in length and comprised of 5 m panels of 1.3 cm, 2.5 cm, and 5.1 cm stretch mesh and placed perpendicular to the marsh edge. Twelve minnow traps were placed along 4 transects at 1, 5, and 10 m, and were oriented radially toward the center of the island from the marsh edge. All nekton captured were identified to the lowest taxonomic level possible, counted, and measured for standard length, and all individuals of a given species were weighed wet.

We evaluated the estuarine nekton assemblage at each site based on species richness (count of species
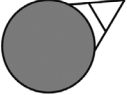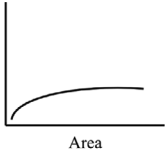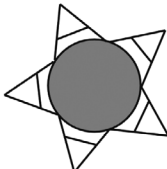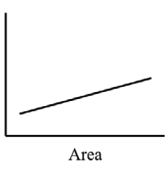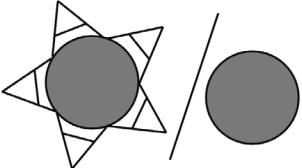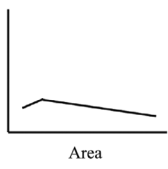
Response variable	Units of measurement	Calculations	Study result	Suspected mechanism
Catch rate	Nekton soak h^{-1}	Number of nekton caught per sampling array divided by time deployed	Area	
Total abundance	Individuals or number	Catch rate multiplied by the number of sampling arrays that fit around a given island perimeter	Area	Edge length or perimeter
Density	Individuals m^{-2}	Total abundance divided by a given island area	Area	Loss of functional habitat in interior of large islands

Fig. 2. Response variables, calculations, simplified graphic of response variable trends in relation to log area (m^2) of a marsh island for the current study, and proposed mechanisms for each metric used to understand fish and crustacean communities across marsh island sites

sampled) and catch rate (number of nekton captured/ net soak time; Fig. 2). We also estimated relative abundance and relative density (Fig. 2) as a scaled comparison across sampling sites but did not analyze these data statistically. Relative abundance was the estimated number of fish and crustaceans that would be present on a marsh island if the entire island was sampled. Relative density of fish and crustaceans was the estimated number m^{-2} across the entire island as sampling gear was deployed at high tide when the marsh platform at each island was flooded. To calculate relative abundance (number per island), we multiplied the catch rate for each island by the number of sampling arrays that would span the perimeter of the island (Fig. 2). This assumes that all fish leave the marsh platform on the ebb tide, which is reasonable, as most nekton require at least 5 cm of water on the marsh surface to survive (Minello et al. 2012) and no island had sub-habitat features (e.g. ponds or pools) for species to occupy while the marsh platform was dry. To calculate relative density (ind. m^{-2}), we divided relative abundance for each marsh island by its area (Fig. 2). These estimations assume equal distribution of nekton across a site and that

each sample collected is representative of each site and time period and allows us to compare across our sampling sites.

2.3. Statistical analysis

To assess the influence of marsh size, perimeter, shoot density along the marsh edge, and adjacent seagrass habitat on both species richness and estuarine nekton catch rates, we ran linear mixed effect models with the 'lme4' package (Bates et al. 2015) in R (version 4.0.5). Our models used fixed factors of log-transformed perimeter, log-transformed area, percent seagrass cover within a 250 m buffer of the marsh, average edge shoot density, and with a random factor of month. Normality was visually assessed using 'qqplot', and homogeneity was tested with a Levene test using the 'car' package (Fox & Weisberg 2019) in R. Optimal models were selected based on Akaike's information criterion (AIC). AIC is a measure of how well observations are explained by a model and accounts for goodness of fit, model complexity, and parsimony (Akaike 1998).

To further explore the relationships between species richness and marsh island area, we also examined the scale-dependent effects of marsh island size (small, medium, and large bins) on species richness using the 'mobr' package in R (McGlinn et al. 2019). We conducted a 2-scale analysis that divided spatial scale into 2 discrete units (local and regional) and calculated species richness at both scales (α- and γ-diversity, respectively) and species turnover (β-diversity). We also ran a multiscale analysis that constructs multiple rarefaction curves to better understand how differences in community structure change continuously across a range of spatial scales. We ran 3 distinct rarefaction curves: a spatial species-based rarefaction (sSBR), a non-spatial species-based rarefaction (nsSBR), and an individual-based rarefaction (IBR). The sSBR is constructed by accumulating plots sampled within a marsh island treatment based on its spatial position (latitude and longitude). The nsSBR is constructed by randomly sampling marsh islands within a size treatment but where the individuals are randomly shuffled among marsh islands while maintaining island-level abundance and treatment-level species abundance distribution. The nsSBR is similar to the sSBR but removes any signal due to spatial aggregation of species. The IBR, the most traditional rarefaction curve, is constructed by pooling individuals across all islands within a treatment and then randomly sampling individuals.

2.4. Quantitative simulations

We conducted quantitative simulations utilizing our relative density estimates to investigate whether a single large or several small marsh islands support more or less estuarine nekton (i.e. numbers of individuals rather than numbers of species). Simulations were based on idealized, circular islands, akin to classical models of island biogeography, to maintain a focus on the fundamental effects of island size, rather than additional, more complex drivers such as island shape. Using field observations, we estimated the total relative abundance of nekton (N) for a given island size and number that would make up a proposed conservation or restoration area (i.e. keeping total habitat amount constant). These estimates take into account both area and perimeter measurements for each individual marsh island so that direct comparisons can be made when overall area is held constant. We multiplied the previously calculated relative density for each island (ind. m^{-2}) by the total area of interest (x). Here, we report simulation results

based on an area of 40 468 m^2 (10 acres), a large but reasonable scale for habitat conservation or restoration based on published examples (Levin et al. 1996, Johnston et al. 2002, Strange et al. 2002, Raposa et al. 2018). We note, however, that our conclusions regarding the optimal SLOSS configuration of marsh islands would remain consistent regardless of the total area of interest (x), as long as individual islands ranged in size between 300 and 55 000 m^2. Rather, changing the total area (x) would evenly affect total relative abundance of nekton (N$_x$) across all island sizes being considered:

$$N_x = \text{ind. m}^{-2} \times x \qquad (1)$$

We ran these calculations for all nekton combined, as well as for ecologically and economically valuable taxa: drums (Scianeidae), flounders (*Paralichthys* spp.), blue crabs *Callinectes sapidus*, and penaeid shrimp (*Farfantepenaeus aztecus* and *Litopenaeus setiferu*s).

3. RESULTS

3.1. Effects of landscape setting on nekton

For the analysis of marsh islands and landscape setting (area, perimeter, adjacent seagrass and marsh plant density) on nekton catch rates, the best supported model (AIC = 892.12, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m672 p045_supp.pdf) incorporated fixed effects of island area and perimeter with a random effect of month. The model showed a clear relationship between catch rates and marsh island area and perimeter (Fig. 3A). The 2 smallest marsh islands (BA2 and CS3) had much lower catch rates (11.31 ± 1.5 [SE] and 16.0 ± 3.4 ind., respectively) compared to all other islands (36.24 ± 2.52). The island with the highest perimeter (BA1) had low catch rates (19.2 ± 3.8 ind.) compared to other islands of a similar size sampled (40.48 ± 1.94 ind.). The highest catch rates (44.2 ± 9.6 ind.) were at the largest marsh island (CS6). Notably, there was large variability in overall catch rates across months reflecting community responses to seasonal changes in water temperature, recruitment phenology, and tidal patterns.

We did not detect a statistically clear relationship between species richness and island area or perimeter from the mixed effects models (Fig. 3B). The best supported model for species richness incorporated marsh plant shoot density along the edge with a random effect of month (AIC = 494.43, Table S2). On
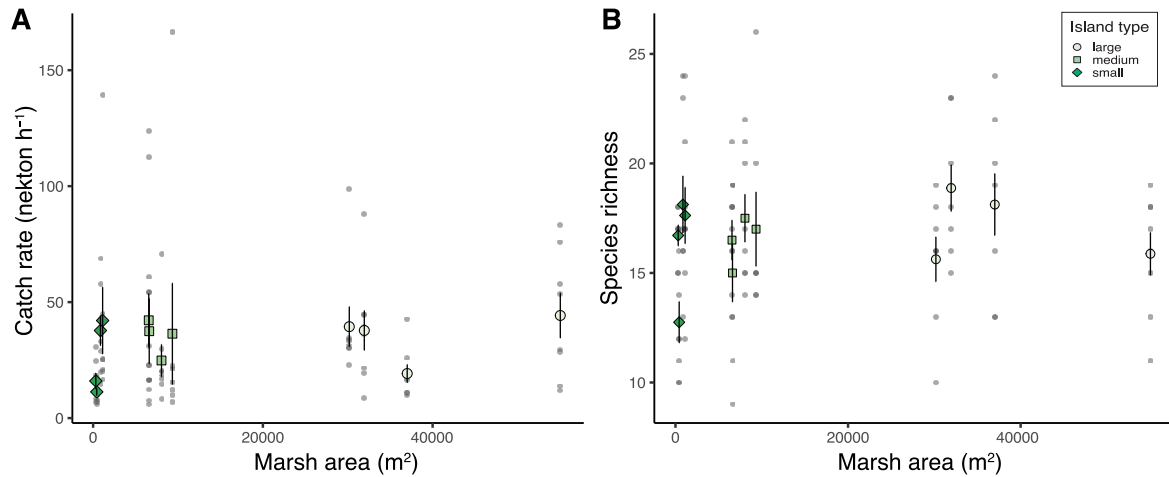
Fig. 3. Influence of marsh island area on (A) catch rates and (B) species richness across small, medium, and large marsh islands. Values are mean ± SE. Gray dots are individual measurements at each site

average, we captured approximately 16 species per site per month (16.59 ± 0.35). The highest species richness observed was 26 species in July 2017 at a medium-sized island (CS2) with an average shoot density of 61.0 ± 6.35 shoots 0.25 m^{-2}, while the lowest was 9 species in August 2017 at another medium-sized island (BA3) with an average shoot density of 9.5 ± 0.71 shoots 0.25 m^{-2}.

The 2-scale analysis on the effect of marsh island size on species richness indicated that when considering the local (α) and regional (γ) scales, there was no clear effect of marsh island size on species richness (α-scale: $F = 0.502$, p = 0.605; γ-scale: $\bar{D} = 7.33$, p = 0.19; Fig. 4A). However, there was a clear effect of marsh island size on the β-diversity or species turnover, whereby species turnover was higher at both small and medium marsh islands
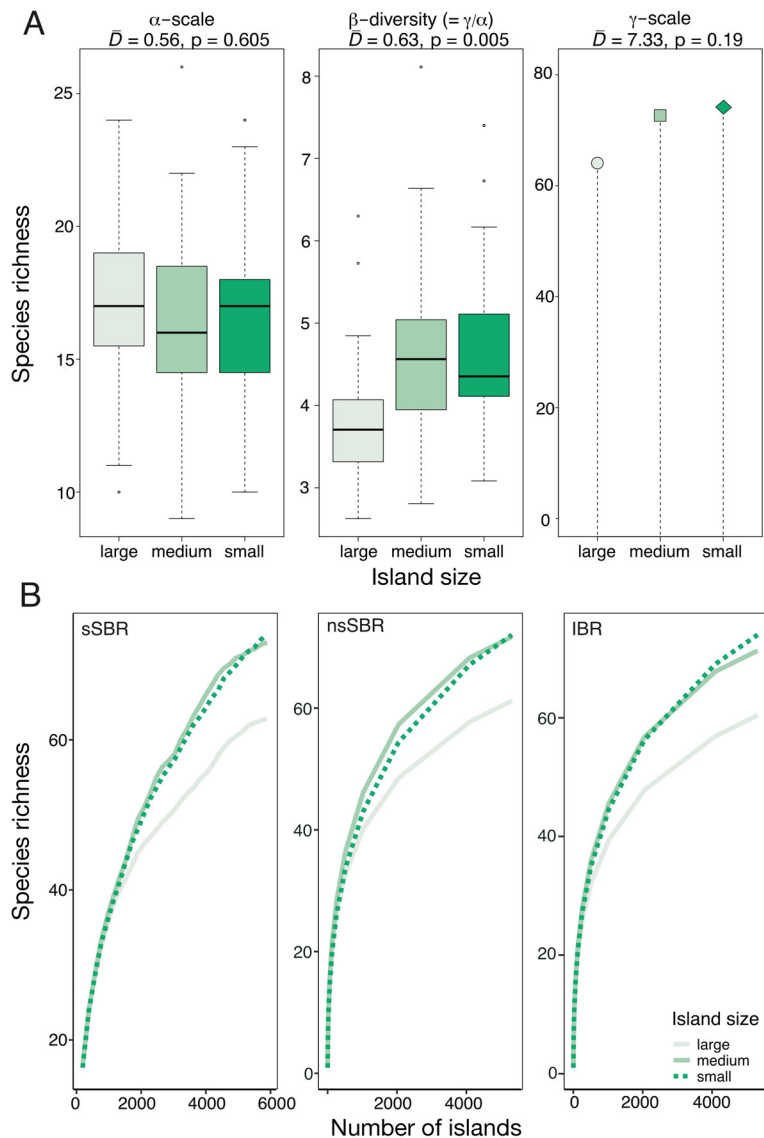
Fig. 4. Results from the (A) 2-scale and (B) multiscale analyses of species richness in relation to marsh island size class. sSBR: spatial species-based rarefaction; nsSBR: non-spatial species-based rarefaction; IBR: individual-based species rarefaction. For box plots, center lines indicate the median value, the interquartile ranges represent 25th and 75th percentiles, lower and upper error lines indicate 10th and 90th percentiles, respectively, and dots indicate outliers. The p-values are based on 999 permutations. Dashed lines in the γ-scale plot are for visual guidance only

than at large marsh islands ($F = 8.09$, p = 0.005; Fig. 4A). There was no clear difference between the different rarefaction curves run for our multiscale analysis. The model output indicated no effect of density on species richness with increased sampling effort and showed that the effects of aggregation and species accumulation distribution cancelled each other out (Fig. S1). Therefore, all 3 rarefaction curves had similar outputs, indicating that small and medium islands support greater species richness than large marsh islands (Fig. 4B).

3.2. Quantitative simulations

Quantitative simulations using relative density estimates indicate that conserving or restoring ~1100 m² (~0.28 acre) circular islands would result in the greatest enhancement of nekton, per total unit area of marsh (Fig. 5). Indeed, these simulations indicate that several ~1100 m² (0.28 acre) islands (totaling 40 468 m² [10 acres] together in our simulations, although these results hold for any total acreage used across island sizes) would support 7 times more nekton than one large 40 468 m² circular island and 1.5 times more nekton than >100 circular islands of ~300 m² (0.07 acre) also totaling 40 468 m² together.

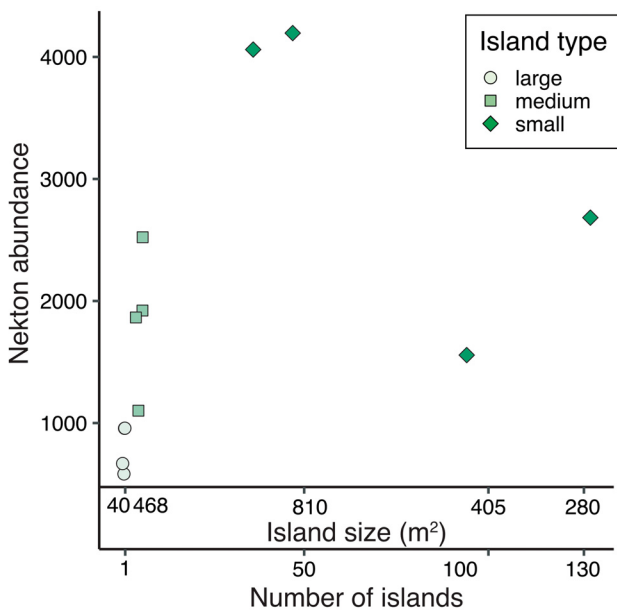When quantitative simulations were conducted for ecologically and economically important taxa, we found that different marsh island size-and-number combinations were required to support the greatest relative abundance of each taxonomic group. Similar to simulations for all taxa, both drums and penaeid shrimps had the highest relative abundances at intermediate-sized islands. Specifically, for the island sizes examined, many ~1100 m² (0.28 acre) islands support 2 times as many drums than other marsh island sizes of equal total area (Fig. 6A). Penaeid shrimps had the highest relative abundance at islands ranging from ~850 to 6500 m² (0.21–1.6 acres) in size (Fig. 6B). The support of flounder species by marsh islands did not follow a clear trend, with the highest relative abundances at a few 6500 m² (1.6 acre) and several 300 m² (0.07 acre) islands (Fig. 6C). Interestingly, the relative abundance of blue crabs peaked with many marsh islands of the smallest sizes (less than ~400 m² [0.1 acre]; Fig. 6D).

4. DISCUSSION

Collectively, our field observations and simulations clearly demonstrate that to provide the greatest support for estuarine nekton, we must consider the landscape setting (e.g. size, adjacent habitat types) of structured coastal habitats. Specifically, we found that overall habitat area and perimeter of a marsh island are key characteristics that can enhance abundance of faunal communities. The results of the quantitative simulations indicate that the highest relative abundance of nekton is achieved with multiple, circular marsh islands of approximately 1100 m² (0.28 acres) in size, an intermediate optimum of marsh island size across the range considered in this study. We also found that the relative abundance of nekton supported by a marsh is greatly diminished on one large circular marsh island of the same area. Further supporting these simulations, our 2-scale and multiscale analyses of species diversity indicated spatial variation in species diversity, whereby higher species turnover occurs at small and medium islands compared to large marsh islands.

As species diversity is typically multidimensional and scale-dependent, there may be high spatial and temporal variation in species richness compared to other diversity metrics not considered in this study (e.g. functional diversity; Chase et. al 2018). As the sampling of our marsh islands spanned 3 interconnected sounds and multiple months, we needed to further address how these varying spatial and temporal scales influenced our seemingly null results between island size and α-diversity. Across all 3 rarefaction curves, which consider spatial variation
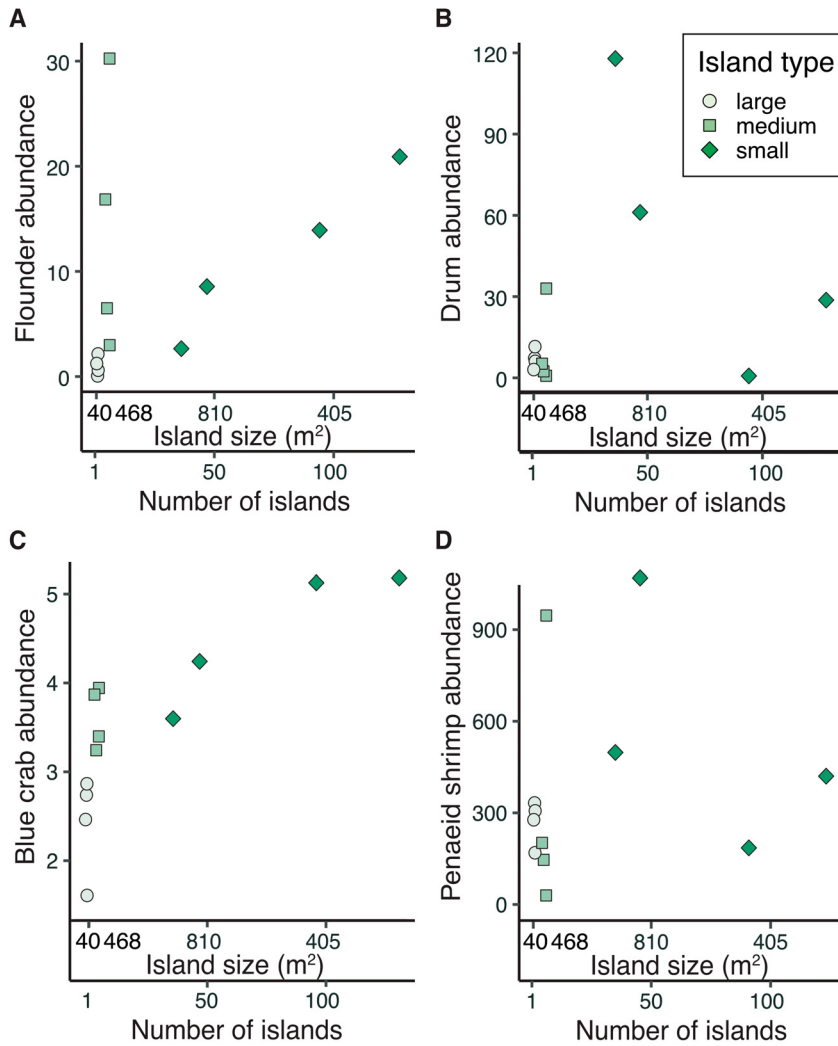

Fig. 5. Conceptual model examining the changes in abundance of all nekton with varying island size and numbers equaling a total area of 40 468.6 m² (10 acres)

Fig. 6. Conceptual model examining the changes in abundance of (A) flounders (*Paralichthys* spp.), (B) drums (Sciaenidae), (C) blue crabs *Callinectes sapidus*, and (D) penaeid shrimp (Penaeidae) with varying island size and numbers equaling a total area of 40 468.6 m² (10 acres)

circular marsh islands may only have a fringing ring of usable habitat along the seaward edge even if the entire marsh platform is flooded, which is consistent with previous studies that have found that marsh seaward edge is the most functional part of this habitat for estuarine species (Peterson & Turner 1994). There were low catch rates at the large marsh island with the greatest perimeter of all sites (BA1) and a perimeter to area ratio of 0.05; however, the total relative abundance was equivalent to other islands with similar areas. Potentially, increased edge provides more overall space for nekton species to move back to the open estuary as the tide recedes and would result in lower overall catch rates but high abundances of transient species. This suggests that a single long slender section of habitat (similar to expansive fringing marshes; Meyer & Posey 2019), rather than circular islands, may increase production or support of organisms due to the high perimeter to area ratio. The support of nekton by one large marsh island may also increase if channels are present, as they (1) create smaller patches of habitat that may flood more evenly and (2) create sub-habitats such as marsh creeks that may allow more fish and crustaceans to utilize the marsh at all tidal stages. However, these channels may also lead to increased erosion and loss of habitat over time.

The functionality of marsh islands and the optimal size and number of islands varies based on the species or functional group examined. For instance, we found that the relative abundances of drums and penaeid shrimps followed similar trends to all nekton, while flounders continued to increase as marsh islands became smaller and more numerous. Previous work has shown that the functional differences among species translate into different sensitivities of biological communities to natural and human-related environmental change and that effective conservation must address these differences (Olden 2003). Correspondingly, conservation practices that have considered species-by-species models (modeling species individually and adding models together) have often outperformed community-based modeling approaches (Hallstan et

among sites, we found that with increased sampling effort, intermediate-sized marsh islands will have higher species richness than singular or few large marsh islands, further supporting a recent review by Fahrig (2020) on SLOSS dynamics across terrestrial, aquatic, and marine habitats.

As marshes are situated at the land–sea interface, abiotic conditions propagated from adjacent coastal habitats may mediate the ability of a marsh to sustain diverse estuarine communities (Ziegler et al. 2021). Decreased support of nekton at the largest marsh islands in terms of both relative abundance and β-diversity (i.e. species turnover) may be due to the abiotic factors such as tidal flooding that control the ability of estuarine species to directly access and move across the marsh platform (Baker et al. 2015). Large

al. 2012). Blue crabs have recently been listed as over-fished in North Carolina waters (NCDMF 2020), and the North Carolina Division of Marine Fisheries has created new blue crab spawning sanctu aries near our study sites. These spawning sanctuaries cover large continuous areas similar to many other coastal man-agement strategies. Our quantitative simulations indi-cate that the smallest marsh islands (400 m^2 [0.1 acre]) with the highest edge to area ratio best support this economically valuable species (both adult and juve-niles; Table S3). Scaling up, conserving many small marsh habitat patches may better protect blue crabs than creating one large spawning sanctuary. This finding is counter to many of the current conservation strategies employed in marine systems, where con-serving an entire sound or large continuous habitat is assumed to be functionally better for estuarine species (i.e. NOAA Habitat Focus Areas). Identifying areas with small patches of marsh or high edge to area ratio, whether circular or long and narrow, may be critical as managers consider efforts to promote ju-venile recruitment and robust blue crab communities to mitigate intense harvest pressure.

In addition, we found differences in β-diversity across marsh islands of varying size. Previous studies have found that fragmentation leading to smaller and increased number of habitat patches has a large effect on β-diversity; however, these outcomes can vary across habitat types (Edge et al. 2017). This is predicted to be due to the process of fragmentation altering the position of habitat patches in relation to other habitat patches and subsequently the ability of a species to move among patches. The configuration of a marsh patch within a seascape (i.e. near or far from seagrass) or the marsh structure itself may af-fect faunal movement and therefore overall β-diver-sity within a system. Further understanding the dif-ferences in β-diversity or species turnover in relation to the regional (γ) diversity could assist in the place-ment of protected areas or design of salt marsh resto-ration within a seascape mosaic to best support fau-nal movement and high biological diversity (Socolar et al. 2016).

We did expect that the habitat features such as marsh plant density and the amount of adjacent structured habitat (i.e. seagrass) would influence the species and number of individuals that utilize a marsh. For instance, Baillie et al. (2015) found that in seagrass beds adjacent to marshes there is increased diversity and abundance of estuarine fauna com-pared to isolated seagrass beds. In contrast, our ana-lyses indicated that the amount of seagrass surround-ing a marsh did not have any effect on either species

richness or the number of estuarine nekton captured exiting the marsh platform. This suggests there may be a 1-way synergy or directional effect in which marshes enhance the function of seagrass communi-ties. In addition, the presence of seagrass may not enhance the function of salt marshes for nekton (i.e. 'habitat redundancy', Geraldi et al. 2009) and may simply provide habitat corridors for predatory spe-cies to move through less conspicuously (Irlandi & Crawford 1997).

We did observe a clear relationship between marsh plant shoot density at the edge of the marsh and spe-cies richness. Increased habitat structure has previ-ously been shown to increase species diversity across both terrestrial and aquatic systems (Willson 1974, Gorman & Karr 1978, Le Hir & Hily 2005). For exam-ple, the amount of live coral cover in a coral reef directly relates to the number of species, and this relationship could be due to increased refuge or food resources among sites with increased habitat struc-ture at the local scale (Bell & Galzin 1984, Roberts & Ormond 1987, Gratwicke & Speight 2005). These dynamics between structured habitat, species rich-ness, and nekton catch rates suggest that landscape setting (patch area and edge) more so than fine-scale habitat variation is important in understanding nurs-ery function across broad spatial and temporal scales. As the dynamics of SLOSS and ecology in general are context dependent, our work suggests there needs to be a more comprehensive under-standing of how the size, shape (e.g. circular vs. long and thin), and configuration of habitats influence the production of individuals, populations, communities, and associated ecosystem services. While more com-plex models may do a better job of capturing the implication of environmental or demographic sto-chasticity (Kingsland 2002), our quantitative simula-tions to determine the optimal size and number of islands provide a simple, yet effective, way to esti-mate the influence of habitat size and shape on the support function for communities and ecologically valuable species. As habitat loss continues to result in the loss of species and reduced ecosystem func-tioning, it is essential to construct simple and easily usable mechanistic models to better predict the out-come of restoration and conservation practices.

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