Evaluating the Role of Habitat Complexity in Structuring Seagrass Communities

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ABSTRACT

Biogenic coastal habitats such as salt marshes, seagrasses, and oyster reefs, support diverse faunal communities and can serve as nursery areas by enhancing the abundance, growth, and survival of juvenile fish and crustaceans. The structure and complexity of these biogenic habitats can strongly influence the composition of marine faunal communities and contribute to their roles as nursery areas. It is imperative to understand how nursery areas are defined in the ecological literature as these definitions are applied to nursery area management across the United States. Further, the relative importance of how habitat structural attributes, which are influenced by abiotic and biotic factors, shape faunal communities within these nursery areas is critical to understand these important coastal ecosystems. My dissertation focuses on (1) how nursery frameworks in the ecological literature have evolved and how these frameworks are applied to state management of nursery areas; (2) how abiotic and biotic factors influence the restoration success and complexity of seagrass meadows; and (3) how, in turn, this habitat complexity influences faunal community composition and structure. For my first chapter, I found six overarching frameworks to define and delineate nursery areas in the ecological literature:

measures of juvenile abundance and vital rates, habitat characteristics, seascape connectivity, populations fitness and contribution to adult biomass, and persistence. Of the 23 coastal states, only seven explicitly protect nursery areas and of these seven states, the aforementioned frameworks are not equally applied. Gathering and analyzing data necessary to integrate higher-order metrics (e.g., connectivity and biomass contribution) to designate nurseries will require significant research investment and greater collaboration between ecologists and fisheries scientists. My second chapter combines two years of observational seagrass and faunal surveys with a habitat preference experiment to investigate to which degree multiple seagrass complexity metrics influence the composition and abundance of faunal communities in North Carolina seagrass beds. Trawl surveys revealed that taller canopied seagrass beds support higher faunal abundances and species richness than shorter canopied beds, however this was not true across all species. There were species-specific relationships between complexity metrics and abundances, with these relationships shifting between the two years of our study, potentially due to the range of sampling months each year. Pinfish (*Lagodon rhomboides)*, the most common fish found in North Carolina seagrass meadows demonstrated a preference for deep seagrass beds, but only preferred taller canopies when these areas also offered increased blade surface area. In Chapter 3, I conducted field surveys of natural seagrass beds to understand the spatio-temporal distribution and morphology of seagrasses in North Carolina coastal sounds and used these observations to inform a field transplantation experiment of the subtropical seagrass species, *Halodule wrightii*. Seagrass morphology differed across sampling months but only canopy height differed across depth. Depth was also influential in transplantation success with higher survival of intertidal seagrass transplants compared to subtidal. Considerations of both structural complexity and physical setting of the habitat are therefore imperative for a comprehensive approach in

understanding how habitats as well as their faunal communities are responding to future changes across ecosystem settings.

Evaluating the Role of Habitat Complexity in Structuring Seagrass Communities

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Abstract

There have been significant conceptual advances for identifying marine nursery habitats within coastal systems used by juvenile fishes and crustaceans. Frameworks for delineating nursery areas now include measures of juvenile abundance, growth, or survival; habitat characteristics; seascape connectivity; population fitness, and contribution to adult biomass (per-unit-area or total). We used all US coastal states as replicate trials to evaluate integration of nursery concepts into fisheries management and found an obvious disconnect between expanding academic interest in nursery roles and management application. Among the few states that afford a subset of coastal environments some nursery status, siting schemes have used relatively low-information metrics (e.g., juvenile density or biogenic structure presence), and it remains unclear what role nursery designations have played in promoting sustainable fisheries. Gathering data necessary to integrate higher-order metrics (e.g., connectivity and biomass contribution) to designate nurseries would require significant research investment and greater collaboration between ecologists and fisheries scientists.

Introduction

Throughout their lifecycles, many organisms undergo ontogenetic habitat shifts, typically to maximize growth while minimizing predation risk that vary as a function of individual body size (Werner and Gilliam 1984). Ontogenetic shifts are especially prevalent in marine and aquatic ecosystems where juvenile organisms have early life-history stages for which mortality may be increased relative to later life stages prior to recruitment to adult habitats (Dahlgren and

Eggleston 2000, Snover 2008, Nakamura et al. 2012). As early as the late 1800s, shallow, coastal areas were noted as important habitats in the early life history stages of many fishes and crustaceans (Peck 1894, Petersen 1896), and subsequently have been generally conceptualized as marine nursery habitats (Pearson 1929, Gunter 1967, Springer 1967, Bass 1978, Dennis 1992, Beck et al. 2001, Minello et al. 2003, Sheridan and Hays 2003, Sheaves et al. 2013, Lefcheck et al. 2019). Since coining of the term 'nursery' in the ecological/fisheries literature, the occurrence of elevated juvenile density, growth, or survival in an area has been presumed to be evidence for a significant functional role of those places or habitats in supporting fishes and crustaceans at population scales. Focus on s shallow-water, structured habitats since the mid-twentieth century have noted the exceptional value of salt marshes, mangrove forests, and seagrass meadows as important juvenile fish habitat relative to unstructured bottom (Gunter 1967, Springer 1967, Boesch and Turrner 1984, Miller et al. 1985, Gibson 1994). These structured habitats have been shown to enhance secondary production of ecologically and economically important species by influencing both foraging and refuge (Boesch and Turner 1984, Beaumont et al. 2007).

Beck et al. (2001) introduced a novel, potentially more rigorous, concept or framework for delineating/prioritizing habitats as a nursery for juveniles of a species based on whether "its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur". In this framework, the production of individuals to adult populations results from any combination of four factors: density, growth, survival, and movement to adult habitats (Beck et al. 2001). In the years since Beck et al. (2001) formally conceptualized the nursery role hypothesis, there has been accelerating interest in developing stronger quantitative links between juvenile habitat quality/quantity and fish and crustacean productivity (e.g., Lefcheck et al. 2019). In the 20+

years since Beck et al. (2001) conceptualized marine nurseries, their work has been cited over 3,000 times, demonstrating the high interest in nursery areas within marine systems. As a part of this accelerating interest, alternative definitions of the nursery concept have arisen, incorporating additional factors, such as habitat extent (effective juvenile habitats; Dahlgren et al. 2006) and connectivity between juvenile habitat patches influencing the focal nekton (fishes and decapod crustaceans) species (seascape nursery concept; e.g., Sheaves et al. 2006) with evaluations of these potential nursery areas increasing as well (Heck et al. 2003, McDevitt-Irwin et al. 2016, Lefcheck et al. 2019). However, many of these evaluations have focused on biomass and survival of individuals rather than the per-unit-area production described by Beck et al. (2001), often due to a lack of available data making production estimates difficult (Lefcheck et al. 2019). Despite considerable advances in nursery concepts within academia that have trended towards more integrative, data-heavy metrics – how and where the nursery habitat concept has been incorporated into fisheries management remains poorly understood.

Concurrent with advances in marine nursery frameworks in the ecological literature, there has been mounting interest in incorporating, where possible, more comprehensive, ecosystem-based management (EBM) strategies into fisheries management (Christensen et al. 1996, Jennings and Kaiser 1998, Pikitch et al. 2004). EBM strategies expand on single-species focused approaches to incorporate species interactions and fish-habitat associations (Pikitch et al. 2004). EBM approaches further allow for adaptive management, wherein management actions and designations can be modified as new information becomes available (Curtin and Prellezo 2010). A holistic approach to EBM requires that data be collected on habitat contribution to production to achieve maximum benefits for managed populations (NOAA NMFS 2002). EBM may also require managing human activities that impact marine systems, including both marine (e.g.,

fishing) and non-marine (e.g., runoff) stressors which may necessitate large-scale watershed management (Guerry 2005, Boesch 2006, Curtin and Prellezo 2010). A critical element of EBM is identification of the management unit which includes both the ecological and social components of the ecosystem (Slocombe 1993). Successful implementation of EBM requires a holistic, multidisciplinary approach as well as continued monitoring of faunal populations and modifications to management actions as needed (Slocombe 1993, Curtin and Prellezo 2010).

A major step towards applying EBM to fisheries in the United States (US) occurred with the 1996 amendment to the 1976 Magnuson-Stevens Fisheries Conservation and Management Act, mandating essential fish habitat (EFH) be designated for all coastal US states. EFH is defined as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" and is identified, mapped, and described by the National Oceanic and Atmospheric Administration (NOAA) in collaboration with management partners (NOAA NMFS 2002). Since the passage of the Magnuson-Stevens Act, fisheries management agencies at national, state, and tribal levels have been working to define, designate, and protect EFH as a way to better conserve important life stages and enhance fisheries, as output (e.g., catch limits, size limits) and input (e.g., limited entry licensing, gear restrictions) control measures alone have frequently proven insufficient to ameliorate fisheries declines (Fluharty 2005). However, many EFH designations have failed to fully identify areas to prioritize for additional protections, but rather identify all or most coastal waters as essential for at least one life stage of the designated species (Fletcher and O'Shea 2000). Because EFH designation does not necessitate specific protections following identification of key habitats, many of these waters are left unprotected, even when designated "essential" (Sarthou 1999, NOAA NMFS 2002). Additionally, EFH is only designated for federally managed species (NOAA NMFS 2002), leaving state-managed

species unprotected by any EFH designations (barring overlap in species' distributions). Given that the EFH definition is broad, and management decisions are made by individual states, approaches employed to protect fish habitats, particularly nursery habitat, are likely to vary widely from state to state.

In this review, we address the following questions: (1) Where and how are nursery areas delineated in US coastal states? (2) How do state nursery delineations align with nursery concepts and frameworks proposed in the ecological literature? and (3) What protections are afforded to areas currently designated by states as nurseries and are those protections designed to enhance factors encompassed in nursery frameworks (e.g., juvenile growth, survival, movement)? First, we identify if and how states designate, manage, and protect nursery areas. From this synthesis, we identify key commonalities and differences between the approaches used by coastal US states to delineate nursery areas and those prescribed by the various nursery concept frameworks proposed within peer-reviewed literature. Finally, we identify future research needs and make recommendations for how to incorporate nursery frameworks into fisheries management.

Key nursery frameworks available to managers

To identify proposed frameworks of nursery areas in the peer-reviewed ecological literature, we employed a snowball search approach. First, we identified recent review and conceptual papers on nursery areas (Sheaves et al. 2015, Litvin et al. 2018, Lefcheck et al. 2019), and used the bibliographies of these papers to find other relevant papers on nursery areas and related concepts. We then consulted the bibliographies of the newly found papers to find additional relevant titles. We continued this approach until we were unable to find additional

citations for earlier papers. This approach allowed us to focus on papers that have promoted and/or advanced nursery conceptual frameworks.

To supplement our snowball methodology, we performed a broader search of nursery areas and associated terms in the SCOPUS literature database (Supplementary Information). These searches yielded nearly 10,000 unique peer-reviewed articles. Article titles and, where necessary, abstracts, were reviewed to confirm the relevance of articles to nursery habitat or related concept designation within coastal and estuarine waters. Articles were considered to fulfill our requirements if they referred to marine nursery areas in their titles or abstracts, including all papers testing a nursery concept by determining nursery value for a habitat area or ecosystem. Papers were also retained that mentioned determination of juvenile habitat, habitat function, or contribution of juveniles to adult habitats and/or populations, even if they did not refer to nursery areas directly. We identified 166 articles returned from our search (just under 2%) that fulfilled these requirements. Between our snowball and database searches we found a total of nineteen papers contributing unique ideas/constructs vis-à-vis nursery area frameworks. Our goal was to be exhaustive in terms of capturing novel frameworks for delineating definitions of nursery habitats rather than capturing all papers referencing or using each framework.

Nursery frameworks in the ecological literature vary widely in their scale and designation method but can be separated into six conceptual frameworks: measures of abundance, individual vital rates, habitat characteristics, connectivity, production contribution, and persistence (Figure 1.1). Measures of abundance applies data, such as catch per unit effort, density (individuals per unit area), or presence/absence, to identify nursery areas (Gunter 1967, Springer 1967, Adams 1976, Bass 1978, Miller et al. 1985, Beck et al. 2001, Pihl et al. 2002, Heupel et al. 2007; Figure 1.1). The framework of individual vital rates is used to designate locations most beneficial to

juveniles based on where juvenile growth and survival are maximized (Springer 1967, Miller et al. 1985, Gibson 1994, Beck et al. 2001; Figure 1.2). The habitat characteristics framework classifies a nursery area based on habitat features, such as shallow estuarine habitats or habitats with structure present (e.g., seagrass, mangroves), that are known to support juveniles of many species (Heincke 1913, Springer 1967, Boesch and Turner 1984, Miller et al. 1985; Figure 1.3). The connectivity framework is based on delineating habitat corridors within large seascapes to define the areas that connect juvenile habitats to each other and to adult habitats as nursery areas (Gillanders et al. 2003, Sheaves et al. 2015, Nagelkerken et al. 2015, Litvin et al. 2018; Figure 1.4). The production contribution framework bases nursery area designation on calculation of contribution of juveniles in a designated habitat recruiting to adult populations, using measurements of abundance, growth, and survival data (Miller et al. 1985, Beck et al. 2001, Dahlgren et al. 2006, Fodrie et al. 2009; Figure 1.5). While the above frameworks could be applicable for shark nursery areas, shark nurseries have consistently been defined separately from those other marine fauna, with a stronger emphasis on juvenile presence as an indicator of nursery function (Springer 1967, Bass 1978, Branstetter 1990, Heupel et al. 2007). Additionally, Heupel et al. (2007) added a requisite of persistence, requiring use of a shark nursery over multiple years which we have included as its own framework: persistence (Figure 1.6). The framework of persistence, while developed with elasmobranchs in mind (Heupel et al. 2007), has largely been ignored in delineating bony fish and crustacean nursery areas, though it has been noted that nursery use can shift across years, indicating persistence may be a necessary component to delineation (see Krauss and Secor 2005).

The connectivity framework can be considered one of the broader frameworks described in the ecological literature. It is intended to encompass both connectivity between adult and

juvenile habitats as well as the seascape nursery concept as defined by Sheaves et al. (2015) and Nagelkerken et al. (2015). The connectivity framework, accounting for ontogenetic shifts in habitat use, moves beyond quantifying structured habitat or production from specific habitat areas and protects habitat mosaics, including the corridors connecting juvenile and adult habitats (Gillanders et al. 2003, Sheaves et al. 2006, Nagelkerken et al. 2015). It additionally encompasses the movement of organic and inorganic materials between habtiat patches within the seascape (Nagelkerken et al. 2015). While the connectivity framework may be the most holistic approach to nursery management, it may also require the most data to designate and enforce, requiring information that is included across multiple of the other aforementioned frameworks (e.g., abundance, habitat characteristics, and productivity) should only portions of the seascape be protected (Sheaves et al. 2015, Nagelkerken et al. 2015). Alternatively, if the entire seascape is to be protected this would likely very little data, if any. .

We recognize that the nursery frameworks outlined in this review possess some overlap in terms of their scope, data needs, and management applications. For example, abundances may be increased in structured areas that also (or are because of) increase individual vital rates in the form of survival or growth (Lefcheck et al. 2019). Additionally, the habitat characteristics framework is partially based on previous literature attributing both increased abundance and increased juvenile survival and growth to the presence of structured habitats (Heck et al. 2003, Lefcheck et al. 2019), linking those three described frameworks. The habitat characteristics framework is more limited than the other frameworks, as it bases designations purely on the presence of a specific structured habitat, such as salt marsh (Boesch and Turner 1984). While positive correlations may exist between habitat structure and abundance, vital rates, and production, not all structured habitats provide increases in these metrics for species of interest

(Lefcheck et al. 2019). Additionally, fauna may consistently be found in specific areas yearly, but designations of nursery areas based on persistence alone may be difficult for initial designations (Heupel et al. 2007). It may therefore be easier to link the persistence framework to an additional metric for designation, allowing persistence of high abundances or high vital rates to demonstrate a greater need for protections. Once designated, persistence can be quantified and any changes to consistent use of the habitat by focal nekton can lead to adaptations to management strategies.

Delineation of nursery areas by US coastal states

To assess if and how coastal US states designate, manage, and protect nursery areas, we conducted a synthesis of state-level fisheries and coastal habitat management documents for Atlantic, Pacific, and Gulf coastal states within the continental US, as well as Alaska and Hawaii. For states that did not designate nursery areas in their management of marine resources, we identified any habitat protection approaches that afford protections to juvenile finfish and crustaceans and/or their habitats. Management documents available via web-based searches were collated into a master database and relevant information on nursery approaches and designations was extracted (Table 1.1). To ensure accurate characterization of habitat designations, methodologies, and metrics, we also conducted interviews with state agency staff responsible for fisheries and coastal habitat management in each state (Supplemental Information). Additionally, we obtained designations and definitions of nursery areas and other non-nursery habitat protections from the *State and Local Authority for Marine Protection* documents, available from the Environmental Law Institute (2014). In addition to the designations of nursery areas and other non-nursery habitat protections by state fisheries management, EFH is designated in all state waters by regional fishery management councils and designations may include habitat areas

of particular concern (NOAA NMFS 2002, 2022). The designations of EFH and habitat areas of particular concern apply for all federally managed species, however there are no clear regulations for affording protections to designated areas and explicit nursery areas do not need to be defined or identified within broad characteristics of EFH (NOAA NMFS 2002, 2022). Therefore, it is important to understand other EBM strategies employed by states to protect nursery areas in conjunction with EFH designations and we have not included EFH management in this review.

Of the 23 US coastal states, including Alaska and Hawaii, only seven states; Alabama, Delaware, North Carolina, Maryland, Mississippi, Texas, and Virginia, explicitly designate areas as nurseries for managed juvenile nekton (Table 1.1, Figure 1.2). The scale at which nursery habitats are designated varied across these states. Some states protect entire bay systems (Mississippi) or secondary/non-major bays (Alabama, Texas), while others protect upriver waters and tributaries to larger bays or sounds, which are not fully designated themselves (Delaware, Maryland, North Carolina, Virginia; Table 1.1). Additionally, the focal species that designated nursery areas seek to protect vary among states. In the case of two states, Alabama and Texas, nursery designations aim to protect a single family of crustacean, the penaeid shrimp. Shrimp nurseries may act as protections for other species, as shrimp juvenile habitats likely overlap with nurseries for other species, particularly when they encompass submerged aquatic vegetation (SAV) habitat (Minello 1999; Alabama; Tables S1.1-S1.2). Thus, shrimp may serve as an umbrella species, where protections for the umbrella species also protect other species (Roberge and Angelstam 2004). In North Carolina, primary and secondary nursery areas are focused on offshore winter-spawned species of economic importance, such as blue crab, brown shrimp, spot, Atlantic croaker, and southern flounder (15A NCAC 03B .1400). All other nursery-designating

states appear to be broader in their nursery designations, such as Maryland protecting all anadromous fish spawning areas rather than designating a subset of species (Table 1.1).

The methods and requirements for identification and delineation of nursery areas differ between the seven nursery-designating states and often do not align well with any single ecological framework (Table 1.1). Of the seven states that designate nursery areas, only Alabama, North Carolina, Mississippi, and Texas base their designations on abundance data of juvenile fishes or crustaceans (Table 1.1; Figure 1.2). Most of these designations are based on juvenile abundance data available at the time of nursery area designation; however, these designations are not regularly updated based on changes in juvenile abundance, even when new data are collected (Table S1.2). For example, Texas nursery areas were originally codified in a 1975 statute using shrimp abundance data collected at that time. However, these nursery designations were not modified until 2000 when rules were overhauled using abundance data from the late 1990s (Table S1.2). Since 2000, there have been no modifications to nursery areas in Texas based on current data, even though routine fisheries independent sampling occurs annually across the entire bay system (Table S1.2). In fact, in the past 20 years, no state has used ongoing fishery independent survey data to assess or modify nursery area designation on a large scale even though fisheries production and nursery roles may vary due to regime shifts or various anthropogenic pressures, necessitating updates to management regulations (Vert-pre et al. 2013, Hutniczak et al. 2019).

Utilizing a different approach to fisheries management and protection, the Chesapeake Bay States (Delaware, Maryland, and Virginia) delineate nursery and spawning areas within tributaries to the Chesapeake Bay, based on data covering adult spawning populations or larvae and egg densities. Otherwise, state designations are based solely on a system's status as a

tributary to a larger bay system with the belief that tributaries serve as both spawning and juvenile habitat (Table 1.1). These three states monitor protected areas for changes in water quality rather than juvenile catch rates / abundances, persistence, or other characteristics (Table 1.1). By monitoring water quality, these states are potentially capturing data reflecting possible habitat decline due to increased nitrogen loads (Orth et al. 2010) or potential for recovery due to enhanced water quality (Greening and Janicki 2006). However, it is unclear whether these nursery areas were chosen based on measured habitat quality as a nursery area or merely designated due to their status as tributaries to the Chesapeake Bay.

Protections afforded by nursery area designations fall into two categories: gear restrictions and seasonal closures or antidegradation policies to maintain water quality (Table 1.1). Alabama, North Carolina, Mississippi, and Texas employ gear restrictions, such as banning the use of commercial fishing gears including trawls and/or gill nets, as well as implementing seasonal closures when juvenile fishes are present (Table 1.1). In addition to gear restrictions and closures, North Carolina also sets restrictions on development within and close to nursery areas to protect these habitats (Table 1.1). Often, the goal of gear restrictions is twofold: saving structured habitat (Auster et al. 1996) and reducing mortality of juvenile fish that may be caught in specific gear types, such as trawls (Diamond et al. 1999). Alternatively, Delaware, Maryland, and Virginia all employ an anti-degradation policy that is focused on preserving water quality standards in the nursery areas (Table 1.1; Figure 1.1). These similarities between states are based on a shared body of water, the Chesapeake Bay (Table 1.1), likely due to structuring of protections under the Chesapeake Bay Watershed Agreement which enables the Chesapeake Bay states to protect habitats similarly. Water quality is often correlated with decreased habitat quality, particularly in SAV beds (Orth et al. 2010), indicating that the goals of these policies are

to protect the spawning and nursery habitats rather than focusing on the fishes themselves. While the nursery management of all seven states likely have a goal of enhancing survival or habitat structure, they often focus on allowable activities rather than preserving nursery function.

While only the seven aforementioned states explicitly employ nursery area frameworks in the protection of juvenile nekton habitats, all coastal states have some level of protection for either juvenile fishes or their habitats (Table 1.1). Among the states without nursery designations, there are several levels of protections for areas that might generally be considered nursery areas and/or habitat for juvenile nekton, such as gear restrictions, seasonal closures, and/or development restrictions (Table 1.1). Some states may rely on a dominant protective mechanism, such as gear restrictions in South Carolina and Georgia, while others may combine several methods to protect juveniles and their habitats. For example, Florida does not designate nursery areas specifically, however, the state closely monitors juvenile fish populations. This monitoring is then used to impose harvest restrictions of species that use state waters as nurseries (e.g., lemon and hammerhead sharks), gear restrictions, and area closures. Area closures in Florida can also be enacted in the form of sanctuaries for areas with known nursery value (Tables S1.1, S1.2). Further, some states (Alaska, California, Hawaii, Louisiana, Oregon, Massachusetts, Rhode Island, and Washington) have designated protected areas, sanctuaries, and/or reserves, with some designated due to the presence of elevated relative abundances of juvenile nekton in the habitats (Tables 1.1, S1.2). The 15 states that include habitat characteristics as a basis for their general, non-nursery specific designations may protect specific habitats due, in part, to their known nursery value (Table 1.1). For example, New Jersey has broad protections for SAV, with one of the stated reasons for protection in management documents as the known use of SAV as nursery areas by juvenile fin fish, bay scallops, and blue crabs (N.J.A.C. 7:7; Tables S1.1, S1.2).

Most states without explicit nursery area designations use measures of species abundance, such as the presence of rare organisms (Maine); or habitat characteristics such as the presence of eelgrass (Massachusetts) to protect waters serving as juvenile habitats (Table 1.1). For many of these states, the protection of waters that serve as high quality juvenile habitat is a co-benefit of broader protection frameworks that also seek to mitigate impacts to adult populations and rely on data sources that are not tailored exclusively to surveying juvenile relative abundance and distribution (Table 1.1). Of note, California mandates that marine protected areas should be sited based on the best, readily available data, meaning data for designations can reflect anything from organismal abundance to tagging data identifying habitat corridors and home ranges (Saarman et al. 2013; Table 1.1). Further, California, Hawaii, Oregon, and Washington all begin their designation methods with proposals from the public and/or private sector, highlighting the perceived importance of public support (Table 1.1). In addition to relying on public input, some states also have defined timelines for review of designations and potential changes. This is particularly true for those states with marine reserve systems, such as Oregon, where managers reassess marine reserves every five years using data collected within and outside of reserves (Table 1.1). Additionally, in a subset of the Oregon marine reserves, larval and juvenile settlement and abundance are being monitored to inform marine reserve efficacy for adults as well as early life stages (Wilson 2021). Given these examples, states without specific habitat protections focusing *solely* on nursery value are often still protecting important habitats for juveniles under an alternative management approach.

Application of ecological nursery frameworks to management: trends and constraints

As ecological frameworks for nursery areas have evolved, they have become increasingly data dependent. For example, calculating the production contribution of juvenile habitats requires habitat-specific densities and size-class distributions for targeted species (zu Ermgassen et al. 2016). Further, estimates of productivity require juvenile fish densities across multiple habitats as well as an understanding of early life history parameters (e.g., survival, specific growth), data which are not available for many species and must be estimated from related species (Blandon and zu Ermgassen 2014). Finally, it may be difficult to attribute production to a single habitat type or location given many species may use multiple habitats throughout their life cycles, including during their time as juveniles (Peterson et al. 2003). It is possible, though, to attribute only a fraction of production for species that are only moderately enhanced by a single habitat and may use other habitats equally or more (Peterson et al. 2003). Given these challenges associated with quantifying habitat contribution to production, it is not surprising that state management agencies are primarily collecting abundance and habitat characteristic data to delineate nursery areas.

Existing state-level fishery monitoring programs or habitat mapping programs allow states to make nursery management decisions based on abundance data collected for stock assessments and/or mapped habitat gain/loss trends (Beddington et al. 2007, Cogan et al. 2009). For example, Alabama, Texas, Mississippi, and North Carolina based initial nursery designations on abundance data collected from multi-year trawl and gill-net monitoring programs (Tables S1.1, S1.2). However, these designations are not revised with updated data from long-term monitoring programs unless a full overhaul is deemed necessary, such as the 2000 overhaul of shrimping rules and regulations in Texas intended to protect nursery areas (Tables S1.1, S1.2). Organisms may also shift nursery use between areas over time (Kraus and Secor 2005),

necessitating the need for long-term monitoring and actions based on persistence of nursery use. Therefore, the high abundance or density of nekton may not indicate nursery areas and complicate which areas may qualify for protections.

The primary and secondary nursery designations seen in North Carolina may have been an intuitive step towards implementing a more connectivity-based approach. Primary and secondary nursery areas are differentiated based on the age and size of nekton using these areas as habitat. Primary nursery areas are those where post-larval settlement and development occur while secondary nursery habitats continue to protect these fish as they develop into sub-adults prior to moving to adult habitats (15A NCAC 03I .0101). Though the efficacy of this management approach has not been tested, it is possible managers were attempting to protect juvenile organisms for longer than they may be present in a single designated nursery area. Identifying primary and secondary nursery areas based on the age of individuals may implicitly be protecting habitat and movement corridors that are necessary for juvenile fauna to migrate to adult habitats.

The seven states with nursery designations appear to use only the relatively low-information-content frameworks of abundance and/or habitat characteristics to identify critical juvenile habitats (Table 1.1; Figure 1.2). Similarly, most states with designations protecting nursery aged nekton but not explicitly labelled as nursery areas also employ measures of abundance and habitat characteristics (Table 1.1; Figure 1.2). One notable exception is California, which designates marine reserves on “best readily available data” for the habitat or region, potentially encompassing all nursery frameworks depending on the data used (Saarman et al. 2013, Table 1.1). While California marine reserves have the potential to use any of the nursery frameworks, the science advisory teams focused on ensuring habitat type protection (habitat

characteristics framework) and using fish population models (population fitness framework) for their designations (Botsford et al. 2014), making California the only state to use population fitness for designation purposes. It should also be of note that some frameworks for designating nursery habitats are more practical within the constraints of data available to state fisheries managers, particularly those based on metrics that can be more easily measured and monitored, such as juvenile abundance in habitats. Ecological differences in managed nearshore habitats and species may also result in the application of different nursery frameworks across states. For example, in the South Atlantic, Florida and North Carolina have abundant seagrass meadows and both incorporate habitat characteristics and abundance data in designations (Figure 1.2D), often focusing on areas with seagrass cover. Alternatively, neither Georgia nor South Carolina host seagrass and use either habitat characteristics or abundance data in designations (Figure 1.2D), with habitat characteristics focused on water body type, rather than presence of a specific habitat (Table 1.2). Thus, it is also important to understand the advantages, disadvantages, and barriers to adoption of each proposed nursery framework for identifying and protecting juvenile habitat within each state.

Similar to management designations, references to putative nurseries in the ecological literature are most typically supported by abundance or habitat type data (Blaber and Blaber 1980, Dulčić et al. 2002, McCallister et al. 2013). Despite the clarification by Beck et al. (2001) that nursery designations should include per unit area production, many synthetic reviews highlight that researchers have – in the absence of quantitative data on fitness or movement - reverted to density, growth, and survivorship metrics in syntheses of nursery dynamics (Heck et al. 2003, McDevitt-Irwin et al. 2016, Lefcheck et al. 2019). Measurements of total nekton densities, regardless of species present, may bias nursery designation, given that nursery habitats

can vary based on species identity and fitness response metrics (Minello et al. 2003). Further complicating nursery designation, according to Beck et al. (2001), nursery habitats must be separate from adult habitats, requiring knowledge of the life history of individual species to be protected. This requirement may complicate designation of specific habitat areas as nurseries, such as coral reefs where both adults and juveniles may use the same overarching habitat but potentially different locations within the reef (e.g., back-reef and reef habitats; Lecchini and Galzin 2005, Adams et al. 2006).

While most management designations do not align with increasingly data-dependent frameworks, both ecologists and federal managers are seeking to better understand the importance of habitat quality, quantity, and connectivity in supporting population health and fisheries productivity. Although not all states designate nursery areas, all states are federally mandated to designate EFH (NOAA NMFS 2002). Once designated, any action that may impact EFH requires consultation with NOAA and development of an environmental impact statement before activities may occur (Rosenberg et al. 2000). While not an explicit protection of nursery areas, EFH designation can protect some habitats from being developed or impacted by other activities (e.g., boating, trawling, nutrient addition). Designation of EFH is based on four levels of data availability: presence/absence; density; growth, reproduction, survival; and production rate (Figure 1.3). These data levels for EFH designation are comprised of multiple nursery frameworks which themselves encompass multiple data levels (Figure 1.3). Even though they do not align directly, obtaining higher EFH data levels may enable states to enact more data-dependent nursery frameworks, such as production contribution (Data level 4 in Figure 1.3). However, like nursery area designation, much of the data used for designating EFH of managed species being measures of abundance (Data levels 1 and 2 in Figure 1.3).

Suggestions/Recommendations

There is a lack of equal application of the six ecological nursery frameworks developed by academic teams over the last 20+ years to state management decisions in coastal US states. To better align with nursery frameworks recently proposed in peer-reviewed literature, state protections may need to be revised to focus more on enhancing the function of putative nursery areas, such as increased survival, growth, or production. Therefore, we have recommendations to both scientists and management agencies to identify research needs and steps to apply nursery frameworks and collected data to nursery management.

For Scientists

Measures of abundance are frequently used by ecologists and fisheries managers as proxies for production (Valentine-Rose et al. 2007). However, this approach typically requires the assumption of a linear, positive relationship between the two, ignoring the impacts of differences in survivorship based on life-history stage and stock size (Iles and Beverton 2000). For instance, in the context of early life-history dynamics, the concentration hypothesis explicitly suggests that the relationship between stock size and recruitment is not linear due to density-dependent growth and mortality at early life-history stages (Iles and Beverton 2000). Additionally, abundance data may not always serve as production proxies of any fixed location as the local abundance of fish can vary greatly through time (Rozas and Hackney 1984, de Ben et al. 1990), including over the course of a single day (i.e., between day and night, (Rooker and Dennis 1991, Mattila et al. 1999). The challenges with using abundance alone are reflected in many production estimates require a combination of biomass, length, movement, mortality, and density measurements rather than solely abundance or density data (Mertz and Myers 1998,

Faunce and Serafy 2008, Yeager et al. 2012, Harborne et al. 2018). We recommend further research to determine whether density and other measures of abundance are acceptable proxies for production contribution for managed species. Likely, increased abundances are linked to increased production, as density is factored into production estimates (zu Ermgassen et al. 2021). However, it is possible that some populations with high abundances may act as demographic sinks due to density-dependent mortality (Fodrie et al. 2009). Therefore, it is important to continue to invest in research, particularly across multiple bodies of water with various habitat types to understand if density can be used as a production proxy for individual species and habitat types. This may allow managers to use readily available density measurements to update protections faster than if more data-intensive production estimates are always required.

Research is also needed to determine how much nursery area (i.e., what percentage of all juveniles within a species/stock) must be protected to ensure sufficient contributions to production. Scientists have recommended a target of at least 20-30% ocean protection in regards to effective MPA management (Bohnsack et al. 2000, Airamé et al. 2003, Sala et al. 2018), emphasizing this should be representative of all habitat types (e.g., seagrass, coral, oysters; Airamé et al. 2003, Green et al. 2009, McLeod et al. 2009). For coral reef ecosystems specifically, the goal of 20-30% no-take protection comes from multiple scientific viewpoints including studies on the exploitation of reef species and fishery failures (Bohnsack et al. 2000) which can be replicated for nursery habitats. Corroboration of this value in terms of protecting 20-30% of nursery areas across all nursery habitat types could further enhance management targets and provide a realizable goal of nursery area protection. Importantly, the 20-30% protection benchmark, should this value hold true across nursery areas, may need to be designated based on areas of high production or density to ensure 20-30% of juveniles as well as

habitat area are being protected. Beyond the total amount of juvenile habitat protection needed to sustain stocks, the shape and configuration of protected areas impacts the amount of edge to interior habitat available which may further influence faunal communities (McLeod et al. 2009) as there may be effects on fauna of being in the edge versus interior of a habitat patch (Baltz et al. 1993; Boström et al. 2006; Carroll et al. 2019). Marine protected area (MPA) management has long debated whether a single large or several small habitat patches should be protected (McNeill and Fairweather 1993; Tjørve 2010), a debate which may arise with regards to nursery area management. MPAs are a type of EBM (Curtin and Prellezo 2010) and may be a helpful corollary for understanding best management practices.

Adult and juvenile faunal distributions are shifting due to climate change, causing species that have previously never been managed by a given state to become present, and at times, abundant (Rijnsdorp et al. 2009, Fodrie et al. 2010 , Morley et al. 2017). Changes in juvenile distribution can cause reduced use of former nursery areas (Brochier et al. 2013, Wahle et al. 2015) or exploitation of new nursery habitats by individual species or faunal assemblages (Barceló et al. 2016, Bangley et al. 2018). However, the impacts of climate change on different life stages of fishes may not be equal (Ong et al. 2015, van de Wolfshaar et al. 2021), with larvae potentially having smaller temperature envelopes than adults, which can influence where juveniles may settle (Rijnsdorp et al. 2009). Further, the shifting distributions of spawning fishes and larval assemblages (Morson et al. 2019) may result in a bottleneck at some life stages (Petitgas et al. 2013, Asch and Erisman 2018, Dahlke et al. 2020). With limited funds, emphasis on how climate change may impact juvenile use of nursery areas as well as any changes in nursery habitat quality (e.g., loss of SAV) is needed. We recommend further research focusing on juvenile distribution shifts, as well as climate change-induced shifts in faunal nursery habitat use

to provide managers with accurate data on which species currently reside in their management areas as juveniles given species distributions may move into or out of management boundaries.

While studies have shown enhancement of density, survival, and growth in specific habitat areas (Heck et al. 2003, Minello et al. 2003, Sheridan and Hays 2003), studies directly measuring production from these habitat areas are almost always lacking (Lefcheck et al. 2019). Potentially, this is because attributing production to a single habitat can be difficult and must often include acknowledgement of use of multiple habitats (Peterson et al. 2003). To estimate production data on more than just juvenile abundance in each habitat area must be collected. This can include metrics of juvenile fish such as size and life history characteristics (zu Ermgassen et al. 2016), environmental variables (Stige et al. 2013), or information on location of origin (Fodrie and Levin 2008). In addition to sampling juvenile populations, adult and subadult populations can be assessed for their location of origin through natural (chemical) tags recorded within the hard parts (e.g., otoliths) of individuals and – increasingly –genomic markers otolith chemistry and elemental fingerprinting (Fodrie and Levin 2008; Fodrie et al. 2020; Hoey et al. 2020). Additionally, advances in acoustic telemetry (Abecasis et al. 2009, Huijbers et al. 2015) can be combined with otolith chemistry and fingerprinting sampling which could provide the critical data necessary for quantifying production of juvenile habitats that can then be a basis for management decisions. It can be challenging, if not impossible given budgetary constraints, to collect in depth data on the growth, survival, and especially production of individual species of juvenile fish within all potential nursery areas in their management boundaries rather than just abundance. Therefore, researchers and management agencies must work together to conduct these studies across species to link habitat areas and types to production measurements to enable state management agencies to enact production-based designations.

For Management Agencies

With limited funding and ability to incorporate new data into management actions, we recommend that managers focus on protecting habitats proposed in the ecological literature to be nursery areas, such as seagrass (Heck et al. 2003), salt marsh (Minello et al. 2003), and mangrove (Sheridan and Hays 2003) habitats (Lefcheck et al. 2019). Protecting presumed nursery areas based on habitat structure will enable states to focus on collecting ecological and habitat data to determine nursery extent. Further, by protecting habitats that are vulnerable to water quality changes and are presumed to serve as nursery areas from previous studies on juvenile-habitat associations, such as seagrasses (Schaffelke et al. 2005, Sofonia and Unsworth 2010, Wagner et al. 2010), states may be able to leverage water quality monitoring to protect the habitat from degradation in addition to more data-heavy production estimates. For example, the water quality improvement plan for the Great Barrier Reef emphasizes water quality monitoring and improvement to protect the habitat from degradation, thus supporting the fish which use the reef as habitat (State of Queensland 2018). Emphasizing habitat management in conjunction with water quality monitoring and improvement may work similarly within the US, enabling collaboration across stakeholder groups to protect fauna from multiple pressures. Stakeholder engagement has been used in fisheries management to include resource-users in management decisions (National Research Council 2008) and is necessary to accurately incorporate EBM into current management at the state level (Curtin and Prellezo 2010).

The movement of many fishes may not align with delineations by regional or state management jurisdictions (e.g., red drum; Bacheler et al. 2009). Therefore, inter-state cooperation is necessary to protect nursery areas for populations where adult and juvenile distributions cross state lines. Acoustic tagging networks across state boundaries may be able to

identify areas of high juvenile use (Simpfendorfer et al. 2010) and link juveniles to adult habitats (Gillanders et al. 2003, Abecasis et al. 2009, Huijbers et al. 2015). While there are other methods for sampling the movement of individuals, managers may be able to leverage acoustic receivers and arrays established by researchers, lowering the funds needed to track individual distributions and movement. Further, other sampling approaches to determine nursery origin such as otolith microchemistry may require personnel and funds that are inaccessible to management agencies. Acoustic telemetry can be used both before setting habitat management areas and after for assessment of size and impact on species of interest (Crossin et al. 2017). Acoustic telemetry was successfully leveraged in the Arctic Ocean to assess management boundary effectiveness for Greenland halibut (Hussey et al. 2017). Though much of the management we have focused on thus far has been state management, the US is broken into eight regional fisheries management councils where regional and participatory fisheries management plans can be created across states to make recommendations to NOAA Fisheries about federally managed species (Jeans 2011). Further, the Atlantic States Marine Fisheries Commission, Pacific States Fisheries Commission, and the Gulf States Fisheries Commission are formed from coastal states bordering the major bodies of water in the United States to monitor and regulate fisheries collectively, demonstrating the ability for cooperative management of highly migratory species or those with large distributions. The Atlantic States Marine Fisheries Commission additionally partners with the Atlantic Coast Fish Habitat Partnership allowing additional cooperative objectives across states (ACFHP 2017). Regulations from these management commissions to protect stocks of highly migratory species may be necessary in the future, particularly as faunal distributions shift with climate change. There may also be a need for these commissions to include species that are managed at the state level within multiple states to ensure juvenile protection across entire

distributions. It is especially important to consider the connectivity between adult and juvenile habitats, such as protecting habitat corridors, particularly for species whose adult and juvenile populations may be 10s to 1,000s of kilometers apart (Gillanders et al. 2003, Fodrie and Levin 2008, Fodrie et al. 2020). Habitat corridors across states will require multi-state cooperation to identify and protect nursery areas, likely through regional management councils for federally managed species.

Determining the size of protected areas is a critical step in ensuring enforceable protections, however this can be difficult, especially when balancing the costs of enforcing strict protections and large areas with the likelihood of public support. While larger marine reserves support elevated density and diversity of fishes relative to smaller reserves (Claudet et al. 2008), it may be more difficult to enforce strict protections over large swaths of water, with reduced enforcement subsequently jeopardizing reserve efficacy (Samoilys et al. 2007, Di Franco et al. 2016). Nursery areas may similarly be in jeopardy of lowered efficacy if their protections are too large to effectively monitor and enforce regulations despite any differences in protections afforded. While potentially less beneficial than larger reserves, reserves of any size positively impact fish density and diversity (Claudet et al. 2008), indicating that no-take zones in small, highly productive areas may positively impact fisheries species. Managing these smaller nursery areas with strict protections could work similarly to MPA networks in which some smaller areas have more stringent protections than others (Sletten et al. 2021). While using guidance from marine protected areas could be beneficial, it is of note that juveniles are not often targeted individuals for recreational or commercial fishing. However, they may be retained as bycatch in commercial fishing or by recreational anglers not following catch restrictions (McPhee et al. 2002, Post et al. 2002, Davies et al. 2009). Further, marine protected area efficacy and nursery

area efficacy, while not identical, are likely to be similar due to the similarly afforded protections such as restricted use or restricted nearby development that may impact the habitat. Therefore, it is important that protections continue to be written with the explicit aim of protecting juveniles and their habitats, even when taking guidance from marine protected areas.

Understanding that it is not possible to protect the nursery areas of all faunal species without protecting the entirety of state waters, priorities must be set regarding species targeted for nursery protection. One possible method is to identify species in decline and seek to determine their nursery areas, rather than attempting to determine nursery areas for all species. If these declining species have overlapping habitats with other species, then all can be protected with the same management, similar to umbrella species management strategies where the protection of one species protects others (Zacharias and Roff 2001). The umbrella species concept has been previously used successfully for a wide variety of terrestrial species including large mammals and owls (Branton and Richardson 2010). There is additional evidence that the umbrella species concept could be used in marine systems for loggerhead sea turtles (Dickson et al. 2022), Chondrichthyes (Osgood et al. 2020), and common snook (Wilson et al. 2022). Alternatively, rather than identifying species in decline, by identifying the production of common species from specific habitats (e.g., seagrass, oysters), rare or cryptic species that use the same habitat may be protected as well. Many areas act as nurseries for multiple species of fish (Rauck and Zijlstra 1978, Nagelkerken et al. 2000, Vasconcelos et al. 2011), so it is unlikely that a nursery area has high contribution to production for a single species and low nursery value for all others, allowing nursery areas of additional species with similar life histories to also be protected. Though, it is of note, that many marine species targeted as umbrella species have broad ranges spanning multiple habitat types, making it difficult to use umbrella species as

indicators of community structure without further understanding how species overlap and interact (Zacharias and Roff 2001).

To best protect nursery areas, managers and researchers must work together to ensure communication of data requests and protections schemes that most benefit the ecosystem. There are many parallels in our recommendations to managers and researchers, demonstrating ways data can be collected to be used by managers efficiently and effectively. The most overarching framework to protect nursery areas is an all-encompassing seascape connectivity framework to protect waters and resources used by juveniles. This would require an EBM approach more so than the more common single-species management schemes and other nursery frameworks. However, to use the connectivity framework to fully encompass all habitats and corridors within an ecosystem, all waters would likely need to be protected (Gillanders et al. 2003, Nagelkerken et al. 2015, Sheaves et al. 2015). With limited funding and interests outside of protection (economically viable recreational or commercial fishing), other protection schemes may need to be considered, even if they do not fully align with the more encompassing connectivity framework. Potentially, the connectivity framework could be integrated into current management with the mindset of protecting all waters at different levels. If this is not possible, additional frameworks would need to be used to determine which areas necessitate higher protection and which may require lowered protections, but these schemes may enable a seascape approach. With all of this in mind, it remains possible to designate and manage nursery areas using higher level frameworks presented here.

We have demonstrated that most US states are designating and protecting nursery areas either through explicit designations or through alternative protections schemes that encompass likely or confirmed nursery areas (Tables 1.1, 1.2; Figure 1.2). However, we also show that these

designations are largely not based upon the most current data-intensive nursery frameworks put forth by ecologists. In order to achieve clearer understanding of how to apply nursery area frameworks to fisheries and habitat management, ecologists and other researchers must identify which data are absolutely necessary to delineate nursery areas, including if abundance can be used as an accurate proxy for production. Concurrently, managers must work with researchers to use necessary data, ideally those data already being collected, to better cite nursery areas and assess their efficacy over time. Clearer understanding of which data to collect and how to apply nursery area frameworks to fisheries and habitat management will help ensure protection of these critical faunal habitats into the future.

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References

Aanesen M, Armstrong CW, Bloomfield HJ, Röckmann C. 2014. What does stakeholder involvement mean for fisheries management? Ecology and Society 19.

Abecasis D, Bentes L, Erzini K. 2009. Home range, residency and movements of Diplodus sargus and Diplodus vulgaris in a coastal lagoon: Connectivity between nursery and adult habitats. Estuarine, Coastal and Shelf Science 85: 525–529.

ACFHP 2021. Conservation Strategic Plan 2017 – 2021. Atlantic Coast Fish Habitat Partnership. (https://www.atlanticfishhabitat.org/wp-content/uploads/2012/10/ACFHPStrategicPlan_2017-1.pdf).

Adams SM. 1976. The ecology of eelgrass, Zostera marina (L.), fish communities. I. Structural analysis. Journal of Experimental Marine Biology and Ecology 22: 269–291.

Adams AJ, Dahlgren CP, Kellison GT, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE. 2006. Nursery function of tropical back-reef systems. Marine Ecology Progress Series 318: 287–301.

Airamé S, Dugan JE, Lafferty KD, Leslie H, McArdle DA, Warner RR. 2003. Applying Ecological Criteria to Marine Reserve Design: A Case Study from the California Channel Islands. Ecological Applications 13: 170–184.

Andreou D, Vacquie-Garcia J, Cucherousset J, Blanchet S, Gozlan RE, Loot G. 2012. Individual genetic tagging for teleosts: an empirical validation and a guideline for ecologists. Journal of Fish Biology 80: 181–194.

Auster PJ, Malatesta RJ, Langton RW, Watting L, Valentine PC, Donaldson CLS, Langton EW, Shepard AN, Babb WG. 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): Implications for conservation of fish populations. Reviews in Fisheries Science 4: 185–202.

Avigliano E, Carvalho B, Velasco G, Tripodi P, Vianna M, Volpedo AV. 2017. Nursery areas and connectivity of the adults anadromous catfish (Genidens barbus) revealed by otolith-core microchemistry in the south-western Atlantic Ocean. Marine and Freshwater Research 68: 931.

Bacheler NM, Paramore LM, Burdick SM, Buckel JA, Hightower JE. 2009. Variation in movement patterns of red drum (Sciaenops ocellatus) inferred from conventional tagging and ultrasonic telemetry. Fishery Bulletin 107: 405–419.

Baillie CJ, Trackenberg SN, Gittman RK, Fodrie FJ. 2022. Evaluating the current productivity and suitability of North Carolina's designated estuarine nursery areas. North Carolina Divistion of Marine Fisheries. Report no. 8066.

Baltz DM, Rakocinski C, Fleeger JW. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36: 109–126.

Bangley CW, Paramore L, Shiffman DS, Rulifson RA. 2018. Increased Abundance and Nursery Habitat Use of the Bull Shark (Carcharhinus leucas) in Response to a Changing Environment in a Warm-Temperate Estuary. Scientific Reports 8: 6018.

Barceló C, Ciannelli L, Olsen EM, Johannessen T, Knutsen H. 2016. Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. Global Change Biology 22: 1155–1167.

Bass AJ. 1978. Problems in studies of sharks in the southwest Indian Ocean. Pages 545–594 in. Sensory biology of sharks, skates, and rays, Hodgson ES, Matthewson RF ed. Office of Naval Research, Department of the Navy, Arlington, VA.

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP. 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. BioScience 51: 633–641.

de Ben WA, Clothier WD, Ditsworth GR, Baumgartner DJ. 1990. Spatio-Temporal Fluctuations in the Distribution and Abundance of Demersal Fish and Epibenthic Crustaceans in Yaquina Bay, Oregon. Estuaries 13: 469.

Blaber SJM, Blaber TG. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17: 143–162.

Blandon A, zu Ermgassen PSE. 2014. Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. Estuarine, Coastal and Shelf Science 141: 1–8.

Boesch DF. 2006. Scientific requirements for ecosystem-based management in the restoration of Chesapeake Bay and Coastal Louisiana. Ecological Engineering 26: 6–26.

Boesch DF, Turner RE. 1984. Dependence of Fishery Species on Salt Marshes: The Role of Food and Refuge. Estuaries 7: 460–468.

Bohnsack JA, Causey B, Crosby MP, Griffis RB, Hixon MA, Hourigan TF, Koltes KH, Maragos JE, Simons A, Tilmant JT. 2000. A rationale for minimum 20-30% no-take protection. Proceedings 9th International Coral Reef Symposium, Bali, Indonesia 5.

Boström C, Jackson EL, Simenstad CA. 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science 68: 383–403.

Botsford LW, White JW, Carr MH, Casell JS. 2014. Marine Protected Area Networks in California, USA. Advances in Marine Biology 69: 205–251.

Branstetter S. 1990. Early Life-History Implications of Selected Carcharhinoid and Lamnoid Sharks of the Northwest Atlantic. Pages 17–28 in. Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, Pratt HL, Gruber SH, Taniuchi T ed. NOAA Technical Report 90, National Marine Fisheries Service, Silver Spring, MD.

Branton M, Richardson JS. 2011. Assessing the Value of the Umbrella-Species Concept for Conservation Planning with Meta-Analysis. Conservation Biology 25: 9–20.

Brewer JF. 2013. From Experiential Knowledge to Public Participation: Social Learning at the Community Fisheries Action Roundtable. Environmental Management 52: 321–334.

Carroll JM, Link to external site this link will open in a new window, Keller DA, Furman BT, Stubler AD. 2019. Rough Around the Edges: Lessons Learned and Future Directions in Marine Edge Effects Studies. Current Landscape Ecology Reports 4: 91–102.

Christensen NL, Bartuska AM, Brown JH, Carpenter S, D'Antonio C, Francis R, Franklin JF, MacMahon JA, Noss RF, Parsons DJ, Peterson CH, Turner MG, Woodmansee RG. 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. Ecological Applications 6: 665–691.

Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, García-Charton J-A, Pérez-Ruzafa Á, Badalamenti F, Bayle-Sempere J, Brito A, Bulleri F, Culioli J-M, Dimech M, Falcón JM, Guala I, Milazzo M, Sánchez-Meca J, Somerfield PJ, Stobart B, Vandeperre F, Valle C, Planes S. 2008. Marine reserves: size and age do matter. Ecology Letters 11: 481–489.

Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM, Raby GD, Cooke SJ. 2017. Acoustic telemetry and fisheries management. Ecological Applications 27: 1031–1049.

Curtin R, Prellezo R. 2010. Understanding marine ecosystem based management: A literature review. Marine Policy 34: 821–830.

Dahlgren CP, Eggleston DB. 2000. Ecological Processes Underlying Ontogenetic Habitat Shifts in a Coral Reef Fish. Ecology 81: 2227–2240.

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE. 2006. Marine nurseries and effective juvenile habitats: Concepts and applications. Marine Ecology Progress Series 312: 291–295.

Davies RWD, Cripps SJ, Nickson A, Porter G. 2009. Defining and estimating global marine fisheries bycatch. Marine Policy 33: 661–672.

Dennis GD. 1992. Island mangrove habitats as spawning and nursery areas for commercially important fishes in the Caribbean. Proceedings of the Forty First Annual Gulf and Caribbean 41: 205–225.

Di Franco A, Thiriet P, Di Carlo G, Dimitriadis C, Francour P, Gutiérrez NL, Jeudy de Grissac A, Koutsoubas D, Milazzo M, Otero M del M, Piante C, Plass-Johnson J, Sainz-Trapaga S, Santarossa L, Tudela S, Guidetti P. 2016. Five key attributes can increase marine protected areas performance for small-scale fisheries management. Scientific Reports 6: 38135.

Diamond SL, Crowder LB, Cowell LG. 1999. Catch and Bycatch: The Qualitative Effects of Fisheries on Population Vital Rates of Atlantic Croaker. Transactions of the American Fisheries Society 128: 1085–1105.

Dickson LCD, Negus SRB, Eizaguirre C, Katselidis KA, Schofield G. 2022. Aerial Drone Surveys Reveal the Efficacy of a Protected Area Network for Marine Megafauna and the Value of Sea Turtles as Umbrella Species. Drones 6: 291.

Dulčić J, Matić S, Kraljević M. 2002. Shallow coves as nurseries for non-resident fish: a case study in the eastern middle Adriatic. Journal of the Marine Biological Association of the United Kingdom 82: 991–993.

Environmental Law Institute. 2014. State and Local Authority for Marine Protection. Environmental Law Institute.

Feldheim K, Gruber S, Dibattista J, Babcock E, Kessel S, Hendry A, Pikitch E, Ashley M, Chapman D. 2013. Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. Molecular ecology 23.

Fletcher KM, O'Shea SE. 2000. Essential Hsh Habitat: Does Calling It Essential Make It So? Environmental Law 30: 51–98.

Fluharty D. 2005. Evolving ecosystem approaches to management of fisheries in the USA. Marine Ecology Progress Series 300: 248–253.

Fodrie FJ, Heck Jr KL, Andrus CFT, Powers SP. 2020. Determinants of the nursery role of seagrass meadows in the sub-tropical Gulf of Mexico: inshore-offshore connectivity for snapper and grouper. Marine Ecology Progress Series 647: 135–147.

Fodrie, FJ, Heck Jr KL, Powers SP, Graham WM, and Robinson KL. 2010. Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. Global Change Biology 16: 48-59.

Fodrie FJ, Herzka SZ. 2008. Tracking juvenile fish movement and nursery contribution within arid coastal embayments via otolith microchemistry. Marine Ecology Progress Series 361: 253–265.

Fodrie FJ, Levin LA. 2008. Linking juvenile habitat utilization to population dynamics of California halibut. Limnology and Oceanography 53: 799–812.

Fodrie FJ, Levin LA, Lucas AJ. 2009. Use of population fitness to evaluate the nursery function of juvenile habitats. Marine Ecology Progress Series 385: 39–49.

Gibson RN. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Netherlands Journal of Sea Research 32: 191–206.

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Marine Ecology Progress Series 247: 281–295.

Greening H, Janicki A. 2006. Toward Reversal of Eutrophic Conditions in a Subtropical Estuary: Water Quality and Seagrass Response to Nitrogen Loading Reductions in Tampa Bay, Florida, USA. Environmental Management 38: 163–178.

Guerry AD. 2005. Icarus and Daedalus: conceptual and tactical lessons for marine ecosystem-based management. Frontiers in Ecology and the Environment 3: 202–211.

Gunter G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. Pages 621–638 in. Estuaries, Lauff GH ed. Washington (DC): American Association for the Advancement of Science.

Harborne AR, Green AL, Peterson NA, Beger M, Golbuu Y, Houk P, Spalding MD, Taylor BM, Terk E, Treml EA, Victor S, Vigliola L, Williams ID, Wolff NH, zu Ermgassen PSE, Mumby PJ. 2018. Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia. Diversity and Distributions 24: 1729–1743.

Heck KL, Hays G, Orth R. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253: 123–136.

Heck KL, Thoman TA. 1984. The Nursery Role of Seagrass Meadows in the Upper and Lower Reaches of the Chesapeake Bay. Estuaries 7: 70–92.

Heincke F. 1913. Investigation on the plaice. I. The plaice fishery and protective regualtions. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 17: 1–153.

Heupel M, Carlson J, Simpfendorfer C. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337: 287–297.

Hoey, JA, Fodrie FJ, Walker Q, Hilton E, Kellison TG, Targett T, Taylor JC, Able KW, and Pinsky ML. 2020. Using multiple natural tags provides evidence for extensive larval dispersal across space and through time in summer flounder. Molecular Ecology 29: 1421-1435.

Huijbers CM, Nagelkerken I, Layman CA. 2015. Fish movement from nursery bays to coral reefs: a matter of size? Hydrobiologia 750: 89–101.

Hussey NE, Hedges KJ, Barkley AN, Treble MA, Peklova I, Webber DM, Ferguson SH, Yurkowski DJ, Kessel ST, Bedard JM, Fisk AT. 2017. Movements of a deep-water fish: establishing marine fisheries management boundaries in coastal Arctic waters. Ecological Applications 27: 687–704.

Hutniczak B, Lipton D, Wiedenmann J, Wilberg M. 2019. Valuing changes in frequency of fish stock assessments. Canadian Journal of Fisheries and Aquatic Sciences 76: 1640–1652.

Iles T, Beverton RJH. 2000. The concentration hypothesis: the statistical evidence. ICES Journal of Marine Science 57: 216–227.

Jakus PM, Fly JM, Wilson JL. 1996. Explaining Public Support for Fisheries Management Alternatives. North American Journal of Fisheries Management 16: 41–48.

Jeans M. 2011. The Role of the Regional Fishery Management Councils in Multi-Sector Spatial Planning: Exploring existing tools and future opportunities.

Jennings S, Kaiser MJ. 1998. The Effects of Fishing on Marine Ecosystems. Pages 201–352 in. Advances in Marine Biology, vol. 34. Elsevier.

Kraus RT, Secor DH. 2005. Application of the nursery-role hypothesis to an estuarine fish. Marine Ecology Progress Series 291: 301–305.

Lecchini D, Galzin R. 2005. Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). Marine Biology 147: 47–58.

Lefcheck JS, Hughes BB, Johnson AJ, Pfirrmann BW, Rasher DB, Smyth AR, Williams BL, Beck MW, Orth RJ. 2019. Are coastal habitats important nurseries? A meta-analysis. Conservation Letters e12645.

Litvin SY, Weinstein MP, Sheaves M, Nagelkerken I. 2018. What Makes Nearshore Habitats Nurseries for Nekton? An Emerging View of the Nursery Role Hypothesis. Estuaries and Coasts 41: 1539–1550.

Marriott A, McCarthy I, Ramsay A, Chenery S. 2016. Discriminating nursery grounds of juvenile plaice (Pleuronectes platessa) in the south-eastern Irish Sea using otolith microchemistry. Marine Ecology Progress Series 546: 183–195.

Mattila J, Chaplin G, Eilers MR, Heck KL, O'Neal JP, Valentine JF. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a Zostera marina bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). Journal of Sea Research 41: 321–332.

McCallister M, Ford R, Gelsleichter J. 2013. Abundance and Distribution of Sharks in Northeast Florida Waters and Identification of Potential Nursery Habitat. Marine and Coastal Fisheries 5: 200–210.

McDevitt-Irwin J, Iacarella J, Baum J. 2016. Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. Marine Ecology Progress Series 557: 133–143.

McLeod E, Salm R, Green A, Almany J. 2009. Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment 7: 362–370.

McNeill SE, Fairweather PG. 1993. Single Large or Several Small Marine Reserves? An Experimental Approach with Seagrass Fauna. Journal of Biogeography 20: 429–440.

McPhee DP, Leadbitter D, Skilleter GA. 2002. Swallowing the bait: is recreational fishing in Australia ecologically sustainable? Pacific Conservation Biology 8: 40–51.

Miller JM, Crowder LV, Moser ML. 1985. Migration ond utilization of estuarine nurseries by juvenile fishes: an evolutionairy perspective. Contribution to Marine Science 27: 338–352.

Minello T, Able K, Weinstein M, Hays C. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Marine Ecology Progress Series 246: 39–59.

Minello TJ. 1999. Nekton Densities in Shallow Estuarine Habitats of Texas and Louisiana and the Identification of Essential Fish Habitat. American Fisheries Society Symposium 22: 43–75.

Morley JW, Batt RD, Pinsky ML. 2017. Marine assemblages respond rapidly to winter climate variability. Global Change Biology 23: 2590–2601.

Nagelkerken I, Sheaves M, Baker R, Connolly RM. 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish and Fisheries 16: 362–371.

Nakamura Y, Hirota K, Shibuno T, Watanabe Y. 2012. Variability in nursery function of tropical seagrass beds during fish ontogeny: timing of ontogenetic habitat shift. Marine Biology 159: 1305–1315.

National Research Council. 2008. *Public Participation in Environmental Assessment and Decision Making*. Washington, DC: The National Academies Press. https://doi.org/10.17226/12434.

NOAA NMFS. 2002. Magnuson-Stevens Act Provisions; Essential Fish Habitat (EFH). Federal Register. (8 September 2020; https://www.federalregister.gov/documents/2002/01/17/02-885/magnuson-stevens-act-provisions-essential-fish-habitat-efh).

NOAA NMFS. 2022. Essential Fish Habitat. NOAA Fisheries. (14 September 2022; https://www.fisheries.noaa.gov/national/habitat-conservation/essential-fish-habitat).

Nutters HM, Pinto da Silva P. 2012. Fishery stakeholder engagement and marine spatial planning: Lessons from the Rhode Island Ocean SAMP and the Massachusetts Ocean Management Plan. Ocean & Coastal Management 67: 9–18.

Orth RJ, Williams MR, Marion SR, Wilcox DJ, Carruthers TJB, Moore KA, Kemp WM, Dennison WC, Rybicki N, Bergstrom P, Batiuk RA. 2010. Long-Term Trends in Submersed Aquatic Vegetation (SAV) in Chesapeake Bay, USA, Related to Water Quality. Estuaries and Coasts 33: 1144–1163.

Osgood G, McCord M, Baum J. 2020. Chondrichthyans as an umbrella species-complex for conserving South African biodiversity. African Journal of Marine Science 42: 81–93.

Pearson JC. 1929. Natural history and conservation of the redfish and other commercial sciaenids on the Texas coast. Bulletin of the Bureau of Fisheries 44: 129–214.

Peterson C, Grabowski J, Powers S. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Marine Ecology Progress Series 264: 249–264.

Pihl L, Cattrijsse A, Codling I, Mathieson S, McLusky DS, Roberts C. 2002. Habitat Use by Fishes in Estuaries and Other Brackish Areas. Pages 10–53 in. Fishes in Estuaries, Elliot, M., Hemingway, K. ed. Blackwell Publishing Ltd.

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ. 2004. Ecosystem-Based Fishery Management. Science 305: 346–347.

Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, Parkinson EA, Paul AJ, Jackson L, Shuter BJ. 2002. Canada's Recreational Fisheries: The Invisible Collapse? Fisheries 27: 6–17.

Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science 66: 1570–1583.

Roberge J-M, Angelstam P. 2004. Usefulness of the Umbrella Species Concept as a Conservation Tool. Conservation Biology 18: 76–85.

Rooker JR, Dennis GD. 1991. Diel, Lunar and Seasonal Changes in a Mangrove Fish Assemblage off Southwestern Puerto Rico. Bulletin of Marine Science 49: 684–698.

Rozas LP, Hackney CT. 1984. Use of Oligohaline Marshes by Fishes and Macrofaunal Crustaceans in North Carolina. Estuaries 7: 213.

Saarman E, Gleason M, Ugoretz J, Airamé S, Carr M, Fox E, Frimodig A, Mason T, Vasques J. 2013. The role of science in supporting marine protected area network planning and design in California. Ocean & Coastal Management 74: 45–56.

Sala E, Lubchenco J, Grorud-Colvert K, Novelli C, Roberts C, Sumaila UR. 2018. Assessing real progress towards effective ocean protection. Marine Policy 91: 11–13.

Samoilys MA, Martin-Smith KM, Giles BG, Cabrera B, Anticamara JA, Brunio EO, Vincent ACJ. 2007. Effectiveness of five small Philippines' coral reef reserves for fish

populations depends on site-specific factors, particularly enforcement history. Biological Conservation 136: 584–601.

Sarthou CM. 1999. An Environmentalist's Perspective on Essential Fish Habitat. American Fisheries Society Symposium 22: 11–22.

Sheaves M, Baker R, Nagelkerken I, Connolly RM. 2015. True Value of Estuarine and Coastal Nurseries for Fish: Incorporating Complexity and Dynamics. Estuaries and Coasts 38: 401–414.

Sheaves M, Johnston R, Johnson A, Baker R, Connolly RM. 2013. Nursery Function Drives Temporal Patterns in Fish Assemblage Structure in Four Tropical Estuaries. Estuaries and Coasts 36: 893–905.

Sheridan P, Hays C. 2003. Are mangroves nursery habitat for transient fishes and decapods? Wetlands 23: 449–458.

Simpfendorfer CA, Wiley TR, Yeiser BG. 2010. Improving conservation planning for an endangered sawfish using data from acoustic telemetry. Biological Conservation 143: 1460–1469.

Sletten J, D'Iorio M, Gleason MG, Driedger A, Vincent T, Colegrove C, Wright D, Zetterlind V. 2021. Beyond the boundaries: How regulation-centered marine protected area information improves ocean protection assessments. Marine Policy 124: 104340.

Slocombe DS. 1993. Implementing Ecosystem-Based Management. BioScience 43: 612–622.

Snover ML. 2008. Ontogenetic Habitat Shifts in Marine Organisms: Influencing Factors and the Impact of Climate Variability. Bulletin of Marine Science 83: 53–67.

Springer S. 1967. Social organization of shark populations. Pages 149–174 in. Sharks, skates, and rays, Gilbert PW, Mathewson RW, Rall DP ed. John Hopkins Press, Baltimore, MD.

Stige L, Hunsicker M, Bailey K, Yaragina N, Hunt GL J. 2013. Predicting fish recruitment from juvenile abundance and environmental indices. Marine Ecology Progress Series 480: 245–261.

Tjørve E. 2010. How to resolve the SLOSS debate: Lessons from species-diversity models. Journal of Theoretical Biology 264: 604–612.

Varjopuro R, Gray T, Hatchard J, Rauschmayer F, Wittmer H. 2008. Introduction: Interaction between environment and fisheries—The role of stakeholder participation. Marine Policy 32: 147–157.

Vert-pre KA, Amoroso RO, Jensen OP, Hilborn R. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. PNAS 110: 1779–1784.

Werner EE, Gilliam JF. 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. Annual Review of Ecology and Systematics 15: 393–425.

Wilson JK, Stevens PW, Blewett DA, Boucek R, Adams AJ. 2023. A new approach to define an economically important fish as an umbrella flagship species to enhance collaborative stakeholder-management agency habitat conservation. Environmental Biology of Fishes 106: 237–254.

Wilson M. 2021. Back With a Splash: Resuming Juvenile Fish Sampling In 2021. Oregon Marine Reserves. (11 July 2022; https://sitemap.oregonmarinereserves.com/2021/07/29/2021-smurf-data/).

Zacharias MA, Roff JC. 2001. Use of focal species in marine conservation and management: a review and critique. Aquatic Conservation: Marine and Freshwater Ecosystems 11: 59–76.

zu Ermgassen PSE, Grabowski JH, Gair JR, Powers SP. 2016. Quantifying fish and mobile invertebrate production from a threatened nursery habitat. Journal of Applied Ecology 53: 596–606.

zu Ermgassen PSE, DeAngelis B, Gair JR, Ermgassen S zu, Baker R, Daniels A, MacDonald TC, Meckley K, Powers S, Ribera M, Rozas LP, Grabowski JH. 2021. Estimating and Applying Fish and Invertebrate Density and Production Enhancement from Seagrass, Salt Marsh Edge, and Oyster Reef Nursery Habitats in the Gulf of Mexico. Estuaries and Coasts 44: 1588–1603.

Tables

Table 1.1: Nursery designation terminology, protections, and identification methods in states with explicit nursery area protections.

State	Terminology Used	Description of Protections Afforded	Identification/Designation Methodology
AL	Nursery Areas	Gear restrictions and area/seasonal closures	Biophysical characteristics
DE	Migratory Fish Spawning and Nursery Designated Use: Outstanding Resource Waters	Antidegradation policy to maintain existing water quality	Proposal and DEQ Board review of exceptional aquatic community (collaborative Chesapeake Bay protections)
MD	Migratory Fish Spawning and Nursery Designated Use: Outstanding Resource Waters	Antidegradation policy to maintain existing water quality	Proposal and DEQ Board review of exceptional aquatic community – based on where eggs and larvae are found (collaborative Chesapeake Bay protections)
MS	Nursery Habitats	Gear restrictions and area/seasonal closures	Set based on historical data and life history traits of species. Continued long-term monitoring but no active assessment of new nursery areas
NC	Primary, Secondary, and Special Secondary Nursery Areas	Gear restrictions and area/seasonal closures; restrictions on development	Proposed based on inshore trawl surveys and areas with similar biophysical properties
TX	Nursery Areas	No Shrimping Allowed	Based on historical data and knowledge of estuarine areas to designate all coastal waters not specifically named as Major Bays or Bait Bays
VA	Migratory Fish Spawning and Nursery Designated Use: Outstanding Resource Waters	Antidegradation policy to maintain existing water quality	Proposal and Division of Environmental Quality Board review of exceptional aquatic community (collaborative Chesapeake Bay protections)

Table 1.2: Nursery designation terminology, protections, and identification methods in states without explicit nursery area protections.

State	Terminology Used	Protections Afforded	Identification/Designation Methodology
AK	Conservation Areas; Anadromous Fish Habitat	GR; AC; SC	Boards of Fisheries and Game recommendations with legislative approval; documentation of fish observed or caught
CA	Marine Life Protected Areas	NTZ; LTA	Stakeholder proposal followed by scientific and policy review using best available science
CT	N/A	GR; AC; SC	Recommendation by Fisheries Division's Habitat Conservation and Enhancement Program
FL	Marine Sanctuaries; Essential Fish Habitat	GR; AC; SC	Habitat characteristics and abundance data
GA	N/A	GR; AC; SC	Based on type of water body (e.g., sounds and estuaries)
HI	Marine Protected Areas; Fish Replenishment Areas	GR; NTZ	Initiated via community and stakeholder discussion; formed into rules by Hawaii Division of Aquatic Resources staff
LA	Sanctuary Areas	GR	All tributaries to Lake Catherine and Lake Pontchartrain
MA	No Name; Cod Conservation Zones	GR; AC; SC; DP	Habitat characteristics (eelgrass habitats); water quality; presence of spawning cod
ME	Beginning with Habitat Focus Areas	DL	Based on natural resource use, water quality, and presence of rare population
NH	Fisheries and Breeding Areas	DP	Case-by-case basis determined at permitting
NJ	Submerged Aquatic Vegetation Habitat	DP	Based on detailed SAV maps from 1980
NY	Significant Coastal Fish and Wildlife Habitats	AR	Recommendations based on rating system focused on ecosystem rarity, species vulnerability, human use, population level, and replaceability
OR	Marine Reserves	GR; HR	Nomination process using expertise of scientists and public; monitored and will be reassessed in 2023 based on ecological monitoring plan
RI	Shellfish and Marine Life Management Areas	GR; HR; DP	Based on fisheries independent and dependent data, habitat data, recommendations from Marine Fishery Council
SC	Outstanding Resource Waters	GR; AC; SC	Based on monitoring programs outside stock assessments
WA	Marine Protected Areas	GR; HR	Public and private proposal to Division of Natural Resources; if approved management plan drafted

Note: Many states have protected areas and named frameworks that play a role in protecting juveniles and/or their habitats. If these frameworks are named, they are listed here. Protections without formal names are listed as N/A
Abbreviations: GR = Gear Restrictions; HR = Harvest restrictions; SC = Seasonal Closures; AC = Area Closures; NTZ = no-take zone; LTA = limited-take area; DP = development prohibitions; DL = Limits on amount and type of discharge into waters, case-by-case development restrictions; AR = actions restricted

Figures

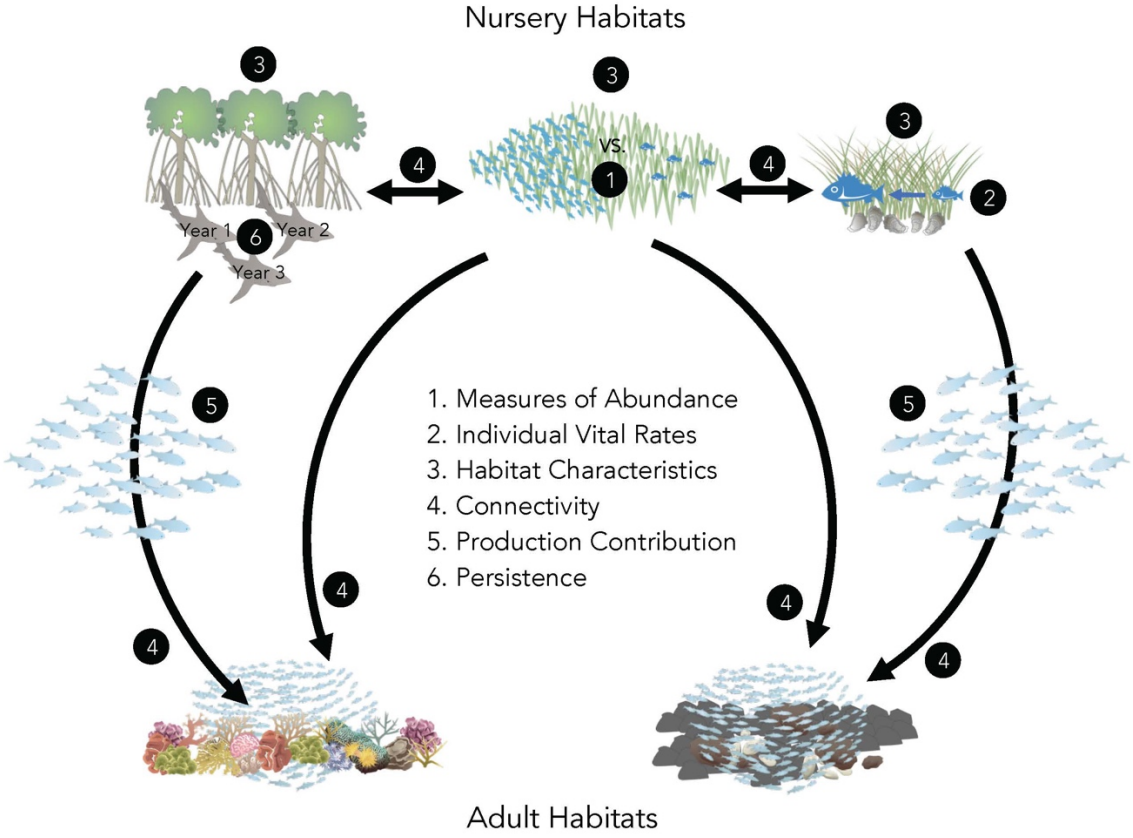

Figure 1.1: Conceptual diagram displaying the six nursery area frameworks from the ecological literature. This diagram displays one or more examples for each framework, but not all possible examples are given here. (1) Measures of abundance (density, presence/absence, abundance), shown here as a large number of fish versus a small number. (2) Individual vital rates (growth, survival), shown as the increase in size of an individual. (3) Habitat characteristics (estuary, shallow water, low salinity, biotic structure), displayed as three structured habitats supporting juvenile fish. (4) Connectivity (migration pathways, seascape features), shown as connections between juvenile habitats as well as adult habitats. Not all possible connections are shown in this diagram. (5) Production contribution (total productivity, population fitness, per unit area contribution), displayed as a large number of individuals moving to adult habitats. (6) Persistence (multi-year use), shown here as an individual using the same nursery habitat over multiple years.

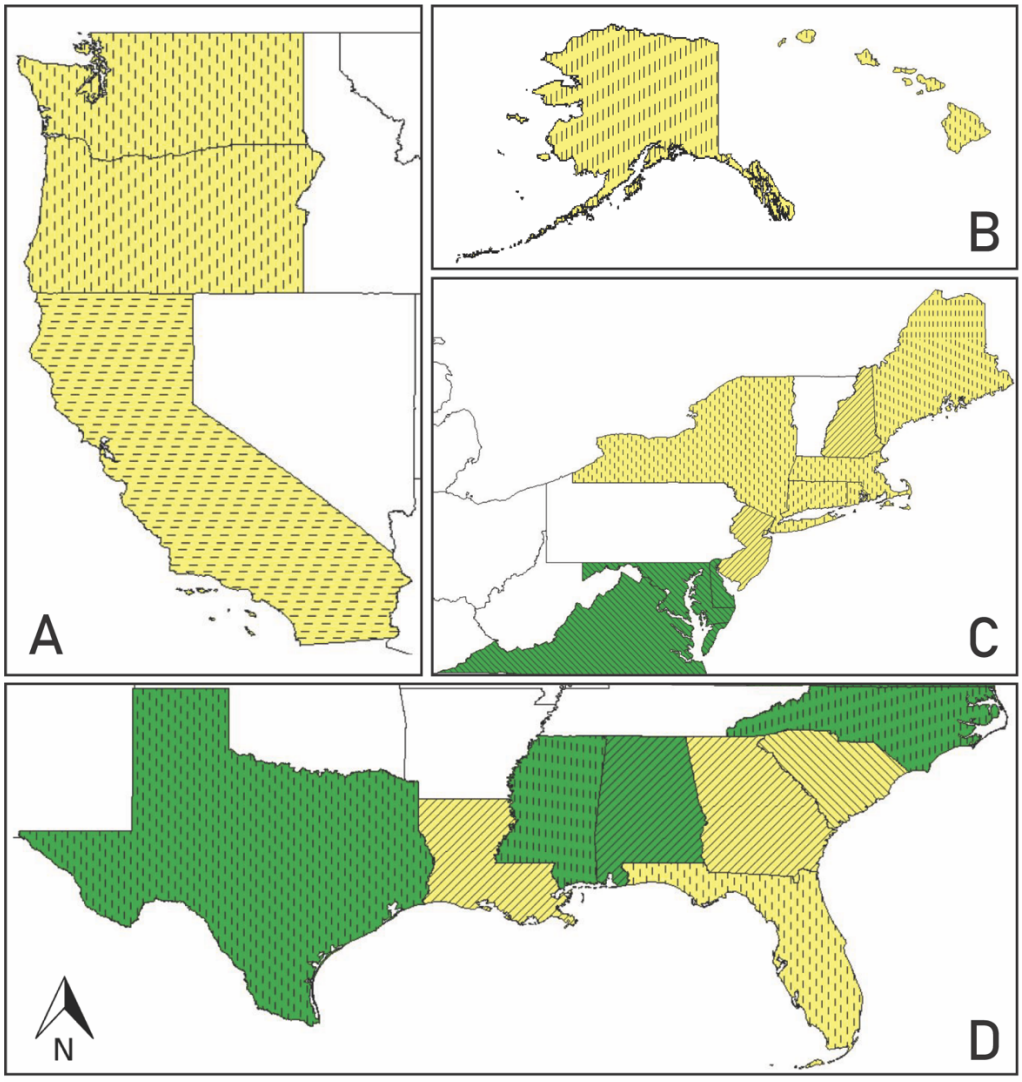

Figure 1.2: Map of coastal states designating nursery areas in the United States on the (A) West coast, (B) Alaska and Hawaii, (C) Northeastern coast, (D) Gulf and Southeastern coast. Green indicates states that explicitly designate nursery areas, yellow indicates states that do not designate nursery areas specifically in their management. Hashing indicates which nursery framework the state employs. Non-nursery specific protections that play a role in protecting juveniles and their habitats are shown using nursery frameworks listed here. // indicates habitat characteristics; \\ indicates measures of abundance; || indicates both habitat characteristics and measures of abundance; = indicates potential for all frameworks.

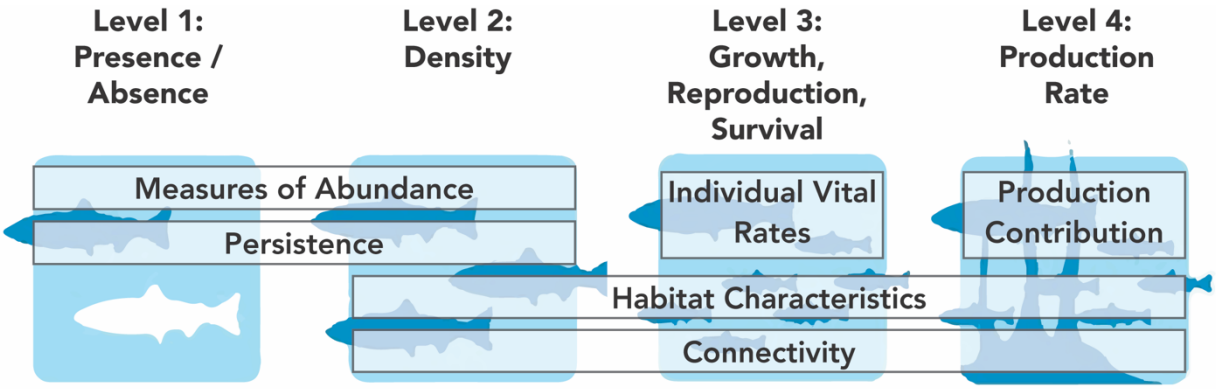

Figure 1.3: Modification of Essential Fish Habitat figure from NOAA Fisheries (NOAA NMFS 2022) EFH data level obtained by each nursery area framework. Note that some frameworks may cross into multiple data levels based on the metric used and available data.

Supplemental Information

SCOPUS search terms for searches conducted on May 28, 2020:

1) "nursery role hypothesis" OR "effective juvenile habitat*" OR "nursery seascape*" OR "juvenile fish habitat*" OR "estuarine-dependent"
2) "nurser*" AND "estuarine" OR "marine" OR "brackish" OR "nearshore" OR "Inshore" OR "coastal" OR "seagrass*" OR "salt marsh*" OR "oyster*" OR "mangrove*" OR "coral*" OR "reef*" OR "decapod*" OR "fish*" AND "Habitat*" OR "landscape" OR "seascape" OR "ecoton"
3) "juvenile*" OR "young of year" AND "estuarine" OR "marine" OR "brackish" OR "nearshore" OR "Inshore" OR "coastal" OR "seagrass*" OR "salt marsh*" OR "oyster*" OR "mangrove*" OR "coral*" OR "reef*" OR "decapod*" OR "fish*" AND "Habitat*" OR "landscape" OR "seascape" OR "ecoton"

Initial contact with states to determine if there are nursery area designations:
Questions asked:

- Does your state manage fisheries in relation to coastal habitats?
- To what extent does your state consider nursery habitats as having a role in conserving and restoring finfish populations?
- Does your state have any official designations for any nursery/critical habitat?
- Could you provide a link to a management plan or document regarding these areas/designations?

Secondary contact with states to confirm nursery designation and gain more information about designation method and alternate designations.
Questions asked of "nursery states"

- What is the designation process for the nursery areas and what data are used to inform the designation?
- What are the protections afforded by the designation of nursery area?
- How is the status of these nursery areas monitored, such as trawl surveys or long-term sampling?

Questions asked of "non-nursery states"

- Can you confirm that your state does not directly manage and protect nursery areas?
- Are there any other designations you may have that are similar to nursery areas meant to protect habitats or areas designated to protect juvenile fish and crustaceans?

Supplemental Tables

Table S1.1: Contact information, date of contact, response type, date, and responder for initial contact with state managers to determine if states designate nursery areas from coastal states where information was not readily available on the state website.

State	State Personnel Initially Contacted	Date of Initial Contact	Date of First Email Response	Questions Answered Over Email?	Email Response Contact	Questions Answered with Phone Call?	Phone Call Date	Phone Call Contact
AK	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
AL	Alabama Department of Conservation and Natural Resources	7/22/20	N/A	N/A	N/A	Y	8/21/20	Kevin Anson, Chief Biologist
CA	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
CT	Connecticut Department of Energy and Environmental Protection	7/15/20	7/15/20	Y	Steve Gephard, Supervising Fisheries Biologist	N/A	N/A	N/A
DE	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
FL	Florida Department of Environmental Protection	7/15/20	N/A	N	Lauren Barth, Wildlife Assistance Biologist	N	8/17/20	Lauren Barth, Wildlife Assistance Biologist
GA	Jan Mckinnon, Manager, Coastal and Ocean Management Program	7/21/20	N/A	N	Jared Flowers, Marine Biologist Supervisor	Y	8/7/20	Jared Flowers, Marine Biologist Supervisor
HI	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
LA	Vickie Amedee, Coastal Resources Scientist	7/22/20		Y	Karl Morgan, Coastal Use Permits & Mitigation Administrator	N/A	N/A	N/A
MA	Marc Carullo, GIS and Habitat Specialist	7/14/20	N/A	N	Todd Callaghan, Coastal and Marine Scientist	Y	8/5/20	Todd Callaghan, Coastal and Marine Scientist
MD	Angel Willey, Natural Resources Biologist	8/5/20	N/A	N/A	N/A	No calls made.	N/A	N/A

						Instead referred to Maryland's Coastal Zone Enhancement plan		
ME	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
MS	Tom Holman, Fisheries Biologist	7/22/20	7/24/20	Y	Rick Burris, Chief Scientific Officer at Mississippi Department of Marine Resources	N/A	N/A	N/A
NC	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
NH	Marine Division of NH State Fish and Game	8/3/20	N/A	N	N/A	Y	8/3/20	Front Desk
NJ	Department of Environmental Protection, Division of Land Use Regulation	7/17/20		Y	Jeffery Brust, Chief, Bureau of Marine Fisheries	N/A	N/A	N/A
NY	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
OR	N/A[1]	N/A	N/A	N/A	N/A	N/A	N/A	N/A
RI	Eric Schneider, Principal Marine Fisheries Biologist	8/21/20	N/A	N	Eric Schneider, Principal Marine Fisheries Biologist	Y	8.28.20	Eric Schneider, Principal Marine Fisheries Biologist
SC	South Carolina Department of Natural Resources	7/21/20	N/A	N	Erin Levesque, Biologist and Director of Waddell Mariculture Center	Y	8/19/20	Erin Levesque, Biologist and Director of Waddell Mariculture Center
TX	Paul Hammerschmidt, Program Specialist at Texas Parks and Wildlife Department	7/20/20	7/21/20	N	Emma Clarkson, Habitat Assessment Team, Team Lead, Corpus Christi	Y	8/7/20	Emma Clarkson, Habitat Assessment Team, Team Lead, Corpus Christi

VA	Nick Meade, Coastal GIS Coordinator	7/21/20	N/A	N/A	N/A	N/A	N/A	N/A
WA	Roberta Davenport, Aquatic Reserves Program Manager	7/17/20	7/17/20	Y	Roberta Davenport, Aquatic Reserves Program Manager	N/A	N/A	N/A

[1] These states not contacted as information was readily available on state webpages and through Environmental Law Institute report.

Table S1.2: Contact information, date of contact, response type, date, and responder for secondary contact with state managers to confirm nursery designation, alternative protection strategies, protections afforded, and designation method from all coastal states.

State	State Personnel Initially Contacted	Date of Initial Contact	Date of First Email Response	Questions Answered Over Email?	Email Response Contact	Questions Answered with Phone Call?	Phone Call Date	Phone Call Contact
AK	Ben Mulligan, Deputy Commissioner, Habitat Section	8/23/21	8/24/21	Y	Rachel Baker, Deputy Commissioner; Benjamin Mulligan, Deputy Commissioner	N	N/A	N/A
AL	Kevin Anson, Chief Biologist	7/26/21	7/26/21	N/A	N/A	Y	7/30/21	Craig Newton, Manager of Shrimp Fisheries and Fishery-Independent Monitoring Program
CA	Becky Ota, Environmental Program Manager	8/23/21	8/23/21	N	N/A	N/A	N/A	N/A
CT	Connecticut Fisheries Division		2/7/22	Y	Matthew Goclowski, Supervising Fisheries Biologist	N	N/A	N/A
DE	Craig Rhoads, Environmental Program Manager	7/26/21	7/26/21	Y	David Wolanski, Environmental Scientist, WAMS	N	N/A	N/A
FL	Alex Reed, Director, Office of Resilience and Coastal Protection	8/16/21	8/17/21	N/A	N/A	Y	8/23/21	CJ Sweetman, PhD. Member of FWC DMFM Team
GA	Jan Mackinnon, Manager, Coastal and Ocean Management Program	8/23/21	N/A	N/A	N/A	N/A	N/A	N/A

HI	HI Division of Aquatic Resources	8/23/21	8/26/21	Y	Ryan Okano, Program Manager, Ecosystem Protection	N	N/A	N/A
LA	Patrick Banks, LDWF Assistant Secretary	8/23/21	8/23/21	Y	Patrick Banks, LSWF Assistant Secretary	N	N/A	N/A
MA	Daniel McKiernan, Director of Fisheries Management and Policy	8/16/21	8/16/21	Y	Mark Rousseau, Division of Marine Fisheries	N	N/A	N/A
MD	Matt Fleming, Director Chesapeake and Coastal Service	7/26/21	8/13/21	Y	Jim Uphoff, Fisheries Biologist	N	N/A	N/A
ME	Kathleen Leyden, Marine Coastal Program Director	8/16/21	N/A	N/A	N/A	N/A	N/A	N/A
MS	Rick Burris, Deputy Director, Office of Marine Fisheries	7/26/21	7/28/21	N/A	N/A	Y	7/28/21	Rick Burris, Chief Scientific Officer at Mississippi Department of Marine Resources
NC	N/A_1	N/A	N/A	N/A	N/A	N/A	N/A	N/A
NH	John Magee, Fish Habitat Biologist	8/16/21	8/17/21	Y	John Magee, Fish Habitat Biologist	N	N/A	N/A
NJ	NJ Office of Policy and Coastal Management	8/23/21	9/13/21	Y	Faelyn Meyers, Watershed and Land Management	N	N/A	N/A
NY	NY Division of Marine Resources	8/20/21	9/21/21	Y	Julia Socrates, Bureau Chief, Marine Habitat	N	N/A	N/A
OR	Oregon Department of Fish and Wildlife	8/23/21	8/23/21	N	N/A	N/A	N/A	N/A
RI	Patrick Barrett, Principal Biologist	8/16/21	8/17/21	Y	Eric Schneider, Principal Marine Fisheries Biologist	N	N/A	N/A

SC	Mel Bell, Director, Office of Fisheries Management	8/23/21	8/24/21	N/A	N/A	Y	8/26/21	Mel Bell, Director, Office of Fisheries Management
TX	Robin Riechers, Director of Coastal Fisheries	7/26/21	7/26/21	N/A	N/A	Y	8/9/21	Robin Riechers, Director of Coastal Fisheries
VA	Randy Owen, Chief of Habitat Management	7/26/21	8/13/21	N	N/A	N/A	N/A	N/A
WA	Washington Division of Fish and Wildlife	8/23/21	N/A	N/A	N/A	N/A	N/A	N/A

[1] This state not contacted as information had been previously confirmed through management webpage, Environmental Law Institute report, or previous exchanges unrelated to the current work.

Chapter 2: Surface area and depth drive faunal community composition in seagrass meadows

Abstract

The complexity of biogenic habitats can strongly influence the size and structure of resident faunal communities. However, the relative importance of habitat attributes, such as area, heterogeneity, and connectivity between habitats, in shaping faunal communities is still up for debate. Seagrasses exhibit high intra- and interspecific morphological variation in traits, such as canopy height and shoot density, making them an ideal system in which to investigate the role of habitat complexity in shaping faunal community structure. However, as in other biogenic habitats, several seagrass complexity metrics are correlated (e.g., surface area necessarily increases as canopy heights increase). As such, identifying the metrics which drive faunal community composition is challenging. Here, we sought to identify and separate the individual effects of seagrass complexity metrics (e.g., shoot density, canopy height) on the composition and abundance of faunal communities in a North Carolina estuary. First, we performed seagrass complexity and associated fauna surveys over two years across 20 seagrass beds. Surveys revealed that taller canopied seagrass beds support higher faunal species richness and abundances than shorter canopied beds. In our first year of surveys, we observed species-specific relationships between canopy height and abundance, with four of eight highly abundant species demonstrating a strong positive relationship with canopy height. We found no relationship between the seagrass species present in the bed or shoot density and faunal richness and abundance measurements, However, our second year of sampling revealed that fauna-canopy height relationships were largely seasonally dependent. Importantly, surveyed beds with taller canopies were found in in deeper water than beds with shorter canopies. Therefore, to explicitly

test the relative importance of canopy height, blade surface area, and water depth in driving habitat choice, we examined habitat preferences of a common seagrass resident (pinfish; *Lagodon rhomboides*) in laboratory mesocosms hosting artificial seagrasses of varying complexities and depths. Pinfish demonstrated a preference for deep seagrass beds, but only preferred taller canopies when these areas also offered increased seagrass blade surface area. Our results indicate that seagrass depth and blade surface area, rather than canopy height, influence faunal community composition. Considerations of both structural complexity and physical setting of the habitat are therefore imperative for a comprehensive approach in understanding how faunal communities and individual species are responding to future changes in habitats across ecosystem settings.

Introduction

The complexity of a habitat can greatly influence the faunal community found within it (Kovalenko et al. 2012). Studies across terrestrial (August 1983, Stein et al. 2014, Basile et al. 2021), aquatic (Shumway et al. 2007, Staudacher and Füreder 2007), and marine (Heck and Wetstone 1977, Friedlander and Parrish 1998, Gratwicke and Speight 2005a, Hauser et al. 2006, Canion and Heck 2009) systems have demonstrated relationships between community composition and habitat complexity. Across ecosystems and taxonomically diverse groups, more complex habitats support larger, more species rich communities (Kohn and Leviten 1976, Heck and Wetstone 1977, Gratwicke and Speight 2005b, Kovalenko et al. 2012, Ghadiri Khanaposhtani et al. 2012, Basile et al. 2021). Measures of habitat complexity include assessments of habitat heterogeneity (Menge et al. 1985, Tews et al. 2004), rugosity (Luckhurst and Luckhurst 1978), interstitial distance (St. Pierre and Kovalenko 2014), shoot density (Canion

and Heck 2009), and plant biomass (Heck and Wetstone 1977) among others. These measures can fit into broad categories of structural complexity (e.g., rugosity, surface area, leaf number; Kovalenko et al. 2012) and spatial or landscape scale complexity (e.g., habitat heterogeneity, fragmentation, and connectivity; Garza 2016). Use of a given complexity category or metric can be study- or habitat-specific. For example, studies on habitats comprised of plants (e.g., seagrass, saltmarsh) may use the size or density of plants as their structural metrics (Canion and Heck 2009, Basile et al. 2021), while studies on reef (e.g., coral or oyster) or rocky habitats may use metrics such as rugosity or the number of holes in the structure (Wilson et al. 2007, Hackradt et al. 2011). On coral reefs, areas of high relief, a measure of complexity, support elevated diversity compared to areas of low relief (Friedlander and Parrish 1998). Increased oyster reef complexity in the form of oyster clusters, as opposed to loose shell piles, can impact predator prey dynamics in oyster reef systems by providing refuge to intermediate predators and their prey and by reducing interference competition among these predators (Grabowski and Powers 2004, Grabowski et al. 2008). While it is understood that increased complexity is often positively correlated with higher abundance and richness of fauna, the complexity metrics purported to be driving these patterns vary across studies (Friedlander and Parrish 1998, Grabowski et al. 2008, Canion and Heck 2009).

Faunal responses to different measures of habitat complexity are not always positive or similar across metrics, even in the same ecosystem. For example, species richness and abundances of faunal communities in kelp forests are positively correlated with holdfast diameter, maximum frond length, and thallus wet weight, but negatively correlated with stipe number per kelp holdfast (Velasco-Charpentier et al. 2021). The impacts of habitat complexity on community dynamics can also differ across scales. In rocky reef and kelp habitats, at a small,

within site scale, increased complexity increases the strength of density-dependent mortality, with more pretty consumed per predator when these predators were at a higher density (Johnson 2006). However, at a larger, across site scale, this relationship reverses with increased complexity decreasing the strength of density-dependent mortality (Johnson 2006). As such, the degree to which complexity metrics reliably predict faunal community structure remains unclear, despite high research effort.

In marine ecosystems, seagrass has acted as a model habitat for exploring the relationship between habitat complexity and community composition and structure for decades (Heck and Wetstone 1977, Heck and Orth 1980, Canion and Heck 2009, Moore and Hovel 2010, Henderson et al. 2017). Seagrasses are found globally (Waycott et al. 2009, McKenzie et al. 2020), exhibit differences in structural complexity both within (Hughes et al. 2009) and between species (Duarte 1991a), and can be manipulated in the field through transplanting, as well as through manipulations of artificial seagrass (Bell et al. 1985, Macreadie et al. 2010). Although several complexity metrics have been suggested to influence faunal community composition, broad agreement over their relative importance is lacking (Heck and Wetstone 1977, Fonseca et al. 1996, Hovel et al. 2002, Canion and Heck 2009, McCloskey and Unsworth 2015, Yeager et al. 2016). For example, McCloskey and Unsworth (2015) found that faunal species richness increased with increased percent cover of seagrass beds in North Wales. Alternatively, in North Carolina, seagrass percent cover explains little variation between seagrass communities (Hovel et al. 2002), except in patchy, fragmented landscapes with low seagrass cover, which leads to decreased epibenthic species abundance and richness, likely due to their lowered movement across habitat patches (Yeager et al. 2016). Further, relative wave exposure and shoot biomass were influential drivers of faunal densities in NC seagrass beds (Hovel et al. 2002). Heck and

Wetstone (1977) also found that total aboveground seagrass biomass dictated macroinvertebrate communities, with higher plant biomass leading to increased macroinvertebrate abundances and species richness. It is important to note that surface area – rather than plant biomass – may have been responsible for these increased abundances, likely increasing protection from predation at high surface areas (Heck and Wetstone 1977). Indeed, in laboratory experiments, amphipods prefer higher surface area seagrasses and demonstrate no preference for differences in seagrass morphology, such as wider blades (Stoner 1980). This preference by amphipods may be due to changing vulnerability to predation in beds with lowered surface area (Stoner 1980). Similarly, in the field, fish abundances positively correlate with seagrass surface area, but not shoot densities (Micheli et al. 2008). However, surface area may only alter community composition and abundance of fauna at low levels of overall complexity (Fonseca et al. 1996). In contrast, benthic macrofauna can show an increase in abundance and diversity with increasing shoot density (Rodil et al. 2021). Further, neither higher meiofauna densities (De Troch et al. 2005) nor epifauna abundances were associated with greater surface area (Virnstein and Howard 1987). Structural complexity may also impact predator success rates, and thus prey abundances, with increased shoot densities or increased surface area per unit biomass preventing predators from capturing infaunal prey due to a decrease in accessibility or an increase in time for a prey item to escape (Orth et al. 1984). There are other cases, however, such as pinfish in turtle grass (*Thalassia testudinum)* meadows where pinfish predation rates on grass shrimp (*Palaemonetes pugio*) do not differ across seagrass densities (Canion and Heck 2009).

In addition to the structure of the seagrass itself, the presence and structure of attached epibiotic organisms, such as epiphytes, may further enhance the complexity of seagrass beds and influence the faunal communities (Hall and Bell 1988, Schneider and Mann 1991, Bologna and

Heck 1999). Some small epifaunal invertebrates have increased abundances in areas of higher epiphytic cover (Hall and Bell 1988, Schneider and Mann 1991), although this could be due to the role of epiphytes as a food source rather than their addition of structure or refuge (Bologna and Heck 1999). Further, increased invertebrate abundances due to epiphytic cover may also enhance the abundance of nekton through food provisioning (Bologna and Heck 1999). In cases where epiphytes improve foraging opportunities for fishes, their presence may play an important role as a structural complexity metric shaping faunal communities.

Physical and landscape-scale processes further complicate analyses of the relative importance of habitat complexity metrics. For example, proximity to patch edges may influence epifaunal density to a greater degree than structural complexity alone (Moore and Hovel 2010). Relationships between physical characteristics of seagrass beds, such as the hydrodynamic energy regime, and faunal densities and richness may vary both spatially and temporally (Hovel et al. 2002). Seagrass habitat provisioning for diverse faunal communities is further dictated by bed depth (França et al. 2012, Whitfield 2017). Differences between water depths may influence seagrass species composition, shoot density, and fragmentation (Fonseca and Bell 1998). Further, deeper beds may provide increased habitat heterogeneity, a form of complexity, as compared to more shallow beds by providing space above the leaf canopy that can be used by motile fauna (Boström et al. 2006). Indeed, epifaunal communities vary among structurally identical artificial seagrasses which varied only in their depth, with increased amphipod abundances in the intertidal and increased penaeid shrimp abundances in the subtidal (Micheli et al. 2008). Species richness has been found to be higher in shallower beds (Hutchinson et al. 2014), with intertidal seagrass beds acting as important nursery areas (Madi Moussa et al. 2020). Structure of faunal assemblage varies among beds of different depths (Hutchinson et al. 2014), as does the relative

difference in assemblage size between bare and vegetated patches (Jenkins et al. 1997). In tidal systems, faunal access to intertidal habitats is influenced by depth, given that habitats will be exposed to air at low tides (West and Zedler 2000, Whitfield 2017). However, the effects of depth on faunal communities may be conflated by differing seagrass communities colonizing subtidal or intertidal areas, particularly when seagrass species are morphologically distinct (Micheli et al. 2008). It is therefore difficult to elucidate whether fine-scale complexity metrics (e.g., shoot density, biomass) as opposed to physical settings (e.g., depth) are driving community differences.

In this study, we conducted observational field surveys to assess how small-scale differences in seagrass complexity across beds influence motile faunal community abundances and composition. We hypothesized that the fine-scale complexity metrics of shoot density, canopy height, seagrass species diversity and composition, and percent cover would be positively correlated with increased motile faunal abundances and species richness in seagrass beds. Results from the observational field studies point towards canopy height as a predictor in faunal community abundance and richness. Because greater seagrass canopy heights occur in deeper water and seagrass surface area increases as canopy height and shoot densities increase (Sirota and Hovel 2006), we conducted a laboratory mesocosm experiment to independently test the influence of water depth, canopy height, and surface area on habitat preference in a common motile, seagrass-associated fish, *Lagodon rhombiodes* (pinfish). We decomposed individual factors of habitat complexity by controlling for surface area and shoot density in the artificial seagrass units deployed in our experimental mesocosms. We hypothesized that the fish would prefer artificial seagrass with taller canopies in deeper areas, independent of changes in surface area and shoot density.

Methods

To test the aforementioned hypotheses, we conducted field observations over two years (April through September 2019 and in June and July 2020) and a laboratory experiment. First, we conducted field observations to test our hypothesis that fine-scale complexity metrics (e.g., higher shoot densities, taller canopy heights) would be positively correlated with increased abundances and species richness in seagrass beds. To test our hypothesis that fauna would show a preference for seagrass with increased canopies in deeper areas, independent of shoot density or surface area, we conducted a mesocosm habitat preference experiment on pinfish from June through August 2022.

Study Site

Our field observational study was conducted in Back Sound, North Carolina, a shallow, well-mixed estuarine system in Carteret County, NC. Back Sound is characterized by high salinity and diurnal tides due to its proximity to the Beaufort and Barden inlets. The seagrass communities of Back Sound are comprised of a mixture of *Zostera marina, Halodule wrightii*, and *Ruppia maritima*, with seagrass dominance changing seasonally throughout the summer and between seagrass beds (Bartenfelder et al. 2022). We sampled six seagrass beds monthly from April through September 2019, with beds randomly selected from 20 mixed community seagrass beds across the entirety of Back Sound and 18 of the 20 beds in June and July 2020 (Figure S2.1). The mesocosm experiment was conducted at the University of North Carolina at Chapel Hill's Institute of Marine Sciences (UNC-IMS) wet-lab facilities with flow-through seawater from Bogue Sound, North Carolina.

Seagrass and Motile Fauna Surveys

From April through September 2019, we sampled motile faunal communities monthly occupying a random subset of six seagrass beds selected from 20 possible sites (IACUC AUP #D358; SEAP Collection Permit #706671, #706481, #1627488; Figure S2.1). North Carolina seagrass communities are highly seasonal with both the grass cover and the fish community changing throughout the spring, summer, and early fall (Field et al. 2021, Bartenfelder et al. 2022; Table S2.1). Our initial sampling took place across six months, encompassing seasonal variation in seagrass and fish presence (Table S2.1). To disentangle differences in the bed communities due to seasonality, we conducted 2020 trawl sampling within a single month (June 15 – July 9, 2020). We sampled 18 seagrass beds in June and July 2020, which coincides with a seasonal peak in motile fauna abundance, the highest seagrass canopy heights observed in 2019 sampling (Figure S2.3), and when both *Z. marina* and *H. wrightii* are present in North Carolina seagrass beds (Bartenfelder et al. 2022).

Seagrass Complexity Metrics

To quantify seagrass complexity metrics and species composition at each site surveyed, we delineated three, 50-m transects across each bed. Where possible, transects were placed parallel to each other in the seagrass bed. In smaller, more patchy beds, transects were placed end to end or perpendicular (though not crossing) to ensure the greatest seagrass presence across the transect. Along each transect, we measured percent cover and canopy height in 0.0625m^2 quadrats placed every five meters. We estimated percent cover according to the North Carolina Vegetation Survey Index (NCVI), which maximizes the ability to distinguish differences between areas of low cover (e.g., 1% and 2%) easier than high cover (e.g., 25% and 26%; Peet et al. 1998). We measured canopy height by taking the heights (in mm) of the 5 tallest seagrass shoots within the quadrat, regardless of seagrass species. A single core was taken along each transect to

quantify the shoot density, shoot length, leaf width, leaf number per shoot, and branch number per shoot (Figure S2.2). Cores were taken at the first quadrat to surpass over 50% cover along the transect or where seagrass cover was the highest if no quadrat had over 50% cover. Core samples were taken with a 10-cm diameter metal corer pushed into the sediment to a depth of 15 cm. The corer was extracted and all material within was sieved to remove sediment and shells. Sieved samples were placed in paint strainer bags and placed on ice for transport back to East Carolina University (ECU) in Greenville, NC, or UNC-IMS in Morehead City, NC, where they were transferred to plastic Ziploc bags and frozen. Core samples remained frozen until processing where they were thawed and processed at ECU or UNC-IMS (Donaher et al. 2021). Additionally, because water depth at low tide was observed to vary across seagrass beds during the 2019 sampling, in 2020, the elevation of the seagrass bed relative to the North American Vertical Datum of 1988 (NAVD88) was taken at the location of each quadrat using a Trimble R10 Real-Time Kinematic (RTK) GPS (0.5-1.0 cm horizontal and 1.0-4.0 cm vertical resolution).

Seagrass cores were thawed in lukewarm water and placed in a tray with a small amount of water. We selected five random shoots of each species and measured the following: shoot length, leaf width, number of leaves per shoot, and number of branches per shoot. In species without branching (*H. wrightii* and non-reproductive *Z. marina*) branch number was recorded as one branch. Aboveground biomass from the subset of measured shoots was placed in a foil to be dried and weighed separately from the rest of the core. The remaining shoots were identified to species, enumerated, and aboveground biomass separated from belowground biomass. Aboveground biomass from each species was placed in separate, pre-weighed foil packets, placed in a 60ºC oven until dry, and massed (Donaher et al. 2021). The mass of the foil packets

was subtracted from the total mass of the sample and packet to give a measurement of the aboveground biomass. We calculated surface area of the seagrass from cores by multiplying the average length, width, and leaf number per shoot by the number of shoots. This was done for each species of seagrass in the core and combined for a measure of total surface area.

In 2020, we also measured epibiont biomass from seagrass cores to better understand how bed depth and seagrass complexity may influence epibiont load. This measurement may provide a proxy for epifaunal abundances, a food source for many mobile fauna (Hall and Bell 1988, Bologna and Heck 1999). Five random shoots of each species were scraped with a glass microscope slide to release epibionts from the blade and length and width of the scraped blades were recorded. Scraped materials were placed in a foil packet, placed in a 60ºC oven until dry, and massed for epibiont load calculations. We calculated epibiont load by diving the weight of all epibionts by the weight of the blade to standardize to the relative load of epibiont, with higher values indicating a higher epibiont load.

Motile Fauna Sampling

In 2019 and 2020, to sample motile fauna, (nekton; all fishes and decapod crustaceans; Aleev and Aleyev 2012), we conducted two tows (two minutes per tow) through the seagrass beds using a 5-m otter trawl (15-m head rope, 2.0-cm body mesh, 0.6-cm cod end mesh, 0.3x0.7-m doors) with a 4-seam balloon design, with floating and lead lines but without a tickler chain (Baillie et al. 2015). The boat was kept at 3 – 4 kilometers per hour during tows as indicated by a GARMIN GPSMAP 78sc handheld GPS unit. All organisms caught in the trawl were identified to the lowest taxonomic level using the Peterson Field Guide to Atlantic Coast Fishes (Robins et al. 1986; Table S2.1). Individuals of each species were enumerated, weighed as a species, and released. Any unknown organisms were placed on ice and transported back to the UNC-IMS for

meristic identification. We recorded distance towed to standardize abundances and weights in statistical analyses, allowing a measure of catch per unit effort (CPUE). We averaged counts and weights between the two tows of each bed to account for sites where low seagrass cover allowed for only a single tow within the bed.

Mesocosm Experiment

We tested our hypothesis that pinfish would show a preference for seagrass with taller canopy heights in deeper areas, independent of shoot density or surface area, we conducted an outdoor mesocosm experiment from June 24 through August 3, 2022, at the UNC-IMS in Morehead City, North Carolina. Pinfish were the most common North Carolina seagrass fish, comprising 60-80% of the catch in our trawl surveys (Tables S2.1, S2.2). Further, pinfish CPUE was also positively correlated with increased canopy height in natural seagrass beds in 2019 (Figure 1; Tables S2.3, S2.4).

Artificial Seagrass Unit Design and Construction

For our choice experiment, we constructed artificial seagrass units (ASUs) with half of each ASU comprised of a tall canopy and half comprised of a short canopy (Figure S2.4). ASUs are a common tool to test for the effects of differences in seagrass structure or landscape configuration without conflating results with increased primary production or seagrass growth (Bell et al. 1985, Bologna and Heck 2000, Lee et al. 2001, Tanner 2006, Moore and Hovel 2010, Hovel et al. 2016). A tall-canopied bed of seagrass will have a higher total surface area than a short canopy bed with the same shoot density and species composition. Similarly, if a tall- and a short-canopied bed share the same surface area, then shoot density necessarily differs between the two. As such, we sought to control for both shoot density and surface area in our experiment by designating three different ASU combinations for our choice assays. The first ASU treatment

combination had one tall canopy and one short canopy ASU with equal shoot densities resulting in double the surface area in the tall canopy ASU. The second and third ASU combinations had equal surface areas across the tall and short canopy choices, which resulted in differences in shoot density between the tall and short canopy ASUs (i.e., the shoot density of the short canopy ASU was twice the shoot density of the tall canopy ASU). The ASUs in the second choice combination each had a total surface area equal to the tall canopy ASU in the equal-shoot-density choice combination and the ASUs in the third combination each had a total surface area equal to the short canopy ASU in the equal-shoot-density choice combination. This resulted in equal shoot density (ESD), equal high surface area (HSA), and equal low surface area (LSA) treatments. We hypothesized that pinfish would show a preference for the taller canopy ASUs in deeper water, regardless of surface area or shoot density.

ASUs were constructed of 1.18 x 0.86 m square pieces of VEXAR mesh with a 2.5 cm hole size. We tied green plastic ribbons to simulate seagrass shoots to the mat such that one half of the mat was covered with short ribbon (15 cm tall) and the other was covered with tall (30 cm tall). We tied the ribbons such that each shoot contained two "leaves" of equal height. We constructed three ASU types: ESD (200 shoots of tall ribbon and 200 shoots of short ribbon), HSA (200 shoots of tall ribbon and 400 shoots of short ribbon), and LSA (100 shoots of tall ribbon and 200 shoots of short ribbon).

Experimental Mesocosm Setup

Mesocosm enclosures were constructed within 4.2 x 1.2 m outdoor metal tanks at the UNC-IMS (Figure S2.4). Enclosures were constructed by sectioning off a 2.34 m length section of the middle of the tank with two 0.4 x 1.2 m pieces of 0.25 cm thick plywood with 3/8" holes drilled throughout to allow for water flow at either end. To create "deep" and "shallow" depth

habitat treatments, one PVC foam board (cut to 1.02 x 1.2 m) was placed randomly on one side of the tank at the bottom ("deep") and one board was placed on the other end of the tank elevated 15 cm above the bottom using bricks ("shallow"). We constructed a 0.15 m tall, 0.3 m long, and 1.2 m wide ramp using two 1.2 m wide pieces of 5 inch triangular "GutterStuff" foam gutter insert. We topped the ramp with PVC foam board and placed it in the center of the tank between the high and low depth areas. All boards were adhered to the tank with 3M heavy duty duct tape and 3M marine adhesive sealant to keep fish from escaping from the enclosure. Once in place, one ASU was placed on one side of the tank and a matching ASU was placed on the other. We placed the ASUs in the tank such that the location of the "tall" and "short" canopies was randomized every day and between the deep and shallow sides. To ensure each ASU treatment (ESD, HSA, LSA) was used in each tank weekly we rotated ASU treatments across tanks daily. Rotation of ASU treatment also allowed each ASU to be unused at least one day a week, ensuring enough time to dry and ensure structurally complex epibionts did not grow. We spread a thin (~1 inch) layer of sand over the ASUs, the foam boards, and the ramp to fully cover the mesocosm enclosure prior to water being added to the tanks. Raw seawater from Bogue Sound was pumped into the tanks until the water reached a depth of 30 cm in the deep portion of the mesocosm enclosure and 15 cm in the shallow area. Flow was then stopped to remove any effect of water movement on the preference of pinfish. After every trial half of the water was fully drained and raw seawater was pumped into tanks to replace the removed water and ensure a depth of 30 cm in the deep portion. This ensured ambient seawater temperature and salinity across trials.

Fish Collection

We collected pinfish for use in the experiment by otter trawl, seine, and minnow trap from Bogue and Back sounds, NC. Once captured fish were kept in 5-gallon buckets fitted with air pumps to maintain oxygen circulation until they could be brought to the UNC-IMS wet lab facility. Fish were kept in 1.8 x 0.45 m holding tanks with flow through filtered sea water from Bogue Sound until use in a trial. Only fish collected within seven days of the trial were used. We checked dissolved oxygen, salinity, and temperature daily, and pH, ammonia, nitrate, and nitrite concentrations weekly. We fed fish daily with a combination of fish flakes and frozen shrimp pieces until satiation. After use in a trial, or after seven days held in the wet lab facilities, we released fish into Bogue Sound (IACUC AUP #D374, #87157; SEAP Collection Permit #706671).

Habitat Preference Trials

Immediately following the filling of the tanks, a single pinfish was moved from holding tanks to the trial arena. Each fish was used only once, for a single trial. Fish were placed gently in the center of the tank above the ramp. Tanks and fish were left undisturbed for 30 minutes at which point the location of the fish was observed visually and recorded. Trials were also recorded with GoPro HERO6 Black cameras to verify the location of pinfish when the observer was unsure of the location at the end of a trial. After recording the location of the fish, it was removed and placed in a holding tank to await release.

Statistical Analyses

Seagrass and Motile Fauna Surveys

We ran a correlation analysis between pairs of the seagrass complexity metrics: canopy height, percent cover, shoot density, shoot length, leaf width, leaf number per shoot, branch number per shoot, and number of seagrass species in bed, to determine which, if any, metrics

were correlated (Tables S2.5, S2.6). We did this for both 2019 and 2020 sampling. We then ran models on one of multiple correlated metrics that has previously been shown as influential for faunal communities and was included in our hypotheses for further analysis to encompass all complexity metrics.

Bayesian generalized linear mixed models (GLMMs; 2019) and generalized linear models (GLMSs; 2020) were used to determine the fixed effects of shoot density (2019), canopy height (2019, 2020), and the identity of seagrass species present (2019, 2020), on the (1) faunal abundance, (2) faunal biomass, (3) species richness, and (4) standardized biomass (total biomass / total abundance; Tables S2.7, S2.8). A linear model (LM) was used to determine the fixed effect of the identity of seagrass species present on the standardized biomass in 2020. A Bayesian GLMM (2019) and a GLM (2020) was used to determine the fixed effect of canopy height on the abundance of individual species of interest (those with 75 or more individuals in 2019 or 50 or more individuals in 2020) at each sampling location from our trawls. We also used a Bayesian GLMM (2019) and GLM (2020) to determine the fixed effect of shoot density on the abundance of gulf flounder (*Paralichthys albigutta*), as previous studies have shown flounder may respond more to shoot density than other characteristics of the seagrass bed (Gilbert 1986, Goldberg et al. 2002, Pullen et al. 2022). A GLM was used to determine the fixed effect of seagrass surface area, depth, and epibiont load on the abundance of fauna caught in 2020. A LM was used to determine the fixed effect of depth on the (1) canopy height, and (2) epibiont load by blade weight of each seagrass bed sampled in 2020. Distance towed was included as an offset in all models with abundance and biomass to standardize abundances and biomass to CPUE. Month and site sampled were included in the model as random effects for all 2019 models. A Bayesian approach was used in 2019 to resolve singularity and obtain reliable estimates for the random effects of

trawl month and site. We created all combinations of the Bayesian models and compared each using leave-one-out cross-validation (LOO) criteria selection. We performed hypothesis testing on Bayesian models to determine if the fixed effect had a non-zero effect on the response variable for all models with a continuous, numerical fixed effect. We used an alpha level of 95% to determine significance after hypothesis testing in 2019 and an alpha level of 0.05 to determine significant p-values for all 2020 models. We used an alpha of 0.1 to determine marginally significant results.

The relationship of standardized biomass and canopy height in 2020 is influenced by a high leverage outlier, due to the presence of a large ray in the catch, however when this point is removed, the results and interpretation do not change, therefore the outlier was included in our analysis. A single seagrass bed was highly influential in our 2020 analyses with highest overall CPUE, faunal biomass, canopy height, and the second highest species richness. This bed is also the only enclosed bed and the only *Z. marina* dominated bed. As we cannot accurately compare this bed to the other samples and the bed was influential in results of our models we conducted all analyses of 2020 data with and without the *Z. marina* dominated bed. Data presented in the manuscript do not include the *Z. marina* bed unless otherwise noted, but all analyses are provided in the supplemental information. There was a single bed with high epibiont load (greater than 2.5 time higher than the second highest load) so we have conducted the analysis with epibiont load twice, once with and once without the outlier.

Mesocosm Experiment

We performed a Bayesian multinomial linear regression analysis on the preference of pinfish between the four habitat options (deep-tall, shallow-tall, deep-short, shallow-short). Each trial included a single fish and single choice, resulting in data including the number of fish

choosing each of the four habitat choices. Each ASU type (equal shoot density, equal surface area – high, and equal surface area – low) was analyzed separately with an identical model. Our models included the random effects of tank used (1 or 2), week of study, and deep side of the tank (left or right) on the choice of the fish. Choice was defined in the categorical family. We performed 100,000 iterations across 4 chains for each model. We visualized diagnostic plots to ensure convergence of chains and appropriateness of model application.

All statistical analyses were performed using the R statistical software using the packages lme4 (Bates et al. 2015) and brms (Bürkner 2017).

Results

Seagrass and Motile Fauna Surveys

In both 2019 and 2020 beds were comprised of a mix of one, two, and three species seagrass species with beds containing solely *H. wrighti,* a mix of *H. wrightii* and *R. maritima* or *Z. marina*, or comprised of all three seagrass species. In 2019, seagrass beds containing *R. maritima* had more branchers per shoot and more leaves per shoot than beds that did not contain *R. maritima* (Table S2.5). In 2020, beds containing *R. maritima* continued to have more branches per shoot than beds not containing *R. maritima* and additionally had increased percent cover than those not containing *R. maritima* (Table S2.5). While leaf width was not correlated with the number of species present, only *Z. marina* has variation in leaf width, with both *R. maritima* and *H. wrightii* leaves consistently measuring at 1 mm wide. In both 2019 and 2020, seagrass beds with taller canopies had higher percent cover and contained longer shoots as measured in core samples (Tables S2.5, S2.6). Additionally, in 2020, beds with taller canopies had increased leaf widths, leaf numbers per shoot, shoot densities, total seagrass biomass, and were found at deeper

depths (Tables S2.6). In both 2019 and 2020 seagrass beds with increased leaf widths also had increased leaf numbers per shoot and increased shoot lengths. This was likely due to an increase in *Z. marina* presence as only *Z. marina* has an increase in leaf width and therefore was included in analyses under the species present per bed. Further, beds with higher number of branches (indicative of *R. maritima)* also had increased number or leaves per shoot. This was additionally included in models under the seagrass species identity. Finally, in 2019 beds with increased shoot densities also had increased aboveground biomass, leaf widths, leaf numbers per shoot, marginally increased percent cover, and marginally decreased shoot lengths (Tables S2.5, S2.6). Because previous studies have found correlations between foundation species diversity, shoot density, and canopy height and faunal metrics (Boström and Bonsdorff 2000, Canion and Heck 2009, Hori et al. 2009), we chose to only investigate the effect of seagrass species identity present in the bed (2019 and 2020), canopy height (2019 and 2020), and shoot density (2019) on faunal communities for these correlated metrics.

We caught a total of 19,465 individuals across all 2019 trawls and 14,448 individuals across the 2020 trawls (Tables S2.1, 2.2). We found no relationship between shoot density and CPUE (Bayesian $R^2 = 0.2818$), total faunal biomass (Bayesian $R^2 = 0.4961$), standardized faunal biomass (Bayesian $R^2 = 0.6205$), or species richness (Bayesian $R^2 = 0.4467$; Figure S2.5; Tables S2.9-S2.17) in 2019 sampling. We also did not see a relationship between seagrass species present in the beds and CPUE, faunal biomass, standardized faunal biomass, or species richness with all credible intervals overlapping in our 2019 analysis (Figure S2.6; Tables S2.9, S2.18-S2.25). In 2020, we continued to find no correlation between the seagrass species composition of the bed and CPUE, faunal biomass, standardized biomass, or species richness (Figure S2.7; Table S2.26).

Our 2019 trawl data did, however, show a positive correlation between canopy height and CPUE, with faunal abundances increasing as canopy height increases (Bayesian $R^2 = 0.5311$; Figure 2.2A; Tables S2.7, S2.27, S2.28). We also found a positive correlation between canopy height and faunal biomass with biomass increasing with increasing canopy height as well as across months (Bayesian $R^2 = 0.5778$; Figure 2.2C; Tables S2.7, S2.29, S2.30). However, the size of individual fauna did not increase with canopy height, as evident by the lack of correlation between standardized biomass and canopy height (Bayesian $R^2 = 0.1336$; Figure 2.2D; Tables S2.7, S2.31, S2.32). We found a significant positive correlation between species richness and the fixed effect of canopy height and the random effect of trawl month (Bayesian $R^2 = 0.5010$), with richness increasing with increasing canopy height. Species richness was highest in August (13.8 $\pm$ 1.6), September (13.2 $\pm$ 0.5), July (12.8 $\pm$ 0.7), and June (11.5 $\pm$ 1.2) and lowest in May (7 $\pm$ 0.5) and April (5.3 $\pm$ 0.8). We did not find a correlation between seagrass surface area as calculated from core samples and CPUE in 2019 (Bayesian $R^2 = 0.2873$; Tables S2.7, S2.35 - S2.36).

In 2020 we continued to find a positive relationship between canopy height and CPUE with CPUE increasing with increasing canopy height when all samples were included in the model ($R^2 = 0.2368$; Figure S2.8; Table S2.37). However, this relationship disappeared when one study site, the only *Z. marina*-dominated seagrass bed sampled in 2020, was removed ($R^2 = 0.0256$; Figure 2.3A; Table S2.38). Without this outlier site, we also found no correlation between canopy height and biomass in 2020 ($R^2 = 0.0067$), and the lack of a correlation between biomass and canopy height persisted when biomass was standardized to the CPUE ($R^2 = 0.0534$; Figure 2.3C,D; Tables S2.38, S2.39). Further, we did not find a correlation between canopy height and species richness in the 2020 sampling ($R^2 = 0.0007$; Figure 2.3B; Table S2.38).

The top four species caught in the trawls by overall abundance in 2019 were pinfish (78.9%), pigfish (*Orthopritis chrysoptera;* 9.4%), anchovy (*Anchoa spp.;* 3.1%), and spot (*Leiostomus xanthurus;* 1.8%; Table S2.1). In 2020 we saw only one species of the top four species change, with most abundant species being pinfish (63.7%), pigfish (24.1%), spot (4.8%), and planehead filefish (*Stephanolepis hispidus*; 1.8%; Table S2.2). In 2019, we found a positive correlation between canopy height and the abundances of pinfish (Bayesian $R^2 = 0.5112$) and pigfish (Bayesian $R^2 = 0.5398$; Figure 2.1A,B; Tables S2.3, S2.4, S2.7, S2.40, S2.41). We found a slight positive correlation between spot abundances in 2019 and seagrass canopy height. However, this was likely due to a single bed with high abundances of spot and high canopy height (Bayesian $R^2 = 0.2644$, Figure 2.1C; Tables S2.7, S2.42, S2.43). We did not include an analysis of anchovy in relation to canopy height as anchovy are not seagrass-associated fish and their high abundances at specific sampling locations is likely due to the schooling nature of the fish passing through the trawl rather than a presence in the seagrass bed itself (Peterson et al. 1980, Rozas and Minello 1998). In 2020, the relationships between canopy height for each of the top four species caught shifted from 2019 results. Of the top four species in 2020, we found only a positive correlation between canopy height and the CPUE of planehead filefish ($R^2 = 0.3545$; Figure 2.4D; Table S2.38). Alternatively, spot showed a marginally significant negative correlation between canopy height and CPUE ($R^2 = 0.0980$; Figure 2.4C; Table S2.38). Neither pinfish ($R^2 = 0.0628$) nor pigfish ($R^2 = 0.0034$) had a correlation between canopy height and CPUE (Figure 2.4A,B; Table S2.38).

In addition, for the species of special interest (those with 75 or more individuals over the sampling period), we found a positive relationship between the canopy height and CPUE of blue crabs (*Callinectes sapidus;* Bayesian $R^2 = 0.2487$) and silver perch (*Bairdiella chrysoura)* in

2019 (Bayesian $R^2 = 0.3476$; Figure S2.9A,F; Tables S2.7, S2.44-S2.47). However, we found no correlation between canopy height and CPUE of blue crabs ($R^2 = 0.0600$) or silver perch ($R^2 = 0.0514$) in 2020 (Figure S2.10; Table S38). In 2019 we found a weak, but positive correlation between canopy height and the combined CPUE of snapper species (*Lutjanus* spp.) and gag grouper (*Mycteroperca microlepis*; Bayesian $R^2 = 0.3768$ Figure S2.9B; Tables S2.7, S2.48, S2.50). Snapper and gag grouper abundances were combined as the abundances of each individual species was too low to include in statistical analyses and these species have similar life histories, entering the North Carolina estuaries juveniles during the summer to use seagrass meadows as nursery areas (Adams 1976, Tzeng et al. 2003, Adamski et al. 2011; Table S2.1). We were unable to investigate the relationship of canopy height and snapper and grouper in 2020 as we did not catch these species in high enough abundances. In 2019 we found no relationship between canopy height and CPUE for planehead filefish (Bayesian $R^2 = 0.6387$) or mojarra species (Gerreidae*;* Bayesian $R^2 = 0.6867$; Figure S2.9C,D; Tables S2.7, S2.50-S2.53). However, in 2020 we found a negative correlation between canopy height and CPUE for mojarra species ($R^2 = 0.2640$; Figure S2.10; Table S2.38). Finally, in 2019 there was no relationship between canopy height (Bayesian $R^2 = 0.1750$) or shoot density (Bayesian $R^2 = 0.1697$) and CPUE of gulf flounder (Figure S2.9E, Tables S2.7, S2.54-S2.57). This relationship remained in 2020 where we found no correlation between canopy height ($R^2 = 0.1186$) or shoot density ($R^2 = 0.0005$) and CPUE of gulf flounder (Figure S2.10; Table S2.38).

We found a marginally significant negative correlation between bed depth relative to local mean sea level (LMSL) and canopy height, with taller canopy heights in deeper beds ($R^2 = 0.1753$; Figure 2.5; Table S2.39). However, we did not observe a correlation between bed depth relative to LMSL and CPUE ($R^2 = 0.0154$; Figure S2.11; Table S2.38). We further found no

correlation between epibiont weight per blade weight and bed depth relative to LMSL (R^2 = 0.0877; Table S2.39). However, when a single bed with high epibiont load (greater than 2.5x higher than the next highest bed) was removed, we did see a significant negative correlation between bed depth relative to LMSL and epibiont load with increased epibiont loads in shallower seagrass beds (R^2 = 0.2658; Table S2.58). We found no correlation between seagrass surface area (R^2 = 0.2368) or epibiont load and CPUE (R^2 = 0.0479; Tables S2.38). When the epibiont load outlier was removed, no relationship between epibiont load and CPUE emerged (R^2 = 0.0043, Table S2.59).

Mesocosm Experiment

When comparing the credible intervals of the models we found a preference for deep habitats for each of the ASU types (Figure 2.6). Contrary to our hypothesis that tall, deep canopies would be preferred regardless of surface area and shoot density, in trials with equal surface area between tall and short canopies, there was no preference for either tall or short canopies regardless of depth (Figure 2.6B,C; Tables S2.60, S2.61). Alternatively, in trials with equal shoot density but an increased surface area in the tall canopies as compared to the short canopies, we found a preference for tall, deep, high surface area canopies (Figure 2.6A; Table S2.62).

In the equal shoot density trials, 26.7% of pinfish chose the deep-short habitat, 51.67% chose the deep-tall habitat, 5% chose the shallow-short habitat, and 16.7% chose the shallow-tall habitat. In the equal low surface area trials, 49.2% of pinfish chose the deep-short habitat, 39% chose the deep-tall habitat, 3.4% chose the shallow-short habitat, and 8.4% chose the shallow-tall habitat. In the equal high surface area trials, 37.7% of pinfish chose the deep-short habitat, 54.1%

chose the deep-tall habitat, 1.6% chose the shallow-short habitat, and 6.6% chose the shallow-tall habitat.

Discussion

Complexity greatly influences the abundance and richness of faunal communities across ecosystems (Heck and Orth 1980, Staudacher and Füreder 2007, Kovalenko et al. 2012, Stein et al. 2014), although the mechanism driving this relationship has remained unclear. Here, we find increased faunal richness, abundance, and biomass in beds with taller canopies as well as taller canopies in deeper beds relative to LMSL. Our habitat choice experiment indicates that perhaps depth and surface area, rather than canopy height, is an important determinant in pinfish habitat choice, and may be driving overall faunal community abundances. Our experimental results are consistent with previous findings that organisms may prefer increased surface area, rather than other metrics that are correlated with surface area (e.g., canopy height, leaf width, plant biomass; Heck and Wetstone 1977, Stoner 1980, Micheli et al. 2008). Additionally, in some areas, the physical setting, namely water depth relative to LMSL results in increased surface area of the habitat structure due to increased canopy heights (Figure 2.5), further modifying community composition and abundance. Further as the mesocosm experiment demonstrates, small, motile fauna, such as pinfish, may prefer deeper habitats over shallow when given a choice. We further demonstrate that fauna may respond to metrics of habitat complexity differently, with only some species responding to the fine-scale metrics quantified in this study. Likely, faunal life-history characteristics play a role in determining how fauna may respond to differences in complexity of their habitat.

This study provides some evidence that seagrass beds with taller canopies, and thus increased total surface area, support more species rich communities and greater motile fauna abundances, than shorter canopied seagrass meadows (Figure 2.2). Previous investigations have found similar increases in abundance (Micheli et al. 2008), as well as decreased predator effectiveness with increased habitat surface area (Orth et al. 1984). Decreased predator effectiveness may, in turn, increase prey abundances, further modifying community composition (Orth et al. 1984). Previous studies have found positive correlations between both faunal richness and densities and shoot density (Boström and Bonsdorff 2000), percent cover (McCloskey and Unsworth 2015), and biomass of the measured foundation species (Hovel et al. 2002, Velasco-Charpentier et al. 2021), all of which we found to be correlated with surface area in our study system in 2019 and most of which were correlated with surface area in our study system in 2020 (Tables S2.5, S2.6). The surface area provided by habitat structure may be influential in shaping faunal communities across habitats (Gladfelter et al. 1980, Dean and Connell 1987), whether terrestrial (Spurr and Warburton 1991), aquatic (Barnes et al. 2013, Labat et al. 2022), or marine, including those outside of seagrass beds (Beck 2000, Kostylev et al. 2005) or in deep, non-coastal habitats (Bergquist et al. 2005). Our results of pinfish habitat preference align with cross-system studies showing surface area is an important determinant in faunal communities across systems (Gladfelter et al. 1980, Kostylev et al. 2005, Barnes et al. 2013).

Shallow waters are often considered refuges for fish communities with greater faunal abundances and lowered predation pressure (Ruiz et al. 1993, Ryer et al. 2010). Therefore, fish may need to seek out shelter in the form of structured habitat (MacDonald et al. 2016) or shaded areas, often provided by a structured habitat (Ellis and Bell 2004). The most common seagrass-associated fish species in North Carolina, pinfish, preferred the deeper offered seagrass habitat

and, within these deeper habitats, preferred areas with higher surface area, rather than tall canopies (Figure 2.6), potentially due to a decreased predator effectiveness in high surface area habitats (Orth et al. 1984). Of note, the depth gradient in our study (<1 m between shallowest and deepest beds; 0.15 m in experimental mesocosms) is far less than previous studies, which include depths of up to, and even over 20 m (Ryer et al. 2010, Jankowski et al. 2015, MacDonald et al. 2016). Previous work has considered shallow water habitats to include those less than 2 m deep (Bradley et al. 2017), so, while we found a preference for deep water, this would still be within the greater context of a shallow water refuge. Therefore, it is important to consider slight differences in depth in shallow water estuaries which may have large implications for faunal community structure across ecosystem types.

Species-specific relationships between abundances and canopy height reveal habitat use and life history strategy are important factors in determining correlations between complexity metrics and faunal abundance. For example, planehead filefish, which consume seagrass-associated animals as well as, to a lesser extent, the seagrass blades themselves (Livingston 1982, Heck et al. 2015, Mancera-Rodríguez and Castro-Hernández 2015) and use seagrass beds as a refuge from predation (Heck and Wilson 1987, Heck and Orth 2006), show higher abundances in seagrass beds with taller canopy heights in 2020, regardless of outlier inclusion (Figures 2.4, S2.12). Epibenthic species, such as planehead filefish, respond strongly to number of seagrass patches at low seagrass cover (Yeager et al. 2016), indicating a strong interaction with their habitats and a potential explanation for the positive relationships between planehead filefish abundances and canopy height. Snapper and grouper, which use seagrass beds as nursery habitat prior to moving offshore to adult habitats at the start of the fall when waters begin to cool (Ross and Moser 1995, Coleman et al. 1999), also demonstrated a positive, though weak,

relationship with canopy height in 2019 (Figure S2.9). Snappers and groupers are highly seasonal in North Carolina and typically only arrive in seagrass beds in the second half of the summer, which was after the end of our 2020 sampling (Adams 1976, Tzeng et al. 2003, Adamski et al. 2011). Pinfish, the most common fish species caught in our sampling, was found in higher abundances in taller canopied seagrass beds in 2019. Pinfish are often found in much higher abundances in seagrass beds, or in structured habitats adjacent to seagrass beds, than in other habitat areas, especially bare sand (Jordan et al. 1996, Irlandi and Crawford 1997). This is likely due to the small size of pinfish recruiting to habitat patches and the increased growth and predation refuge offered by seagrass habitats (Jordan et al. 1996, Levin et al. 1997). High canopies and increased surface area may therefore help protect cryptic species as well as small juveniles of nursery species from predation while providing prey items within the seagrass bed, maximizing growth and survival.

However, not all fauna showed positive relationships with canopy height in our sampled seagrass beds. Alternatively, spot and mojarra, which are often found in marsh channels and less-structured habitats rather than seagrass beds (Szedlmayer and Able 1996, Nagelkerken et al. 2001, United States National Marine Fisheries Service et al. 2006), were not correlated with seagrass canopy height in 2019 (Figures 2.1, S2.9) and were negatively correlated with canopy height in 2020 (Figures 2.4, S2.10). Taller canopies may impede the feeding strategies of spot and mojarra, explaining their reduced abundances in tall-canopied seagrass beds. Finally, gulf flounder, a benthic organism residing in seagrass beds for cover and food (Gilbert 1986), did not demonstrate a relationship between abundances and canopy height (Figures S2.7, S2.10) or shoot density. As a benthic ambush predator, too high of a canopy or shoot density may negatively impact a flounder's ability to move within the habitat and search for prey. Indeed, flounder may

be less associated with the densest patches of seagrass and may be found in bare sand habitats adjacent to seagrass rather than the dense seagrass itself (Goldberg et al. 2002, Pullen et al. 2022). Though we did not observe a relationship between flounder abundance and shoot density as seen in previous studies, it is possible that our sampling design biased our results. We only measured shoot density in areas of high seagrass cover (2019) and in 3-5 cores overall (2019 and 2020), likely biasing our results to high shoot density areas only and making inferences difficult. However, the species-specific responses to canopy height observed in this study are similar to those found in previous studies within seagrass ecosystems (Schneider and Mann 1991, Hovel et al. 2002), other marine systems (Cocheret de la Morinière et al. 2004, Newman et al. 2015), and extending to terrestrial (Cousin and Phillips 2008, Hewson et al. 2011) and aquatic (O'Connor 1991, Eitzmann and Paukert 2010) systems, as well. However, here, by combining field surveys and a mesocosm experiment, we were able to control for covarying complexity metrics that are often difficult to tease apart.

Observed relationships between faunal abundances and canopy height and depth, including species-specific relationships, were highly influenced by a single seagrass bed sampled in 2020 that hosted higher faunal abundances than all other beds. This bed was the only *Z. marina* dominated bed, had the tallest canopies, was one of the five deepest beds, and is surrounded by a marsh complex protecting it from wave energy and linking the seagrass bed to adjacent marsh and oyster reefs. All else equal, wider seagrass blades increase surface area (De Troch et al. 2005), so the larger blade widths of *Z. marina* may yield an overall higher surface area than *H. wrightii,* even at lower shoot densities. The landscape context of a habitat may also be a large determinant in species abundances (Moore et al. 2011, Angelini et al. 2015, Baillie et al. 2015). Cryptic species may particularly prefer continuous, sheltered, high surface area beds

such as this (Yeager et al. 2016) and proximity to other coastal habitats (e.g., salt marsh, bivalve reefs) has previously been shown to increase the size and species richness of associated communities (Baillie et al. 2015, Goodridge Gaines et al. 2022). Therefore, due to the many unique attributes of this site, we are unable to determine the exact attribute driving faunal abundances.

In contrast to the findings of our mesocosm experiment, we did not observe clear patterns in abundance from our trawl surveys based on surface area of the seagrass bed. Likely, this is because we did not capture the true surface area of the bed, but rather a snapshot of 3-5 cores within the bed. In 2019, these were the areas with the highest seagrass cover, inflating the surface area estimates in beds that had few areas of high cover. Additionally, 3-5 core samples are likely insufficient to accurately describe fish-available surface area across a seagrass bed. Similarly, the estimates of surface area are constrained by our measurement of only a small subset of shoots rather than all blades within the shoot. Improvement can be made on our surface area estimates by increasing core and fine-scale measurement sample sizes. We also found no correlation between bed depth relative to LMSL and catch during the sampling in 2020 when the *Z. marina* dominated bed was excluded from analyses (Figure S2.11). However, this could be because we trawled within 3 hours of high tide regardless of bed depth relative to LMSL. Trawling at or near high tide resulted in similar water depths across all sites trawled regardless of relative bed depth. We were also limited in our ability to derive within-bed variation from the trawl data, as trawls capture fish from the entire bed while seagrass metrics, such as relative surface area and depth, may change within the bed. Although these sampling artifacts complicate our ability to determine drivers of abundance and richness observationally, we were able to investigate these drivers

further in the laboratory mesocosm experiment. The agreement between our three studies points towards depth and seagrass surface area as important drivers in structuring faunal communities.

Our research highlights the importance of considerations of surface area, as well as the physical setting of depth of seagrass beds. However, future studies are needed to determine if these patterns hold true across ecosystems, as well as within a single continuous habitat patch. Future studies could focus on small-scale differences within a single habitat to determine if surface area and depth matter at a small, within patch scale. Additionally, larger scale investigations of surface area and community composition across landscapes containing multiple habitat types may inform the importance of surface area and depth at a much larger scale. These studies can be done across marine and aquatic ecosystems including oyster and coral reefs, kelp, and lake or pond ecosystems, as well as in terrestrial systems. Though terrestrial systems do not have water depth, a different measure of physical setting such as elevation could be used for comparison (Rowe-Rowe and Meester 1982, Sam et al. 2019). Understanding the scale at which communities are influenced by their habitat structure will be necessary to understand how communities may be impacted by habitat degradation or potential restoration.

Complexity of a habitat influences the structure of the community residing within. Using a combination of field observations and a laboratory mesocosm experiment, we show habitat surface area and depth, a mix of structural complexity and physical setting, are most influential in shaping faunal communities. Small changes in depth (0.15 – 1 m) can have large impacts on the structure of the habitat itself as well as faunal preferences. Previous studies across habitat types often investigate structural complexity (Heck and Orth 1980, Hauser et al. 2006, Basile et al. 2021), with fewer investigating physical setting (McLachlan et al. 1993, Fonseca and Bell 1998) or both structural complexity and physical setting together (Hovel et al. 2002). Our results

show that structural complexity does not arise independent of physical setting and integrating small-scale changes in physical setting and structural complexity may be necessary to understand faunal communities across complex habitats, potentially explaining contrasting results from previous studies. Our results also highlight the need for understanding species-specific habitat interactions due to life history characteristics that may influence structural or depth preferences, sometimes differing from community-wide trends. It is imperative to take a comprehensive approach to understanding how fauna may respond to future changes in habitats and across ecosystem settings by using community- and species-specific responses, as well as considering the influence of both the structural complexity of the habitat and the physical setting.

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References

Adams, S. M. 1976. The ecology of eelgrass, Zostera marina (L.), fish communities. I. Structural analysis. Journal of Experimental Marine Biology and Ecology 22:269–291.

Adamski, K. M., J. A. Buckel, K. W. Shertzer, G. B. Martin, and J. C. Taylor. 2011. Developing Fishery-Independent Indices of Larval and Juvenile Gag Abundance in the Southeastern United States. Transactions of the American Fisheries Society 140:973–983.

Aleev, Iu. G., and Y. G. Aleyev. 2012. Nekton. Springer Netherlands, Netherlands.

Angelini, C., T. van der Heide, J. N. Griffin, J. P. Morton, M. Derksen-Hooijberg, L. P. M. Lamers, A. J. P. Smolders, and B. R. Silliman. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B: Biological Sciences 282:20150421.

August, P. V. 1983. The Role of Habitat Complexity and Heterogeneity in Structuring Tropical Mammal Communities. Ecology 64:1495–1507.

Baillie, C. J., J. M. Fear, and F. J. Fodrie. 2015. Ecotone Effects on Seagrass and Saltmarsh Habitat Use by Juvenile Nekton in a Temperate Estuary. Estuaries and Coasts 38:1414–1430.

Barnes, J. B., I. P. Vaughan, and S. J. Ormerod. 2013. Reappraising the effects of habitat structure on river macroinvertebrates. Freshwater Biology 58:2154–2167.

Bartenfelder, A., W. J. Kenworthy, B. Puckett, C. Deaton, and J. C. Jarvis. 2022. The Abundance and Persistence of Temperate and Tropical Seagrasses at Their Edge-of-Range in the Western Atlantic Ocean. Frontiers in Marine Science 9:917237.

Basile, M., I. Storch, and G. Mikusiński. 2021. Abundance, species richness and diversity of forest bird assemblages – The relative importance of habitat structures and landscape context. Ecological Indicators 133:108402.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Beck, M. W. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. Journal of Experimental Marine Biology and Ecology 249:29–49.

Bell, J. D., A. S. Steffe, and M. Westoby. 1985. Artificial seagrass: How useful is it for field experiments on fish and macroinvertebrates? Journal of Experimental Marine Biology and Ecology 90:171–177.

Bergquist, D., C. Fleckenstein, J. Knisel, B. Begley, I. MacDonald, and C. Fisher. 2005. Variations in seep mussel bed communities along physical and chemical environmental gradients. Marine Ecology Progress Series 293:99–108.

Bologna, P. A. X., and K. L. Heck. 1999. Macrofaunal associations with seagrass epiphytes Relative importance of trophic and structural characteristics. Journal of Experimental Marine Biology and Ecology 242:21–39.

Bologna, P. A. X., and K. L. Heck. 2000. Impacts of Seagrass Habitat Architecture on Bivalve Settlement. Estuaries 23:449.

Boström, C., and E. Bonsdorff. 2000. Zoobenthic community establishment and habitat complexity-the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series 205:123–138.

Boström, C., E. L. Jackson, and C. A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science 68:383–403.

Bradley, M., R. Baker, and M. Sheaves. 2017. Hidden Components in Tropical Seascapes: Deep-Estuary Habitats Support Unique Fish Assemblages. Estuaries and Coasts 40:1195–1206.

Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software 80:1–28.

Canion, C., and K. Heck. 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. Marine Ecology Progress Series 393:37–46.

Cocheret de la Morinière, E., I. Nagelkerken, H. van der Meij, and G. van der Velde. 2004. What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? Marine Biology 144:139–145.

Coleman, F., C. Koenig, A. M. Eklund, and C. Grimes. 1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. American Fisheries Society Symposium 23:233–242.

Cousin, J. A., and R. D. Phillips. 2008. Habitat complexity explains species-specific occupancy but not species richness in a Western Australian woodland. Australian Journal of Zoology 56:95.

Davis, J., K. Pitt, A. Olds, A. Harborne, and R. Connolly. 2017. Seagrass corridors and tidal state modify how fish use habitats on intertidal coral reef flats. Marine Ecology Progress Series 581:135–147.

De Troch, M., L. Vandepitte, M. Raes, E. Suàrez-Morales, and M. Vincx. 2005. A field colonization experiment with meiofauna and seagrass mimics: effect of time, distance and leaf surface area. Marine Biology 148:73–86.

Dean, R. L., and J. H. Connell. 1987. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. Journal of Experimental Marine Biology and Ecology 109:217–247.

Donaher, S. E., C. J. Baillie, C. S. Smith, Y. S. Zhang, A. Albright, S. N. Trackenberg, E. H. Wellman, N. Woodard, and R. K. Gittman. 2021. Bivalve facilitation mediates seagrass recovery from physical disturbance in a temperate estuary. Ecosphere 12:e03804.

Duarte, C. M. 1991a. Allometric scaling of seagrass form and productivity. Marine Ecology Progress Series 77:289–300.

Duarte, C. M. 1991b. Seagrass depth limits. Aquatic Botany 40:363–377.

Duarte, C. M., N. Marbà, D. Krause-Jensen, and M. Sánchez-Camacho. 2007. Testing the predictive power of seagrass depth limit models. Estuaries and Coasts 30:652–656.

Eitzmann, J. L., and C. P. Paukert. 2010. Longitudinal Differences in Habitat Complexity and Fish Assemblage Structure of a Great Plains River. The American Midland Naturalist 163:14–32.

Ellis, W. L., and S. S. Bell. 2004. Conditional use of mangrove habitats by fishes: Depth as a cue to avoid predators. Estuaries 27:966–976.

Field, D., W. J. Kenworthy, and D. Carpenter. 2021. Metric Report: Extent of Submerged Aquatic Vegetation, High-Salinity Estuarine Waters (REVISED). Page 19 pp. Albemarle-Pamlico National Estuary Partnership, Raleigh, NC.

Fonseca, M., and S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Marine Ecology Progress Series 171:109–121.

Fonseca, M. S., and J. S. Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Marine Ecology Progress Series 29:15–22.

Fonseca, M. S., D. L. Meyer, and M. O. Hall. 1996. Development of planted seagrass beds in Tampa Bay, Florida, USA. II. Faunal components. Marine Ecology Progress Series 132:141–156.

França, S., R. P. Vasconcelos, V. F. Fonseca, S. E. Tanner, P. Reis-Santos, M. J. Costa, and H. N. Cabral. 2012. Predicting fish community properties within estuaries: Influence of habitat type and other environmental features. Estuarine, Coastal and Shelf Science 107:22–31.

Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224:1–30.

Garza, C. 2016. Landscape Complexity Effects on Fisheries: Insights from Marine Landscape Ecology. Current Landscape Ecology Reports 1:1–9.

Ghadiri Khanaposhtani, M., M. Kaboli, M. Karami, and V. Etemad. 2012. Effect of Habitat Complexity on Richness, Abundance and Distributional Pattern of Forest Birds. Environmental Management 50:296–303.

Gilbert, C. R. 1986. Species Profiles. Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida). Southern, Gulf, and Summer Flounders. Page 35. Florida State Museum, Gainesville, FL.

Gladfelter, W. B., J. C. Ogden, and E. H. Gladfelter. 1980. Similarity and Diversity Among Coral Reef Fish Communities: A Comparison between Tropical Western Atlantic (Virgin Islands) and Tropical Central Pacific (Marshall Islands) Patch Reefs. Ecology 61:1156–1168.

Goldberg, R., B. Phelan, J. Pereira, S. Hagan, P. Clark, A. Bejda, A. Calabrese, A. Studholme, and K. W. Able. 2002. Variability in habitat use by young-of-the-year winter flounder,Pseudopleuronectes americanus, in three northeastern U.S. estuaries. Estuaries 25:215–226.

Goodridge Gaines, L. A., C. J. Henderson, J. D. Mosman, A. D. Olds, H. P. Borland, and B. L. Gilby. 2022. Seascape context matters more than habitat condition for fish assemblages in coastal ecosystems. Oikos 2022:e09337.

Grabowski, J. H., A. R. Hughes, and D. L. Kimbro. 2008. Habitat complexity influences cascading effects of multiple predators. Ecology 89:3413–3422.

Grabowski, J., and S. Powers. 2004. Habitat complexity mitigates trophic transfer on oyster reefs. Marine Ecology Progress Series 277:291–295.

Gratwicke, B., and M. Speight. 2005a. Effects of habitat complexity on Caribbean marine fish assemblages. Marine Ecology Progress Series 292:301–310.

Gratwicke, B., and M. R. Speight. 2005b. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650–667.

Hackradt, C. W., F. C. Félix-Hackradt, and J. A. García-Charton. 2011. Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. Marine Environmental Research 72:235–247.

Hall, M., and S. Bell. 1988. Response of Small Motile Epifauna to Complexity of Epiphytic Algae on Seagrass Blades. Journal of Marine Research 46:613–630.

Hauser, A., M. Attrill, and P. Cotton. 2006. Effects of habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts. Marine Ecology Progress Series 325:93–100.

Heck, K., F. Fodrie, S. Madsen, C. Baillie, and D. Byron. 2015. Seagrass consumption by native and a tropically associated fish species: potential impacts of the tropicalization of the northern Gulf of Mexico. Marine Ecology Progress Series 520:165–173.

Heck, K. L., and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449–464 Estuarine Perspectives. Elsevier.

Heck, K. L., and R. J. Orth. 2006. Predation in Seagrass Beds. Pages 537–550 *in* A. W. D. Larkum and C. M. Duarte, editors. Seagrasses: Biology, Ecology and Conservation. Springer Netherlands, Dordrecht.

Heck, K. L., and G. S. Wetstone. 1977. Habitat Complexity and Invertebrate Species Richness and Abundance in Tropical Seagrass Meadows. Journal of Biogeography 4:135–142.

Heck, K. L., and K. A. Wilson. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. Journal of Experimental Marine Biology and Ecology 107:87–100.

Henderson, C. J., B. L. Gilby, S. Y. Lee, and T. Stevens. 2017. Contrasting effects of habitat complexity and connectivity on biodiversity in seagrass meadows. Marine Biology 164:117.

Hewson, C. M., G. E. Austin, S. J. Gough, and R. J. Fuller. 2011. Species-specific responses of woodland birds to stand-level habitat characteristics: The dual importance of forest structure and floristics. Forest Ecology and Management 261:1224–1240.

Hori, M., T. Suzuki, Y. Monthum, T. Srisombat, Y. Tanaka, M. Nakaoka, and H. Mukai. 2009. High seagrass diversity and canopy-height increase associated fish diversity and abundance. Marine Biology 156:1447–1458.

Hovel, K. A., A. M. Warneke, S. P. Virtue-Hilborn, and A. E. Sanchez. 2016. Mesopredator foraging success in eelgrass (Zostera marina L.): Relative effects of epiphytes, shoot density, and prey abundance. Journal of Experimental Marine Biology and Ecology 474:142–147.

Hovel, K., M. Fonseca, D. Myer, W. Kenworthy, and P. Whitfield. 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Marine Ecology Progress Series 243:11–24.

Hughes, A. R., J. J. Stachowicz, and S. L. Williams. 2009. Morphological and physiological variation among seagrass (Zostera marina) genotypes. Oecologia 159:725–733.

Hutchinson, N., G. P. Jenkins, A. Brown, and T. M. Smith. 2014. Variation with Depth in Temperate Seagrass-Associated Fish Assemblages in Southern Victoria, Australia. Estuaries and Coasts 37:801–814.

Irlandi, E. A., and M. K. Crawford. 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110:222–230.

Jankowski, M., N. Graham, and G. Jones. 2015. Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: implications for the depth-refuge hypothesis. Marine Ecology Progress Series 540:203–215.

Jenkins, G. P., H. M. A. May, M. J. Wheatley, and M. G. Holloway. 1997. Comparison of Fish Assemblages Associated with Seagrass and Adjacent Unvegetated Habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with Emphasis on Commercial Species. Estuarine, Coastal and Shelf Science 44:569–588.

Johnson, D. W. 2006. Predation, Habitat Complexity, and Variation in Density-Dependent Mortality of Temperate Reef Fishes. Ecology 87:1179–1188.

Jordan, F., M. Bartolini, C. Nelson, P. E. Patterson, and H. L. Soulen. 1997. Risk of predation affects habitat selection by the pinfish Lagodon rhomboides (Linnaeus). Journal of Experimental Marine Biology and Ecology 208:45–56.

Kohn, A. J., and P. J. Leviten. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia 25:199–210.

Kostylev, V. E., J. Erlandsson, M. Y. Ming, and G. A. Williams. 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. Ecological Complexity 2:272–286.

Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: approaches and future directions. Hydrobiologia 685:1–17.

Labat, F., C. Piscart, and G. Thiébaut. 2022. Invertebrates in small shallow lakes and ponds: a new sampling method to study the influence of environmental factors on their communities. Aquatic Ecology 56:585–603.

Lee, S. Y., C. W. Fong, and R. S. S. Wu. 2001. The effects of seagrass (Zostera japonica) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. Journal of Experimental Marine Biology and Ecology 259:23–50.

Levin, P., R. Petrik, and J. Malone. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. Oecologia 112:55–63.

Livingston, R. J. 1982. Trophic Organization of Fishes in a Coastal Seagrass System. Marine Ecology Progress Series 7:1–12.

Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49:317–323.

MacDonald, C., T. C. L. Bridge, and G. P. Jones. 2016. Depth, bay position and habitat structure as determinants of coral reef fish distributions: Are deep reefs a potential refuge? Marine Ecology Progress Series 561:217–231.

Macreadie, P. I., J. S. Hindell, M. J. Keough, G. P. Jenkins, and R. M. Connolly. 2010. Resource distribution influences positive edge effects in a seagrass fish. Ecology 91:2013–2021.

Madi Moussa, R., F. Bertucci, H. Jorissen, C. Gache, V. P. Waqalevu, V. Parravicini, D. Lecchini, and R. Galzin. 2020. Importance of intertidal seagrass beds as nursery area for coral reef fish juveniles (Mayotte, Indian Ocean). Regional Studies in Marine Science 33:100965.

Mancera-Rodríguez, N. J., and J. J. Castro-Hernández. 2015. Feeding ecology of the planehead filefish Stephanolepis hispidus (Pisces: Monacanthidae), in the Canary Islands area. Revista de biología marina y oceanografía 50:221–234.

McCloskey, R. M., and R. K. F. Unsworth. 2015. Decreasing seagrass density negatively influences associated fauna. PeerJ 3:e1053.

McKenzie, L. J., L. M. Nordlund, B. L. Jones, L. C. Cullen-Unsworth, C. Roelfsema, and R. K. F. Unsworth. 2020. The global distribution of seagrass meadows. Environmental Research Letters 15:074041.

McLachlan, A., E. Jaramillo, T. E. Donn, and F. Wessels. 1993. Sandy Beach Macrofauna Communities and their Control by the Physical Environment: A Geographical Comparison. Journal of Coastal Research:27–38.

Menge, B. A., J. Lubchenco, and L. R. Ashkenas. 1985. Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. Oecologia 65:394–405.

Micheli, F., M. J. Bishop, C. H. Peterson, and J. Rivera. 2008. Alteration of seagrass species composition and function over two decades. Ecological Monographs 78:225–244.

Moore, E. C., and K. A. Hovel. 2010. Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. Oikos 119:1299–1311.

Moore, C. H., K. Van Niel, and E. S. Harvey. 2011. The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. Ecography 34:425–435.

Nagelkerken, I., S. Kleijnen, T. Klop, R. van den Brand, E. de la Morinière, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Marine Ecology Progress Series 214:225–235.

Newman, S. P., E. H. Meesters, C. S. Dryden, S. M. Williams, C. Sanchez, P. J. Mumby, and N. V. C. Polunin. 2015. Reef flattening effects on total richness and species responses in the Caribbean. Journal of Animal Ecology 84:1678–1689.

O'Connor, N. A. 1991. The effects of habitat complexity on the macroinvertebrates colonising wood substrates in a lowland stream. Oecologia 85:504–512.

Orth, R. J., K. L. Heck, and J. van Montfrans. 1984. Faunal Communities in Seagrass Beds: A Review of the Influence of Plant Structure and Prey Characteristics on Predator: Prey Relationships. Estuaries 7:339–350.

Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A Flexible, Multipurpose Method for Recording Vegetation Composition and Structure. Castanea 63:262–274.

Pullen, M., D. Gerber, M. S. Thomsen, and S. P. Flanagan. 2022. Seasonal Dynamics of Faunal Diversity and Population Ecology in an Estuarine Seagrass Bed. Estuaries and Coasts 45:2578–2591.

Robins CR, Ray GC, Society NA, Federation NW. 1986. A Field Guide to Atlantic Coast Fishes of North America. Houghton Mifflin.

Rodil, I. F., A. M. Lohrer, K. M. Attard, J. E. Hewitt, S. F. Thrush, and A. Norkko. 2021. Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications. Biodiversity and Conservation 30:3023–3043.

Ross, S. W., and M. L. Moser. 1995. Life history of juvenile fof, Mycteroperca microlepis, in North Carolina estuaries. Bulletin of Marine Science 56:222–237.

Rowe-Rowe, D. T., and J. Meester. 1982. Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. African Zoology 17:202–209.

Rozas, L. P., and W. E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77:101–106.

Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Marine Ecology Progress Series 99:1–16.

Ryer, C., B. Laurel, and A. Stoner. 2010. Testing the shallow water refuge hypothesis in flatfish nurseries. Marine Ecology Progress Series 415:275–282.

Sam, K., B. Koane, D. C. Bardos, S. Jeppy, and V. Novotny. 2019. Species richness of birds along a complete rain forest elevational gradient in the tropics: Habitat complexity and food resources matter. Journal of Biogeography 46:279–290.

Schneider, F. I., and K. H. Mann. 1991. Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. Journal of Experimental Marine Biology and Ecology 145:119–139.

Shumway, C. A., H. A. Hofmann, and A. P. Dobberfuhl. 2007. Quantifying habitat complexity in aquatic ecosystems. Freshwater Biology 52:1065–1076.

Spurr, E. B., and B. Warburton. 1991. Methods of Measuring the Proportions of Plant Species Present in Forest and Their Effect on Estimates of Bird Preferences for Plant Species. New Zealand Journal of Ecology 15:171–175.

St. Pierre, J. I., and K. E. Kovalenko. 2014. Effect of habitat complexity attributes on species richness. Ecosphere 5:art22.

Staudacher, K., and L. Füreder. 2007. Habitat Complexity and Invertebrates in Selected Alpine Springs (Schütt, Carinthia, Austria). International Review of Hydrobiology 92:465–479.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.

Stoner, A. 1980. Perception and Choice of Substratum by Epifaunal Amphipods Associated with Seagrasses. Marine Ecology Progress Series 3:105–111.

Szedlmayer, S. T., and K. W. Able. 1996. Patterns of Seasonal Availability and Habitat Use by Fishes and Decapod Crustaceans in a Southern New Jersey Estuary. Estuaries 19:697.

Tanner, J. E. 2006. Landscape ecology of interactions between seagrass and mobile epifauna: The matrix matters. Estuarine, Coastal and Shelf Science 68:404–412.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

Tzeng, M. W., J. A. Hare, and D. G. Lindquist. 2003. Ingress of transformation stage gray snapper, Lutjanus griseus (Pisces: Lutjanidae) through Beaufort Inlet, North Carolina. Bulletin of Marine Science 72:18.

United States. National Marine Fisheries Service, Puerto Rico. Department of Natural and Environmental Resources, Inc. Louis Berger, and Inc. Reef Research, editors. 2006. Habitat use/habitat zoning study, Cayo Aurora, Guanica Natural Reserve, Puerto Rico : final report.

Velasco-Charpentier, C., F. Pizarro-Mora, N. P. Navarro, and N. Valdivia. 2021. Disentangling the links between habitat complexity and biodiversity in a kelp-dominated subantarctic community. Ecology and Evolution 11:1214–1224.

Virnstein, R. W., and R. K. Howard. 1987. Motile epifauna of marine macrophytes in the Indiant River Lagoon, Florida. I. Comparisons among three species of seagrasses from adjacent beds. Bulletin of Marine Science 41:1–12.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J.

Kenworthy, F. T. Short, and S. L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences 106:12377–12381.

West, J. M., and J. B. Zedler. 2000. Marsh-Creek Connectivity: Fish Use of a Tidal Salt Marsh in Southern California. Estuaries 23:699.

Whitfield, A. K. 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. Reviews in Fish Biology and Fisheries 27:75–110.

Wilson, S. K., N. A. J. Graham, and N. V. C. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151:1069–1076.

Yeager, L. A., D. A. Keller, T. R. Burns, A. S. Pool, and F. J. Fodrie. 2016. Threshold effects of habitat fragmentation on fish diversity at landscapes scales. Ecology 97:2157–2166.

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Figures

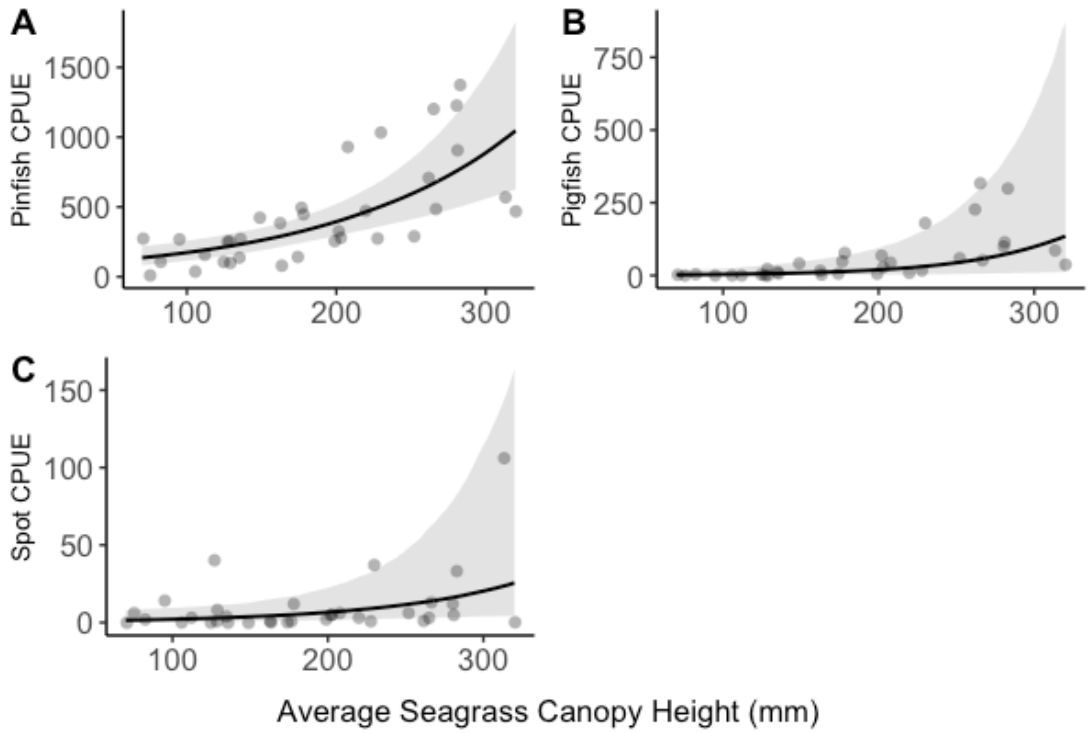

Figure 2.1: Seagrass canopy height plotted on the x-axis and CPUE of the three most abundant motile fauna species outside of anchovy, (A) pinfish, *Lagodon rhomboides*; (B) pigfish, *Orthopritis chrysoptera*; and (C) spot, *Leiostomus xanthurus* captured in 2019 trawl surveys plotted on the y-axis. Lines denoted here are Bayesian GLMMs with 95% credible intervals.

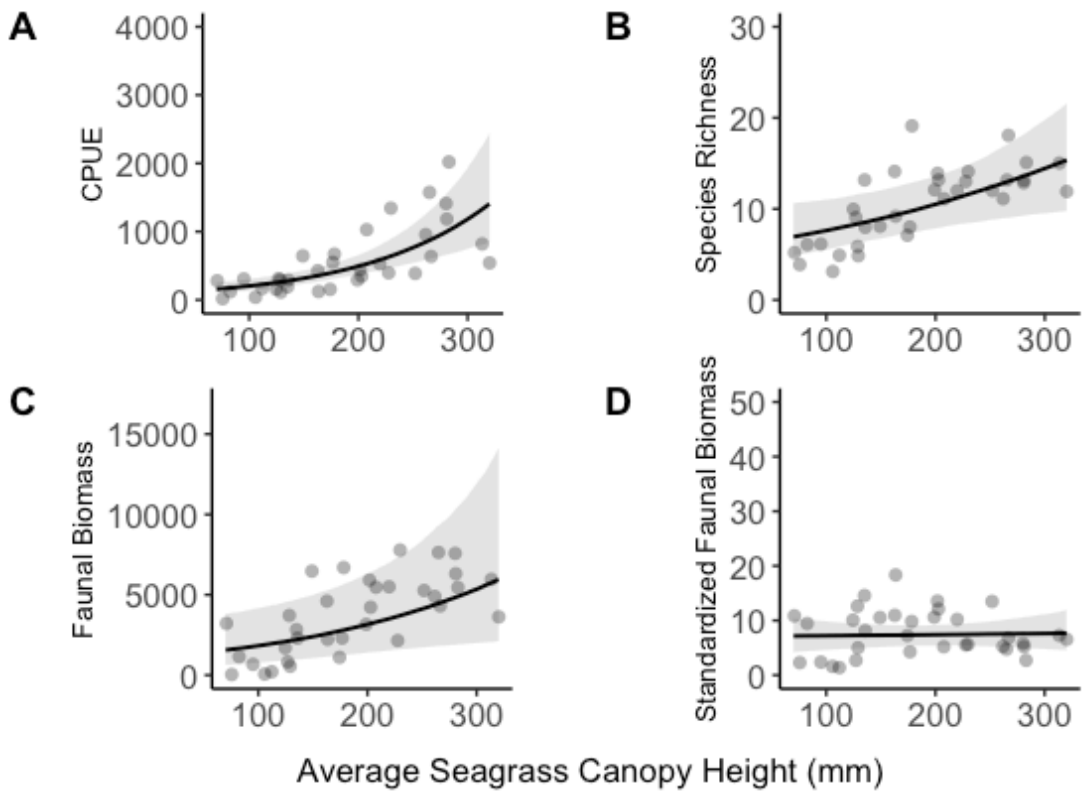

Figure 2.2: Average 2019 seagrass canopy height in beds trawled plotted on the x-axis with motile fauna (A) Catch per unit effort (CPUE) (B) Species Richness (C) Biomass and (D) Standardized Biomass (Biomass / CPUE) plotted on the y-axis. Lines denoted here are Bayesian generalized linear mixed models (GLMM) with 95% credible intervals.

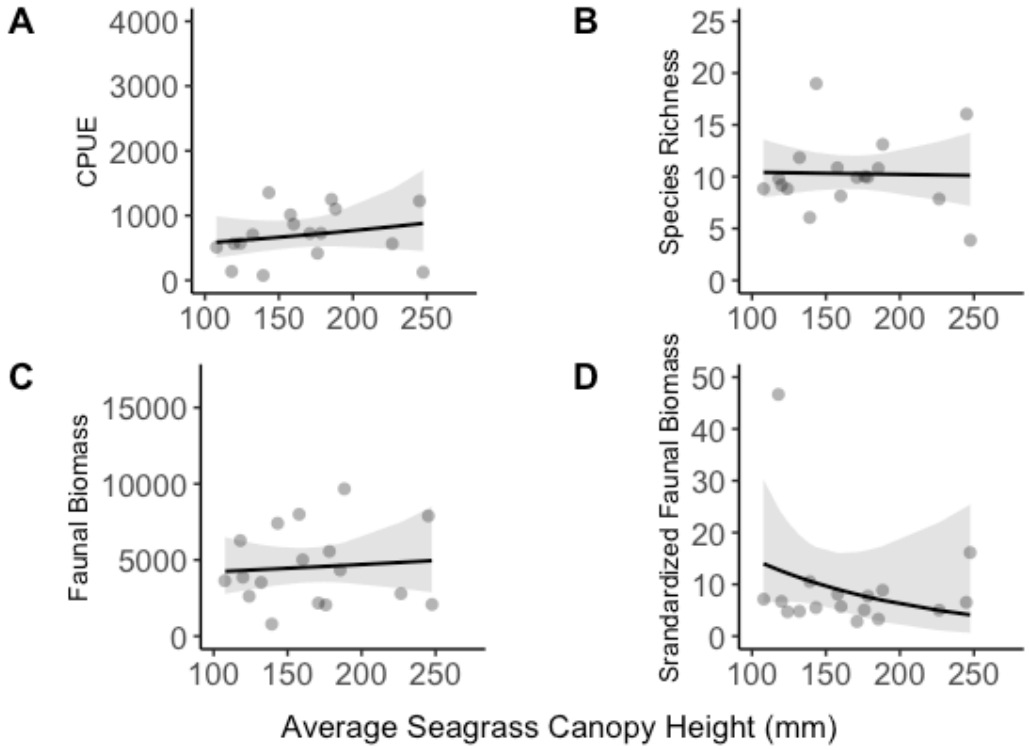

Figure 2.3: Average 2020 seagrass canopy height in beds trawled plotted on the x-axis with motile fauna (A) CPUE (B) Species Richness (C) Biomass and (D) Standardized Biomass (Biomass / CPUE) plotted on the y-axis. Plots and models do not include the outlier, *Z. marina* dominated seagrass bed. Lines denoted here are GLMs with 95% confidence intervals.

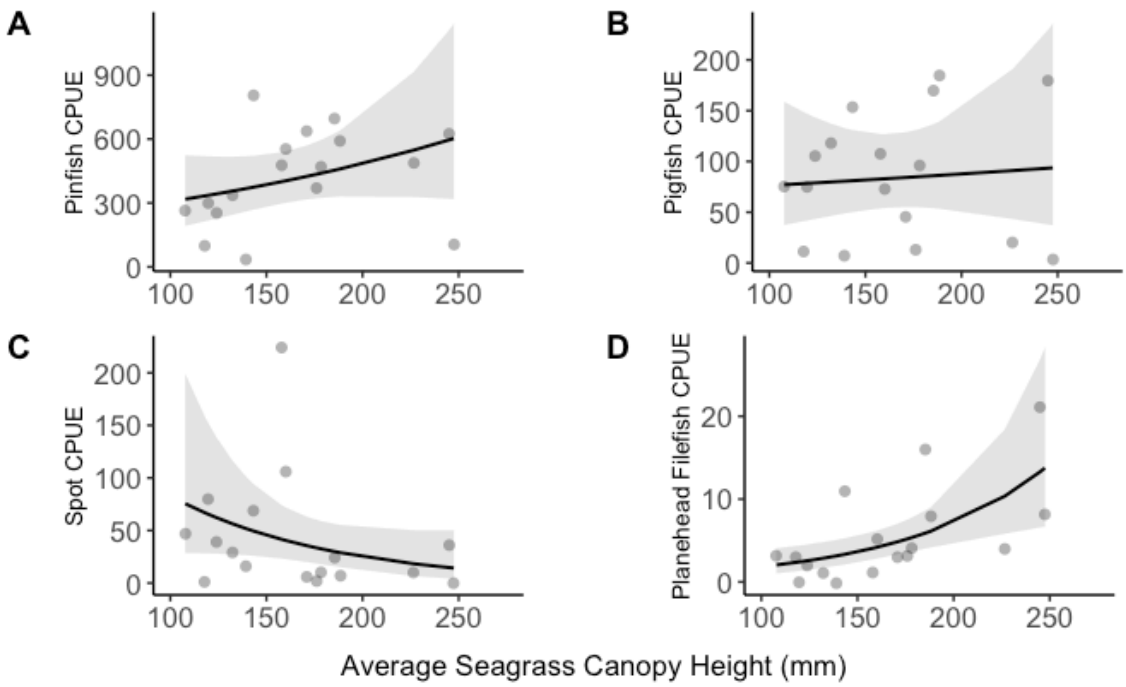

Figure 2.4: Seagrass canopy height plotted on the x-axis and CPUE of the four most abundant motile fauna species, (A) pinfish, *Lagodon rhomboides;* (B) pigfish, *Orthopritis chrysoptera*; (C) spot, *Leiostomus xanthurus*; and (D) planehead filefish, *Stephanolepis hispidus*) captured in 2020 trawl surveys plotted on the y-axis. Plots and models do not include the outlier *Z. marina* dominated seagrass bed. Lines denoted here are GLM with 95% confidence intervals.

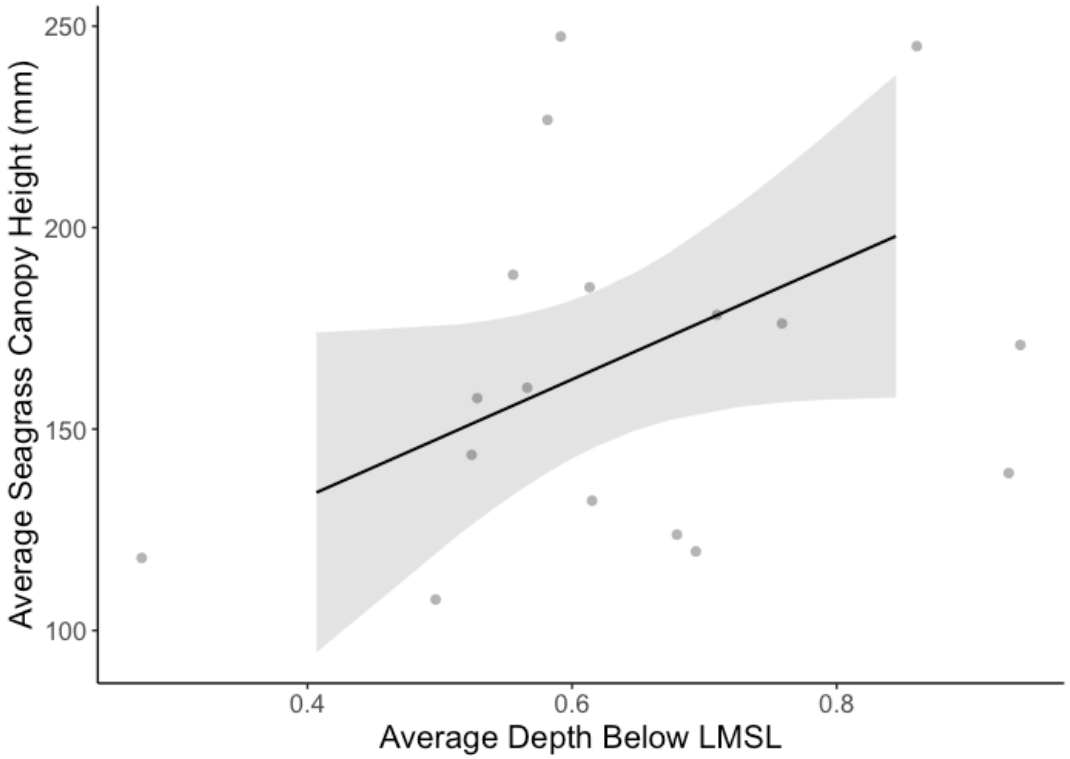

Figure 2.5: Average depth relative LMSL of seagrass beds measured in 2020 plotted on the x-axis with average canopy height per bed plotted on the y-axis. Higher values for depth indicate deeper beds. Plot and models do not include the outlier *Z. marina* dominated seagrass bed. Line denoted here is a linear model (lm) prediction with 95% confidence interval with an R^2 value of 0.1753.

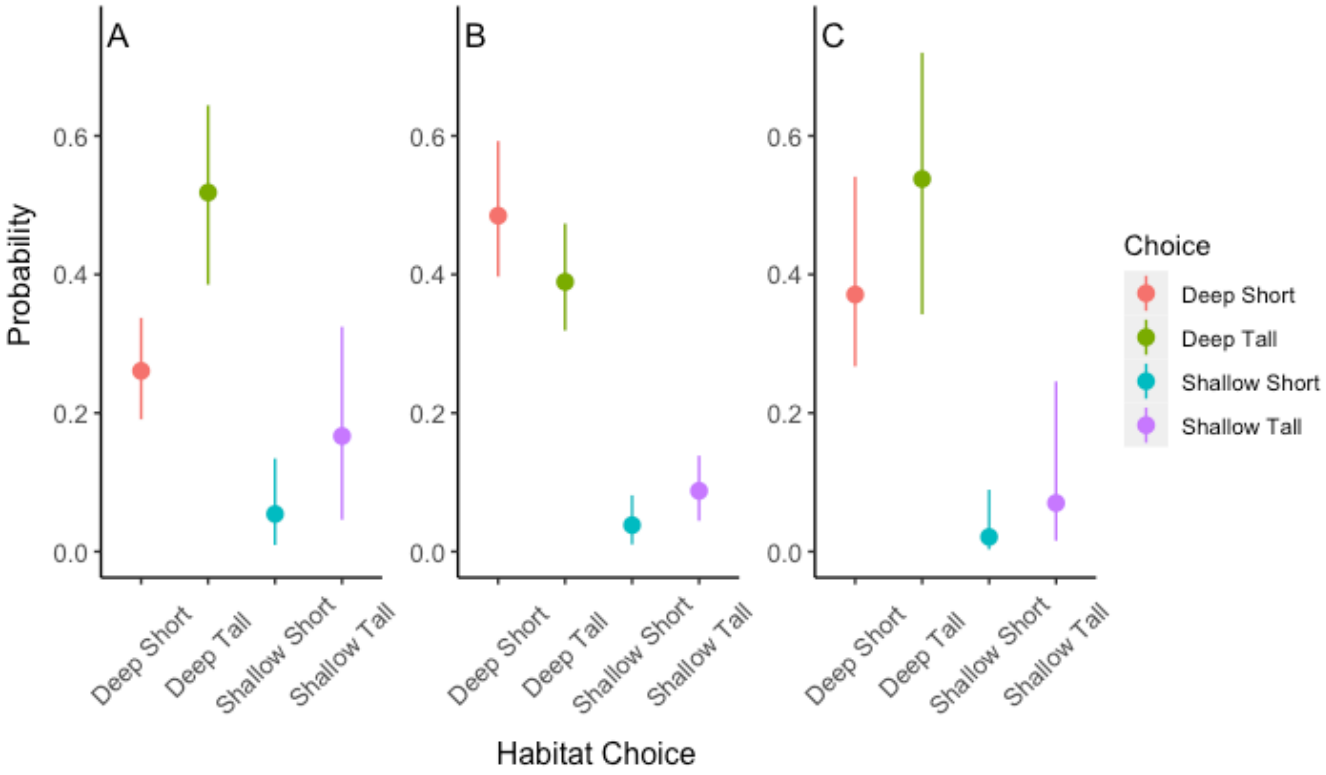

Figure 2.6: Bayesian multinomial mixed model of pinfish habitat preference with ASUs having (A) equal shoot density, (B) low equal surface area, and (C) high equal surface area. Probability of choosing habitat is plotted on the x-axis and habitats are plotted on the y-axis. Error bars denote 95% credible intervals.

Supplemental Figures

Figure S2.1: Map of seagrass bed locations in Back Sound, North Carolina, sampled in 2019 and 2020. Each white point denotes a single seagrass site.

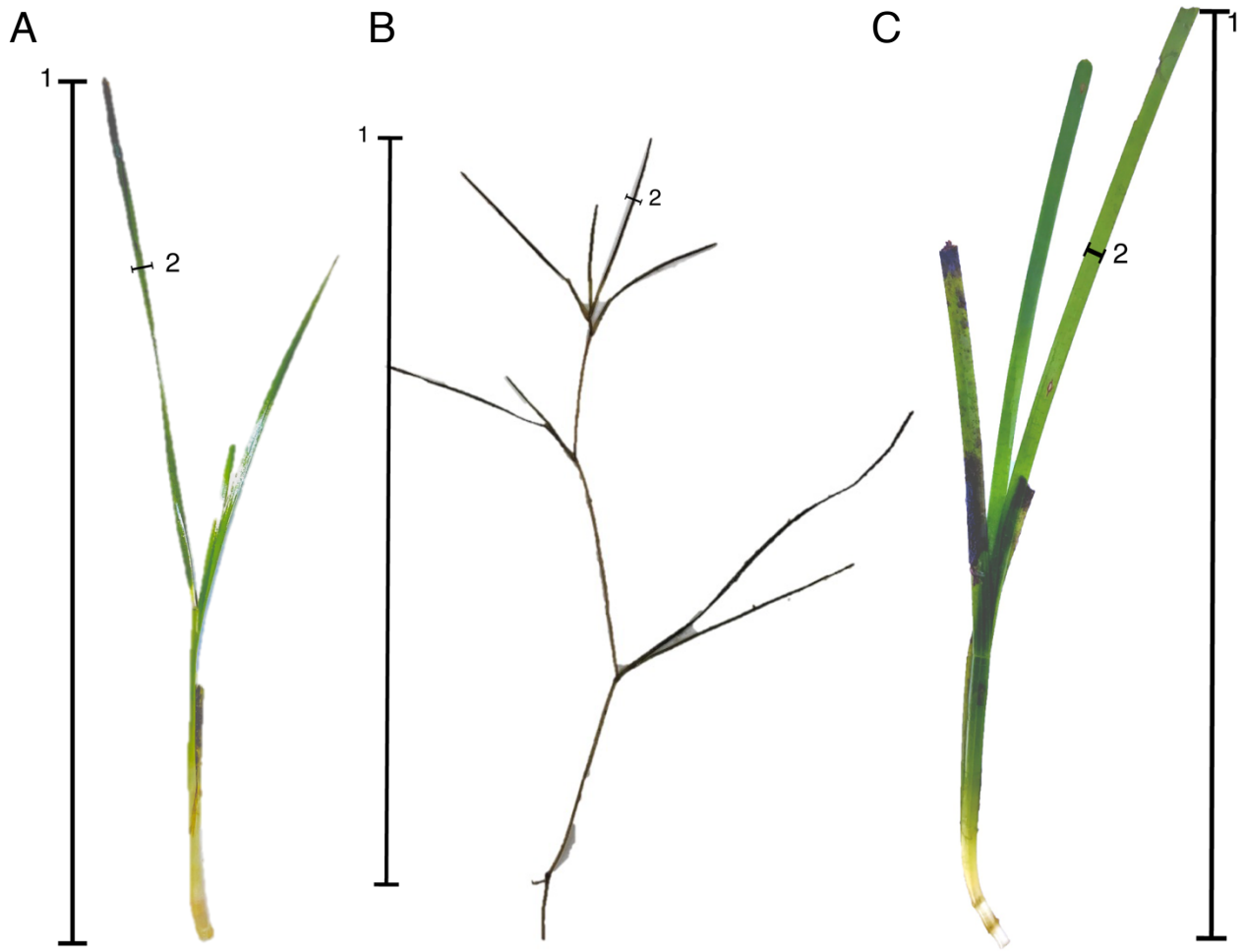

Figure S2.2: Image of a single shoot of (A) *H. wrightii,* (B) *R. maritima*, and (C) *Z. marina* with the (1) shoot length and (2) leaf width demarcated. The shoots of *H. wrightii* and *Z. marina* have four leaves and one branch. The shoot of *R. maritima* has eight leaves and four branches. Images of *H. wrightii* and *Z. marina* courtesy of S. Donaher.

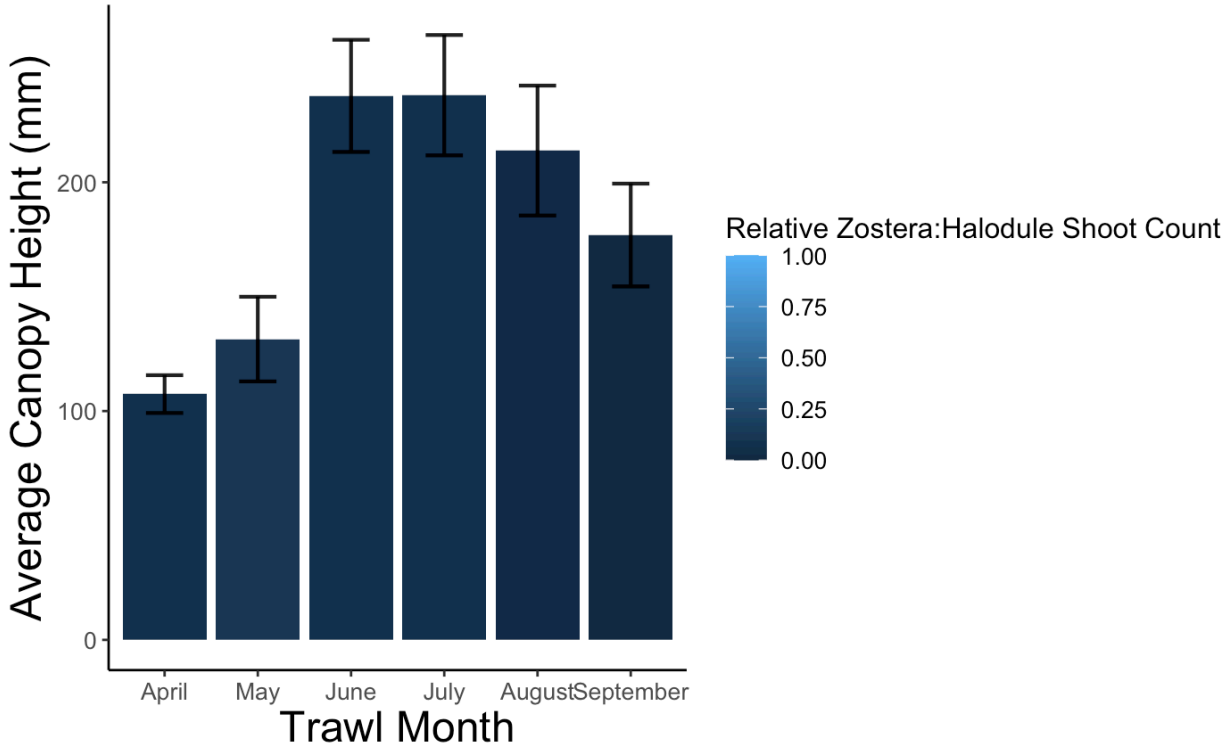

Figure S2.3: Average canopy height across seagrass beds for each month of 2019 sampling. Color denotes dominance of *H. wrightii* or *Z. marina* based on shoot count measured from cores with darker blue indicating *H. wrightii* dominance and lighter blue indicating *Z. marina* dominance.

Figure S2.4: Photo of the outdoor mesocosm enclosures. Equal shoot density ASU is shown here with tall canopy on the right of both the shallow (top) and deep (bottom) elevations. The ramp is shown here as the bare area between the deep and the shallow.

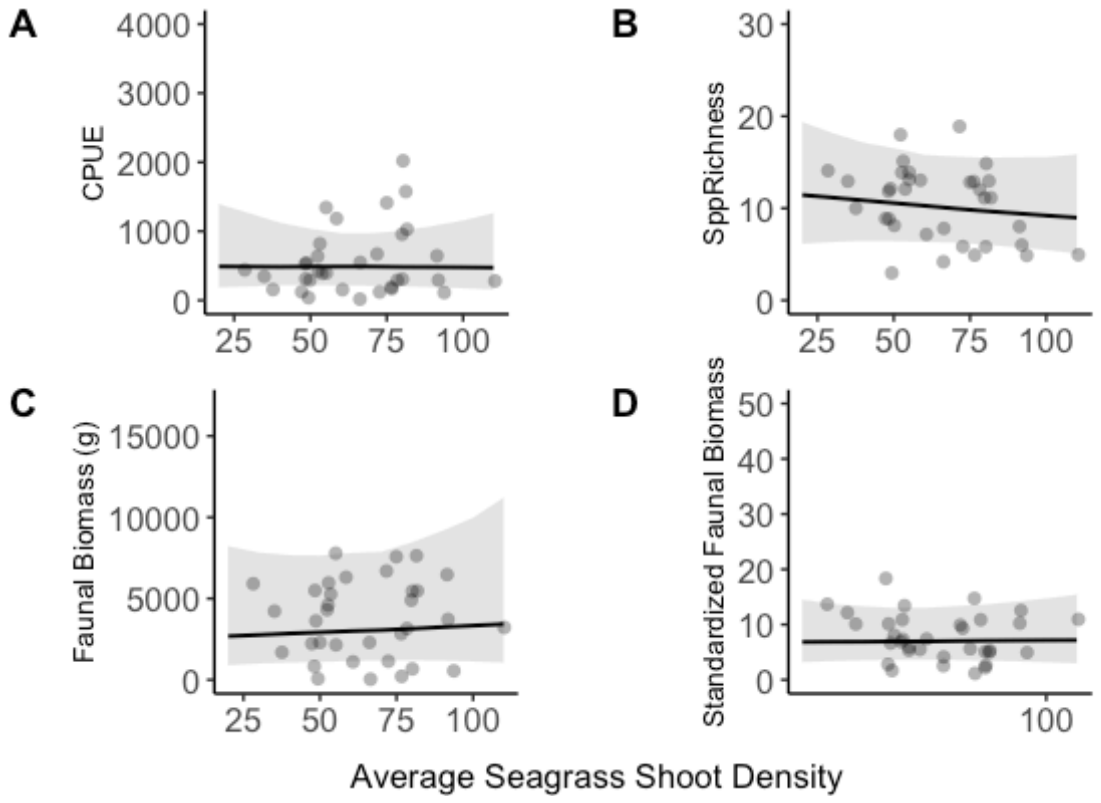

Figure S2.5: Average 2019 seagrass shoot density per 10-cm-diameter core in beds trawled plotted on the x-axis with motile fauna (A) CPUE (B) species richness (C) biomass and (D) standardized faunal biomass plotted on the y-axis. Lines denoted here are Bayesian glmm predictions with 95% credible intervals.

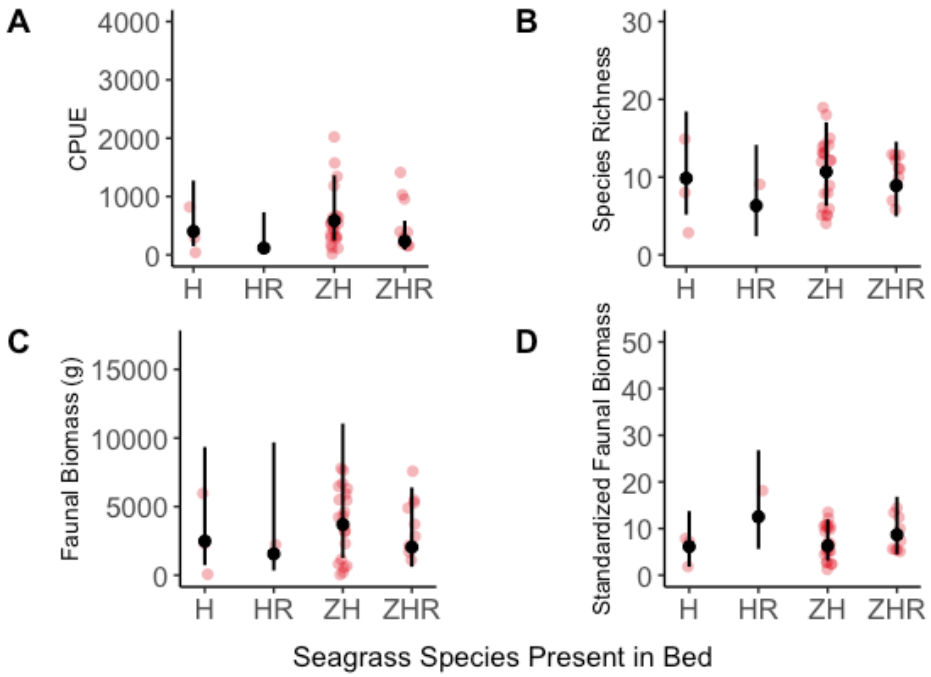

Figure S2.6: Seagrass species composition in beds trawled in 2019 plotted on the x-axis with motile fauna (A) CPUE (B) species richness (C) biomass and (D) standardized faunal biomass plotted on the y-axis. Points are Bayesian GLMM predictions with lines denoting 95% credible intervals. H indicates *H. wrightii,* R indicates *R. maritima*, and Z indicated *Z. marina*.

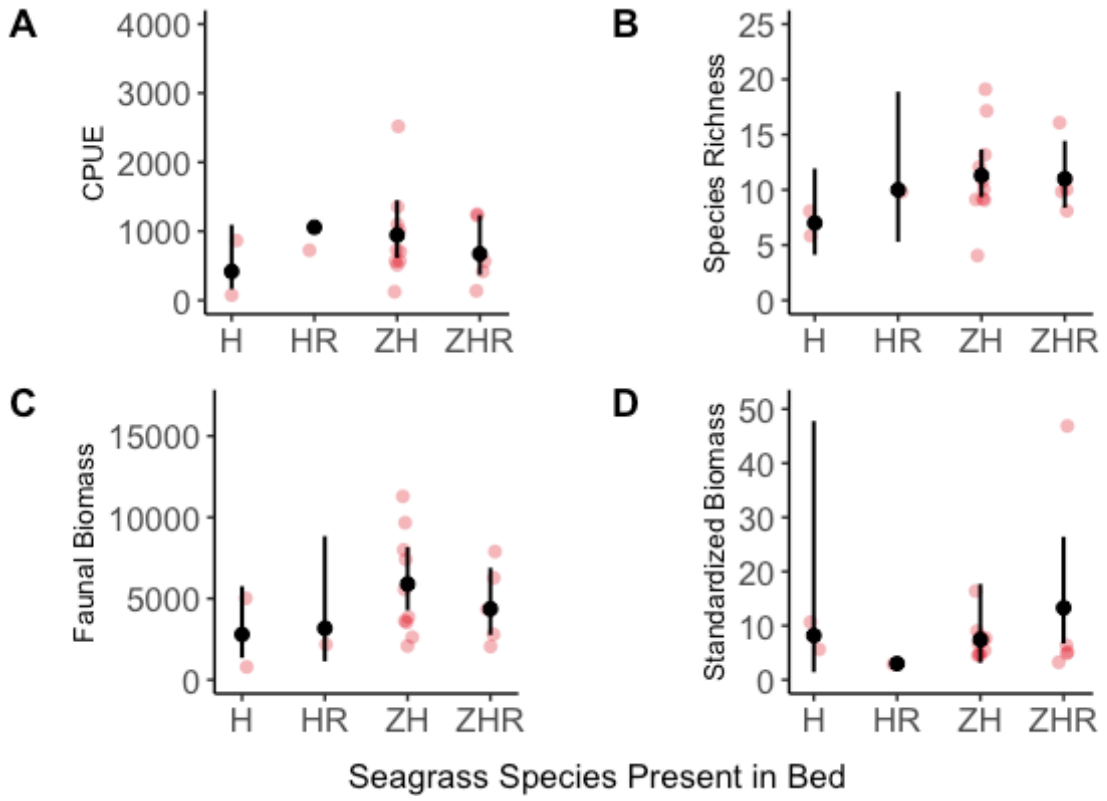

Figure S2.7: Seagrass species composition in beds trawled in 2020 plotted on the x-axis with motile fauna (A) CPUE (B) species richness (C) biomass and (D) standardized biomass plotted on the y-axis. Black points are GLM predictions with lines denoting 95% confidence intervals. The *Z. marina* dominated bed has been included in these analyses. H indicates *H. wrightii,* R indicates *R. maritima*, and Z indicated *Z. marina*.

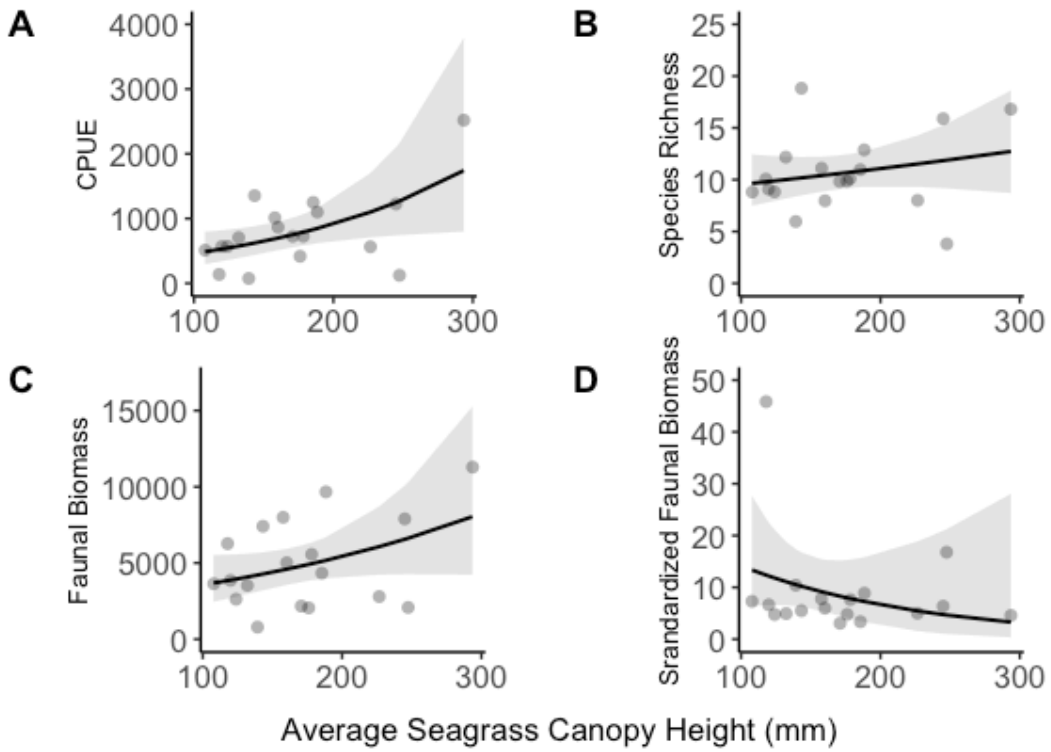

Figure S2.8: Average 2020 seagrass canopy height in beds trawled plotted on the x-axis with motile fauna (A) CPUE (B) Species Richness (C) Biomass and (D) Standardized Biomass (Biomass / CPUE) plotted on the y-axis. Lines denoted here are GLM predictions with 95% confidence intervals. The *Z. marina* dominated seagrass bed has been included in these plots and models.

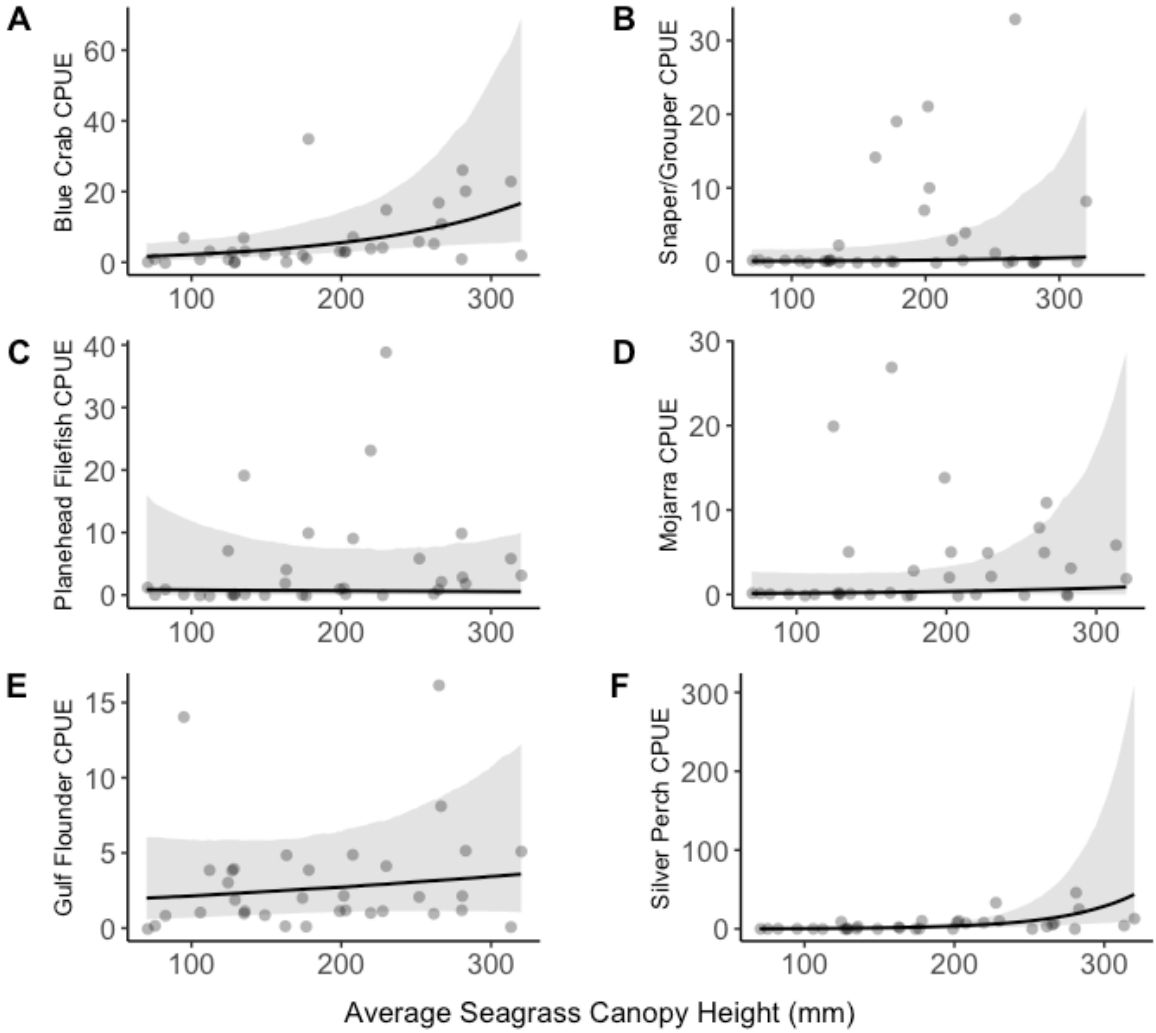

Figure S2.9: Average 2019 canopy height in beds trawled plotted on the x-axis with CPUE for (A) blue crabs (*Callinectes sapidus)* (B) snapper species and gag grouper (*Lutjanus spp.* and *Mycteroperca microlepis)* (C) planehead filefish (*Stephanolepis hispidus)* (D) mojarra (*Gerreidae)* (E) gulf flounder (*Paralichthys albigutta)* (F) silver perch (*Bairdiella chrysoura)* plotted on the y-axis. Lines denote Bayesian GLMM predictions with 95% credible intervals

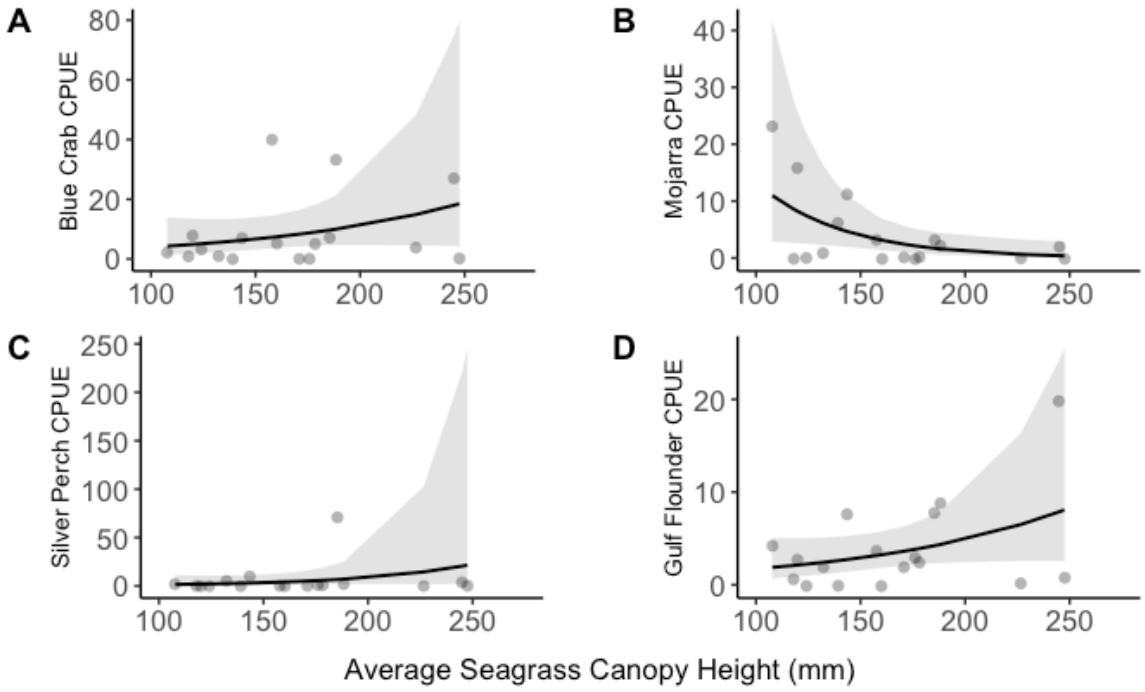

Figure S2.10: Average 2020 canopy height in beds trawled plotted on the x-axis with CPUE for (A) blue crabs (*Callinectes sapidus)* (B) mojarra *(Gerreidae)* (C) silver perch (*Bairdiella chrysoura)* (D) gulf flounder (*Paralichthys albigutta)* plotted on the y-axis. Lines denoted here are GLM predictions with 95% confidence intervals. The *Z. marina* dominated seagrass bed has been removed from these plots and models.

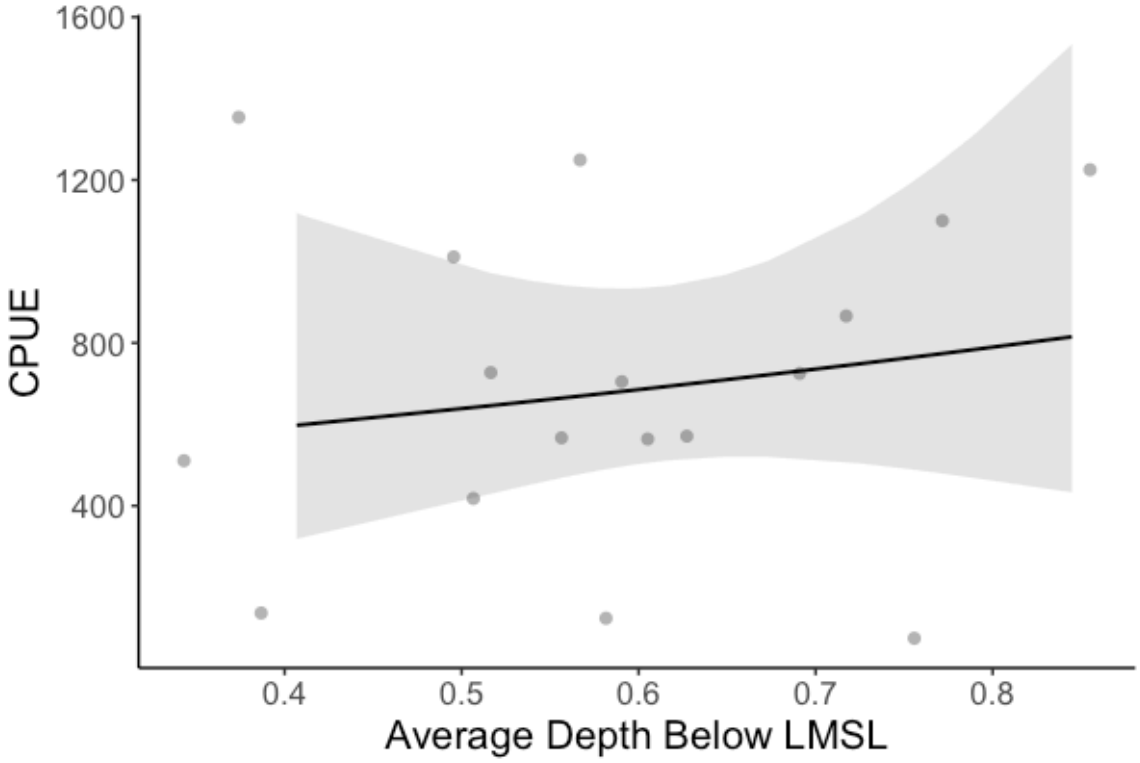

Figure S2.11: Average seagrass bed depth relative LMSL measured in 2020 plotted on the x-axis with CPUE of motile fauna from 2020 trawls plotted on the y-axis. A higher depth value indicates a deeper bed. The *Z. marina*-dominated bed has been removed from this figure and model. Line denoted here is GLM predictions with 95% confidence intervals.

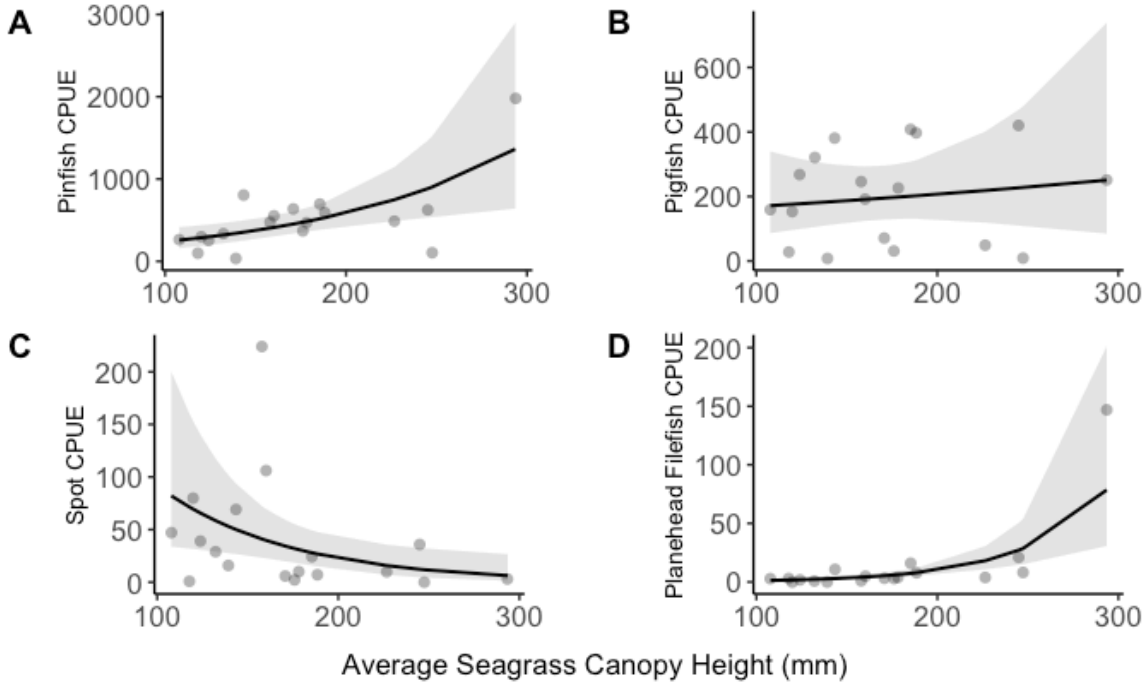

Figure S2.12: Seagrass canopy height plotted on the x-axis and CPUE of the four most abundant motile fauna species (pinfish, *Lagodon rhomboides;* pigfish, *Orthopritis chrysoptera*; spot, *Leiostomus xanthurus*; and planehead filefish, *Stephanolepis hispidus*) captured in 2020 trawl surveys plotted on the y-axis. Lines denoted here are GLM predictions with 95% confidence intervals. The *Z. marina* dominated seagrass bed has been included in these plots and models.

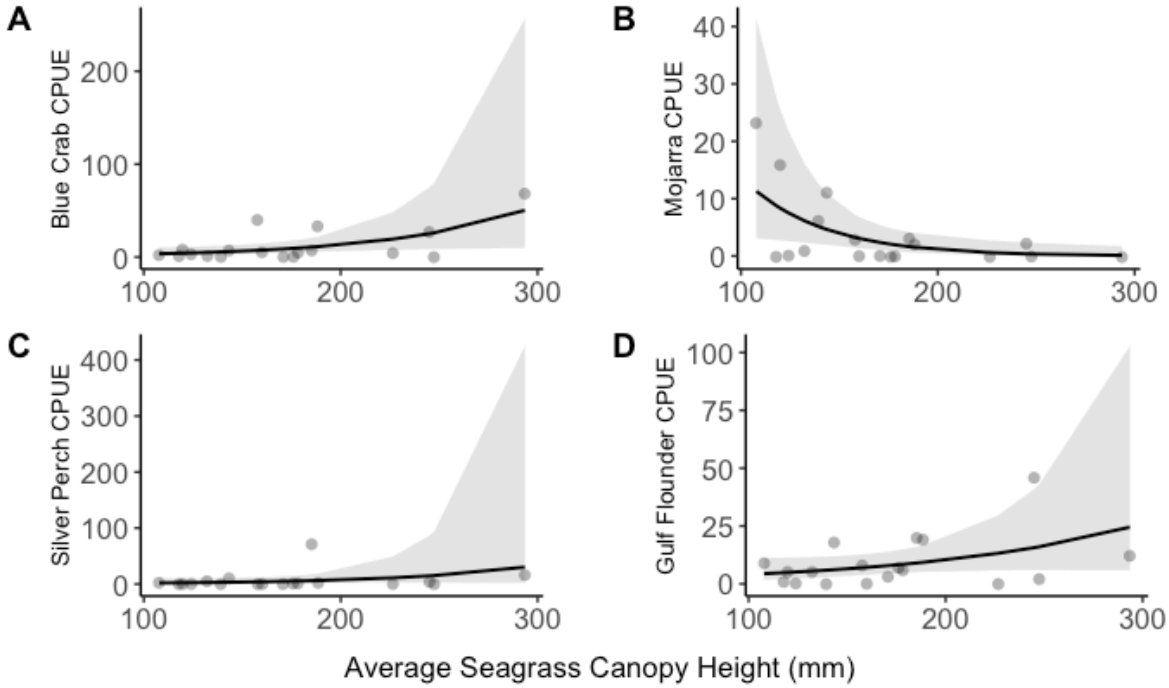

Figure S2.13: Average 2020 canopy height in beds trawled plotted on the x-axis with CPUE for (A) blue crabs (*Callinectes sapidus)* (B) mojarra *(Gerreidae)* (C) silver perch (*Bairdiella chrysoura)* (D) gulf flounder (*Paralichthys albigutta)* plotted on the y-axis. Lines denoted here are GLM predictions with 95% confidence intervals. The *Z. marina* dominated seagrass bed has been included in these plots and models.

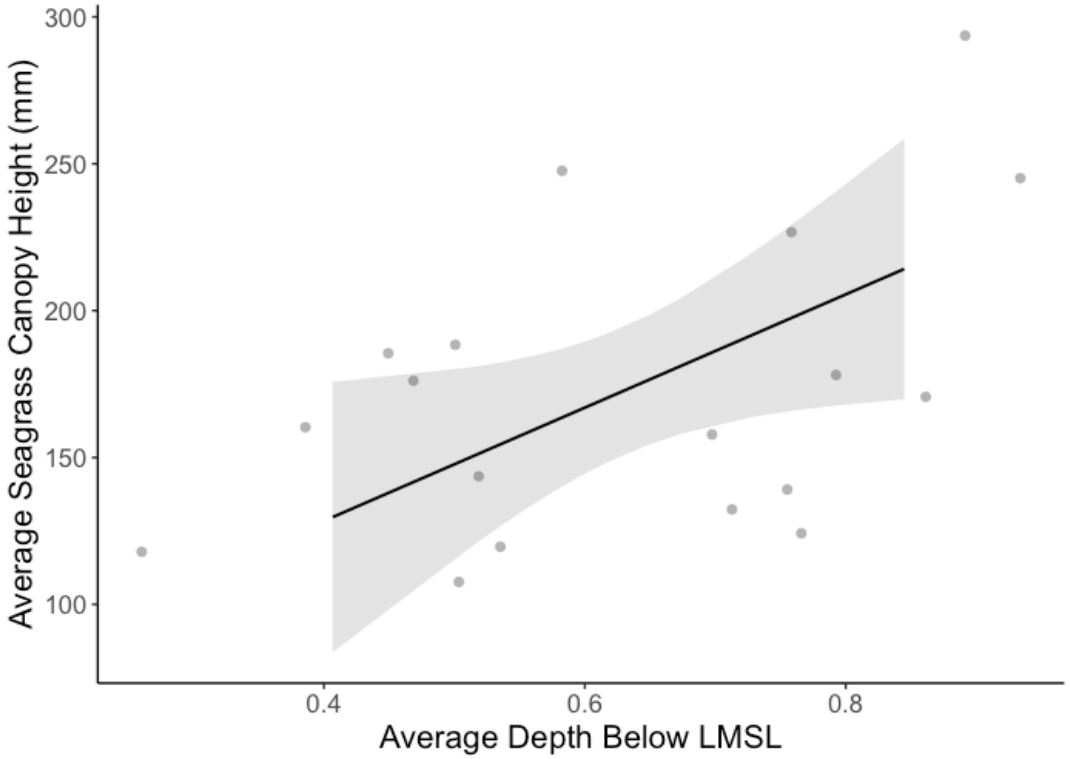

Figure S2.14: Average depth of seagrass beds relative to LMSL measured in 2020 plotted on the x-axis with average canopy height per bed plotted on the y-axis. A higher depth value indicates a deeper bed. The *Z. marina*-dominated bed has been included in this plot and model. Line denoted here is a linear model prediction with 95% confidence intervals.

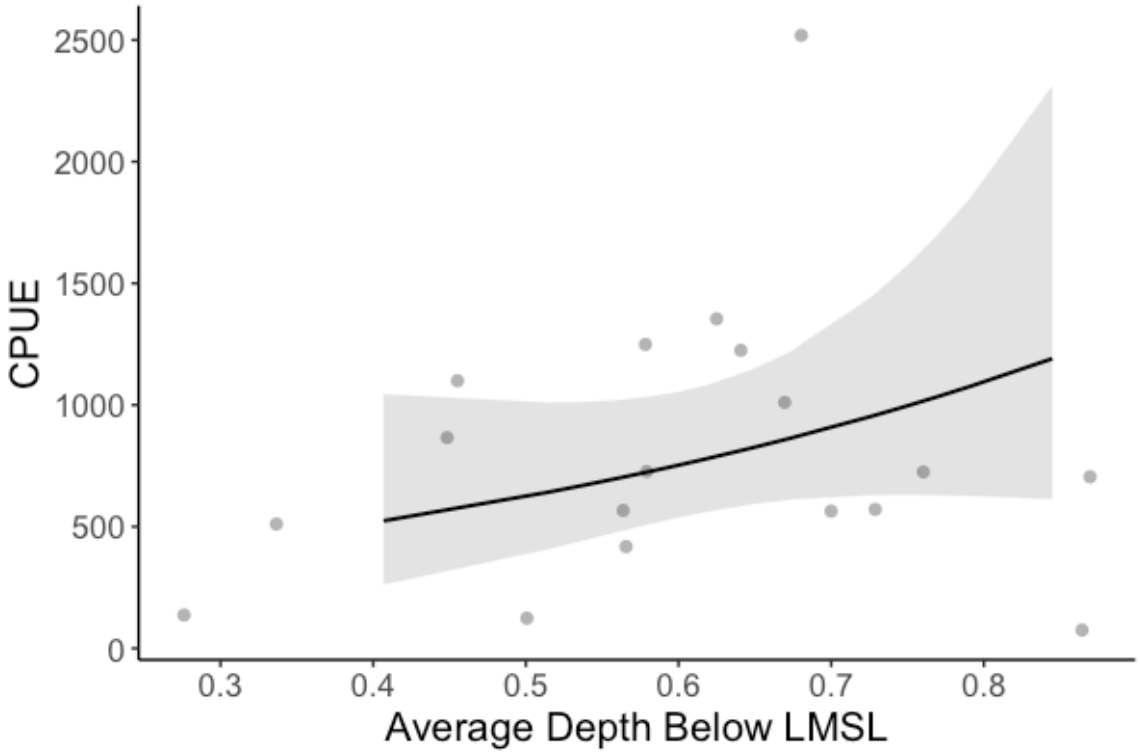

Figure S2.15: Average seagrass bed depth below LMSL measured in 2020 plotted on the x-axis with CPUE of motile fauna from 2020 trawls plotted on the y-axis. A higher depth value indicates a deeper bed. The *Z. marina* dominated bed has been included in this plot and model. Line denoted here is GLM prediction with 95% confidence intervals.

Supplemental Tables

Table S2.1: All fauna caught in our 2019 trawls. Numbers here denote averages and (standard error) across beds standardized to two 100m tows) for each month of the trawl.

Scientific Name	Common Name	April	May	June	July	August	September
Fish							
Anchoa spp.	Anchovy	1.24 (0.74)	23.91 (22.26)	27.8 (26.14)	15.16 (8.76)	6.09 (5.08)	0.964 (0.572)
Archosargus probatocephalus	Sheepshead	0 (0)	0 (0)	0.32 (0.21)	0.64 (0.42)	1.64 (0.88)	0.67 (0.22)
Bairdiella chrysoura	Silver Perch	0 (0)	0.44 (0.44)	4.88 (3.03)	12.67 (5.48)	5.28 (1.66)	4.02 (1.88)
Carangoides bartholomaei	Yellow Jack	0 (0)	0 (0)	0.08 (0.08)	0 (0)	0 (0)	0 (0)
Centropristis striata	Black Sea Bass	0 (0)	0 (0)	0 (0)	0.14 (0.14)	0.13 (0.13)	0 (0)
Chilomycterus schoepfi	Striped Burrfish	0.56 (0.36)	0.26 (0.16)	0.25 (0.25)	0.25 (0.16)	0.26 (0.26)	0.22 (0.22)
Citharichthys spilopterus	Bay Whiff	0 (0)	0 (0)	0 (0)	0 (0)	0.13 (0.13)	0 (0)
Cynoscion nebulosus	Speckled Sea Trout	0 (0)	0 (0)	0 (0)	0 (0)	0.13 (0.13)	0 (0)
Diplodus holbrooki	Spottail Pinfish	0 (0)	0.94 (0.49)	6.19 (3.75)	4.16 (2.03)	0.46 (0.21)	0.45 (0.26)
Gerreidae	Mojarra	0 (0)	0 (0)	1.769 (0.857)	4.404 (2.610)	6.494 (3.211)	4.33 (2.711)
Halichoeres bivittatus	Slippery Dick	0 (0)	0 (0)	0 (0)	0 (0)	0.131 (0.131)	0 (0)
Hypsoblennius hentzi	Feather Blenny	0 (0)	0.125 (0.125)	0.08 (0.08)	0.163 (0.105)	0 (0)	0 (0)
Lagodon rhomboides	Pinfish	114.93 (37.28)	228.54 (45.83)	611.25 (114.18)	386.56 (126.76)	291.04 (63.88)	264.16 (26.45)
Leiostomus xanthurus	Spot	10.55 (5.27)	0.41 (0.28)	6.08 (3.32)	17.2 (10.76)	4.5 (1.96)	2.67 (0.79)
Lutjanus analis	Mutton Snapper	0 (0)	0 (0)	0 (0)	0 (0)	0.56 (0.42)	1.04 (0.4)
Lutjanus chrysurus	Yellowtail Snapper	0 (0)	0 (0)	0 (0)	0 (0)	0.16 (0.16)	0 (0)

Lutjanus griseus	Grey / Mangrove Snapper	0 (0)	0 (0)	0 (0)	0 (0)	6.69 (3.8)	8.41 (1.79)
Lutjanus synagris	Lane Snapper	0 (0)	0 (0)	0 (0)	0.62 (0.54)	1.07 (0.33)	1.4 (0.64)
Menidia spp.	Silverside	0.11 (0.11)	0 (0)	0 (0)	0 (0)	0.13 (0.13)	0 (0)
Micropogonias undulatus	Atlantic Croaker	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.22 (0.22)
Monacanthidae	Filefish[1]	0 (0)	0 (0)	0.12 (0.12)	0 (0)	0 (0)	0 (0)
Mycteroperca microlepis	Gag Grouper	0 (0)	0 (0)	0 (0)	0 (0)	0.54 (0.27)	0 (0)
Opisthonema oglinum	Atlantic Thread Herring	0 (0)	0 (0)	0 (0)	0.09 (0.09)	0 (0)	0 (0)
Opsanus tao	Oyster Toadfish	0 (0)	0 (0)	0.16 (0.16)	0.14 (0.14)	0 (0)	0 (0)
Orthopritis chrysoptera	Pigfish	0 (0)	13.71 (6.17)	110.84 (37.32)	55.21 (22.4)	25.51 (9.28)	24.94 (11.65)
Paralichthys albigutta	Gulf Flounder	3.34 (1.58)	0.68 (0.26)	3.51 (1.4)	1.43 (0.49)	3.39 (0.98)	0.82 (0.34)
Pomatomus saltatrix	Bluefish	0 (0)	0 (0)	0.53 (0.53)	0.12 (0.12)	0.41 (0.41)	0 (0)
Sciaenops ocellatus	Red Drum	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0 (0)
Sphoeroides maculatus	Northern Pufferfish	0 (0)	0.11 (0.11)	0.74 (0.3)	0.26 (0.26)	0.13 (0.13)	0.44 (0.44)
Sphyraena spp.	Sennet / Barracuda	0 (0)	0.39 (0.26)	1.43 (0.72)	0.07 (0.07)	0 (0)	0.22 (0.22)
Stenotomus caprinus	Longspine Porgy	0 (0)	0.27 (0.27)	0 (0)	0 (0)	0 (0)	0 (0)
Stephanolepis hispidus	Planehead Filefish	0 (0)	0.3 (0.19)	2.3 (1.18)	7.85 (4.98)	8.55 (3.12)	0.87 (0.36)
Sygnathus sp.	Pipefish	0.53 (0.32)	0 (0)	0.21 (0.13)	1.08 (0.73)	0.69 (0.38)	0.38 (0.22)
Synodus foetens	Inshore Lizardfish	0 (0)	0.13 (0.13)	0 (0)	0.12 (0.12)	0 (0)	0 (0)
	UnID Postlarval Fish[2]	0.22 (0.22)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Rays							
Dasyatis americana	Southern Stingray	0 (0)	0.26 (0.16)	0.11 (0.11)	0 (0)	0 (0)	0.2 (0.2)

	Crab						
Callinectes sapidus	Blue Crab	3.9 (1.79)	1.14 (0.45)	5.4 (2.23)	8.97 (3.21)	8.2 (4.1)	2.51 (0.06)
Libinia spp.	Spider/Decorator Crab	0 (0)	0 (0)	0 (0)	0.51 (0.25)	0 (0)	0 (0)
Portunus spp.	Swimming Crab	0 (0)	0 (0)	0 (0)	0.26 (0.26)	0 (0)	0 (0)
	Lobster						
Panulirus spp.	Spiny Lobster	0.11 (0.11)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	Shrimp						
Palaemon spp.	Grass Shrimp	0.14 (0.14)	0 (0)	0.1 (0.1)	0.73 (0.73)	0 (0)	0 (0)
Penaeus aztecus	Brown Shrimp	0 (0)	0 (0)	0 (0)	1.09 (0.54)	0.53 (0.39)	0 (0)
Tozeuma carolinense	Arrow Shrimp	0.46 (0.46)	0 (0)	0 (0)	0 (0)	0.13 (0.13)	0.2 (0.2)

[1]This individual was not a planehead filefish but could not be identified to the species level. Therefore it was kept separate in species richness analyses.

[2]This unidentified fish was not included in species richness estimates as it was likely a larval fish from a captured species.

Table S2.2: All fauna caught in our 2020 trawls. Sum column sums across all beds and average is the average across all 18 beds. It is of note two of our sites were only towed once and standardized to 100m while all other sites were towed twice and their trawls combined.

Scientific Name	Common Name	Sum	Average (Standard Error)
Fish			
Anchoa spp.	Anchovy	34.649	1.925 (0.989)
Archosargus probatocephalus	Sheepshead	25.66	1.43 (0.6)
Bairdiella chrysoura	Silver Perch	87.28	4.85 (2.86)
Carangoides bartholomaei	Yellow Jack	3.1	0.17 (0.1)
Chasmodes bosquianus	Striped Blenny	0.82	0.05 (0.05)
Chilomycterus schoepfi	Striped Burrfish	2.78	0.16 (0.08)
Diplodus holbrooki	Spottail Pinfish	4.94	0.27 (0.27)
Fistularia spp.	Cornetfish	2.47	0.14 (0.1)
Gerreidae	Mojarra	62.17	3.45 (1.49)
Hypleurochilus geminatus	Crested Blenny	0.64	0.04 (0.04)
Hypsoblennius hentzi	Feather Blenny	2.98	0.16 (0.08)
Lagodon rhomboides	Pinfish	7803.47	433.53 (99)
Leiostomus xanthurus	Spot	600.65	33.37 (11.23)
Lutjanus synagris	Lane Snapper	1.8	0.1 (0.1)
Micropogonias undulatus	Atlantic Croaker	1.65	0.09 (0.06)
Opisthonema oglinum	Atlantic Thread Herring	1.88	0.1 (0.07)
Opsanus tao	Oyster Toadfish	2.86	0.16 (0.12)
Orthopritis chrysoptera	Pigfish	3072.8	170.71 (29.57)
Paralichthys albigutta	Gulf Flounder	139.16	7.73 (2.31)
Paralichthys dentatus	Summer Flounder	0.67	0.04 (0.04)
Pomatomus saltatrix	Bluefish	11.51	0.64 (0.55)
Sphoeroides maculatus	Northern Pufferfish	2.91	0.16 (0.16)
Sphyraena spp.	Sphyraenid (Sennet/Barracuda)	13.89	0.77 (0.38)
Stenotomus caprinus	Longspine Porgy	0.88	0.05 (0.05)
Stephanolepis hispidus	Planehead Filefish	222.69	12.37 (7.99)

Sygnathus spp.	Pipefish	11.78	0.66 (0.38)
Synodus foetens	Lizardfish, Inshore	7.03	0.39 (0.17)
	Rays		
Dasyatis americana	Southern Stingray	1.72	0.1 (0.07)
Dasyatis sabina	Atlantic Stingray	0.83	0.04 (0.04)
	Cephalopods		
Decapodiformes spp.	Squid	0.77	0.04 (0.04)
	Crabs		
Achelous spinimanus	Blotched Swimming Crab	3.96	0.22 (0.22)
Callinectes sapidus	Blue Crab	194.54	10.81 (4.24)
Libinia spp.	Spider/Decorator Crab	28.31	1.57 (0.62)
	Shrimp		
Penaeus spp.	Commercial Shrimp	46.18	2.56 (1.186)

Table S2.3: Loo Criteria table of all Bayesian generalized linear mixed models compared to fit best model of the fixed effect of canopy height on abundance of pinfish. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model2 (site)	-0.4	1.2
Model1 (full)	-0.9	0.7
Model4 (no random)	-11	5.2

Table S2.4: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month on the abundance of pinfish (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.19	0.17	0.01	0.63	1	1264	1279

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-1.16	0.35	-1.85	-0.47	1	2505	1406
Canopy Height	0.01	0	0	0.01	1	3670	2573

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	2.91	0.75	1.62	4.59	1	2705	2438

Table S2.5: Statistical table of ANOVA to test for relationships across seagrass metrics. Significant p-values at the 0.05 alpha level are bolded and significant p-values at the 0.1 alpha level are italicized.

Year	Response Variable	Fixed Effect	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
2019	Leaf Number per Shoot	Species Present	3, 32	2.2571	0.75237	8.6609	**0.0002**
2019	Branch Number per Shoot	Species Present	3, 32	1.26361	0.4212	19.13	**<0.0001**
2019	Shoot Density	Species Present	3, 32	953.3	317.78	08913	0.4562
2019	Aboveground Biomass	Species Present	3, 32	0.9093	0.303111	2.1263	0.1163
2019	Leaf Width	Species Present	3, 32	0.13233	0.044111	1.0718	0.3748
2019	Canopy Height	Species Present	3, 32	2992	997.2	0.1776	0.9108
2019	Total Percent Cover	Species Present	3, 32	1.2041	0.40137	0.556	0.6479
2019	Shoot Length	Species Present	3, 32	885.7	295.24	0.396	0.7567
2019	Canopy Height	Total Percent Cover	3, 32	79730	26576.5	8.2596	**0.0003**
2019	Shoot Density	Total Percent Cover	3,32	2250.8	750.28	2.3745	*0.0885*
2019	Aboveground Biomass	Total Percent Cover	3, 32	0.4293	0.14311	0.9083	0.4479
2019	Leaf Width	Total Percent Cover	3, 32	0.19857	0.06619	1.6934	0.1881
2019	Leaf Number per Shoot	Total Percent Cover	3, 32	0.2378	0.079251	0.5284	0.666
2019	Branch Number per Shoot	Total Percent Cover	3, 32	0.08474	0.028247	0.4799	0.6985
2019	Shoot Length	Total Percent Cover	3, 32	3803.4	1267.8	1.9377	0.1433
2019	Seagrass Surface Area	Total Percent Cover	3, 32	306062430	102020810	2.9427	**0.0478**
2020	Branch Number per Shoot	Species Present	3, 14	0.23832	0.07944	8.8787	**0.0015**
2020	Total Percent Cover	Species Present	3, 14	2.3	0.76667	2.9009	*0.0721*
2020	Shoot Density	Species Present	3, 14	1198.6	399.54	1.164	0.3584
2020	Aboveground Biomass	Species Present	3, 14	0.06334	0.021113	0.2644	0.8499

2020	Leaf Number per Shoot	Species Present	3, 14	0.48139	0.16046	2.3629	0.1152
2020	Leaf Width	Species Present	3, 14	0.48207	0.16069	1.2582	0.3266
2020	Canopy Height	Species Present	3, 14	2708	903.16	0.2978	0.8264
2020	Canopy Height	Total Percent Cover	2, 15	9780	4889.8	2.0725	0.1604
2020	Shoot Density	Total Percent Cover	2, 15	279.6	139.8	0.3663	0.6993
2020	Aboveground Biomass	Total Percent Cover	2, 15	0.1194	0.059698	0.8433	0.4497
2020	Leaf Width	Total Percent Cover	2, 15	0.0008	0.000401	0.0027	0.9974
2020	Leaf Number per Shoot	Total Percent Cover	2, 15	0.05387	0.02934	0.2931	0.7501
2020	Branch Number per Shoot	Total Percent Cover	2, 15	0.077119	0.038560	2.0191	0.1673
2020	Shoot Length	Total Percent Cover	2, 15	86.3	43.17	0.0805	0.9231
2020	Seagrass Surface Area	Total Percent Cover	2, 15	32886963	16443482	0.6924	0.5157

Table S2.6: Results from pearson correlation analysis between seagrass metrics in 2019 and 2020. Significant p-values at the 0.05 alpha level are bolded and significant p-values at the 0.1 alpha level are italicized.

Year	X	Y	Pearson Correlation Coefficient	P Value
2019	Canopy Height	Shoot Length	0.5116	**0.0014**
2019	Canopy Height	Shoot Density	-0.1876	0.2733
2019	Canopy Height	Leaf Width	-0.2103	0.2183
2019	Canopy Height	Branch Number per Shoot	-0.687	0.6904
2019	Canopy Height	Aboveground Biomass	0.2553	0.1329
2019	Canopy Height	Leaf Number per Shoot	-0.0495	0.7744
2019	Shoot Density	Leaf Width	0.4071	**0.014**
2019	Shoot Density	Leaf Number per Shoot	0.3747	**0.024**
2019	Shoot Density	Aboveground Biomass	0.436	**0.0079**
2019	Shoot Density	Branch Number per Shoot	0.1584	0.3563
2019	Shoot Density	Shoot Length	-0.3260	*0.0524*
2019	Aboveground Biomass	Leaf Width	0.2440	0.1516
2019	Aboveground Biomass	Branch Number per Shoot	0.3560	**0.0331**
2019	Aboveground Biomass	Shoot Length	0.4815	**0.0029**
2019	Aboveground Biomass	Leaf Number per Shoot	0.3456	**0.0390**
2019	Leaf Width	Leaf Number per Shoot	0.3536	**0.0344**
2019	Leaf Width	Branch Number per Shoot	-0.0036	0.9834
2019	Leaf Width	Shoot Length	-0.4049	**0.0143**
2019	Branch Number per Shoot	Shoot Length	-0.02766	0.8728
2019	Branch Number per Shoot	Leaf Number per Shoot	0.6962	**<0.0001**
2019	Shoot Length	Leaf Number per Shoot	-0.2434	0.1526
2019	Seagrass Surface Area	Shoot Density	0.6348	**<0.0001**
2019	Seagrass Surface Area	Aboveground Biomass	0.8313	**<0.0001**
2020	Canopy Height	Shoot Length	0.7835	**0.0001**
2020	Canopy Height	Shoot Density	-0.4126	*0.089*

2020	Canopy Height	Leaf Width	0.7413	**0.0004**
2020	Canopy Height	Aboveground Biomass	0.4365	*0.07*
2020	Canopy Height	Leaf Number per Shoot	0.5387	**0.021**
2020	Canopy Height	Branch Number per Shoot	0.2043	0.4161
2020	Canopy Height	Depth Relative LMSL	0.4632	*0.0529*
2020	Shoot Density	Leaf Width	-0.6530	**0.0033**
2020	Shoot Density	Branch Number	0.3148	0.2033
2020	Shoot Density	Shoot Length	-0.6595	**0.0029**
2020	Shoot Density	Aboveground Biomass	0.2819	0.257
2020	Shoot Density	Leaf Number per Shoot	-0.3064	0.2162
2020	Aboveground Biomass	Leaf Width	0.0978	0.6995
2020	Aboveground Biomass	Branch Number per Shoot	0.1429	0.5715
2020	Aboveground Biomass	Shoot Length	0.3260	0.1868
2020	Aboveground Biomass	Leaf Number per Shoot	0.2292	0.3604
2020	Leaf Width	Leaf Number per Shoot	0.5995	**0.0085**
2020	Leaf Width	Branch Number per Shoot	-0.1139	0.6527
2020	Leaf Width	Shoot Length	0.7627	**0.0002**
2020	Branch Number per Shoot	Shoot Length	0.0897	0.7234
2020	Branch Number per Shoot	Leaf Number per Shoot	0.5148	**0.0288**
2020	Shoot Length	Leaf Number per Shoot	0.6915	**0.0015**
2020	Seagrass Surface Area	Shoot Density	0.5027	**0.0335**
2020	Seagrass Surface Area	Aboveground Biomass	0.7814	**0.0001**

Table S2.7: Family of Bayesian generalized linear mixed models for 2019 data analyses.

Response Variable	**Fixed Effect**	**Family**
CPUE	Shoot Density	Negative Binomial
Faunal Biomass	Shoot Density	Negative Binomial
Species Richness	Shoot Density	Negative Binomial
Standardized Biomass	Shoot Density	Gaussian (log link)
CPUE	Canopy Height	Negative Binomial
Faunal Biomass	Canopy Height	Negative Binomial
Species Richness	Canopy Height	Negative Binomial
Standardized Biomass	Canopy Height	Gaussian (log link)
CPUE	Seagrass Species Present	Negative Binomial
Faunal Biomass	Seagrass Species Present	Negative Binomial
Species Richness	Seagrass Species Present	Negative Binomial
Standardized Biomass	Seagrass Species Present	Gaussian (log link)
Planehead Filefish Abundance	Canopy Height	Negative Binomial
Spot Abundance	Canopy Height	Negative Binomial
Pinfish Abundance	Canopy Height	Negative Binomial
Pigfish Abundance	Canopy Height	Negative Binomial
Mojarra Abundance	Canopy Height	Negative Binomial
Silver Perch Abundance	Canopy Height	Negative Binomial
Blue Crab Abundance	Canopy Height	Negative Binomial
Gulf Flounder Abundance	Canopy Height	Negative Binomial
Snapper/Grouper Abundance	Canopy Height	Negative Binomial
Gulf Flounder Abundance	Shoot Density	Negative Binomial

Table S2.8: Family of generalized linear models for 2020 data analyses.

Response Variable	Fixed Effect	Family
CPUE	Canopy Height	Negative Binomial
Faunal Biomass	Canopy Height	Negative Binomial
Species Richness	Canopy Height	Negative Binomial
Standardized Biomass	Canopy Height	Gaussian (log link)
CPUE	Seagrass Species Present	Negative Binomial
Faunal Biomass	Seagrass Species Present	Negative Binomial
Species Richness	Seagrass Species Present	Negative Binomial
Planehead Filefish Abundance	Canopy Height	Negative Binomial
Spot Abundance	Canopy Height	Negative Binomial
Pinfish Abundance	Canopy Height	Negative Binomial
Pigfish Abundance	Canopy Height	Negative Binomial
Mojarra Abundance	Canopy Height	Negative Binomial
Silver Perch Abundance	Canopy Height	Negative Binomial
Blue Crab Abundance	Canopy Height	Negative Binomial
Gulf Flounder Abundance	Canopy Height	Negative Binomial
Gulf Flounder Abundance	Shoot Density	Negative Binomial
CPUE	Seagrass Surface Area	Negative Binomial
CPUE	Depth Relative LMSL	Negative Binomial
CPUE	Epibiont Load	Negative Binomial

Table S2.9: Results from hypothesis testing on Bayesian models that the fixed effect has a non-zero effect on the response variable. Bold probabilities indicate those above 95% probability. Probabilities over 90% are italicized.

Response Variable	Fixed Effect	Estimate	Est. Error	CI Lower	CI Upper	Evid Ratio	Post. Prob
CPUE	Shoot Density	0	0.01	-0.01	0.01	0.86	0.46
Biomass	Shoot Density	0	0.01	-0.01	0.02	1.91	0.66
Standardized Biomass	Shoot Density	0	0.01	-0.01	0.01	1.18	0.54
Species Richness	Shoot Density	0	0	-0.01	0	0.37	0.27
CPUE	Canopy Height	0.01	0	0.1	0.1	Inf	**1**
Biomass	Canopy Height	0.01	0	0	0.01	116.65	**0.99**
Standardized Biomass	Canopy Height	0	0	0	0	1.38	0.58
Species Richness	Canopy Height	0	0	0	0	132.33	**0.99**
CPUE	Surface Area	0.36	0.48	-0.44	1.12	3.65	0.78
Pigfish Abundance	Canopy Height	0.02	0	0.01	0.02	Inf	**1**
Flounder Abundance	Canopy Height	0	0	0	0.01	3.32	0.77
Flounder Abundance	Shoot Density	0	0.01	-0.03	0.02	0.62	0.38
Spot Abundance	Canopy Height	0.01	0.01	0	0.02	92.02	**0.99**
Pinfish Abundance	Canopy Height	0.01	0	0.01	0.01	Inf	**1**
Planehead Filefish Abundance	Canopy Height	0	0.01	-0.01	0.01	0.53	0.35
Blue Crab Abundance	Canopy Height	0.01	0	0	0.02	159	**0.99**
Mojarra Abundance	Canopy Height	0.01	0.01	-0.01	0.03	4.1	0.8
Silver Perch Abundance	Canopy Height	0.02	0.01	0.01	0.03	Inf	**1**
Snapper and Grouper Abundance	Canopy Height	0.01	0.01	0	0.02	9.87	*0.91*

Table S2.10: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of shoot density on faunal abundance. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero . When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-1	1.3
Model2 (site)	-3.8	2.8
Model4 (no random)	-17.2	4.8

Table S2.11: Statistical table of Bayesian generalized linear mixed model with fixed effect of shoot density and random effect of trawl month on the abundance of fish caught (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.67	0.39	0.15	1.80	1.01	580	314

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	0.73	0.65	-0.52	2.03	1	1420	1417
Shoot Density	0	0.01	-0.02	0.02	1	1261	831

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	2.08	0.53	1.22	3.28	1	2310	2402

Table S2.12: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of shoot density on faunal biomass. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-1.1	0.7
Model2 (site)	-11.2	3.4
Model4 (no random)	-12.2	6.3

Table S2.13: Statistical table of Bayesian generalized linear mixed model with fixed effect of shoot density and random effect of trawl month on the biomass of fish caught (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects							
~Trawl Month (Number of levels: 6)							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.08	0.46	0.5	2.24	1	856	1041
Population-Level Effects							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	2.35	0.66	1.07	3.69	1	1497	1603
Shoot Density	0	0.01	-0.01	0.02	1	2680	2500
Family Specific Parameters							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	2.71	0.7	1.51	4.25	1	2263	2503

Table S2.14: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of shoot density on faunal biomass standardized by faunal abundance. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model1 (full model)	0	0
Model3 (month)	-4.7	3.2
Model4 (no random)	-11.6	4.5
Model2 (site)	-12.4	4.3

Table S2.15: Statistical table of Bayesian generalized linear mixed model with fixed effect of shoot density and random effects of trawl month and site on the biomass of fish standardized by total faunal abundance (model 1). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Site (Number of levels: 17)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.33	0.11	0.12	0.57	1	935	1273

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.72	0.35	0.30	1.62	1	1200	1631

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.91	0.46	0.98	2.84	1	1535	2352
Shoot Density	0	0.01	-0.01	0.01	1	2290	2744

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	2.14	0.49	1.41	3.29	1	802	1704

Table S2.16: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of shoot density on species richness. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-0.9	0.2
Model4 (no random)	-11	3.4
Model2 (site)	-12.1	3.4

Table S2.17: Statistical table of Bayesian generalized linear mixed model with fixed effect of shoot density and random effect of trawl month on species richness (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.49	0.25	0.19	1.18	1	868	1107

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	2.48	0.35	1.75	3.13	1	1459	1528
Shoot Density	0	0	-0.01	0.01	1	3013	2900

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	95.71	75.19	18.81	295.81	1	2677	2601

Table S2.18: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of seagrass species present in the bed on the faunal abundance. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-0.9	0.5
Model2 (site)	-12.3	3.9
Model4 (no random)	-26.1	6.5

Table S2.19: Statistical table of Bayesian generalized linear mixed model with fixed effect of seagrass species present in the bed and random effect of trawl month on faunal abundance (model 3). H indicates *H. wrightii*, R indicates *R. maritima*, and Z indicates *Z. marina*. The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.91	0.38	0.40	1.91	1	1142	1670

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	0.51	0.53	-0.53	1.56	1	1441	1801
HR Present	-1.20	0.80	-2.67	0.50	1	2570	2325
HZ Present	0.37	0.39	-0.46	1.09	1	2395	2558
HRZ Present	-0.56	0.44	-1.43	0.30	1	2432	2378

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	3.24	0.88	1.73	5.15	1	2162	2420

Table S2.20: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of seagrass species present in the bed on the faunal biomass. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-0.5	0.3
Model2 (site)	-14.3	4.0
Model4 (no random)	-15.3	6.9

Table S2.21: Statistical table of Bayesian generalized linear mixed model with fixed effect of seagrass species present in the bed and random effect of trawl month on faunal biomass (model 3). H indicates *H. wrightii*, R indicates *R. maritima*, and Z indicates *Z. marina*. The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.20	0.50	0.58	2.49	1	1103	1604

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	2.33	0.61	1.15	3.55	1	1384	1256
HR Present	-0.42	0.80	-1.87	1.27	1	2399	2464
HZ Present	0.38	0.40	-0.48	1.10	1	2170	1809
HRZ Present	-0.21	0.45	-1.13	0.65	1	2068	2155

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	3.15	0.83	1.75	5.01	1	2237	1991

Table S2.22: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of seagrass species present in the bed on the faunal biomass standardized by faunal abundance. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model1 (full model)	0	0
Model3 (month)	-4.3	2.4
Model2 (site)	-18.7	6.8
Model4 (no random)	-18.9	7.7

Table S2.23: Statistical table of Bayesian generalized linear mixed model with fixed effect of seagrass species present in the bed and random effect of trawl month on faunal biomass standardized by faunal abundance (model 1). H indicates *H. wrightii*, R indicates *R. maritima*, and Z indicates *Z. marina*. The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Site (Number of levels: 17)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.18	0.11	0.01	0.43	1.01	758	2020

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.69	0.34	0.28	1.57	1	1107	1210

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.75	0.66	0.59	2.62	1.01	716	379
HR Present	0.77	0.64	-0.01	1.88	1.01	691	329
HZ Present	0.09	0.58	-0.48	1.09	1.01	766	323
HRZ Present	0.41	0.60	-0.22	1.39	1.01	718	332

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	2.29	0.48	1.49	3.33	1.01	592	812

Table S2.24: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model for the fixed effect of seagrass species present in the bed on the species richness. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-1.3	0.5
Model4 (no random)	-15.5	3.2
Model2 (site)	-16.5	3.3

Table S2.25: Statistical table of Bayesian generalized linear mixed model with fixed effect of seagrass species present in the bed and random effects of trawl month on species richness (model 3). H indicates *H. wrightii*, R indicates *R. maritima*, and Z indicates *Z. marina*. The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.54	0.26	0.22	1.24	1	842	1411

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	2.31	0.31	1.68	2.93	1.00	1516	1856
HR Present	-0.47	0.45	-1.41	0.39	1	2808	2654
HZ Present	0.07	0.24	-0.40	0.55	1	2301	2320
HRZ Present	-0.11	0.25	-0.59	0.41	1	2339	2216

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	106.97	83.03	19.61	330.05	1	2566	2482

Table S2.26: Statistical table of generalized linear model with fixed effect of seagrass species present in the seagrass bed on the response variables with *Z. marina* dominated bed excluded. Significant p-values at the 0.05 level are bolded.

Response Variable	DF	Deviance	Residual Deviance	Pr(>Chi)
CPUE	3, 13	1.7542	18.061	0.625
Faunal Biomass	3, 13	2.8012	17.659	0.4233
Standardized Biomass	3, 13	142.64	1511.3	0.7466
Species Richness	3, 13	2.7427	15.641	0.433

Table S2.27: LOO Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on faunal abundance. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model2 (site)	0	1
Model1 (full model)	-0.8	0.6
Model4 (no random)	-14.9	6

Table S2.28: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effect of trawl month on the abundance of fish caught (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.19	0.16	0.01	0.62	1	1460	1971

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-1.05	0.34	-1.71	-0.36	1	3852	3042
Canopy Height	0.01	0	0.01	0.01	1	4469	3166

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	3.21	0.82	1.83	5	1	3072	2306

Table S2.29: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on faunal biomass. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full model)	-1.4	0.6
Model4 (no random)	-3.4	5.6
Model2 (site)	-7.8	2.5

Table S2.30: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effect of trawl month on the biomass of fish caught (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects
~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.86	0.41	0.3	1.87	1	823	1142

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.53	0.57	0.44	2.71	1	1457	1854
Canopy Height	0.01	0	0	0.01	1	2515	2355

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	2.97	0.76	1.64	4.61	1	1879	2140

Table S2.31: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on standardized faunal biomass. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_dff
Model2 (site)	0	0
Model4 (no random)	-0.20	0.80
Model3 (month)	-6.52E+04	2.43E+04
Model1 (full)	-1.11E+13	7.49E+12

Table S2.32: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effect of trawl site on the standardized biomass of fish caught (model 2). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Site (Number of levels: 17)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.2	0.15	0.01	0.58	1.03	160	323

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.91	0.86	0.99	2.6	1.03	367	128
Canopy Height	0	0	0	0	1.03	12.07	104

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	4.29	0.86	3.11	6.6	1.08	33	25

Table S2.33: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on species richness. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full)	-0.4	0.3
Model4 (no random)	-2.1	1.5
Model2 (site)	-2.5	1.4

Table S2.34: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effect of trawl month on the species richness of fish caught (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.26	0.18	0.02	0.72	1	810	844

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.73	0.26	1.24	2.27	1	1913	2161
Canopy Height	0	0	0	0.1	1	2620	2633

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	102.52	79.31	20.06	318.82	1	2493	2762

Table S2.35: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of surface area on total faunal abundance. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full)	-0.6	1.0
Model2 (site)	-1.6	2.2
Model4 (no random)	-14.6	5.4

Table S2.36: Statistical table of Bayesian generalized linear mixed model with fixed effect of surface area and random effect of trawl month on the total abundance of fish caught (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects
~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.59	0.41	0.06	1.58	1.01	338	436

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.56	4.63	-11.07	7.15	1.00	1094	1149
Surface Area	0.33	0.48	-0.67	1.22	1.00	1118	1125

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	2.09	0.53	1.21	3.25	1.00	1072	566

Table S2.37: Statistical table of generalized linear model results with *Z. marina* dominated bed included. Significant p-values at the 0.05 level are bolded and at the 0.1 level are italicized.

Response Variable	Fixed Effect	Estimate	Std. Error	DF	Z Value	Pr(>|Z|)
CPUE	Canopy Height	0.006862	0.003036	17	2.257	**0.024**
Faunal Biomass	Canopy Height	0.004195	0.002503	17	1.676	*0.0937*
Species Richness	Canopy Height	0.001489	0.001509	17	0.987	0.324
CPUE	Bed Depth Relative LMSL	-1.8717	1.3813	17	-1.355	0.175
Pigfish Abundance	Canopy Height	0.002038	0.004223	17	0.483	0.629
Gulf Flounder Abundance	Canopy Height	0.009225	0.005671	17	1.627	0.104
Gulf Flounder Abundance	Shoot Density	-0.005804	0.01669	17	-0.348	0.728
Spot Abundance	Canopy Height	-0.013855	0.005618	17	-2.466	**0.0137**
Pinfish Abundance	Canopy Height	0.008974	0.002949	17	3.043	**0.00234**
Planehead Filefish Abundance	Canopy Height	0.021835	0.003987	17	5.477	**4.33E-08**
Blue Crab Abundance	Canopy Height	0.014267	0.006447	17	2.213	**0.0269**
Mojarra Abundance	Canopy Height	-0.02493	0.01001	17	-2.49	**0.0128**
Silver Perch Abundance	Canopy Height	0.01486	0.01043	17	1.425	0.1543
CPUE	Seagrass Surface Area	7.758 e-6	3.711 e-5	17	0.209	0.8344
CPUE	Epibiont Load	0.4786	0.4590	17	1.043	0.29706

Table S2.38: Statistical table of generalized linear model results with *Z. marina* dominated bed excluded. Significant p-values at the 0.05 level are bolded and at the 0.1 level are italicized.

Response Variable	Fixed Effect	Estimate	Std. Error	DF	Z Value	Pr(>|Z|)
CPUE	Canopy Height	0.002861	0.003681	16	0.777	0.437
Faunal Biomass	Canopy Height	0.001084	0.003007	16	0.36	0.718
Species Richness	Canopy Height	-0.0002069	0.0018956	16	-0.109	0.913
Planehead Filefish Abundance	Canopy Height	0.013627	0.004353	16	3.131	**0.00174**
Spot Abundance	Canopy Height	-0.011906	0.006945	16	-1.714	*0.0865*
Pinfish Abundance	Canopy Height	0.004575	0.003552	16	1.288	0.198
Pigfish Abundance	Canopy Height	0.001392	0.005135	16	0.271	0.786
Mojarra Abundance	Canopy Height	-0.02394	0.01068	16	-2.242	**0.0250**
Silver Perch Abundance	Canopy Height	0.0188	0.01372	16	1.371	0.1705
Blue Crab Abundance	Canopy Height	0.010452	0.008217	16	1.272	0.2034
Gulf Flounder Abundance	Canopy Height	0.010446	0.006634	16	1.575	0.115
Gulf Flounder Abundance	Shoot Density	-0.002844	0.028488	16	-0.1	0.92
CPUE	Bed Depth Relative LMSL	-0.7074	1.2841	16	-0.551	0.582
CPUE	Seagrass Surface Area	2.508 e-5	3.23 e-5	16	0.776	0.437
CPUE	Epibiont Load	0.3712	0.4030	16	0.921	0.35693

Table S2.39: Statistical table of generalized linear model (GLM) and linear model (LM) results with *Z. marina* dominated bed excluded from analyses. Significant p-values at the 0.05 level are bolded and at the 0.1 level are italicized.

Response Variable	Fixed Effect	Estimate	Std. Error	DF	t Value	Pr(>|t|)
Standardized Faunal Biomass	Canopy Height (GLM)	-0.008729	0.008454	16	-1.033	0.3182
Canopy Height	Bed Depth Relative LMSL (LM)	-145.31	81.36	15	-1.786	*0.0943*
Epibiont Load	Bed Depth Relative LMSL (LM)	-0.9261	0.7712	15	-1.201	0.248

Table S2.40: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on abundance of pigfish. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model1 (full)	0	0
Model3 (month)	-1.3	2.1
Model2 (site)	-7.6	3.8
Model 4 (no random)	-54.6	12.1

Table S2.41: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month and trawl site on the abundance of pigfish (model 1). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Site (Number of levels: 17)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.5	0.26	0.06	1.08	1	1104	1112

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.89	0.94	0.6	4.19	1	1232	1496

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-5.68	1.08	-7.76	-3.45	1	1481	1985
Canopy Height	0.02	0	0.01	0.02	1	2125	2181

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	1.87	0.71	0.84	3.57	1	1609	2194

Table S2.42: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on abundance of spot. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full)	-0.6	0.7
Model2 (site)	-4.9	2.5
Model4 (no random)	-53.4	15.1

Table S2.43: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month on the abundance of spot. The model includes 4 chains, each with 2000 iterations (model 3). 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.29	0.6	0.4	2.8	1	1157	1416

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-5.88	1.18	-8.3	-3.64	1	2207	2280
Canopy Height	0.01	0.01	0	0.02	1	2127	2277

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	0.69	0.23	0.34	1.23	1	2466	2630

Table S2.44: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on abundance of blue crab. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (fll)	-0.1	1.5
Model2 (site)	-0.5	1.9
Model4 (no random)	-23.8	5.8

Table S2.45: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month on the abundance of blue crab (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.57	0.4	0.04	1.6	1	1106	1618

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-5.67	0.77	-7.21	-4.13	1	2454	2347
Canopy Height	0.01	0	0	0.02	1	2750	1922

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	1.27	0.44	0.63	2.3	1	2740	2511

Table S2.46: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on abundance of silver perch. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model2 (site)	0	0
Model1 (full)	-0.5	0.8
Model12 (site)	-0.5	2.1
Model4 (no random)	-45.3	11.5

Table S2.47: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl site on the abundance of silver perch (model 2). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Draws: 4 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmupdraws = 4000							
Group-Level Effects							
~Site (Number of levels: 17)							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.06	0.72	0.05	2.73	1	555	1258
Population-Level Effects							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-8.72	1.56	-12.14	-5.97	1	828	645
Canopy Height	0.02	0.01	0.01	0.04	1	1602	1781
Family Specific Parameters							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	0.59	0.34	0.22	1.38	1.01	706	289

Table S2.48: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on the combined abundance of snapper and grouper species. Best fit models using LOO cross validation have the a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full)	0	0.7
Model2 (site)	-12.9	4.4
Model4 (no random)	-71.2	10.3

Table S2.49: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month on the combined abundance of snapper and grouper species (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	4.05	1.68	1.77	8.2	1	1674	1831

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-9.34	2.27	-14.13	-5.08	1	1570	1352
Canopy Height	0.01	0.01	-0.01	0.03	1	2558	1979

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	0.85	0.52	0.24	2.19	1	1940	2038

Table S2.50: Loo Criteria table of all Bayesian generalized linear mixed models compared to fit best model of the fixed effect of canopy height on abundance of planehead filefish. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model1 (full)	0	0
Model3 (month)	-10.8	2.7
Model2 (site)	-17.6	4.6
Model4 (no random)	-62.2	10.9

Table S2.51: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month and trawl site on the abundance of planehead filefish (model 1). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Site (Number of levels: 17)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.25	0.42	0.6	2.25	1	1162	1577

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	2.7	1.14	1.15	5.61	1	1455	2043

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-5.5	1.68	-8.92	-2.27	1	1327	1598
Canopy Height	0	0.01	-0.01	0.01	1	1480	1627

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	31.33	46.62	1.09	160.14	1.01	1001	1162

Table S2.52: Loo Criteria table of all Bayesian generalized linear mixed models compared to fit best model of the fixed effect of canopy height on abundance of mojarra. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model1 (full)	0	0
Model3 (month)	-13.7	3.2
Model2 (site)	-15.9	2.9
Model4 (no random)	-61.4	10.5

Table S2.53: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month and trawl site on the abundance of mojarra (model 1). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Site (Number of levels: 17)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.95	0.7	0.89	3.59	1	709	559

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	2.87	1.35	1.07	6.32	1.01	1473	2274

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-8.25	2.27	-12.97	-4.04	1	1067	1491
Canopy Height	0.01	0.01	-0.01	0.03	1	1080	1573

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	31.33	47.11	0.69	168.11	1	843	612

Table S2.54: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of canopy height on abundance of gulf flounder. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full)	-0.8	1.7
Model2 (site)	-2.8	2.8
Model4 (no random)	-18.3	5.5

Table S2.55: Statistical table of Bayesian generalized linear mixed model with fixed effect of canopy height and random effects of trawl month on the abundance of gulf flounder(model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.84	0.47	0.13	1.98	1	852	822

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-4.99	0.76	-6.51	-3.51	1	2013	2276
Canopy Height	0	0	0	0.01	1	3344	2968

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	1.83	0.91	0.74	4.35	1	2166	1689

Table S2.56: Loo Criteria table of all Bayesian generalized linear mixed models compared to best fit model of the fixed effect of seagrass shoot density on the abundance of gulf flounder. Best fit models using LOO cross validation have a difference in expected log predictive density (elpd_diff) value closest to zero. When the difference in elpd (elpd_diff) was equal across models we chose the model with lowest standard error (se_diff).

	elpd_diff	se_diff
Model3 (month)	0	0
Model1 (full)	-0.8	2.0
Model2 (site)	-1.6	3.3
Model4 (no random)	-17.7	5.1

Table S2.57: Statistical table of Bayesian generalized linear mixed model with fixed effect of seagrass shoot density and random effects of trawl month on the abundance of gulf flounder (model 3). The model includes 4 chains, each with 2000 iterations. 1000 warmup, thin = 1, and total post-warmup draws of 4000.

Group-Level Effects

~Trawl Month (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.92	0.52	0.16	2.21	1	841	1010

Population-Level Effects

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-4.25	0.94	-6.04	-2.31	1	2215	2114
Shoot Density	0	0.01	- 0.03	0.02	1	2220	1960

Family Specific Parameters

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
shape	1.82	0.91	0.73	4.00	1	2494	1671

Table S2.58: Statistical Table of linear model results with the epibiont outlier excluded from analyses. Inclusion or exclusion of the *Z. marina* dominated bed is indicated in the response variable column as "Z included" or "Z excluded". Significant p-values at the 0.05 level are bolded and at the 0.1 level are italicized.

Response Variable	Fixed Effect	Estimate	Std. Error	DF	t Value	Pr(>|t|)
Epibiont Load (Z excluded)	Bed Depth Relative LMSL	-0.7995	0.3551	14	-2.252	**0.040927**
Epibiont Load (Z included)	Bed Depth Relative LMSL	-0.6858	0.3580	15	-1.916	*0.074682*

Table S2.59: Statistical Table of generalized linear model results with the epibiont outlier excluded from analyses. Inclusion or exclusion of the *Z. marina* dominated bed is indicated in the response variable column as "Z included" or "Z excluded". Significant p-values at the 0.05 level are bolded and at the 0.1 level are italicized.

Response Variable	Fixed Effect	Estimate	Std. Error	DF	z Value	Pr(>|z|)
CPUE (Z excluded)	Epibiont Load	0.2256	0.8369	15	0.270	0.7875
CPUE (Z included)	Epibiont Load	0.9435	0.9235	16	1.022	0.307

Table S2.60: Statistical table from Bayesian multinomial linear regression on the preference of pinfish between four habitat choices in the equal surface area (high) trials. Random effects of tank used, week of study, and deep side of tank were included. The model includes 4 chains, each with 100000 iterations. 50000 warmup, thin = 50, and total post-warmup draws of 4000.

Group-Level Effects:

~DeepSide (Number of levels: 2)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	1.19	1.22	0.03	4.51	1	3883	3853
sd(muShallowShort_Intercept)	2.5	2.76	0.07	9.09	1	4091	3817
sd(muShallowTall_Intercept)	1.76	1.67	0.07	6.09	1	3942	3940

~Tank (Number of levels: 2)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	1.32	1.36	0.05	4.77	1	3762	3615
sd(muShallowShort_Intercept)	2.34	2.44	0.07	8.94	1	4063	3864
sd(muShallowTall_Intercept)	1.4	1.51	0.03	5.27	1	4056	3890

~Week (Number of levels: 6)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	0.51	0.47	0.02	1.65	1	3983	3973
sd(muShallowShort_Intercept)	2	1.93	0.07	6.82	1	4049	3389
sd(muShallowTall_Intercept)	2.63	1.93	0.25	7.6	1	3821	3873

Population-Level Effects:

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	0.34	1.23	-2.23	2.8	1	3612	3852
sd(muShallowShort_Intercept)	-2.91	2.66	-8.54	1.95	1	3453	3501
sd(muShallowTall_Intercept)	-2.01	2.06	-6.53	1.84	1	4160	3915

Table S2.61: Statistical table from Bayesian multinomial linear regression on the preference of pinfish between four habitat choices in the equal surface area (low) trials. Random effects of tank used, week of study, and deep side of tank were included. The model includes 4 chains, each with 100000 iterations. 50000 warmup, thin = 50, and total post-warmup draws of 4000.

Group-Level Effects:

~DeepSide (Number of levels: 2)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	1.18	1.29	0.03	4.59	1	3895	3666
sd(muShallowShort_Intercept)	1.73	1.77	0.06	6.13	1	4060	3917
sd(muShallowTall_Intercept)	1.38	1.38	0.04	5.06	1	3962	3872

~Tank (Number of levels: 2)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	1.06	1.24	0.03	4.52	1	3879	3910
sd(muShallowShort_Intercept)	2.69	2.56	0.11	9.2	1	4029	3931
sd(muShallowTall_Intercept)	1.31	1.41	0.04	4.84	1	3918	3963

~Week (Number of levels: 7)

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	0.43	0.38	0.01	1.46	1	3878	3956
sd(muShallowShort_Intercept)	1.41	1.33	0.05	4.78	1	3754	4163
sd(muShallowTall_Intercept)	0.97	0.86	0.04	3.29	1	4434	4144

Population-Level Effects:

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	-0.19	1.2	-2.68	2.4	1	4168	3689
sd(muShallowShort_Intercept)	-2.49	2.28	-7.25	2.04	1	3808	3528
sd(muShallowTall_Intercept)	-1.52	1.5	-4.38	1.69	1	3836	3891

Table S2.62: Statistical table from Bayesian multinomial linear regression on the preference of pinfish between four habitat choices in the equal shoot density trials. Random effects of tank used, week of study, and deep side of tank were included. The model includes 4 chains, each with 100000 iterations. 50000 warmup, thin = 50, and total post-warmup draws of 4000.

Group-Level Effects:							
~DeepSide (Number of levels: 2)							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	1.12	1.24	0.03	4.6	1	4284	4096
sd(muShallowShort_Intercept)	2.87	2.54	0.16	9.11	1	3873	3860
sd(muShallowTall_Intercept)	1.51	1.39	0.05	4.96	1	3783	3560
~Tank (Number of levels: 2)							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	1.07	1.2	0.03	4.34	1	4127	4141
sd(muShallowShort_Intercept)	1.44	1.51	0.05	5.1	1	3760	3856
sd(muShallowTall_Intercept)	1.48	1.43	0.05	5.23	1	3668	3477
~Week (Number of levels: 7)							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	0.6	0.51	0.02	1.89	1	4020	3573
sd(muShallowShort_Intercept)	0.96	0.9	0.03	3.33	1	4102	3918
sd(muShallowTall_Intercept)	0.95	0.79	0.04	2.93	1	4039	3796
Population-Level Effects:							
	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(muDeepTall_Intercept)	0.52	1.19	-2.07	2.83	1	3823	3929
sd(muShallowShort_Intercept)	-1.74	2.1	-6.56	2.2	1	4075	3618
sd(muShallowTall_Intercept)	-0.49	1.49	-3.47	2.5	1	4032	3441

Table S2.63: Statistical table of generalized linear model with fixed effect of seagrass species present in the seagrass bed on the response variables with *Z. marina* dominated bed included. Significant p-values at the 0.05 level are bolded.

Response Variable	DF	Deviance	Residual Deviance	Pr(>Chi)
CPUE	3, 14	2.4889	19.397	0.4773
Faunal Biomass	3, 14	4.0964	18.811	0.2512
Standardized Biomass	3, 14	153.47	1520.7	0.7025
Species Richness	3, 14	4.4423	16.736	0.2175

Table S2.64: Statistical Table of generalized linear model (GLM) and linear model (LM) results with *Z. marina* dominated bed included in analyses. Significant p-values at the 0.05 level are bolded and at the 0.1 level are italicized.

Response Variable	Fixed Effect	Estimate	Std. Error	DF	t Value	Pr(>|t|)
Standardized Faunal Biomass	Canopy Height (GLM)	-0.00797	0.007438	17	-1.071	0.29985
Canopy Height	Bed Depth Relative LMSL (LM)	-192.83	92.24	16	-2.091	*0.0529*
Epibiont Load	Bed Depth Relative LMSL (LM)	-0.8394	0.7334	16	-1.145	0.2692

Chapter 3: Evaluating habitat provisioning and restoration potential of a subtropical seagrass species in a temperate estuary

Abstract

Accelerating human-induced losses of biogenic coastal ecosystems has prompted interest on how to restore these critical habitats. In North Carolina, the temperate, habitat-forming seagrass *Zostera marina* may be replaced by the tropical habitat-forming seagrass, *Halodule wrightii,* and the widespread seagrass, *Ruppia maritima* as waters warm. We sought to understand how abiotic (e.g., water depth) and biotic factors (e.g., seagrass species composition) influence the distribution of *H. wrightii*, as well as its restoration potential and associated faunal community. We conducted surveys to characterize the spatio-temporal distribution and morphology of natural seagrass beds in coastal North Carolina and conducted a restoration experiment to test the effect of transplantation depth (intertidal vs. subtidal) on 1) *H. wrightii* restoration success and 2) the associated faunal community. Surveyed seagrass beds were largely dominated by *H. wrightii* from April to September 2019. Seagrass species composition and within-species morphology differed across sampling months, but only canopy height differed across depths. Intertidal *H. wrightii* transplants persisted >18 months post-restoration; whereas, nearly all subtidal transplants were lost within six months. We found no difference in faunal community abundance or structure between transplanted and control plots across depths. However, these communities were less abundant and less rich than those sampled in a nearby natural reference seagrass bed. Our results suggest that although *H. wrightii* is highly abundant in North Carolina seagrass beds, small scale transplantation does not lead to successful restoration or host communities as abundant as natural beds, despite intertidal transplants surviving better than subtidal. Greater understanding of the role of *H. wrightii* as faunal habitat and increased

focus on identifying best practices for its restoration are critical to sustain and enhance ecosystem functioning in changing estuaries.

Introduction

Structurally complex coastal habitats formed by foundation species, such as salt marshes, coral reefs, and seagrass meadows, provide multiple ecosystem services including shoreline protection, nutrient cycling, carbon sequestration, and as habitats for juvenile organisms resulting in their classification as nursery areas (Beaumont et al. 2007, Waycott et al. 2009, Barbier et al. 2011, Dennis 1992, Beck et al. 2001, Minello et al. 2003, Sheridan and Hays 2003, Sheaves et al. 2013, Lefcheck et al. 2019). In particular, seagrass meadows serve as nursery areas for large and diverse faunal communities, enabling juvenile nekton to mature through high-mortality life stages more quickly than they would in other habitats (Heck and Thoman 1984, Beck et al. 2001, Heck Jr. et al. 2003, Lefcheck et al. 2019). Additionally, despite covering less than 0.2% of the world's oceans, seagrasses provide nursery habitat to 21.5% of the species on the FAO's "top 25 most landed species" list (FAO 2016).

Despite their recognized importance in nutrient cycling, sediment stabilization, water quality improvement, and habitat provisioning (Duarte 2002), global seagrass extent has declined by roughly 30% relative to coverage records from 1879 (Waycott et al. 2009). Currently, seagrass is being lost at an estimated rate of 2-5% per year, with annual rates possibly as high as 7% per year and increasing (Waycott et al. 2009). Therefore, restoration efforts have increased in recent decades to combat these losses and preserve ecosystem functioning (Zhang et al. 2018). While some projects have seen high success rates (>85% survival of transplants; Bastyan and Cambridge 2008, Balestri and Lardicci 2012), seagrass

restoration can be extremely costly and outcomes are highly variable (Bayraktarov et al. 2016). This is due in part to a lack of information about environmental conditions that will promote growth and establishment of restored seagrasses (van Katwijk et al. 2009). Therefore, important factors to consider prior to implementing seagrass restoration projects include proper citing (e.g., energy regime, depth) and restoration strategy (e.g., seed planting, adult transplantation; Fonseca et al. 1998, van Katwijk et al. 2009, Bayraktarov et al. 2016).

Depth is an important environmental variable in predicting seagrass survival and restoration success (Duarte 1991, Sheridan et al. 1998, Aoki et al. 2020), as light required for photosynthesis declines with depth, while deeper waters provide protection from desiccation and UV/thermal stress (Duarte 1991, Fonseca and Bell 1998, Duarte et al. 2007). Water depth can also influence seagrass morphology, with decreased blade widths, increased leaf area, decreased leaf biomasss, and decreased leaf production rates due to decreased light availability (Thayer et al. 1984, Lee and Dunton 1997, Olesen et al. 2002). Depth may also play a role in the habitat functioning of seagrass beds, with some fish preferring deeper seagrasses over shallower beds (see chapter 2). Further, intertidal seagrass beds can be exposed at low tides, limiting the type and abundance of organisms that can remain in these habitats. Thus, it is imperative to understand how depth influences seagrass bed presence, composition, and morphology, as well as habitat provisioning for motile fauna.

The Outer Banks of North Carolina represent a valuable study system to investigate the factors affecting seagrass composition and restoration success. In North Carolina, seagrasses face threats such as thermal stress from climate change, nutrient loading from runoff, and increased storminess (NC Department of Environmental Quality 2021). These stressors have led to declines of over 10% of high salinity submerged aquatic vegetation in

southern areas of the state between surveys conducted in 2006/2007 and 2013, with no clear signs of recovery (Field et al. 2021, NC Department of Environmental Quality 2021). Therefore, there is a strong need to develop restoration techniques to proactively increase seagrass habitat extent. Additionally, the semi-diurnal tidal system of North Carolina may further increase the stress of intertidal habitats due to the twice daily low tides increasing the temperatures and potential of desiccation the seagrasses are experiencing (Fonseca et al. 1998, Suykerbuyk et al. 2016). North Carolina meadows are comprised of one to three of the following seagrass species: *Halodule wrightii, Ruppia maritima,* and *Zostera marina*. Previous restoration efforts in North Carolina's high salinity waters have focused on restoring *Z. marina*, a species at its southernmost extent in North Carolina rather than either *H. wrightii* or *R. maritima* (Kenworthy et al. 1980, Fonseca et al. 1990, Zhang et al. 2021).

In contrast to *Z. marina, H. wrightii* is much less studied with regards to successful restoration practices. In fact, a 2016 meta-analysis on seagrass restoration found over 200 restoration studies on *Z. marina,* but only 58 on *H. wrightii* worldwide (van Katwijk et al. 2016). Previous studies of North Carolina faunal communities have found *Z. marina* to host larger and more diverse communities compared to *H. wrightii* (Micheli et al. 2008), potentially explaining the focus on *Z. marina* restoration. However, *H. wrightii* may be a better candidate species for restoration in North Carolina due to its higher temperate tolerance and increasing dominance as compared to *Z. marina,* particularly in the warmer summer months (Wilson and Lotze 2019, Bartenfelder et al. 2022). *H. wrightii* can also rapidly expand into recently disturbed areas within a seagrass meadow at the start of its growing season in the late spring/early summer and has the potential to become as dense as the surrounding seagrass bed within one year after disturbance (Donaher et al. 2021). Moreover, due to the range and

heat tolerance limitations of temperate *Z. marina*, subtropical *H. wrightii* is likely to become increasingly dominant in coastal North Carolina with climate change (Micheli et al. 2008, Wilson and Lotze 2019, Aoki et al. 2020, Bartenfelder et al. 2022). Therefore, understanding best practices for restoring *H. wrightii* in these communities is critical should temperatures warm above the tolerance threshold for *Z. marina*, leading to its extirpation in the region.

To address knowledge gaps in *H. wrightii* distribution and restoration practices, we combined field surveys and an experimental transplantation to address the following questions: (1) how do abiotic (i.e., depth) and biotic factors (i.e., species composition) influence the distribution and morphology of a habitat-forming seagrass*, H. wrightii* and (2) how does depth impact the restoration success of *H. wrightii* and its associated motile fauna? We hypothesized (*H1*) that *H. wrightii* would co-occur with *R. maritima* at shallower depths and *Z. marina* at deeper depths, and that *H. wrightii* would be seasonally dominant in the mid- to late-summer. We further hypothesized (*H2*) that *H. wrightii* shoot heights would increase with depth, but other morphological traits (e.g., leaf number per shoot, leaf width) would decrease with increasing depth. We hypothesized (*H3*) that the restoration potential of *H. wrightii* would be equivalent across subtidal and intertidal depths within the natural depth range of *H. wrightii*. However, we hypothesized (*H4*) that motile faunal use of restored (transplanted) *H. wrightii* would increase with depth and seagrass cover.

Methods

Study Sites

This study was conducted in Back Sound within the Albemarle-Pamlico estuarine system in Carteret County, North Carolina. Back Sound is a shallow, well-mixed estuarine system

characterized by high salinity and diurnal tides due to its proximity to the Beaufort and Barden inlets. North Carolina is at the transition zone of temperate and subtropical ecosystems, impacting the composition of seagrass species within meadows (Field et al. 2021, NC Department of Environmental Quality 2021). Seagrass composition and seasonal trends have shifted over time within this transition zone due to warming temperatures as well changes in water clarity (Micheli et al. 2008, NC Department of Environmental Quality 2021, Bartenfelder et al. 2022).

The transplantation experiment was conducted in Back Sound near the Harker's Island public boat ramp in Carteret County, North Carolina (34º43'25.07" N, 76º34'47.04" W). This site is characterized by a large, continuous seagrass bed with a matrix of salt marsh, oyster reefs, and sandy habitats (Figure S3.2). The natural seagrass bed at the restoration location is dominated by *H. wrightii*, interspersed with *R. maritima* and *Z. marina*, with the presence of *Z. marina* declining in the mid to late summer after a spring and early summer peak (*personal observation*, Field et al. 2021, NC Department of Environmental Quality 2021).

Seagrass Survey Design

To test *H1* and *H2*, we conducted two years (2019 and 2020) of seagrass surveys, assessing how meadow composition, complexity, and seagrass morphology varied monthly over the 2019 growing season (April-September) and with depth in June and July 2020 (Thayer et al. 1984, Zhang et al. 2021, Donaher et al. 2021). In 2019, each month we randomly selected six beds from 20 mixed community seagrass beds across the entirety of Back Sound to sample (Zhang et al. 2021; Figure S3.1). At each site we delineated three, 50-m transects across each bed to quantify meadow complexity and species composition. Where possible, transects were placed parallel to each other in the seagrass bed. In smaller, more patchy beds, transects were placed end

to end or perpendicularly to ensure the greatest seagrass presence across the transect. Along each transect, we measured percent cover of *Z. marina* and *H. wrightii/R. maritima* and canopy height in 0.0625-m^2 quadrats placed every five meters. We combined *H. wrightii* and *R. maritima* for percent cover measurements as it is difficult to visually distinguish between *H. wrightii* and *R. maritima* in the field. We estimated percent cover according to the North Carolina Vegetation Survey Index (NCVI), which maximizes the ability to distinguish differences between areas of low cover (e.g., 1% and 2%) more easily than high cover (e.g., 25% and 26%; Peet et al. 1998). Canopy height was quantified as the mean of the 5 tallest seagrass shoots within the quadrat, regardless of species. A single core was taken along each transect at the first sampling location to surpass 50% cover or where seagrass cover was the highest if no quadrat had over 50% cover.

Core samples were taken with a 10-cm diameter metal corer pushed into the sediment to a depth of 15 cm and sieved in the field to remove sediment and shells. Core samples were frozen until processing at which point they were thawed and processed (Donaher et al. 2021) for shoot density, shoot length, leaf width and number per shoot, and branch number per shoot. *R. maritima* and *H. wrightii* can be distinguished in the lab so seagrass metrics analyzed during core processing could be attributed to individual species. Within each core, we haphazardly selected five shoots of each species and measured shoot length, leaf width, number of leaves per shoot, and number of branches per shoot (*R. maritima* and reproductive shoots of *Z. marina* only; Figure S3.3). *H. wrightii* and vegetative *Z. marina* shoots do not display branching; therefore, branch number was recorded as one. Aboveground biomass from the subset of measured shoots was dried at 60ºC and massed separately from the rest of the core. The remaining shoots were identified to species, enumerated, separated into above- and belowground biomass, dried and massed as described above (Donaher et al. 2021).

To quantify seagrass composition during peak productivity and to assess how meadow composition, complexity, and seagrass morphology varied across depths, we sampled 18 seagrass beds in June and July 2020, which coincided with the highest seagrass canopy heights observed in 2019 sampling, and when *H. wrightii, R. maritima,* and *Z. marina* are all present in North Carolina seagrass beds (Bartenfelder et al. 2022; Figure 3.1). Seagrass bed composition was measured in five haphazardly placed 0.0625-m^2 quadrats throughout the meadow. Percent cover and canopy height were measured in each quadrat identically to the 2019 sampling design. Additionally, the elevation of the seagrass bed relative to the North American Vertical Datum of 1988 (NAVD88) was taken at the location of each quadrat using a Trimble R10 Real-Time Kinematic (RTK) GPS (0.5-1.0 cm horizontal and 1.0-4.0 cm vertical resolution) as a proxy for bed inundation. Seagrass cores were processed as described above for our 2019 sampling. In addition, to better understand how bed depth and seagrass complexity may influence abundances of seagrass-associated epifauna, which are a food source for many nekton (Hall and Bell 1988, Bologna and Heck 1999), we measured epibiont load. Five haphazardly selected shoots of each species were scraped with a glass microscope slide to release epibionts from the blade, and length and width of the scraped blades were recorded. Scraped epibionts were dried and massed as described above. Epibiont load was standardized by blade weight such that higher values indicate an increased epibiont presence with increased blade size, and therefore available surface area for epibiont colonization, varied widely across samples.

Seagrass Transplantation Experimental Design

To test how depth influences restoration success and faunal community composition, we conducted a transplantation experiment in Back Sound, North Carolina informed by our seagrass surveys. We delineated 2m by 2m plots for our experiment with the following treatments:

intertidal transplanted (N=5), subtidal transplanted (N=6), intertidal bare sand (N=6), subtidal bare sand (N=5), and natural reference seagrass (>75% cover of *H. wrightii,* N=5). All natural seagrass reference plots were at the intertidal depth range, as there was no nearby natural *H. wrightii* seagrass bed occurring at the subtidal depth range.

In April 2021 we used a Trimble R10 RTK GPS to identify sites at two elevation categories informed by prior-described surveys: subtidal (-0.6 m – -0.8 m NAVD88) and intertidal (-0.4 m – -0.55 m NAVD88). These elevation categories correlated to a depth of 0.5 – 0.6 m below local mean sea level (LMSL) for subtidal and 0.3 – 0.45 m below LMSL for intertidal plots (Gittman et al. 2018). Intertidal plots were selected such that they would be exposed at spring tides but remain submerged during neap tides (Figure S3.4).

H. wrightii predominantly exhibits clonal growth in North Carolina, with few documentations of flowering plants and low genetic diversity indicating high rates of cloning (Ferguson et al. 1993, Fonseca and Bell 1998, Digiantonio et al. 2020). Transplanting also allows for standardization of shoot density, clump size, initial canopy height, and percent cover across plots and depths. Therefore, transplanting adult *H. wrightii* shoots is a practical method (Fonseca et al. 1998), especially in North Carolina where seed collection is likely to be challenging.

Halodule wrightii Transplantation

On April 26 – 28, 2021, we transplanted 23 clumps comprised of 15 shoots of *H. wrightii* each from a nearby (<400 m) seagrass bed into 2-m by 2-m plots in a grid arrangement (Figure S3.5). To assess initial conditions and variability across treatments, we measured the biomass of eight randomly selected clumps (including all roots and rhizomes) collected for planting, ($\bar{x}$ = 0.605 $\pm$ 0.058 g dry weight) and quantified shoot lengths from ten random clumps, five assigned "subtidal" and five assigned "intertidal." We followed the staple method as described by Fonseca

et al. (1998; Figure S3.6B). Care was taken while transplanting to ensure intact roots and rhizomes were included within each clump rather than individual, unconnected shoots of *H. wrightii*. Clumps were anchored to the sediment with lawn staples to minimize transplant loss until their root system became established in the transplant location (Figure S3.6). High winds during initial planting efforts and stingray activity within a transplanted plot, caused the loss of many transplants within the first week. Therefore, we conducted a supplemental transplant on May 25, 2021 to replace all lost clumps for 23 total clumps per plot. We measured the biomass of an additional eight clumps from this planting to ensure minimal differences in clump size between April and May ($\overline{x} = 0.639 \pm 0.1$ g dry weight). Bi-monthly from June through October 2021 2022 we counted the number of remaining clumps transplanted in each plot out of the original 23.

Faunal Monitoring

To assess faunal communities associated with transplanted seagrass relative to reference natural seagrass and bare sand sites, we employed three separate approaches: minnow traps and standardized monitoring units for the recruitment of fish (SMURFs; Ammann 2004) for fishes and macroinvertebrates, and squid pops as a proxy for consumption. Bi-monthly, we deployed baited minnow traps in all 27 transplanted, bare sand, and natural reference seagrass plots. We baited the traps with two pieces of dry dog food (Yarnall and Fodrie, 2020). Each minnow trap was placed in the center of the plot to avoid placement directly on transplanted clumps. Traps were deployed within two hours of low tide during a neap tide for 24 hours, recovered, and all fish and crustaceans within traps were identified to the lowest taxonomic level, enumerated, and wet-weighed before being released (Table S3.1; IACUC AUP #371; SEAP Collection Permit #706671, #706481, #1627488). Minnow traps samples were standardized to 24-hour

deployments to account for any trap that may have been retrieved slightly early or late of the 24-hour mark, giving a measure of catch per unit effort (CPUE).

Concurrently with minnow trap deployments, we conducted 24-hour squid-pop consumption assays (Duffy et al. 2015). Consumption assays give a measure of relative feeding intensity, and thus predation pressure, of consumers of small motile organisms within our plots (Duffy et al. 2015). Measures of consumption and predation pressure can then be used to identify areas that may act as a refuge for small and juvenile fauna (Lefcheck et al. 2021). Squid-pops were comprised of a 1.3-cm-diameter circular piece of dried squid attached to a garden stake with a 5-cm-long piece of monofilament line (Duffy et al. 2015, Lefcheck et al. 2021). Squid-pops were deployed one hour prior to low tide and placed so that the dried squid was 20 cm above the substrate. Consumption was checked one-, two-, and 24 hours post deployment. Consumption was rated as consumed, partially consumed, or intact. Any active predation was also noted as partially consumed and, when identifiable, the species preying upon the squid-pop was recorded. The proportion consumed in each plot across all sampling dates was averaged and average plot consumption was included in the model (see statistical analyses below).

Finally, we conducted two-week deployments of SMURFs each month to capture larval and juvenile fish and crustaceans entering the site (Figure S3.7; Ammann 2004). SMURFs were deployed between plots in subtidal and intertidal bare sand and within intertidal seagrass reference plots. SMURFs could not be placed within transplanted plots, as the large size and method of anchoring (sand screws) would negatively impact transplanted plots. SMURFs were constructed as described in Yarnall 2021. After two-weeks, SMURFs were removed, and all organisms within were flushed and collected and placed preserved in labelled jars with 70% ethanol for later identification. Organisms were identified to the lowest taxonomic level,

enumerated, and the first 10 individuals of each species haphazardly selected from each SMURF were measured to the nearest mm (total length for fishes and shrimp; carapace width for crabs; Tables S3.2, S3.3).

Statistical Analyses

Seagrass Surveys

Linear mixed models (LMMs) and generalized linear mixed models (GLMMs) were used to determine the relationship between the fixed effect of 2019 sampling month and the random effect of seagrass site on seagrass composition and morphology metrics (Table S3.4). A LMM was used to determine the fixed effect of *H. wrightii* and *R. maritima* percent dominance by biomass and the random effect of site on the canopy height of the bed. We then used Tukey's post-hoc tests to assess pairwise differences for any significant results between sampling months. We delineated beds as "low" versus "high" cover for the percent cover analysis of *H. wrightii* and *Z. marina* in order to understand how overall seagrass cover may be impacted by month and depth. For analyses we gave cover of 0-50% a score of 0 and cover from 50-100% a score of 1. We conducted a one-way analysis of variance (ANOVA) on data from 2019 and 2020 separately to test if there were differences across seagrass species in their (1) average shoot length, (2) leaf width, (3) leaf number per shoot, (4) branch number per shoot, and (5) shoot count per bed. We then performed Tukey's post-hoc tests to assess pairwise differences for any significant results across species.

Linear models (LMs) and generalized linear models (GLMs) were used to determine the fixed effect of seagrass bed elevation, hereafter referred to as depth relative to LMSL, on the 2020 measurements of seagrass composition and morphology metrics (Table S3.5). A LM was used to determine the fixed effect of *H. wrightii* and *R. maritima* percent dominance by biomass

on the average canopy height of the bed. We scored percent cover of *H. wrightii* and *Z. marina* as either 0 or 1 as described above. and ran a binomial GLM to test for effects of depth on the percent cover of *H. wrightii* and *Z. marina*. No models were run on seagrass morphological metrics that had no variance across samples (e.g., leaf width of *H. wrightii* and *R. maritima*, Table 3.1).

Seagrass Transplantation Experiment

Differences in depth between the "subtidal" and "intertidal" plots were assessed using ANOVA models with the fixed effect of depth category on the measured depth relative to LMSL of the plots. To ensure that depths were similar (1) between the transplanted, bare sand, and natural reference seagrass plots in the intertidal depth category and (2) between transplanted and bare sand plots in the subtidal depth category, we conducted an ANOVA with the fixed effect of transplantation category (transplanted vs. bare sand vs. natural reference seagrass [intertidal only]) on the measured depth relative to LMSL of the plots. Finally, we compared the lengths of shoots planted across treatment plots using an ANOVA with the fixed effect of depth category (intertidal, subtidal) on the average shoot length of clumps to be planted.

We used a LMM to analyze the fixed effect of plot type (subtidal vs. intertidal), date, and their interaction on the number of clumps remaining during 2021 checks and included plot number as a random effect. We also used a LMM to analyze the fixed effect of date on the number of clumps remaining in intertidal plots in 2022 and included plot number as a random effect. We conducted a one-way ANOVA to determine differences in minnow trap CPUE across the natural reference seagrass, intertidal and subtidal transplanted, and bare sand plots. We then used a Tukey's post-hoc test to assess pairwise differences for statistically significant ANOVA results. A quasipoisson GLM was used to analyze the fixed effects of depth treatment, number of

clumps remaining in transplanted seagrass and their interaction on minnow trap CPUE. We did not include any plots where all transplanted clumps had been lost at the time of sampling as these could no longer be considered 'transplanted.'

We used multivariate analyses to determine if minnow trap or SMURF community composition differed across plot types. Prior to all analyses, we removed samples with zero catch (no community data), as well as rare species, which were considered as those species which were caught only once across all samples. For all multivariate analyses (unless otherwise noted) catch data were log x+1 transformed and then, following transformation, a Bray-Curtis similarity matrix was created. We visually represented the communities through non-metric multidimensional scaling (NMDS) and conducted a permutational multivariate analysis of variance (PERMANOVA), permutational multivariate analysis of dispersion (PERMDISP), and similarity percentages breakdown (SIMPER) analyses using fixed and random effects as described below.

Due to a lack of subtidal natural reference seagrass plots in our experiment, separate analyses were conducted (1) to compare across only intertidal plots comparing natural reference seagrass, transplanted seagrass, and bare sand, and (2) to compare transplanted and bare sand plots in both the subtidal and intertidal. First, to compare across only intertidal plots we conducted a PERMANOVA with the fixed effects of date and plot category (natural reference seagrass, transplanted seagrass, bare sand), their interaction, and the random effect of plot number nested within category to account for repeated sampling. We then conducted a pairwise PERMANOVA for pairs of the factor plot category within each date. PERMDISP were conducted for plot category and date and, finally we conducted a SIMPER analysis to determine species driving differences across plot types. Second, to compare transplanted and bare sand

plots in the intertidal and subtidal we investigated whether communities differed according to transplantation category (transplanted vs. bare), depth category (subtidal vs. intertidal), or the interaction of both. Due to small sample size across dates and treatments, we were unable to analyze the subtidal and intertidal transplanted and bare sand plots across dates, so we (1) analyzed trap catches from the first sampling time point (June 17, 2021), (2) analyzed trap catches from the final sampling time point (September 9, 2021), and (3) summed samples across dates for each plot and analyzed the total community caught in each plot across the sampling period. We conducted PERMANOVAs with the fixed effects of transplantation category, depth category, and their interaction. We conducted PERMDISPs on the transplantation and depth categories to ensure homogeneity of dispersion.

Because SMURFS could not be placed inside transplanted plots, we compared communities sampled across: (1) intertidal plots (natural reference seagrass and intertidal bare sand) and (2) across depths (subtidal and intertidal bare sand). We conducted PERMANOVAs with the fixed effects of date, plot category (natural reference seagrass vs. intertidal bare sand and intertidal bare sand vs. subtidal bare sand), their interaction, and the random effect of plot number nested within plot category to account for repeated sampling of the plots. We next ran PERMDISP on the plot category and date for each analysis to ensure homogeneity of dispersion. Finally, we ran a SIMPER analysis on the shallow plots only between natural reference seagrass and intertidal bare sand plots.

We then compared communities caught via SMURF sampling to those from minnow traps to compare species caught across the entire sampling period in each sampling method. Sampling methods can be biased, particularly in targeting specific life stages, so combining methods in projects can give clearer indications of the communities and detect differences

between sampling events or treatments (Layman and Smith 2001, Franco et al. 2012, Flannery and Przeslawski 2015). For this analysis, catches across all dates for each plot and gear type were aggregated. SMURFs and minnow traps have differing gear efficiencies when standardized to a similar timeframe. Because we were interested in species richness and identity and not the abundance of each species, we transformed catch data into presence/absence data with 1 representing present and 0 representing absent. We split the SMURF and minnow trap comparisons into two categories (1) natural reference seagrass plots only and (2) intertidal and subtidal bare sand plots only. We did not include transplanted plots in our analyses as SMURFs were unable to be deployed in transplanted plots. For the natural reference seagrass plots, we ran a PERMANOVA with the fixed effect of sampling gear method. We then ran a PERMDISP on sampling gear to ensure homogeneity of dispersion and a SIMPER analysis to determine species driving differences across gear types. For the analysis of bare sand plots only we ran a PERMANOVA with the fixed effects of gear type, plot depth, and their interaction. We then ran PERMDISPs on plot depth and gear type. Finally, we ran a SIMPER analysis to determine species driving differences across the sampling gear.

Finally, quasibinomial GLMs were used to analyze (1) the fixed effects of restoration transplantation category (transplanted vs. bare sand control) and depth treatment (intertidal vs. subtidal) on proportion of squid-pops consumed at one and two hours for the transplanted and bare sand plots and (2) the fixed effect of habitat type (natural reference seagrass, bare sand, and transplanted seagrass) on proportion of squid-pops consumed at one and two hours post deployment for all intertidal plots. All squid pops were consumed after 24 hours, regardless of plot type, so no models were run. Tukey's post-hoc tests were used to assess pairwise differences for any significant treatment or interaction effects from the models.

All LMs, LMMs, GLMs, and GLMMs for both the observational seagrass surveys and manipulative field experiment were conducted in R statistical software using the package lme4 (Bates et al. 2015). All community analyses for the manipulative field experiment were conducted in Primer7 software (Anderson et al. 2008).

Results

Seagrass Surveys

Seagrass beds were comprised of one, two, or three seagrass species, with the highest seagrass diversity (i.e., the most beds with 3 co-occurring species) observed in June and July 2019 (Figure 3.1). Percent cover ranged from 0% to 75% per bed for both *H. wrightii* and *Z. marina* (Table S3.6). Seasonal composition shifts were evident, with *H. wrightii* and *R. maritima* contribution to percent cover increasing from April through September ($F_{5,23.75} = 5.3309$, $p = 0.0020$; Figure S3.8; Tables S3.7, S3.8). Aboveground biomass for *H. wrightii* was highest in June and July. In comparison, *R. maritima* aboveground biomass was highest in June, and *Z. marina* biomass peaked in May ($p < 0.05$; Figure S3.9; Tables S3.7, S3.9-S3.13). Percent cover of *H. wrightii* + *R. maritima* also shifted seasonally with increased cover of *H. wrightii* + *R. maritima* during June-July compared to April-May ($\chi^2_5 = 16.992$, $p = 0.0045$; Tables S3.9, S3.14). *Z. marina* percent cover did not shift during the sampling period with low (<50%) cover in all months sampled ($\chi^2_5 = 6.0526$, $p = 0.03011$; Table S3.9). *Z. marina* shoot counts were highest in May and lowest in September ($\chi^2_5 = 35.219$, $p < 0.0001$), while *R. maritima* shoot counts were highest in June and lowest in April and September, when it was not present in the seagrass beds ($\chi^2_3 = 2.3258$, $p < 0.0001$; Figure S3.10, Tables S3.9, S3.15, S3.16). There was also a shift in overall shoot count of the beds over time with highest shoot densities in June and

lowest in September ($p < 0.05$; Figure S3.10; Tables S3.9, S3.14, S3.17). However, shoot count of *H. wrightii* did not differ across months ($\chi^2_5 = 5.5519$, $p = 0.3523$; Figure S3.10; Table S3.9).

Field measures of seagrass canopy height varied across months and was lower in April and May compared to all other months ($p < 0.05$; Figure S3.11; Tables S3.7, S3.18). Canopy height did not, however, vary based on the dominance of *H. wrightii* + *R. maritima* by biomass over *Z. marina* ($F_{1,33.969} = 1.4252$, $p = 0.2408$; Figure S3.12; Table S3.7). Structurally, *Z. marina* had narrower leaf widths and lower leaf numbers per shoot in July and August as compared to April – June ($p < 0.05$; Figures S3.13, S3.14; Tables S3.7, S3.19, S3.20). *Z. marina* exhibited the highest branching of leaves per shoot (indicative of reproductive shoots) in April, with no variation across other months ($F_{4,16.381} = 3.9216$, $p = 0.0204$; Figure S3.15; Tables S3.7, S3.21). *Z. marina* shoots were shortest in August as compared to all other months ($p < 0.05$; Figure S3.16, Table S3.7). *R. maritima* shoot length differed across months with longest shoots present in June ($p < 0.05$; Figure S3.16; Tables S3.9, S3.22). *R. maritima* had fewer branches in August than in June and July ($p < 0.05$; Figure S3.15; Tables S3.9, S3.23), while the number of leaves per shoot for *R. maritima* did not differ across months ($F_{3,3.9632} = 0.89$, $p = 0.5195$; Figure S3.14; Table S3.7). *H. wrightii* demonstrated no macroscale variation in leaf width across samples (Table 3.1). However, the length of *H. wrightii* shoots increased from April through July and then decreased in August and September, while the number of leaves per shoot of *H. wrightii* increased monthly from April through September, except for June when leaf number peaked ($p < 0.05$; Figures S3.14, S3.16; Tables S3.9, S3.24, S3.25). Across seagrass species, *R. maritima* had the highest number of leaves per shoot while *H. wrightii* had the highest shoot count and shoot lengths and *Z. marina* had the widest leaves ($p < 0.05$; Figure S3.17; Tables S3.26, S3.27).

In June and July 2020, seagrass beds were also comprised of a mix of one, two, and three species beds with a majority of the beds a mix of *H. wrightii* and *Z. marina* (Figure 3.1). Percent cover ranged from 0% to 75% for both *H. wrightii* and *Z. marina* (Table S3.28). The average depth of the shallowest measured seagrass bed was 0.41 $\pm$ 0.01 m below LMSL while the average depth of the deepest measured seagrass bed was 0.84 $\pm$ 0.06 m below LMSL. The overall deepest depth measured was 1.01 m below LMSL and the shallowest measured depth was 0.32 m below LMSL.

While the metrics of seagrass presence (cover, dominance, biomass) differed across months, none of these metrics differed across bed depth when sampled in June and July 2020 ($p > 0.05$; Figure S3.18, S3.19; Tables S3.29, S3.30, S3.31). *H. wrightii* shoot count decreased with depth, and shoots length was positively correlated with depth ($p < 0.05$; Figures S3.20, S3.21; Tables S3.29, S3.30). Similarly, canopy height of the bed had a marginally significant increase in height with depth ($F_{1,16} = 4.3705$, $p = 0.0529$; Figure 3.2, Table S3.29). The shoot lengths of *R. maritima* ($F_{1,4} = 1.5506$, $p = 0.2810$) and *Z. marina* ($F_{1,13} = 0.643$, $p = 0.4370$), however, did not differ across bed depths (Figures S3.21, S3.22; Table S3.29). All other measures of seagrass morphology did not differ across depths ($p > 0.05$, Figures S3.21-S3.25; Table S3.29). We further found no difference in epibiont load across depths ($F_{1,16} = 1.31$, $p = 0.2692$; Table S3.29). Measured *H. wrightii* shoots from both 2019 and 2020 seagrass surveys showed no differences in measurable leaf width, and, despite varying across months, showed minimal variation in leaf number per shoot overall (2.78 $\pm$ 0.04).

R. maritima had the highest number of leaves per shoot while *H. wrightii* had the highest shoot count and *Z. marina* had the widest leaves ($p < 0.05$; Figure S26; Tables 3.1, S3.32, S3.33).

Z. marina shoots were only marginally longer than both *H. wrightii* and *R. maritima* ($F_{2,35}$ = 2.628, p = 0.0865; Figure S3.26; Table S3.32).

Seagrass Transplantation Experiment

We transplanted *H. wrightii* at two elevations informed by the range of natural seagrass elevations measured June and July 2020 surveys (0.32 m – 1.01 m below local mean sea level). In the *H. wrightii* transplantation experiment, intertidal plots had a mean depth of 0.40 $\pm$ 0.01 m below LMSL and subtidal plots had a mean depth of 0.58 $\pm$ 0.02 m below LMSL ($F_{1,25}$ = 114.61, p < 0.001; Figure S3.27; Table S3.34). There was no difference in depth below LMSL within the intertidal ($F_{2,13}$ = 0.5132, p = 0.610) or subtidal elevation categories ($F_{1,9}$ = 0.0966, p = 0.763; Figure S3.27; Table S3.35-S3.37). There was no difference in the initial mean shoot length of *H. wrightii* clumps transplanted to subtidal (76 $\pm$ 3 mm) versus intertidal plots (81 $\pm$ 3 mm; $F_{1,8}$ = 1.376, p = 0.2745; Table S3.38). The number of transplanted *H. wrightii* clumps declined over time from 23 clumps per plot on May 25, 2021, to 8.4 $\pm$ 2.8 clumps in intertidal plots, and 1.3 $\pm$ 0.8 clumps in subtidal plots on October 5, 2021 (Figure 3.3). Intertidal plots lost *H. wrightii* clumps at a significantly slower rate than the subtidal plots over the 2021 sampling period ($t_{92.14}$ = 3.425 p = 0.0009; Figure 3.3; Table S3.39). By April 2022, no subtidal plots contained transplanted clumps. In comparison, *H. wrightii* clumps in intertidal plots declined from 8.4 $\pm$ 2.8 clumps on June 8, 2022, to 0.8 $\pm$ 0.8 clumps remaining on October 4, 2022 ($t_{38.9998}$ = -4.666, p < 0.001; Figure 3.3; Table S3.40).

The mean faunal CPUE in minnow traps deployed in intertidal natural reference seagrass plots was 18.1 $\pm$ 0.8, 1.2 $\pm$ 0.3 in subtidal bare sand plots, and 1.8 $\pm$ 0.4 in subtidal transplanted plots. The mean CPUE in intertidal bare sand plots was 2.6 $\pm$ 0.4 and 1.6 $\pm$ 0.6 in intertidal transplanted plots ($F_{4,22}$ = 170.34, p < 0.0001; Figure 3.4; Tables S3.41, S3.42). Minnow trap

CPUE decreased as number of clumps remaining decreased ($F_{1,59} = 9.68$, $p = 0.0029$, Figure S3.28, Table S3.43). However, there was no difference in CPUE between intertidal and subtidal transplanted plots ($F_{1,58} = 0.061$, $p = 0.874$) nor was there a difference in the rate at which CPUE decreased with decreasing clump number between intertidal and subtidal plots ($F_{1,57} = 3.1567$, $p = 0.087$; Figure S3.28; Table S3.43).

Faunal communities differed across sampling date and plot type (PERMANOVA $p < 0.0001$), as well as across plots (PERMANOVA $p = 0.0085$; Table 3.44). Specifically, catches in natural reference seagrass meadows were dissimilar to catches from both the intertidal transplanted and intertidal bare sand plots (Figure S3.29). However, some of these differences may be attributed to differences in within group dispersion of plot type with more variation within transplanted seagrass and bare sand communities than natural reference seagrass communities (PERMDISP $F_{2, 73} = 17.178$, $p < 0.001$; Tables S3.45, S3.46). Communities sampled in natural reference seagrass using minnow traps differ from both the intertidal transplanted and intertidal bare sand plots ($p < 0.05$) for all dates except the final sampling where natural reference seagrass and transplanted communities are only marginally different from each other (PERMANOVA $p = 0.0534$; Table S3.47). Communities observed in intertidal transplanted and bare sand plots were similar in composition regardless of sampling date (PERMANOVA $p > 0.05$; Table S3.47). Differences between natural reference seagrass and intertidal transplanted and bare sand plots were driven by higher abundances of pinfish (*Lagodon rhomboides)*, pigfish (*Orthopristis chrysoptera*), blue crabs (*Callinectes sapidus*), and planehead filefish (*Stephanolepis hispidus*) in natural reference seagrass plots (Table S3.48). There were no differences in faunal communities captured in intertidal and subtidal plots regardless of transplantation category or date (PERMANOVA $p > 0.05$; Tables S3.49-S3.57).

Communities caught in the SMURF sampling across the intertidal plots were similar over time (PERMANOVA p = 0.2068) and between natural reference seagrass and bare sand plots (PERMANOVA p = 0.7978; Table S3.58). However, communities differed between intertidal natural reference seagrass and intertidal bare sand plots (PERMANOVA p = 0.0216) potentially due to greater variance in community assemblages in bare plots compared to natural reference seagrass plots (PERMDISP $F_{1,39}$ = 8.2527 p = 0.021, Tables S3.58-S3.60). There were also only slight differences in species abundance across plot types (SIMPER) and within the NMDS plots, demonstrating a high degrees of overlap between communities captured in natural reference seagrass and bare sand plots (Figure S3.30; Table S3.61). We saw no differences in communities observed within the SMURF samples between intertidal and subtidal bare sand plots (PERMANOVA p = 0.7607), across dates (PERMANOVA p = 0.114), or between plot types across dates (PERMANOVA p = 0.7354; Table S3.62-S3.64).

The motile fauna communities sampled within the seagrass plots were different across gear types (minnow trap versus SMURF, PERMANOVA p = 0.0088; Tables S3.65, S3.66). Cluster analysis indicated communities observed grouped by gear type (60% similarity, Figure S3.31). Differences in species caught are due to the capture of motile fish (pigfish; spottail pinfish, *Diplodus holbrookii*; and mummichog *Fundulus heteroclitus*) in minnow traps, but not in SMURFs (Table S3.67). The presence of species caught in bare sand plots did not differ based on depth (PERMANOVA p = 0.6384) or between gear type across dates (PERMANOVA p = 0.6802). However, species did differ across gear type (PERMANOVA p < 0.0001) with much larger variance within the minnow trap samples than within the SMURF samples (PERMDISP $F_{1,19}$ = 18.221, p < 0.001; Tables S3.68-S3.70). Differences across gear type are due to higher catch rates of motile species in the minnow traps (pinfish, pigfish) and higher catch rates of less

mobile species in the SMURFs (mud crabs; blenniiformes; skilletfish, *Gobiesox strumosus*; blotched swimming crabs, *Portunus spinimanus;* and blue crabs; Table S3.71).

After one hour, the proportion of squid pops consumed was greatest in subtidal bare sand plots (0.62 $\pm$ 0.13) and lowest in intertidal transplanted plots (0.20 $\pm$ 0.08; Figure 3.5). Across subtidal and intertidal bare sand and transplanted seagrass plots we found higher consumption in subtidal plots as compared to intertidal plots ($F_{1,19}$ = 7.5534, p = 0.0132) regardless of transplantation category or the interactions between depth and transplantation category (p > 0.05; Table 3.72). However, after one hour within only intertidal plots, consumption was marginally different across plots with highest consumption in the bare sand and lowest in the transplanted seagrass plots ($F_{2,13}$ = 2.9727, p = 0.0865; Figure 3.5C; Table S3.73). After two hours, the proportion of squid pops consumed was 0.77 $\pm$ 0.10 in deep bare sand, 0.79 $\pm$ 0.04 in deep transplanted plots, 0.83 $\pm$ 0.05 in shallow bare sand, 0.52 $\pm$ 0.10 in shallow transplanted plots, and 0.77 $\pm$ 0.08 for natural reference seagrass (Figure 3.5). After two hours, consumption across subtidal and intertidal bare sand and transplanted seagrass plots differed by plot type, with consumption significantly higher in intertidal bare sand plots as compared to intertidal transplanted plots ($F_{1,18}$ = 5.0037, p = 0.0382, Figure 3.5B; Tables S3.74, S3.75). After two hours consumption did not differ between either subtidal transplanted and subtidal bare sand plots and any other plot type (p > 0.05; Figure 3.5B; Tables S3.74, S3.75). Within just the intertidal plots two hours post deployment, consumption of squid pops varied ($F_{2,13}$ = 4.6107, p = 0.0307), with lower consumption in transplanted plots as compared to bare sand plots (z = 3.034, p = 0.0245; Figure 3.5D; Tables S3.76, S3.77). However, natural reference seagrass plots were only marginally higher than transplanted (z = 2.294, p = 0.0924) and did not differ from consumption in bare sand plots (z = -0.639, p = 0.8017; Figure 3.5D; Tables S3.76, S3.77).

Discussion

Restoration of seagrasses through adult transplantation or planting seeds has been the primary method to combat seagrass loss and restore ecosystem functioning (Fonseca et al. 1998, Reynolds et al. 2016, van Katwijk et al. 2016). However, seagrass restoration often depends on understanding the native seagrass makeup and distribution for greatest success (Tan et al. 2020, Pazzaglia et al. 2021). Here, we show that *H. wrightii* is the dominant seagrass species in North Carolina in sampled beds from April through September and this dominance did not change with depth relative to LMSL. While the morphology of all three seagrass species changed temporally, morphology did not vary with depth regardless of seagrass species. Based on our results, *H. wrightii* may have high potential for restoration using adult transplants, but potentially only in shallow, intertidal areas, despite naturally occurring in deeper, subtidal beds (Figure 3.2). This is similar to *Z. marina* restoration by seed in which seedlings are more resilient in depths that exclude the shallowest and deepest portions of the natural range (Aoki et al. 2020). Further, our small-scale transplantation of *H. wrightii* did not host as abundant faunal communities as the natural reference seagrass beds, indicating that we may not have restored seagrass ecosystem functioning in the form of faunal habitat during our sampling period.

North Carolina seagrass meadows have long been studied due to their habitat provisioning and the unique co-occurrence of three seagrass species: *H. wrightii, R. maritima,* and *Z. marina* (Micheli et al. 2008, Field et al. 2021, Bartenfelder et al. 2022). Similar to past studies, and agreeing with our hypothesis(H1), we observed seagrass beds comprised of a mix of one, two, and three species with metrics of seagrass bed composition (biomass, shoot count, cover, and dominance) changing from April through September (Micheli et al. 2008,

Bartenfelder et al. 2022, Figure 3.1). The shift in seagrass composition of the beds in this study throughout the spring and summer is likely related to the optimal temperatures and growing season for each seagrass species present in our study, as *Z. marina* prefers cooler, more temperate temperatures than both *H. wrightii* and *R. maritima* (Thayer et al. 1984, Micheli et al. 2008). Though seagrass composition changed over time, *H. wrightii* was the dominant seagrass compared to *Z. marina* regardless of sampling month with only a single *Z. marina* dominated bed sampled in 2020 (Figures 3.1-3.2). Although *H. wrightii* is thought to be temperature limited in colder months, we found high dominance of *H. wrightii* in the spring (April and May), a period previously characterized by dominance of *Z. marina* rather than *H. wrightii,* particularly in deeper beds (Micheli et al. 2008, Bartenfelder et al. 2022). Seagrass distributions may be highly influenced by depth, particularly in North Carolina where deeper beds are characterized by higher presence and abundance of *Z. marina* (Thayer et al. 1984, Micheli et al. 2008). Beds sampled in this study were generally shallow (<1 m) and randomly selected, therefore, though it is possible dominance of seagrass is shifting in the spring away from dominance of *Z. marina*, it is likely that based on random draw we may have missed the deeper, high *Z. marina* cover beds at their peak dominance.

Seagrass morphology shifted over the course of the active growing season, which can be indicative of seagrass health and tolerance to stressors (Lee and Dunton 1997, York et al. 2013), as well as sexual reproductive output (Kuo and Hartog 2006). Morphology of both *R. maritima* and *Z. marina* sexually reproductive shoots differ from vegetative shoots (Kuo and Hartog 2006). This morphology change is most evident by the increased number of branches per shoot of *Z. marina* in April and *R. maritima* in June and July (Figure S3.15). Additionally, seagrasses often show changes in distribution (Thayer et al. 1984, Micheli et al. 2008), morphology, and

structure based on changing depth (Olesen et al. 2002, Enríquez and Pantoja-Reyes 2005) and light availability (Fitzpatrick and Kirkman 1995, Longstaff et al. 1999). During times of light stress seagrasses have fewer, shorter leaves and lose overall biomass (Fitzpatrick and Kirkman 1995, Enríquez and Pantoja-Reyes 2005, Biber et al. 2009). However, this was not observed in our system as the distribution of *H. wrightii* and *Z. marina* as well as most measured seagrass morphology metrics did not differ with depth. Interestingly, we found an increase in *H. wrightii* shoot length, rather than a decrease with increased bed depth, despite the high light requirement of *H. wrightii* (Biber et al. 2009). Because surveyed beds in this study were generally shallow (<1 m relative LMSL) with little variation in depth (0.4 m), variation in light availability may not have been great enough to observably impact morphology or distribution across depths.

Studies have recommended that seagrass transplantation for restoration should occur within the local depth range of natural seagrass (Fonseca et al. 1998, van Katwijk et al. 2009). The presence of *H. wrightii* across sampled depths (0.32 – 1.01 m below LMSL) indicates that *H. wrightii* transplants could succeed and persist both in the subtidal (0.51 – 1.01 m below LMSL) and intertidal zones (0.32 – 0.43 m below LMSL). However, contrary to our hypothesis (H3), *H. wrightii* transplant survival was higher in shallow, intertidal plots than deeper, subtidal plots. Notably, transplanted clumps remained present in one intertidal plot 18 months post restoration (Figure 3.3). These results suggest that *H. wrightii* transplantation for restoration may be more likely to succeed at intertidal depths despite its natural occurrence in the subtidal. However, much like previous restoration studies, overall mortality of transplants was high (Bayraktarov et al. 2016, van Katwijk et al. 2016), suggesting that while intertidal transplanting may enhance persistence of transplants, in our study it did not lead to restoration success. Previous exploration of seagrass restoration across depths have also found distinct

depth thresholds for where restored grasses cannot persist (Aoki et al. 2020), which may be different than the observed depths of naturally occurring seagrasses (Fonseca et al. 1998). Our results appear to support the existence of these distinct thresholds, as the natural depths of *H. wrightii* measured in our seagrass surveys and in previous studies (Ferguson et al. 1993, Biber et al. 2008) are noticeably deeper than the subtidal transplantation treatment of 0.584 $\pm$ 0.018 m below LMSL. Though we were not successful at restoring *H. wrightii*, it can colonize rapidly after a disturbance and, in established meadows, may be able to colonize new areas (Donaher et al. 2021), a potential mechanism for expansion following successful transplantation.

While the mechanism for what caused a faster decline in *H. wrightii* transplants in subtidal plots when compared to intertidal plots is unknown, we observed heavy sedimentation in both 2021 and 2022, particularly throughout the end of August and September. Lawn staples used to stabilize transplanted clumps were initially placed flush with the sediment surface but were eventually buried, subsequently indicating burial-related mortality of transplants (Fonseca et al. 1998). Alternatively, though not measured, the speed of currents can shape seagrass landscapes, with increased currents leading to decreased percent cover and seedling recruitment (Fonseca and Bell 1998, Fonseca et al. 1998).

The low number of initial transplants per plot in our study may have negatively impacted our restoration success in both the intertidal and subtidal which may be enhanced by changing the method used (van Katwijk et al. 2016, Zhang et al. 2021). Scaling up planting by increasing transplant number and the aerial extent of restoration leads to increased survival and mean growth rate of restored seagrasses (van Katwijk et al. 2016). Plantings are likely more stressed than established beds, which may rely on facilitation from adjoining shoots at

the deep edge of large beds (Fonseca et al. 1998). Harnessing both intra- and interspecific facilitations may be an additional approach to enhance restoration success (Valdez et al. 2020, Zhang et al. 2021). Large, dense seagrass beds also reduce scouring and aid in sediment trapping and stabilization, thus improving water quality, and resulting in more resilient restoration efforts (Aoki et al. 2020). Further, increasing the genetic diversity of seagrass plants included in a restoration project can enhance the survival and growth of restored grasses (Reynolds et al. 2012). Therefore, the presumed low genetic diversity in *H. wrightii* in North Carolina due to almost exclusive cloning (Ferguson et al. 1993, Fonseca and Bell 1998, Digiantonio et al. 2020) may have lowered our restoration success (Williams 2001, van Katwijk et al. 2009, Reynolds et al. 2012).

Faunal communities in the transplanted plots did not reach abundances equal to those in the natural reference seagrass bed regardless of depth (Figure 3.4). Rather transplanted plots had similar abundances and community composition to bare sand control plots and, contrary to our hypothesis, did not vary across depth. However, we did find significantly more abundant faunal communities in natural reference seagrass as compared to bare sand and transplanted plots. We may be measuring such drastic differences in faunal abundances in the natural reference seagrass and transplanted plots due to the large difference in cover, biomass, and surface area of the natural reference seagrass bed compared to transplanted areas. Greater cover, biomass, and surface may increase a beds' value as a nursery area (Orth et al. 1984, Hovel et al. 2002, McCloskey and Unsworth 2015). Interestingly, while the faunal abundances across intertidal and subtidal bare sand and transplanted plots were equivalent, there were more individuals caught in minnow traps in bare sand than transplanted plots while the opposite was true for deeper, subtidal areas despite minnow traps adding additional

structure to the unstructured bare sand (Layman and Smith 2001; Figure 3.4B). In mangrove habitats, small fish will seek out refuge in the form of shaded areas with increased water depth while these same fish are found in more open, well-lit foraging grounds in shallow water due to increased predation pressure in deeper water (Ellis and Bell 2004). In contrast, in unvegetated habitats small fish are found more often in shallow water due to the presence of larger predatory organisms in deeper nearby waters but were more abundant in deeper waters when submerged aquatic vegetation was more prevalent in the study area (Ruiz et al. 1993). Our study supported this finding where fish may seek refuge in seagrass in deeper waters whereas it may be unnecessary to seek out the same refuge in shallow areas that likely lack a strong predator presence.

Decreased consumption of squid-pops, a proxy for predation, in intertidal compared to subtidal plots after one hour, but not two hours is likely due to a lack of access by consumers to intertidal plots at low tide. Fish may leave shallow areas at low tide to prevent stranding, even when beds are not completely exposed (Sogard et al. 1989), returning to shallow seagrass beds rapidly after low tide (Espadero et al. 2020). Interestingly, consumption was lowest in intertidal, transplanted seagrass plots and highest in intertidal bare sand plots at the two-hour check, indicating a potential role of transplanted seagrass as a refuge from predation. A small increase in seagrass cover from bare sand may provide valuable habitat and refuge from common squid-pop consumers, such as blue crabs (*Callinectes sapidus*; personal observations, Duffy et al. 2015, Rodemann and Brandl 2017). Previous studies found the presence of artificial vegetation decreased predation of softshell clams (*Mya arenaria*) and juvenile blue crabs by adult blue crabs compared to bare sand, even at low densities of cover (Blundon and Kennedy 1982, Orth and van Montfrans 1982). Faunal abundance increased with increasing number of clumps per

plot, further pointing towards the transplanted plots as valuable habitat and a potential refuge for fauna. Though, the communities in these plots did not reach abundances or compositions equal to the of the natural seagrass reference plots regardless of clump number, likely due to the large increase in cover provided by the natural seagrass compared to both bare sand and transplanted plots (Orth et al. 1984, Hovel et al. 2002, McCloskey and Unsworth 2015).

Distribution of seagrass species at their range limits in North Carolina are shifting with climate change which may lead to spatio-temporal differences in morphology and seagrass species composition in beds (Lee and Dunton 1997, Micheli et al. 2008, Bartenfelder et al. 2022). As seagrass losses continue (Waycott et al. 2009, NC Department of Environmental Quality 2021), it is imperative to understand and document the composition and structure of natural seagrass beds, as well as best practices for restoring these critical habitats. Our results indicate that *H. wrightii* is a common seagrass species in Back Sound, North Carolina during the spring and summer months. However, additional widespread seagrass surveys are needed to confirm the dominance of *H. wrightii* over a larger spatial scale. In our study, seagrass presence and morphology varied temporally, as in previous analyses (Micheli et al. 2008, Bartenfelder et al. 2022), but not spatially with depth. However, *H. wrightii* restoration success did vary with depth, with subtidal restoration failing within 6-12 months of transplantation, followed by intertidal transplantation failure at 18 months. Previous studies near our restoration site have documented the beneficial impacts of inter- and intraspecific facilitation on restoration of *Z. marina* and mixed assemblages (Zhang et al. 2021), as well as *H. wrightii* disturbance recovery (Donaher et al. 2021). It may therefore be critical to determine if, and how facilitation can be harnessed (e.g., bigger clump sizes or restoring with bivalves) to improve the restoration success of *H. wrightii*, particularly if seagrasses continue to be lost (NC Department of Environmental

Quality 2021, Zhang et al. 2021). Further, transplanted beds supported fewer species and abundances of fauna than natural seagrass beds. Increased focus on uncovering best practices for restoring *H. wrightii* should continue with focus on how to enhance the success found restoring *H. wrightii* in intertidal depths within its natural distribution to restore ecosystem functioning.

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References

Ammann, A. J. 2004. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. Journal of Experimental Marine Biology and Ecology 299:135–154.

Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.

Aoki, L. R., K. J. McGlathery, P. L. Wiberg, and A. Al-Haj. 2020. Depth Affects Seagrass Restoration Success and Resilience to Marine Heat Wave Disturbance. Estuaries and Coasts 43:316–328.

Balestri, E., and C. Lardicci. 2012. Nursery-propagated plants from seed: a novel tool to improve the effectiveness and sustainability of seagrass restoration. Journal of Applied Ecology 49:1426–1435.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169–193.

Bartenfelder, A., W. J. Kenworthy, B. Puckett, C. Deaton, and J. C. Jarvis. 2022. The Abundance and Persistence of Temperate and Tropical Seagrasses at Their Edge-of-Range in the Western Atlantic Ocean. Frontiers in Marine Science 9:917237.

Bastyan, G. R., and M. L. Cambridge. 2008. Transplantation as a method for restoring the seagrass Posidonia australis. Estuarine, Coastal and Shelf Science 79:289–299.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bayraktarov, E., M. I. Saunders, S. Abdullah, M. Mills, J. Beher, H. P. Possingham, P. J. Mumby, and C. E. Lovelock. 2016. The cost and feasibility of marine coastal restoration. Ecological Applications 26:1055–1074.

Beaumont, N. J., M. C. Austen, J. P. Atkins, D. Burdon, S. Degraer, T. P. Dentinho, S. Derous, P. Holm, T. Horton, E. van Ierland, A. H. Marboe, D. J. Starkey, M. Townsend, and T. Zarzycki. 2007. Identification, definition and quantification of goods and services provided by marine biodiversity: Implications for the ecosystem approach. Marine Pollution Bulletin 54:253–265.

Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. BioScience 51:633–641.

Biber, P. D., C. L. Gallegos, and W. J. Kenworthy. 2008. Calibration of a Bio-optical Model in the North River, North Carolina (Albemarle–Pamlico Sound): A Tool to Evaluate Water Quality Impacts on Seagrasses. Estuaries and Coasts 31:177–191.

Biber, P. D., W. J. Kenworthy, and H. W. Paerl. 2009. Experimental analysis of the response and recovery of Zostera marina (L.) and Halodule wrightii (Ascher.) to repeated light-limitation stress. Journal of Experimental Marine Biology and Ecology 369:110–117.

Blundon, J. A., and V. S. Kennedy. 1982. Refuges for infaunal bivalves from blue crab, Callinectes sapidus (Rathbun), predation in Chesapeake Bay. Journal of Experimental Marine Biology and Ecology 65:67–81.

Bologna, P. A. X., and K. L. Heck. 1999. Macrofaunal associations with seagrass epiphytes Relative importance of trophic and structural characteristics. Journal of Experimental Marine Biology and Ecology 242:21–39.

Dennis, G. D. 1992. Island mangrove habitats as spawning and nursery areas for commercially important fishes in the Caribbean. Proceedings of the Forty First Annual Gulf and Caribbean 41:205–225.

Digiantonio, G., L. Blum, K. McGlathery, K. van Dijk, and M. Waycott. 2020. Genetic mosaicism and population connectivity of edge-of-range Halodule wrightii populations. Aquatic Botany 161:103161.

Donaher, S. E., C. J. Baillie, C. S. Smith, Y. S. Zhang, A. Albright, S. N. Trackenberg, E. H. Wellman, N. Woodard, and R. K. Gittman. 2021. Bivalve facilitation mediates seagrass recovery from physical disturbance in a temperate estuary. Ecosphere 12:e03804.

Duarte, C. M. 1991. Seagrass depth limits. Aquatic Botany 40:363–377.

Duarte, C. M. 2002. The future of seagrass meadows. Environmental Conservation 29:192–206.

Duarte, C. M., N. Marbà, D. Krause-Jensen, and M. Sánchez-Camacho. 2007. Testing the predictive power of seagrass depth limit models. Estuaries and Coasts 30:652–656.

Duffy, J. E., S. L. Ziegler, J. E. Campbell, P. M. Bippus, and J. S. Lefcheck. 2015. Squidpops: A Simple Tool to Crowdsource a Global Map of Marine Predation Intensity. PLOS ONE 10:e0142994.

Ellis, W. L., and S. S. Bell. 2004. Conditional use of mangrove habitats by fishes: Depth as a cue to avoid predators. Estuaries 27:966–976.

Enríquez, S., and N. I. Pantoja-Reyes. 2005. Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass Thalassia testudinum. Oecologia 145:234–242.

Espadero, A. D. A., Y. Nakamura, W. H. Uy, P. Tongnunui, and M. Horinouchi. 2020. Tropical intertidal seagrass beds: An overlooked foraging habitat for fishes revealed by underwater videos. Journal of Experimental Marine Biology and Ecology 526:151353.

FAO, editor. 2016. Contributing to food security and nutrition for all. Rome.

Ferguson, R. L., B. T. Pawlak, and L. L. Wood. 1993. Flowering of the seagrass Halodule wrightii in North Carolina, USA. Aquatic Botany 46:91–98.

Field, D., W. J. Kenworthy, and D. Carpenter. 2021. Metric Report: Extent of Submerged Aquatic Vegetation, High-Salinity Estuarine Waters (REVISED). Page 19 pp. Albemarle-Pamlico National Estuary Partnership, Raleigh, NC.

Fitzpatrick, J., and H. Kirkman. 1995. Effects of prolonged shading stress on growth and survival of seagrass Posidonia australis in Jervis Bay, New South Wales, Australia. Marine Ecology Progress Series 127:279–289.

Fonseca, M., and S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Marine Ecology Progress Series 171:109–121.

Fonseca, M., W. Kenworthy, D. Colby, K. Rittmaster, and G. Thayer. 1990. Comparisons of fauna among natural and transplanted eelgrass Zostera marIna meadows: criteria for mitigation. Marine Ecology Progress Series 65:251–264.

Fonseca, M. S., W. J. Kenworthy, and G. W. Thayer. 1998. Guidelines for the Conservation and Restoration of Seagrasses in the United States and Adjacent Waters. NOAA Coastal Ocean Office, Silver Spring, MD.

Gittman, R. K., F. J. Fodrie, C. J. Baillie, M. C. Brodeur, C. A. Currin, D. A. Keller, M. D. Kenworthy, J. P. Morton, J. T. Ridge, and Y. S. Zhang. 2018. Living on the Edge: Increasing Patch Size Enhances the Resilience and Community Development of a Restored Salt Marsh. Estuaries and Coasts 41:884–895.

Hall, M., and S. Bell. 1988. Response of Small Motile Epifauna to Complexity of Epiphytic Algae on Seagrass Blades. Journal of Marine Research 46:613–630.

Heck Jr., K. L., G. Hays, and R. J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253:123–136.

Heck, K. L., and T. A. Thoman. 1984. The Nursery Role of Seagrass Meadows in the Upper and Lower Reaches of the Chesapeake Bay. Estuaries 7:70–92.

Hovel, K., M. Fonseca, D. Myer, W. Kenworthy, and P. Whitfield. 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Marine Ecology Progress Series 243:11–24.

Infantes, E., L. Eriander, and P. Moksnes. 2016. Eelgrass (Zostera marina) restoration on the west coast of Sweden using seeds. Marine Ecology Progress Series 546:31–45.

Jarvis, J., K. Moore, and W. Kenworthy. 2012. Characterization and ecological implication of eelgrass life history strategies near the species' southern limit in the western North Atlantic. Marine Ecology Progress Series 444:43–56.

van Katwijk, M. M., A. R. Bos, V. N. de Jonge, L. S. A. M. Hanssen, D. C. R. Hermus, and D. J. de Jong. 2009. Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Marine Pollution Bulletin 58:179–188.

van Katwijk, M. M., A. Thorhaug, N. Marbà, R. J. Orth, C. M. Duarte, G. A. Kendrick, I. H. J. Althuizen, E. Balestri, G. Bernard, M. L. Cambridge, A. Cunha, C. Durance, W. Giesen, Q. Han, S. Hosokawa, W. Kiswara, T. Komatsu, C. Lardicci, K.-S. Lee, A. Meinesz, M. Nakaoka, K. R. O'Brien, E. I. Paling, C. Pickerell, A. M. A. Ransijn, and J. J. Verduin. 2016. Global analysis of seagrass restoration: the importance of large-scale planting. Journal of Applied Ecology 53:567–578.

Kenworthy, W. J., M. S. Fonseca, J. Homziak, and G. W. Thayer. 1980. Development of a transplanted seagrass (Zostera marina L.) meadow in Back Sound, Carteret County, North Carolina. Proceedings of the Seventh Annual Conference on the Restoration and Creation of Wetlands:175–193.

Kuo, J., and C. den Hartog. 2006. Seagrass Morphology, Anatomy, and Ultrastructure. Pages 51–87 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: Biology, Ecology and Conservation. Springer Netherlands, Dordrecht.

Lee, K.-S., and K. H. Dunton. 1997. Effect of in situ light reduction on the maintenance, growth and partitioning of carbon resources in Thalassia testudinum banks ex König. Journal of Experimental Marine Biology and Ecology 210:53–73.

Lefcheck, J. S., B. B. Hughes, A. J. Johnson, B. W. Pfirrmann, D. B. Rasher, A. R. Smyth, B. L. Williams, M. W. Beck, and R. J. Orth. 2019. Are coastal habitats important nurseries? A meta-analysis. Conservation Letters:e12645.

Lefcheck, J. S., B. W. Pfirrmann, F. J. Fodrie, J. H. Grabowski, A. R. Hughes, and A. R. Smyth. 2021. Consumption rates vary based on the presence and type of oyster structure: A seasonal and latitudinal comparison. Journal of Experimental Marine Biology and Ecology 536:151501.

Longstaff, B. J., N. R. Loneragan, M. J. O'Donohue, and W. C. Dennison. 1999. Effects of light deprivation on the survival and recovery of the seagrass Halophila ovalis (R.Br.) Hook. Journal of Experimental Marine Biology and Ecology 234:1–27.

Marion, S. R., and R. J. Orth. 2010. Innovative Techniques for Large-scale Seagrass Restoration Using Zostera marina (eelgrass) Seeds. Restoration Ecology 18:514–526.

McCloskey, R. M., and R. K. F. Unsworth. 2015. Decreasing seagrass density negatively influences associated fauna. PeerJ 3:e1053.

Micheli, F., M. J. Bishop, C. H. Peterson, and J. Rivera. 2008. Alteration of seagrass species composition and function over two decades. Ecological Monographs 78:225–244.

Minello, T., K. Able, M. Weinstein, and C. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Marine Ecology Progress Series 246:39–59.

NC Department of Environmental Quality. 2021. Coastal Habitat Protection Plan 2021 Amendment:287.

Olesen, B., S. Enríquez, C. Duarte, and K. Sand-Jensen. 2002. Depth-acclimation of photosynthesis, morphology and demography of Posidonia oceanica and Cymodocea nodosa in the Spanish Mediterranean Sea. Marine Ecology Progress Series 236:89–97.

Orth, R. J., W. C. Dennison, J. S. Lefcheck, C. Gurbisz, M. Hannam, J. Keisman, J. B. Landry, K. A. Moore, R. R. Murphy, C. J. Patrick, J. Testa, D. E. Weller, and D. J. Wilcox. 2017. Submersed Aquatic Vegetation in Chesapeake Bay: Sentinel Species in a Changing World. BioScience 67:698–712.

Orth, R. J., K. L. Heck, and J. van Montfrans. 1984. Faunal Communities in Seagrass Beds: A Review of the Influence of Plant Structure and Prey Characteristics on Predator: Prey Relationships. Estuaries 7:339–350.

Orth, R. J., S. R. Marion, K. A. Moore, and D. J. Wilcox. 2010. Eelgrass (Zostera marina L.) in the Chesapeake Bay Region of Mid-Atlantic Coast of the USA: Challenges in Conservation and Restoration. Estuaries and Coasts 33:139–150.

Orth, R. J., and J. van Montfrans. 1982. Predator-prey interactions in a Zostera marina (eelgrass) ecosystem in the lower Chesapeake Bay, Virginia. Pages 81–94 Interactions of Resident Consumers in a Temperate Estuarine Seagrass Community: Vaucluse Shore, Virginia, USA. VIMS-SRAMSOE 267.

Pazzaglia, J., H. M. Nguyen, A. Santillán-Sarmiento, M. Ruocco, E. Dattolo, L. Marín-Guirao, and G. Procaccini. 2021. The Genetic Component of Seagrass Restoration: What We Know and the Way Forwards. Water 13:829.

Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A Flexible, Multipurpose Method for Recording Vegetation Composition and Structure. Castanea 63:262–274.

Reynolds, L. K., K. J. McGlathery, and M. Waycott. 2012. Genetic Diversity Enhances Restoration Success by Augmenting Ecosystem Services. PLOS ONE 7:e38397.

Reynolds, L. K., M. Waycott, K. J. McGlathery, and R. J. Orth. 2016. Ecosystem services returned through seagrass restoration. Restoration Ecology 24:583–588.

Rodemann, J., and S. Brandl. 2017. Consumption pressure in coastal marine environments decreases with latitude and in artificial vs. natural habitats. Marine Ecology Progress Series 574.

Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Marine Ecology Progress Series 99:1–16.

Sheaves, M., R. Johnston, A. Johnson, R. Baker, and R. M. Connolly. 2013. Nursery Function Drives Temporal Patterns in Fish Assemblage Structure in Four Tropical Estuaries. Estuaries and Coasts 36:893–905.

Sheridan, P., and C. Hays. 2003. Are mangroves nursery habitat for transient fishes and decapods? Wetlands 23:449–458.

Sheridan, P., G. McMahan, K. Hammerstrom, and W. Pulich Jr. 1998. Factors Affecting Restoration of Halodule wrightii to Galveston Bay, Texas. Restoration Ecology 6:144–158.

Sogard, S. M., G. V. N. Powell, and J. G. Holmquist. 1989. Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 2. Diel and tidal patterns. Environmental Biology of Fishes 24:81–92.

Suykerbuyk, W., L. L. Govers, T. J. Bouma, W. B. J. T. Giesen, D. J. de Jong, R. van de Voort, K. Giesen, P. T. Giesen, and M. M. van Katwijk. 2016. Unpredictability in seagrass restoration: analysing the role of positive feedback and environmental stress on Zostera noltii transplants. Journal of Applied Ecology 53:774–784.

Tan, Y. M., O. Dalby, G. A. Kendrick, J. Statton, E. A. Sinclair, M. W. Fraser, P. I. Macreadie, C. L. Gillies, R. A. Coleman, M. Waycott, K. van Dijk, A. Vergés, J. D. Ross, M. L. Campbell, F. E. Matheson, E. L. Jackson, A. D. Irving, L. L. Govers, R. M. Connolly, I. M. McLeod, M. A. Rasheed, H. Kirkman, M. R. Flindt, T. Lange, A. D. Miller, and C. D. H. Sherman. 2020. Seagrass Restoration Is Possible: Insights and Lessons From Australia and New Zealand. Frontiers in Marine Science 7.

Thayer, G. W., W. J. Kenworthy, and M. S. Fonseca. 1984. The Ecology of Eelgrass Meadows of the Atlantic Coast: A Community Profile. Fish and Wildlife Service, U.S. Department of the Interior.

Valdez, S. R., Y. S. Zhang, T. van der Heide, M. A. Vanderklift, F. Tarquinio, R. J. Orth, and B. R. Silliman. 2020. Positive Ecological Interactions and the Success of Seagrass Restoration. Frontiers in Marine Science 7.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short, and S. L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences 106:12377–12381.

Williams, S. L. 2001. Reduced Genetic Diversity in Eelgrass Transplantations Affects Both Population Growth and Individual Fitness. Ecological Applications 11:1472–1488.

Wilson, K. L., and H. K. Lotze. 2019. Climate change projections reveal range shifts of eelgrass Zostera marina in the Northwest Atlantic. Marine Ecology Progress Series 620:47–62.

Yarnall, A. H. 2021. Community Structure and Dynamics in Estuarine Seagrass Systems Across Habitat Configurations, Environmental Gradients, and Spatial Scales. Ph.D., The University of North Carolina at Chapel Hill, United States -- North Carolina.

Yarnall, A. H., and F. J. Fodrie. 2020. Predation patterns across states of landscape fragmentation can shift with seasonal transitions. Oecologia 193:403–413.

York, P. H., R. K. Gruber, R. Hill, P. J. Ralph, D. J. Booth, and P. I. Macreadie. 2013. Physiological and Morphological Responses of the Temperate Seagrass Zostera muelleri to Multiple Stressors: Investigating the Interactive Effects of Light and Temperature. PLOS ONE 8:e76377.

Zhang, Y., W. Cioffi, R. Cope, P. Daleo, E. Heywood, C. Hoyt, C. Smith, and Brian. Silliman. 2018. A Global Synthesis Reveals Gaps in Coastal Habitat Restoration Research. Sustainability 10:1040.

Zhang, Y. S., R. K. Gittman, S. E. Donaher, S. N. Trackenberg, T. van der Heide, and B. R. Silliman. 2021. Inclusion of Intra- and Interspecific Facilitation Expands the Theoretical Framework for Seagrass Restoration. Frontiers in Marine Science 8.

Zhou, Y., P. Liu, B. Liu, X. Liu, X. Zhang, F. Wang, and H. Yang. 2014. Restoring Eelgrass (Zostera marina L.) Habitats Using a Simple and Effective Transplanting Technique. PLOS ONE 9:e92982.

Figures

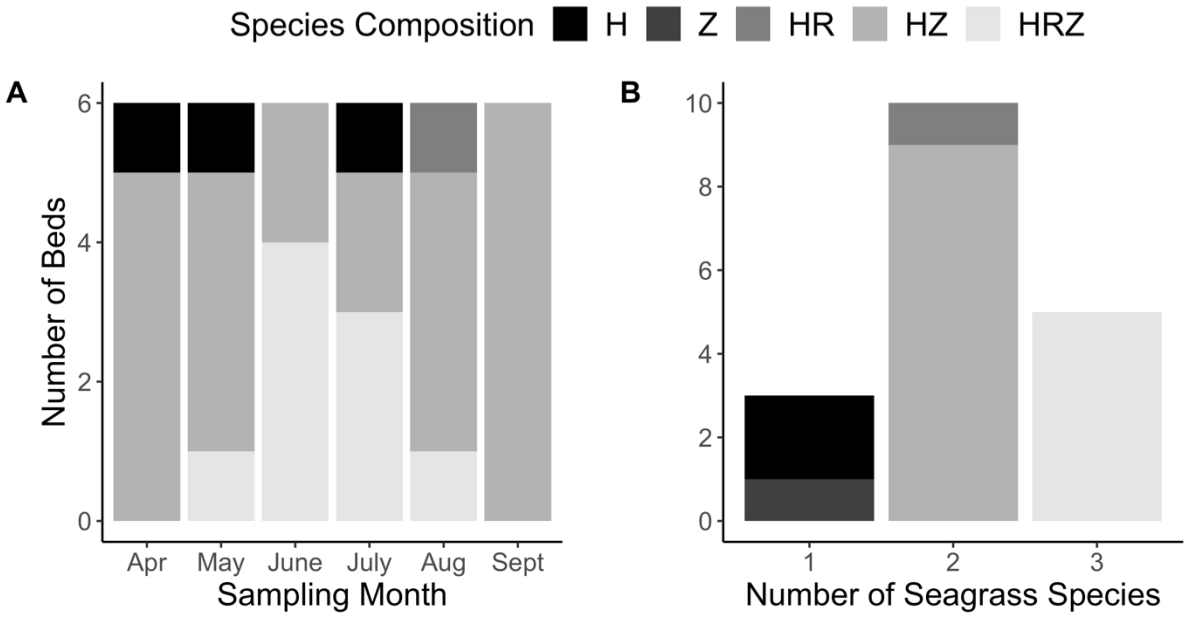

Figure 3.1: The species composition of each surveyed bed (A) across months (N = 6 per month) in 2019 and (B) across the number of beds comprised of 1, 2, and 3 seagrass species in 2020 (N = 18). Color denotes the makeup of the beds by seagrass presence. H indicates *H. wrightii*, R indicates *R. maritima*, and Z indicates *Z. marina*.

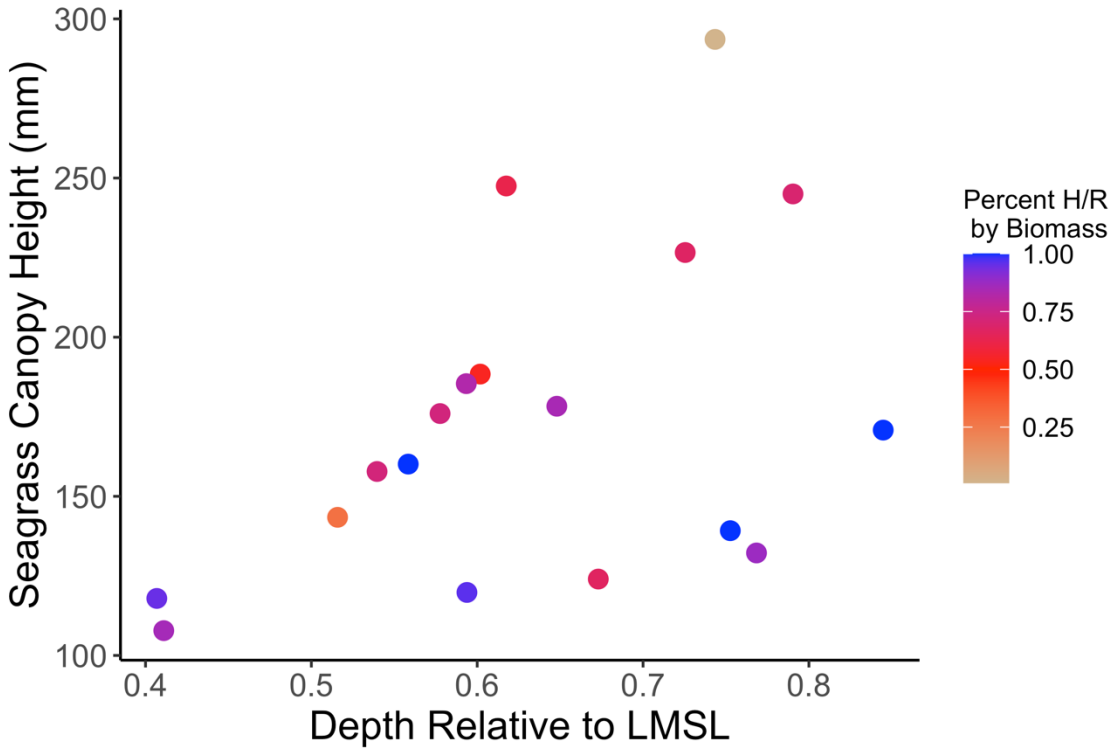

Figure 3.2: Canopy height and depth relative to local mean sea level (LMSL) of each seagrass bed sampled in 2020. The color of the dot indicates dominance of the seagrass bed by biomass with blue indicating a higher proportion of *H. wrightii* and *R. maritima* combined, red indicating a mix of *H. wrightii / R. maritima* and *Z. marina*, and tan indicating dominance of *Z. marina.*

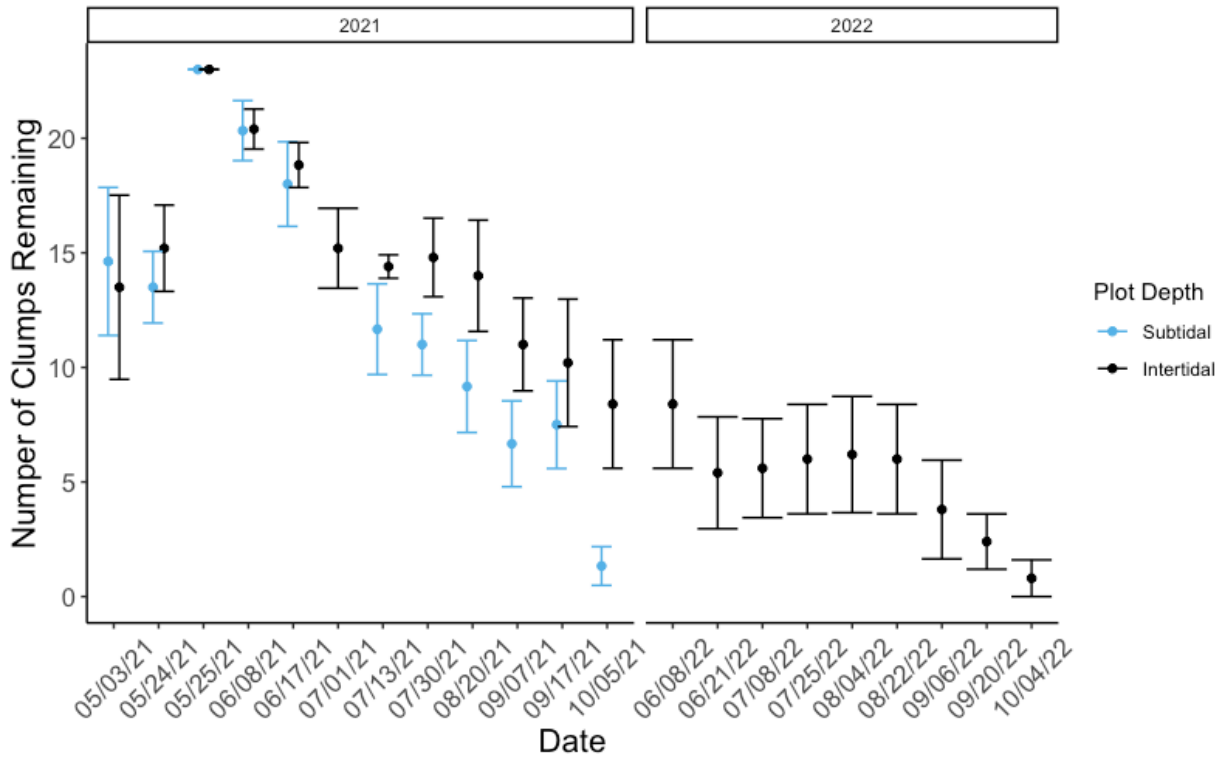

Figure 3.3: Mean number of transplanted *H. wrightii* clumps remaining in subtidal (blue) and intertidal (black) plots in 2021 and 2022. Error bars indicate standard error.

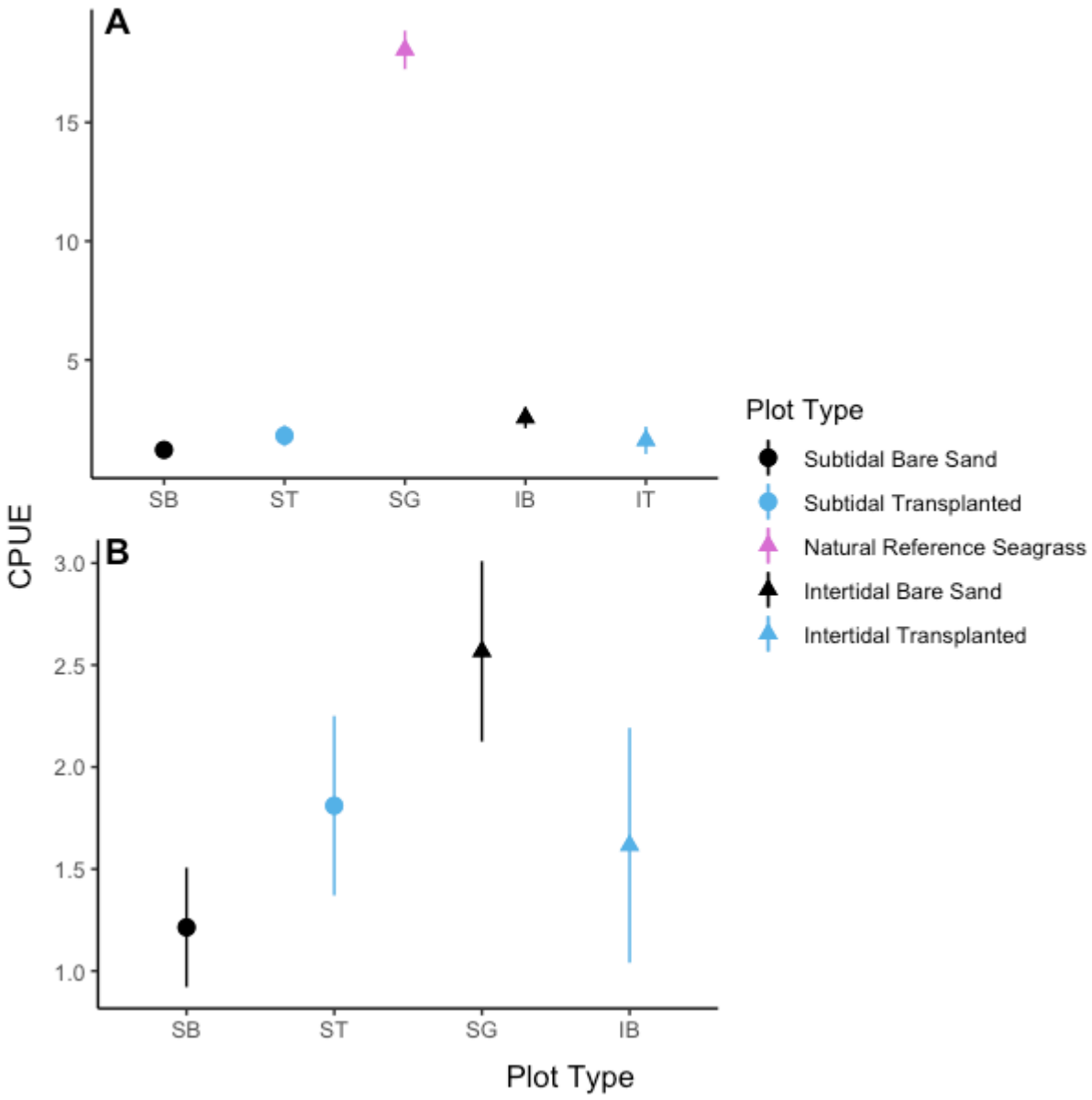

Figure 3.4**:** Motile fauna CPUE as a function of plot type. A and B show the same data; however, B is a closer view of sand flat and transplanted plots to allow better distinguishment between catch rates. Color denotes transplantation category and shape denotes elevation category. Error bars denote standard error.

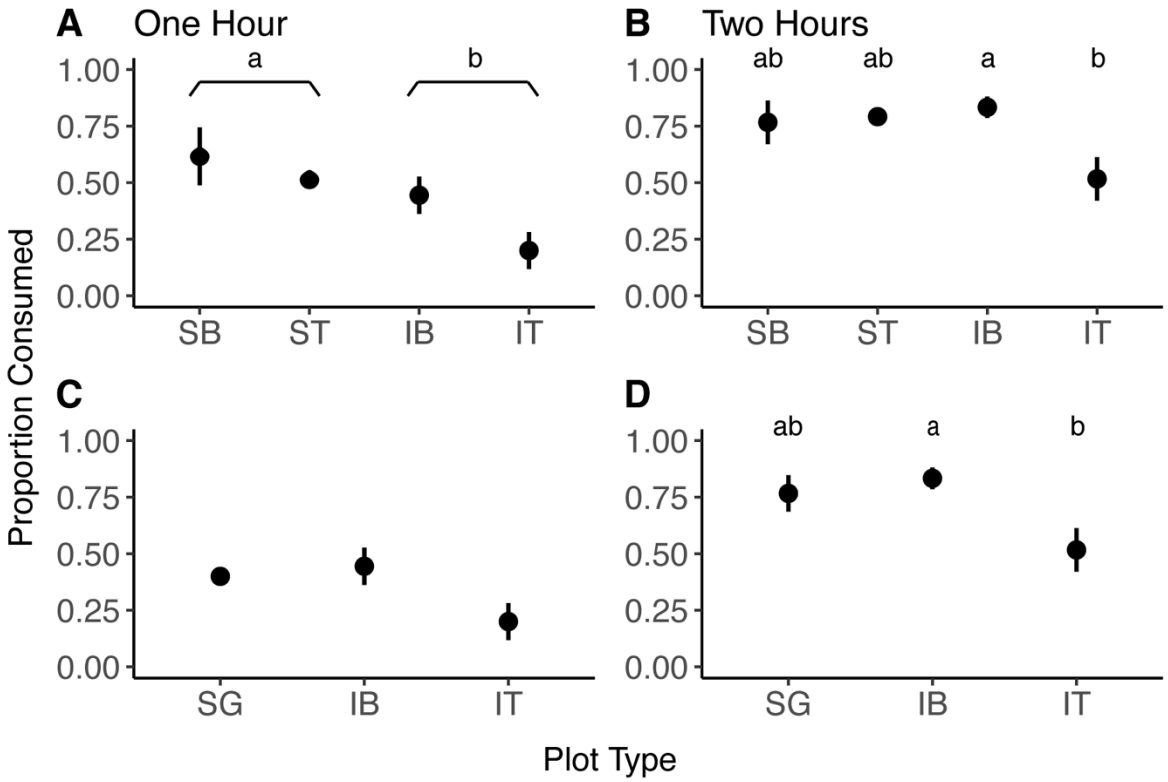

Figure 3.5: Proportion of squid pops consumed as a factor of plot type after one (A, C) and two (B, D) hours. Comparisons are for bare sand and transplanted plots across intertidal and subtidal areas (A, B) and across only intertidal habitats (C, D). SB denotes subtidal bare sand, ST denotes subtidal transplanted, IB denotes intertidal bare sand, IT denotes intertidal transplanted, and SG denotes natural reference seagrass. Dots are average across plots with bars denoting standard error. Letters above plots indicate significant ($p < 0.05$) results from ANOVA and Tukey's post-hoc tests.

Tables

Table 3.1: Mean (standard error) of seagrass composition and morphology metrics for 2019 and 2020 across the bed, *H. wrightii*, *R. maritima*, and *Z. marina*. Any metric not measured for the specific species or bed is left blank.

	Year	Bed	*H. wrightii*	*R. maritima*	*Z. marina*
Canopy Height (mm)	2019	184.26 (12.04)	-	-	-
	2020	173 (12.15)	-	-	-
Average Shoot Length (mm)	2019	-	125.84 (5.25)	88.08 (7.44)	105.46 (6.7)
	2020	-	92.81 (2.76)	93.01 (9.73)	111.69 (8.87)
Aboveground Biomass (g)	2019	0.92 (0.07)	0.72 (0.05)	0.05 (0.02)	0.15 (0.03)
	2020	0.76 (0.06)	0.49 (0.04)	0.04 (0.02)	0.23 (0.06)
Leaf Width (mm)	2019	-	1 (0)	1 (0)	2.11 (0.1)
	2020	-	1 (0)	1 (0)	2.21 (0.05)
Leaf Number per Shoot	2019	-	2.78 (0.05)	4.94 (0.38)	3.81 (0.14)
	2020	-	2.88 (0.04)	3.67 (0.28)	3.28 (0.12)
Shoot Count	2019	63.84 (3.13)	56.32 (2.84)	3.82 (1.42)	3.69 (0.80)
	2020	71.12 (4.43)	59.55 (4.49)	5.97 (2.95)	5.6 (1.07)
Branch Number per Shoot	2019	-	1 (0)	3.26 (0.35)	1.06 (0.04)
	2020	-	1 (0)	2.07 (0.25)	1 (0)
***H. wrightii* + *R. maritima* Percent by Biomass**	2019	85.54 (2.61)	-	-	-
	2020	73.59 (6.14)	-	-	-
Epibiont Load (grams / gram of seagrass)	2020	0.64 (0.09)	-	-	-

Supplemental Figures

Figure S3.1: Map of seagrass bed locations in Back Sound, North Carolina, sampled in 2019 and 2020. Each white point denotes a single seagrass site.

Figure S3.2. Map of restoration site. Circles represent intertidal transplanted (N=5), stars represent subtidal transplanted (N=6), triangles represent intertidal bare sand (N=6), diamonds represent subtidal bare sand (N=5), and squares represent seagrass control plots (N=5).

Figure S3.3: Image of a single shoot of *Z. marina* with the (A) shoot length and (B) leaf width demarcated. This shoot has four leaves and one branch. Image courtesy of S. Donaher.

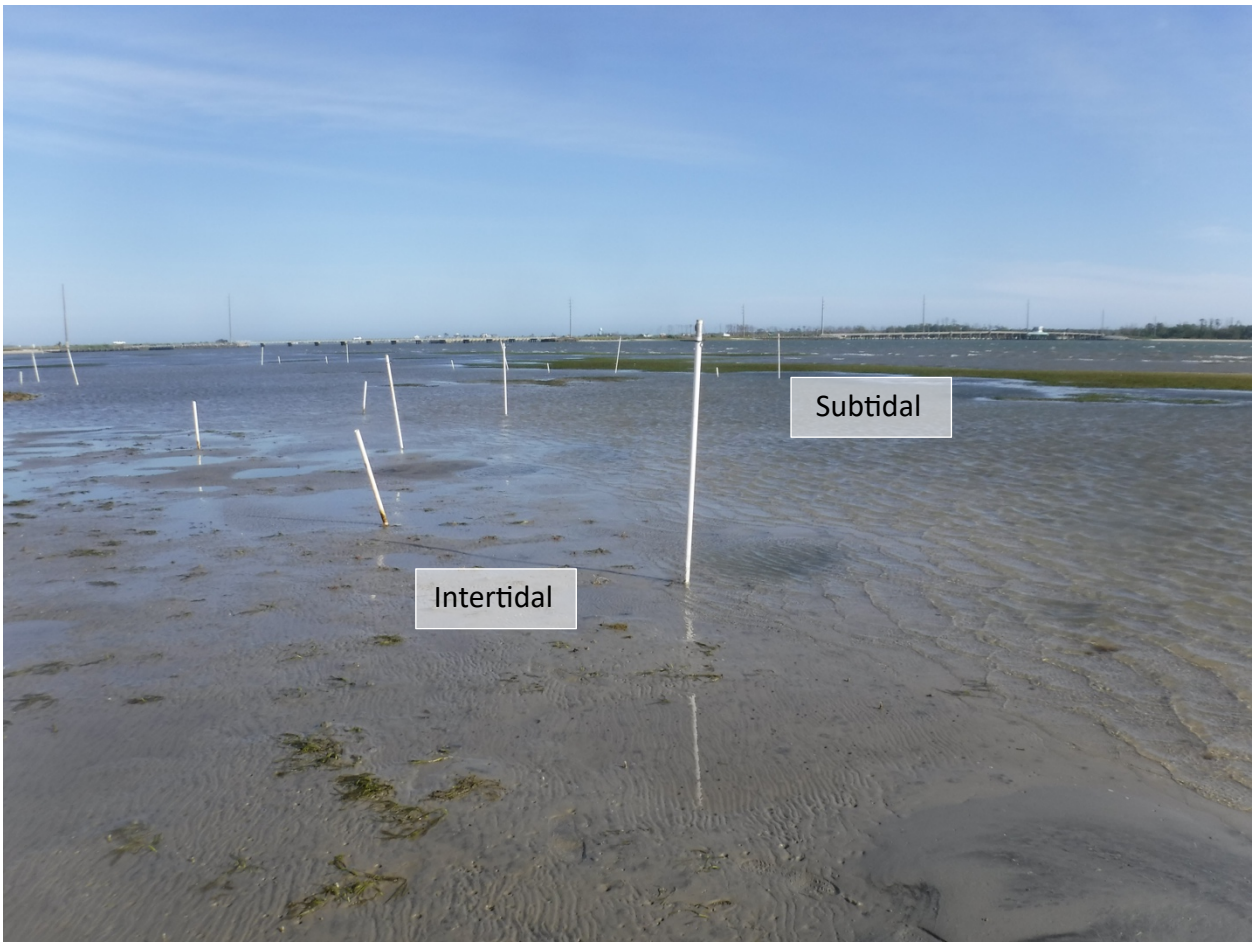

Figure S3.4: Image of restoration site with shallow, intertidal (close) and deep, subtidal (far) plots shown at low tide.

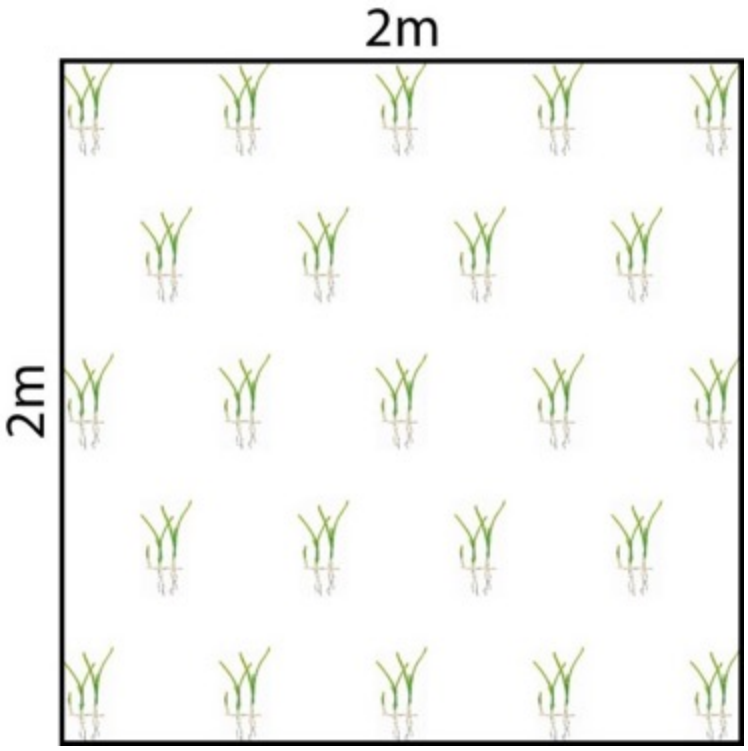

Figure S3.5: Diagram representing the transplantation scheme of *H. wrightii* in the manipulative field experiment. Diagram created from figures using the University of Maryland Center for Environmental Science media library.

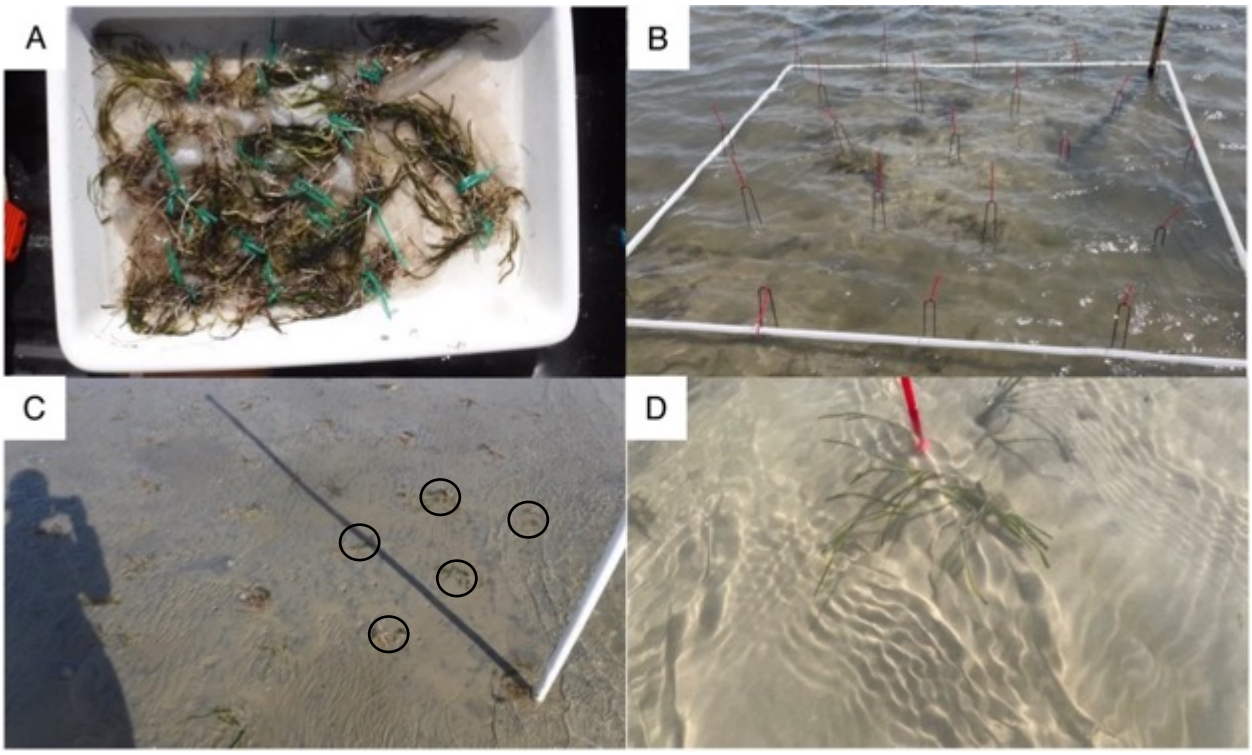

Figure S3.6: (A) Clumps of 15 shoots of *H. wrightii* to be planted in (B) 2 m x 2 m plot with 23 clumps total marked by lawn staples. (C) A restored plot after planting with a few clumps circled for ease of view and (D) a close-up of a planted clump with all roots and rhizomes covered with sand.

Figure S3.7: A standardized monitoring unit for the recruitment of fish (SMURF) deployed in a natural reference seagrass plot.

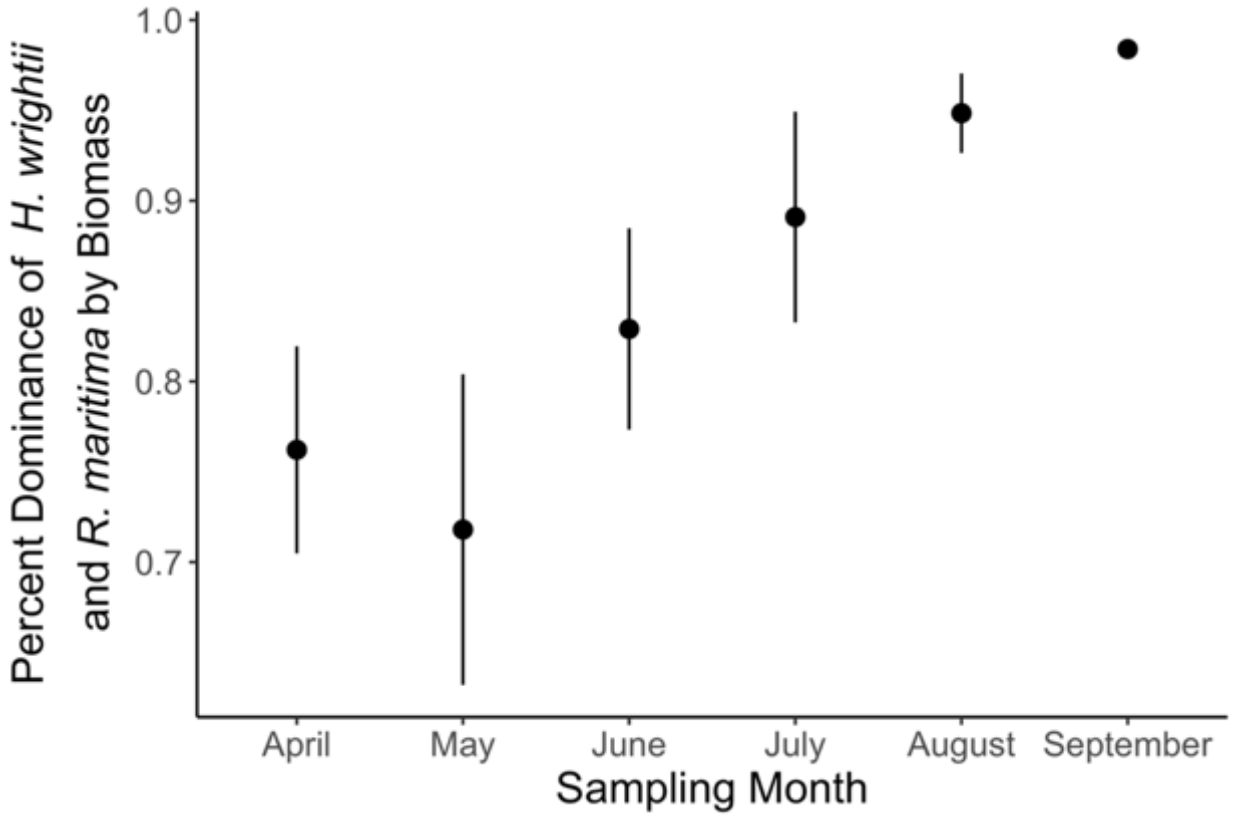

Figure S3.8: Percent dominance of *H. wrightii* and *R. maritima* in 2019 over *Z. marina* plotted on the y-axis with sampling month plotted on the x-axis. Values are means and with standard error bars.

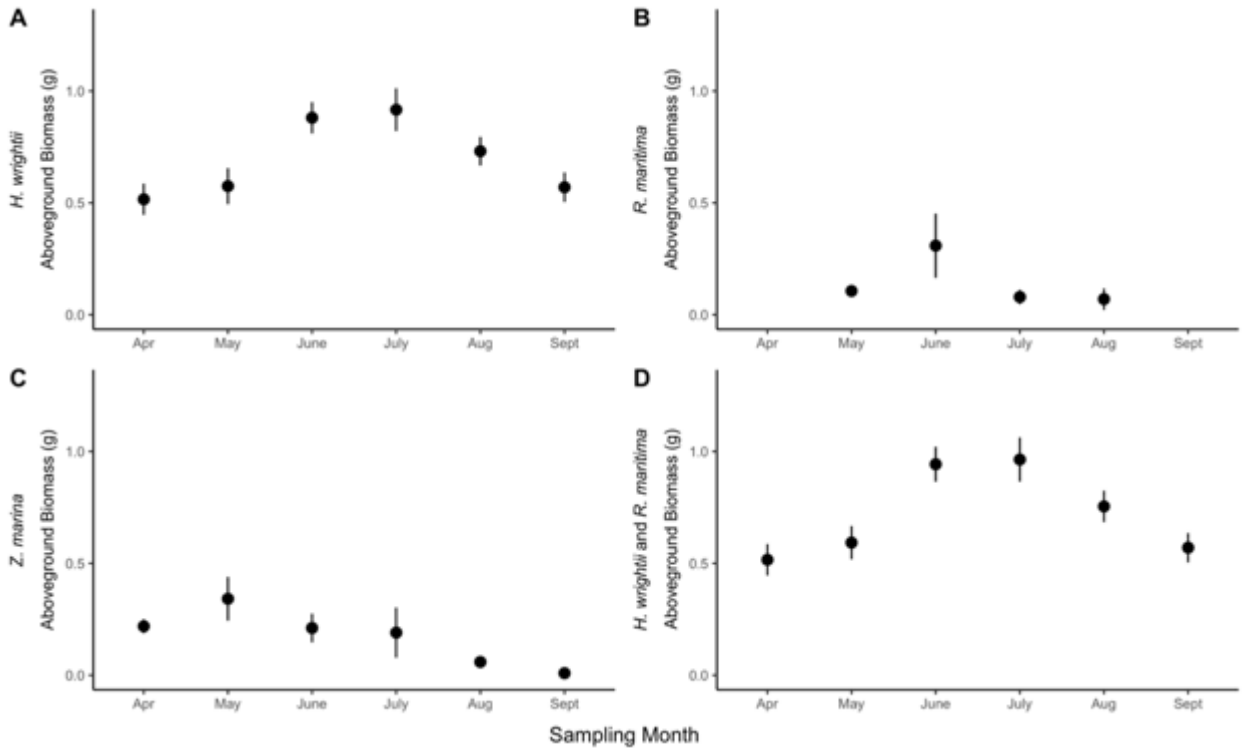

Figure S3.9: Sampling month plotted on the x-axis with the aboveground biomass in grams of (A) *H. wrightii,* (B) *R. maritima,* (C) *Z. marina,* and (D) the combined biomass of *H. wrightii* and *R. maritima* plotted on the y-axis. Means across beds are plotted with error bars denoting standard error.

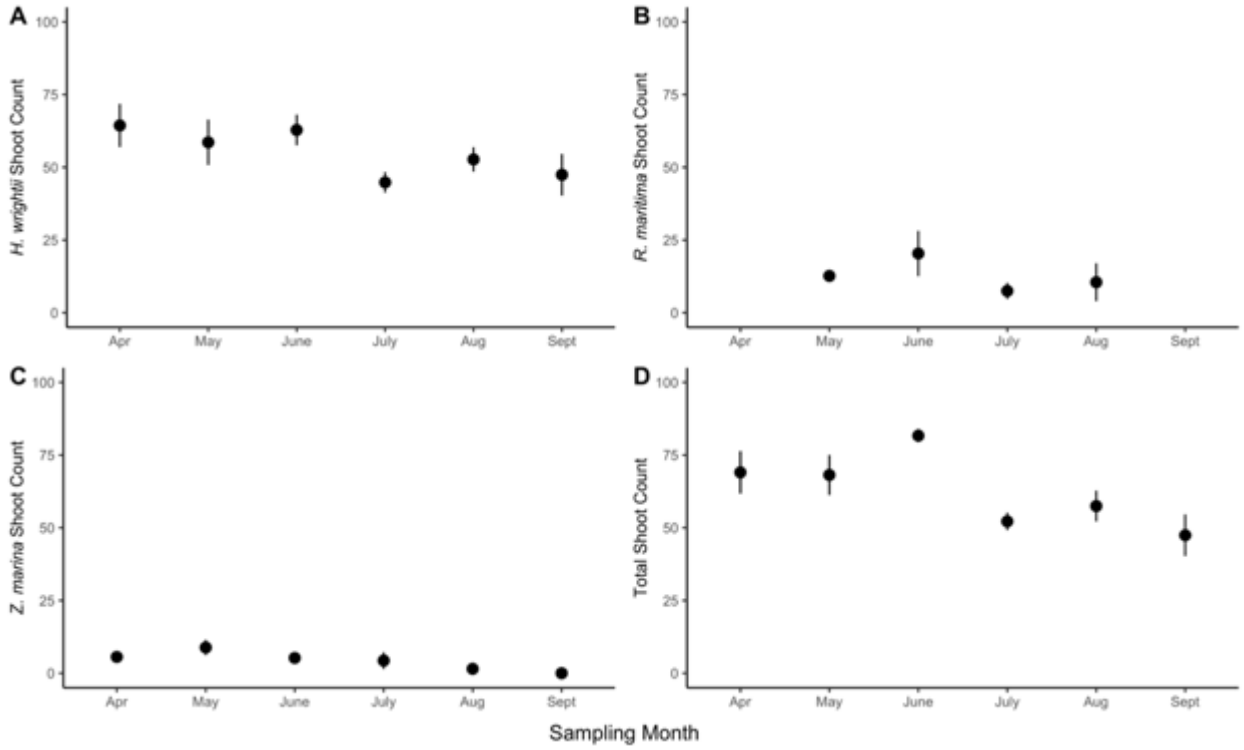

Figure S3.10: Sampling month plotted on the x-axis with the shoot density per 10 cm diameter core of (A) *H. wrightii,* (B) *R. maritima,* (C) *Z. marina,* and (D) the total shoot count of all three seagrass species plotted on the y-axis. Means across beds are plotted with error bars denoting standard error.

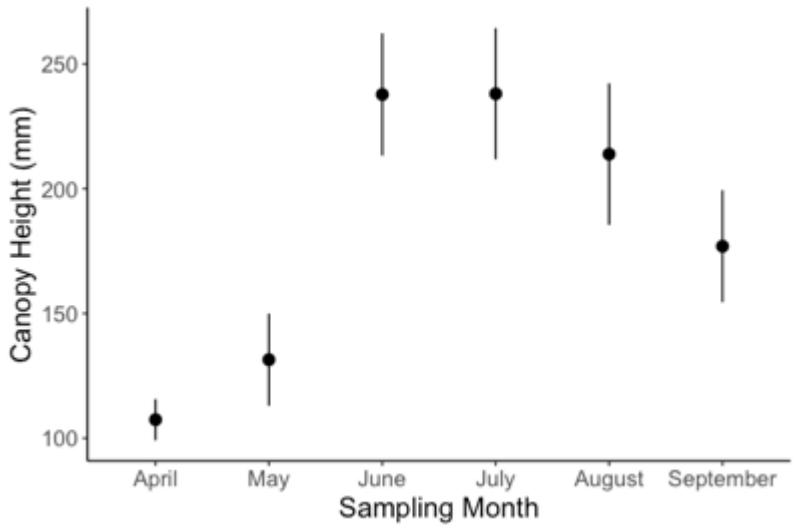

Figure S3.11: Sampling month plotted on the x-axis with the canopy height in millimeters plotted on the y-axis. Means across beds are plotted with error bars denoting standard error.

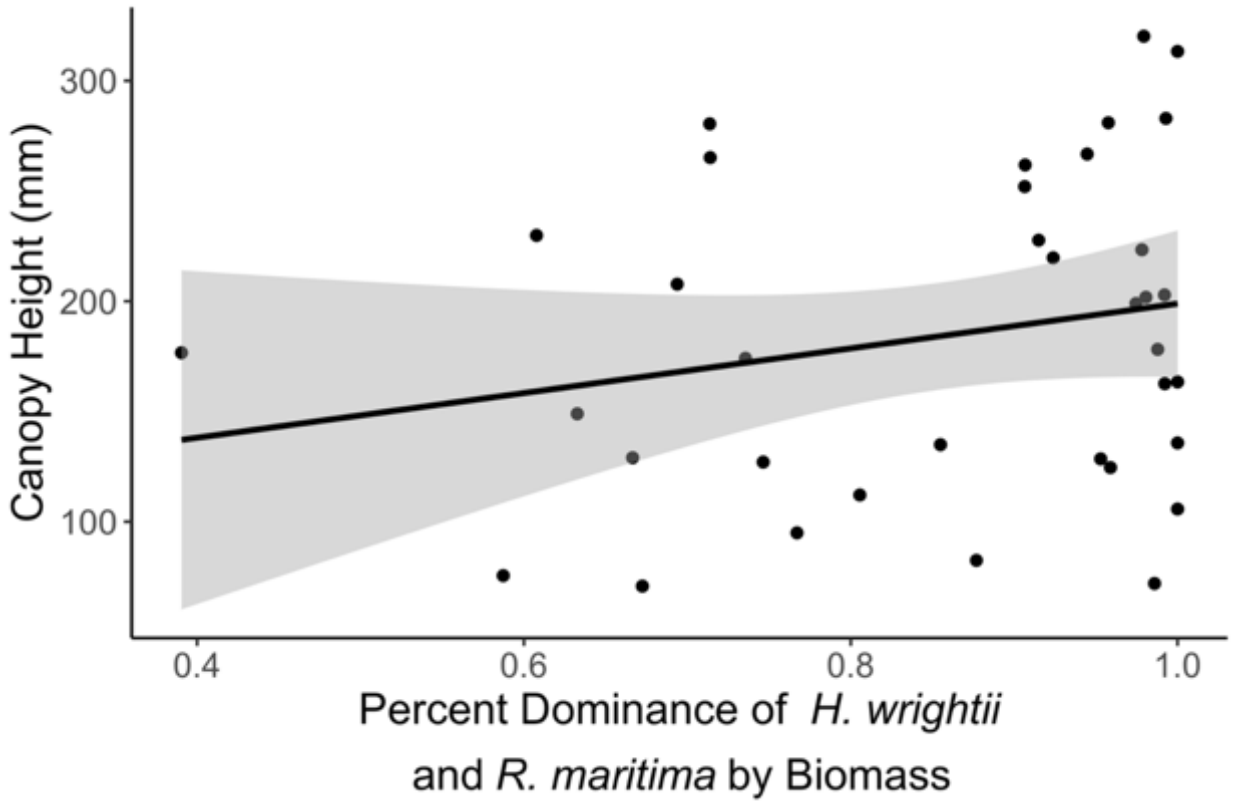

Figure S3.12: The dominance of *H. wrightii* and *R. maritima* by biomass over *Z. marina* plotted on the x-axis and the canopy height in mm plotted on the y-axis. The linear mixed model predictions and 95% confidence interval are plotted over the values.

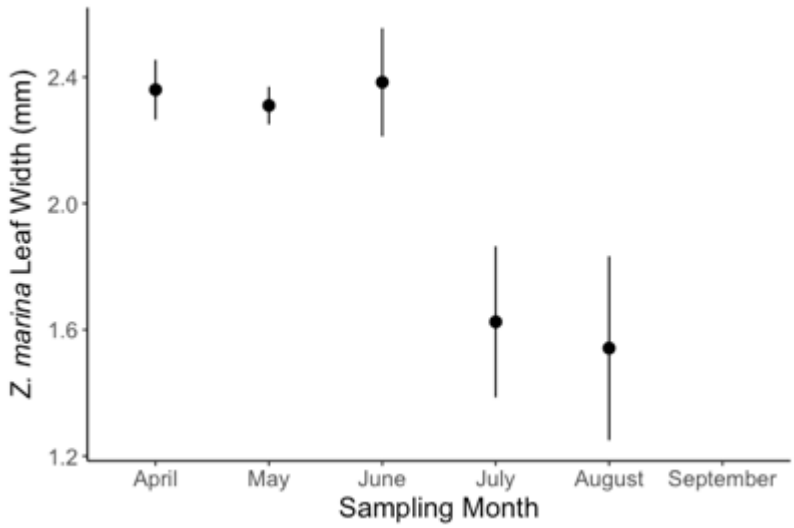

Figure S3.13: The sampling month plotted on the y-axis and the leaf width of *Z. marina* in millimeteres plotted on the x-axis. Means across beds are plotted and error bars denote standard error. *H. marina* and *R. maritima* are not shown as there is no variation in their leaf widths across individual shoots.

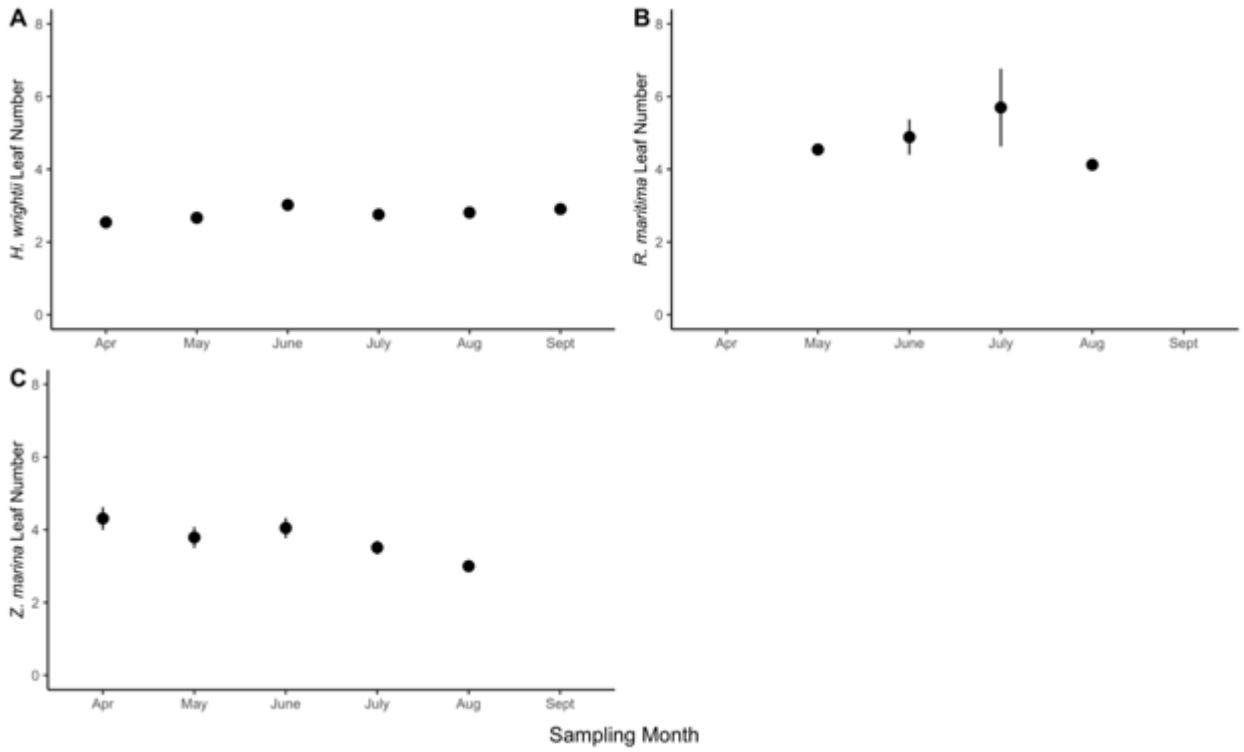

Figure S3.14: Sampling month plotted on the x-axis with the leaf number per shoot of (A) *H. wrightii,* (B) *R. maritima,* and (C) *Z. marina* plotted on the y-axis. Means across beds are plotted with error bars denoting standard error.

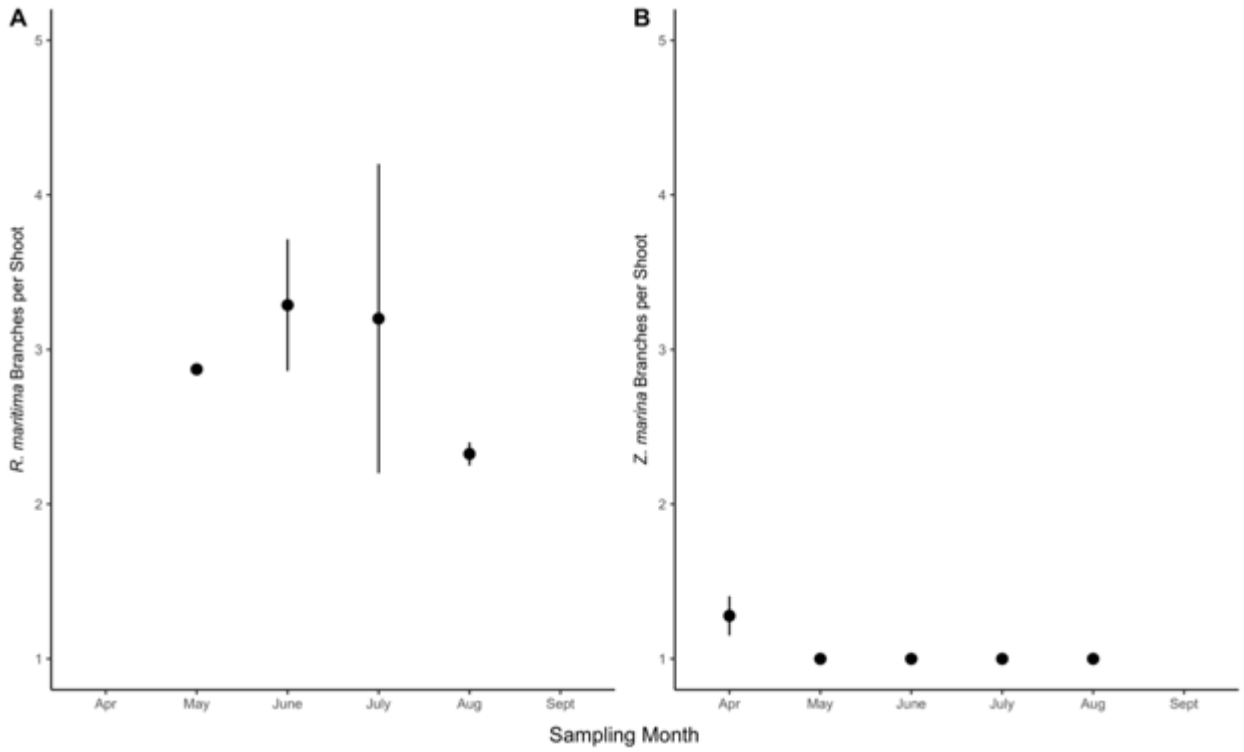

Figure S3.15: Sampling month plotted on the x-axis with number of branches per shoot of (A) *R. maritima* and (B) *Z. marina* plotted on the y-axis. Means across beds are plotted with error bars denoting standard error. Branch number of *H. wrightii* is not shown as it does not vary across shoots.

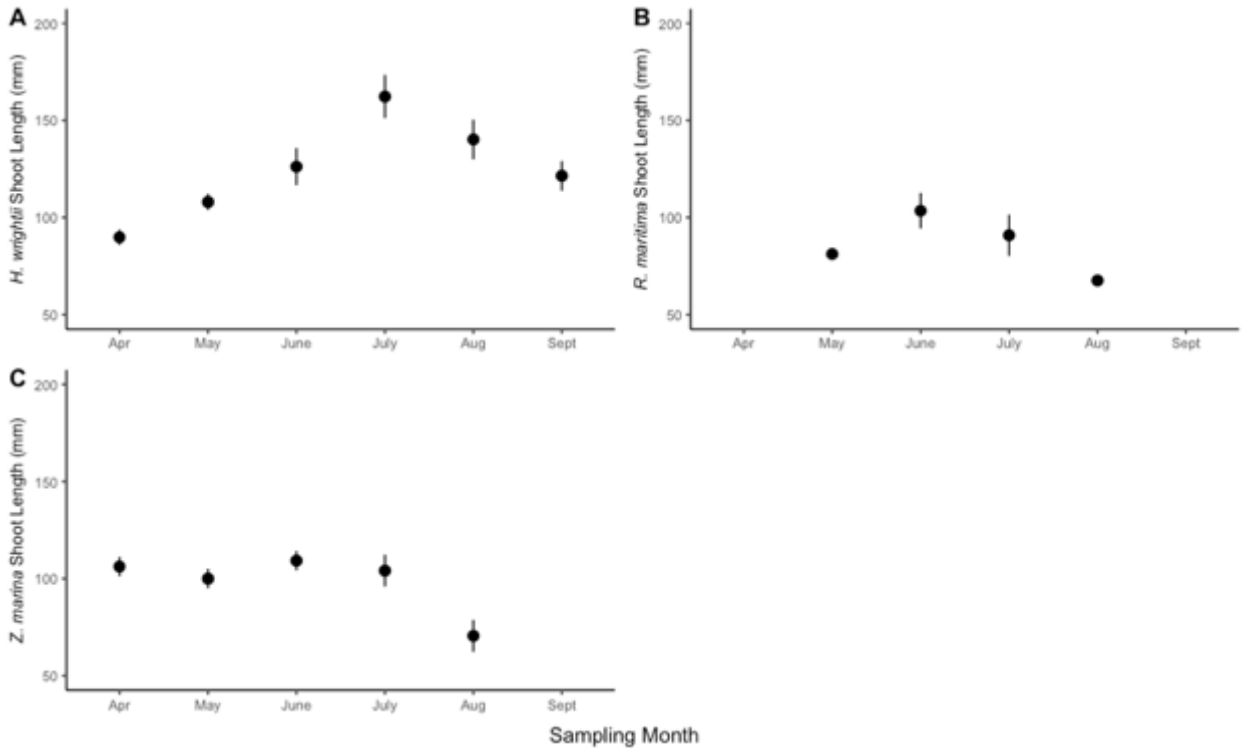

Figure S3.16: Sampling month plotted on the x-axis with the shoot length in millimeters of (A) *H. wrightii,* (B) *R. maritima,* and (C) *Z. marina* plotted on the y-axis. Means across beds are plotted with error bars denoting standard error.

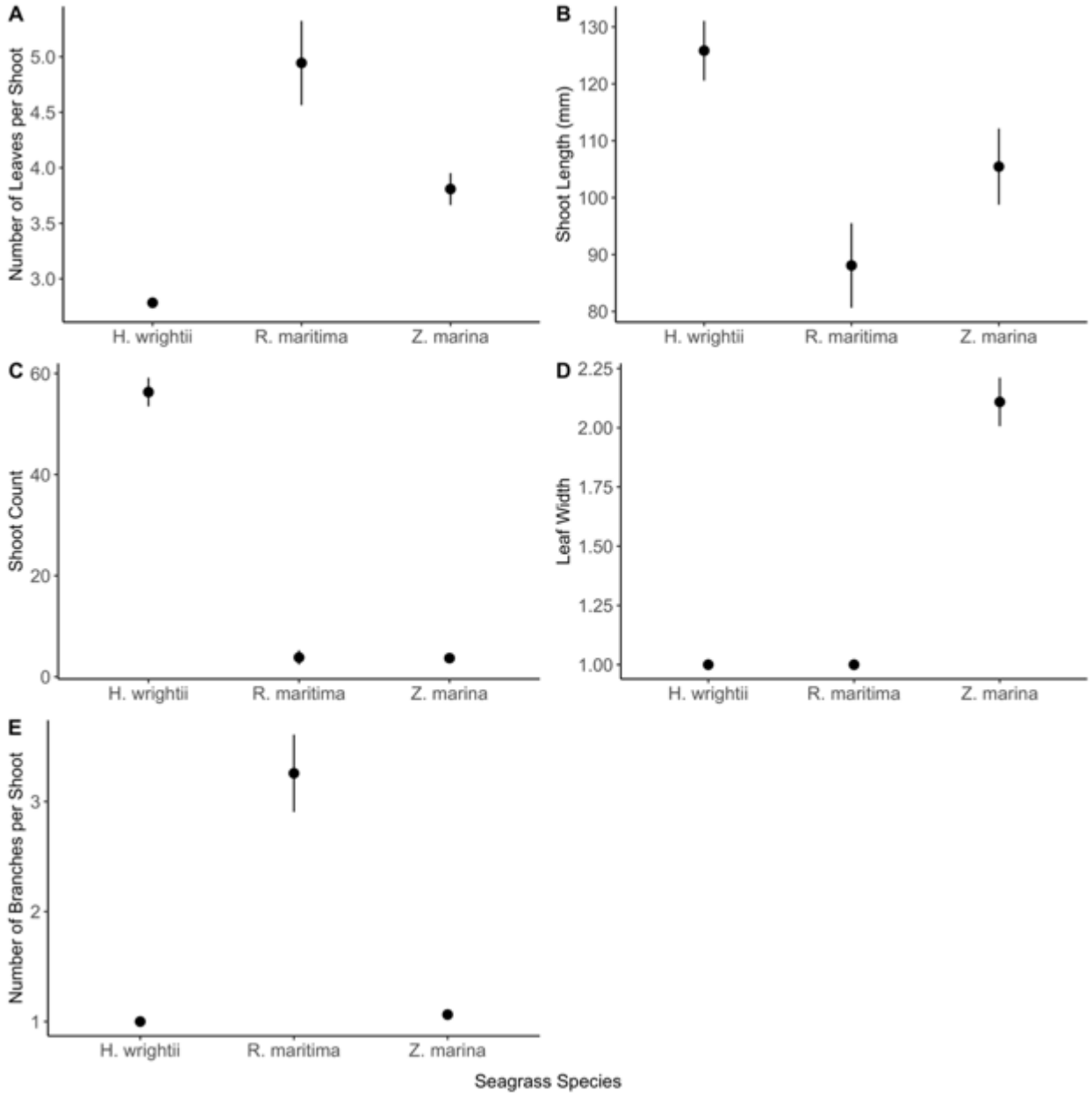

Figure S3.17: Seagrass species plotted on the x-axis with (A) number of leaves per shoot, (B) shoot length in mm, (C) shoot count per 10 cm diameter core, (D) leaf width in mm, (E) and number of branches per shoot plotted on the y-axis. Means across all beds and sampling months are plotted with error bars denoting standard error.

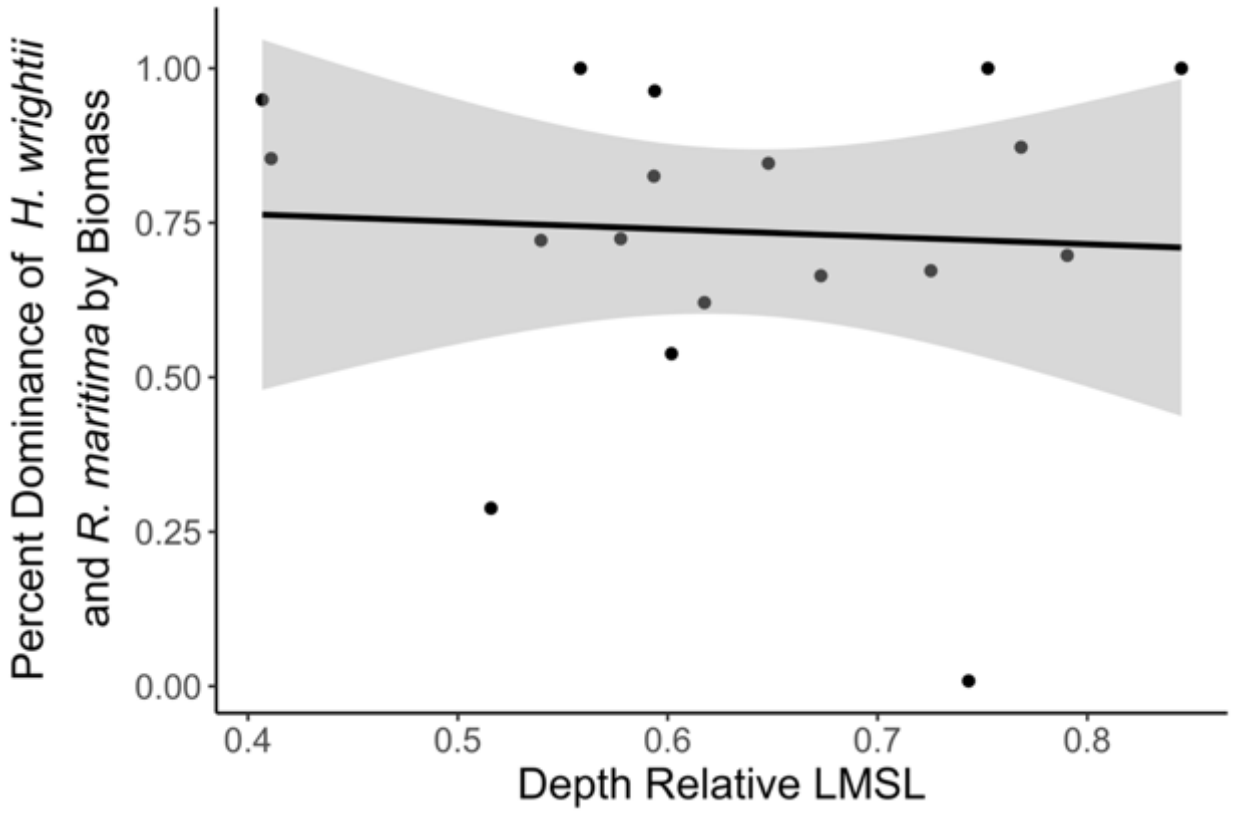

Figure S3.18: Depth relative to LMSL in m plotted on the x-axis with percent dominance of *H. wrightii* and *R. maritima* over *Z. marina* by biomass plotted on the y-axis. The line denoted here is a LMM prediction with a 95% confidence interval.

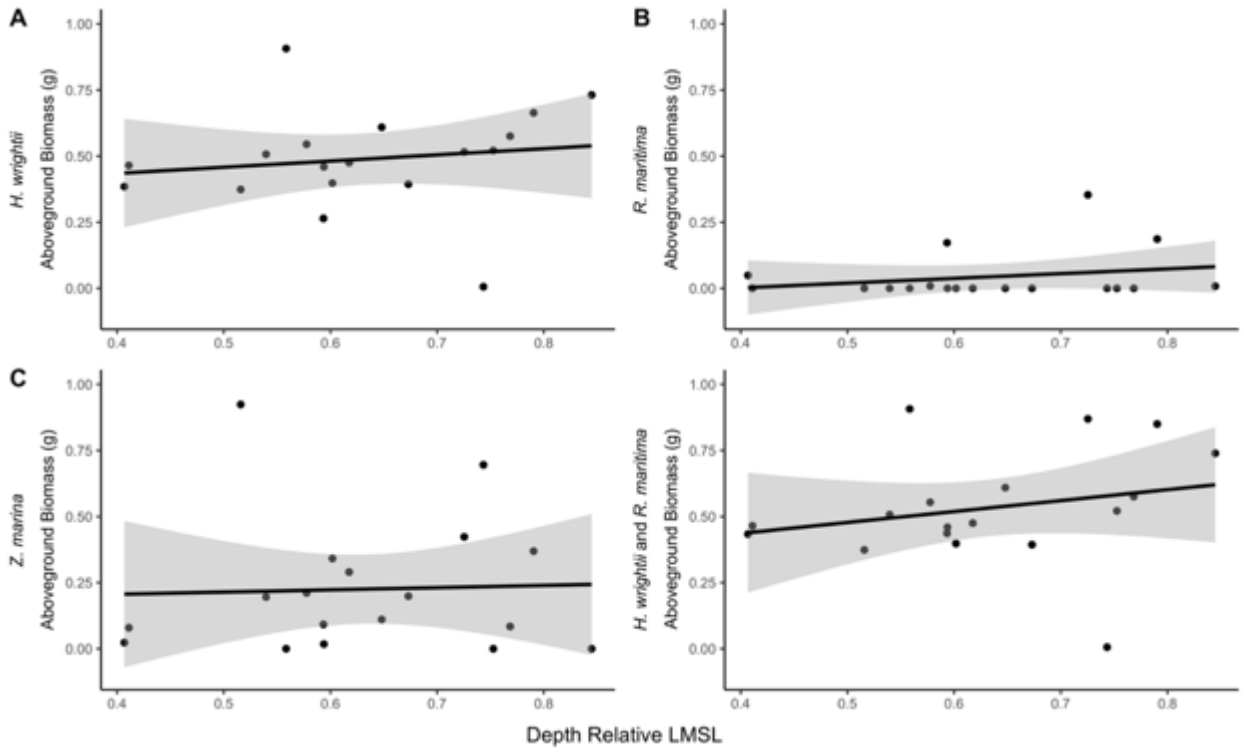

Figure S3.19: Depth relative to LMSL in m plotted on the x-axis with aboveground biomass in grams of (A) *H. wrightii*, (B) *R. maritima*, (C) *Z. marina*, and (D) *H. wrightii* and *R. maritima* combined plotted on the y-axis. The lines denoted here are LMM predictions with 95% confidence intervals for *H. wrightii, Z. marina,* and *H. wrightii* and *R. maritima* combined and GLMM predictions with 95% confidence interval for *R. maritima*.

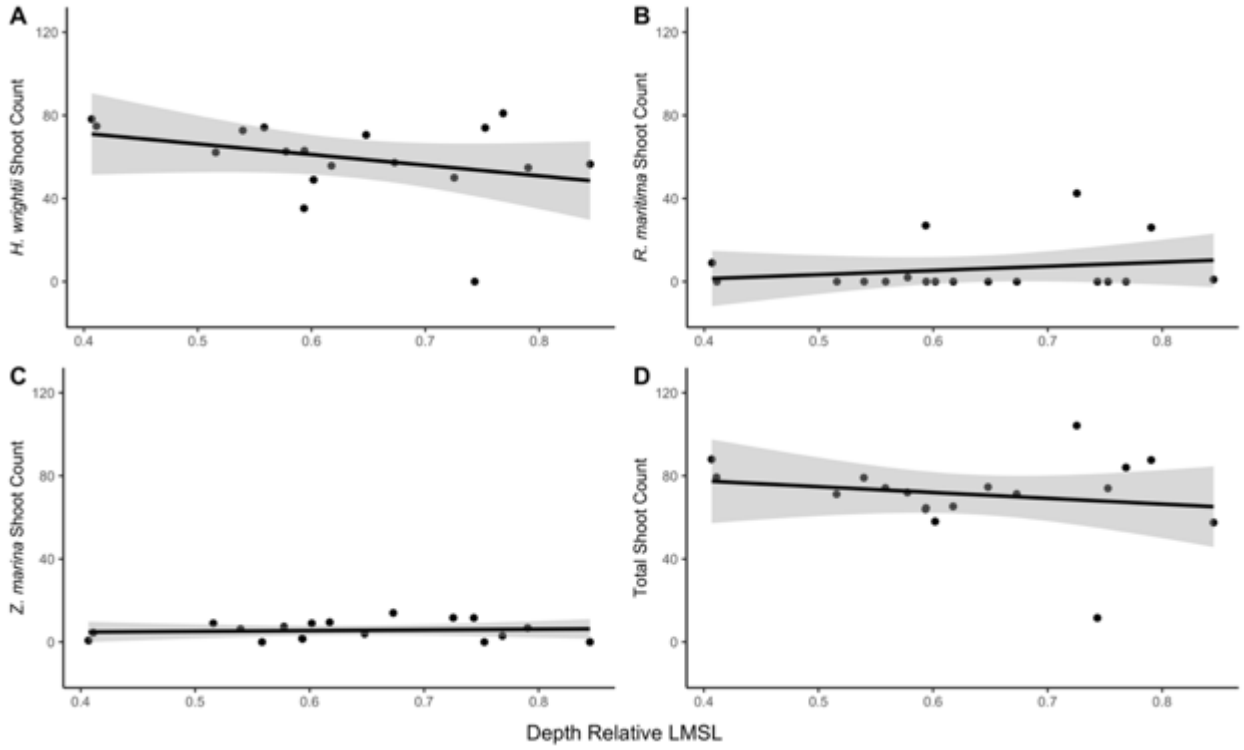

Figure S3.20: Depth relative to LMSL in m plotted on the x-axis with shoot count per 10 cm diameter core of (A) *H. wrightii*, (B) *R. maritima*, (C) *Z. marina*, and (D) total of all three seagrass species combined plotted on the y-axis. The lines denoted here are GLMM predictions with 95% confidence intervals.

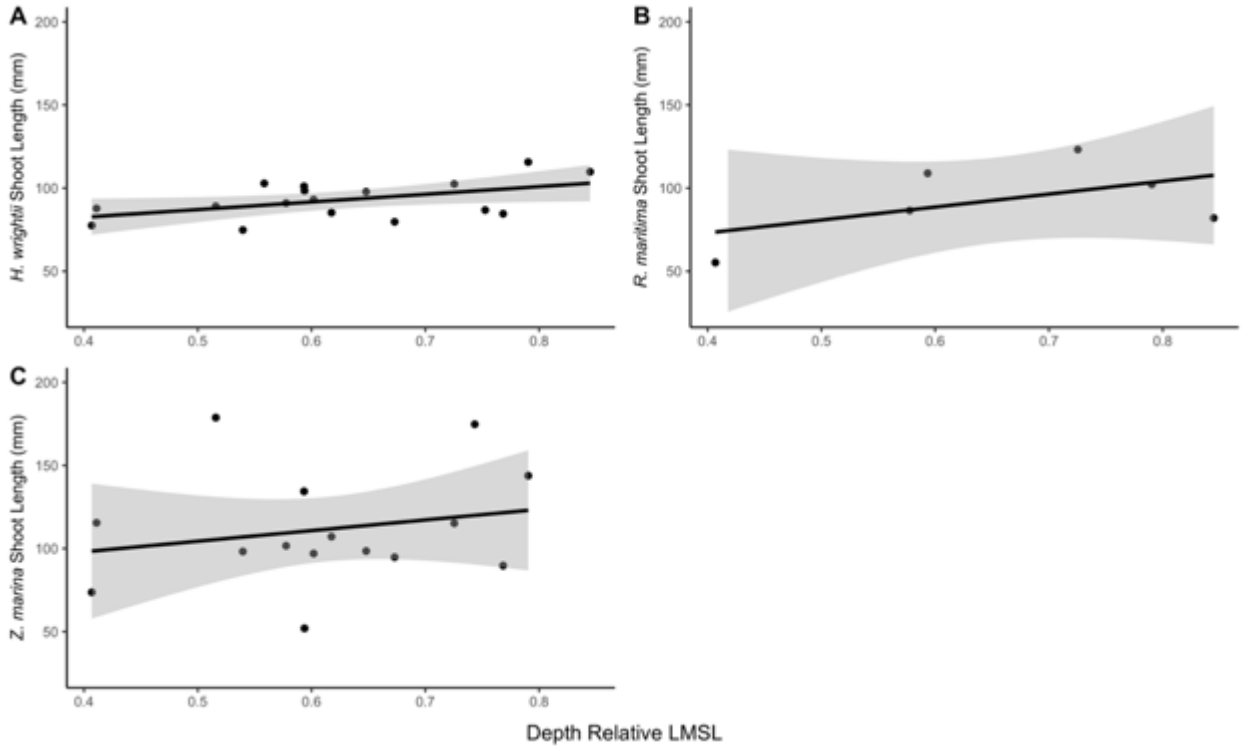

Figure S3.21: Depth relative to LMSL in m plotted on the x-axis with shoot length in meters of (A) *H. wrightii*, (B) *R. maritima*, (C) *Z. marina*, and (D) *H. wrightii* and *R. maritima* combined plotted on the y-axis. The lines denoted here are LMM predictions with 95% confidence intervals.

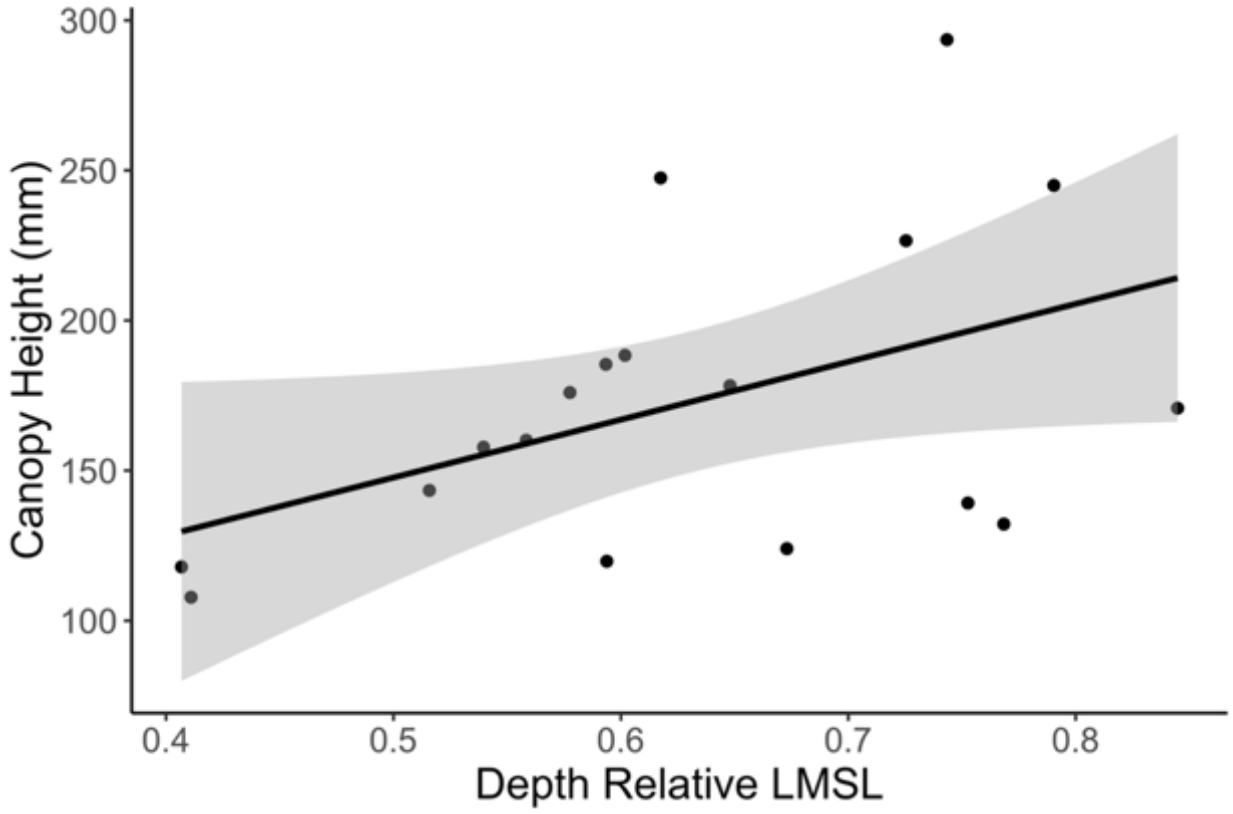

Figure S3.22: Depth relative to LMSL in m plotted on the x-axis with canopy height in mm plotted on the y-axis. The line denoted here is a LMM prediction with a 95% confidence interval.

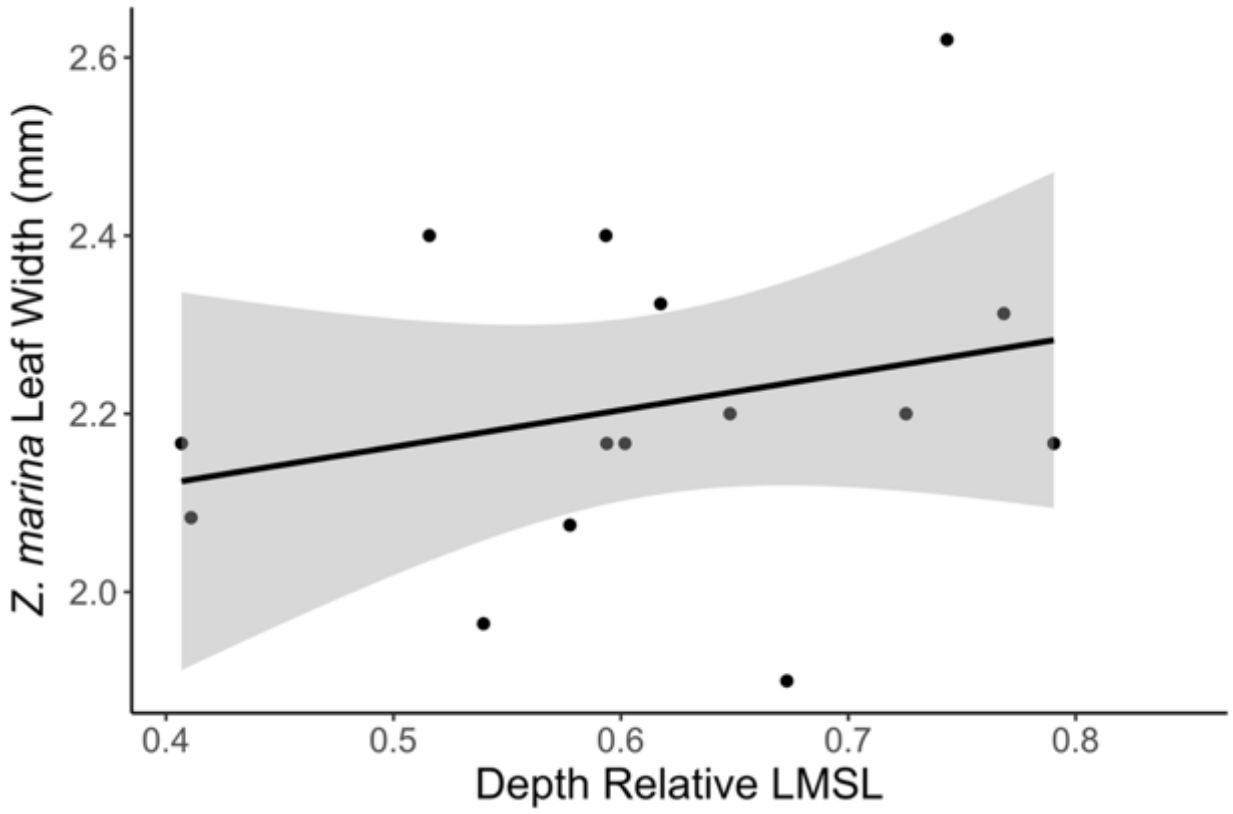

Figure S3.23: Depth relative to LMSL in m plotted on the x-axis with leaf width of *Z. marina* in millimeters plotted on the y-axis. The line denoted here is a LMM prediction with a 95% confidence interval.

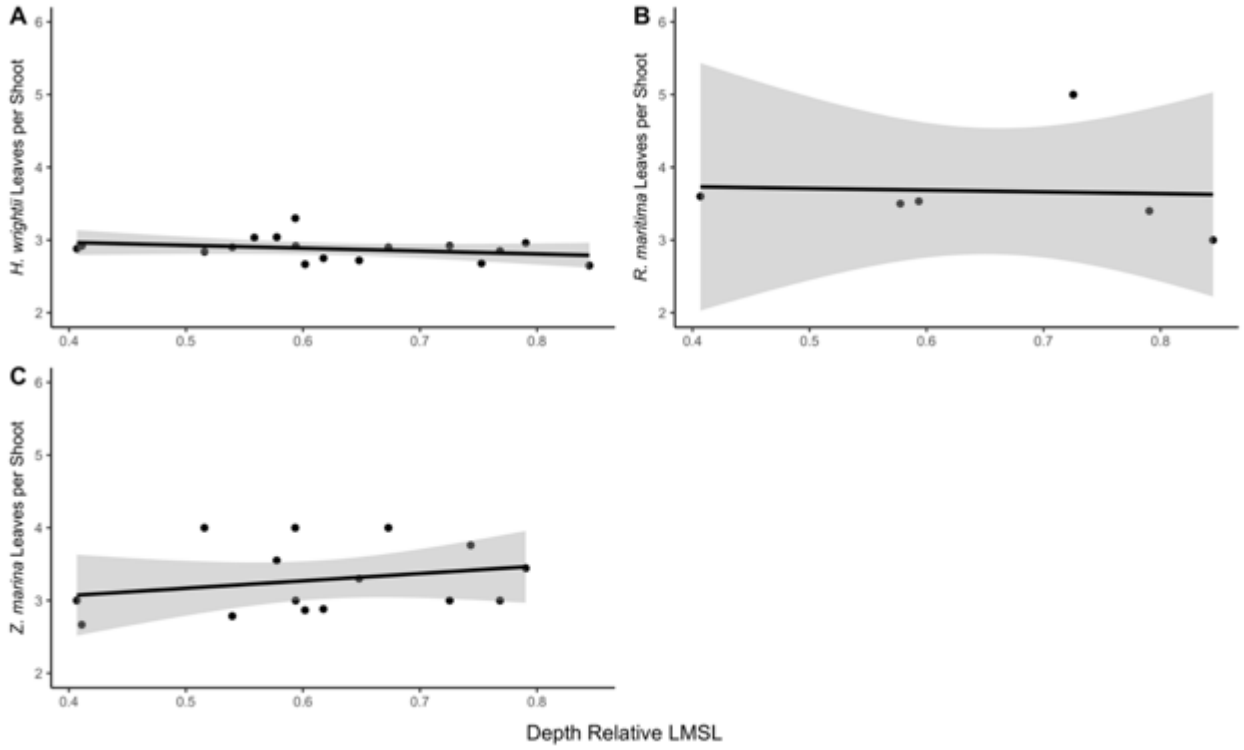

Figure S3.24: Depth relative to LMSL in m plotted on the x-axis with leaf number per shoot of (A) *H. wrightii*, (B) *R. maritima*, and (C) *Z. marina* plotted on the y-axis. The lines denoted here are LMM predictions with 95% confidence intervals.

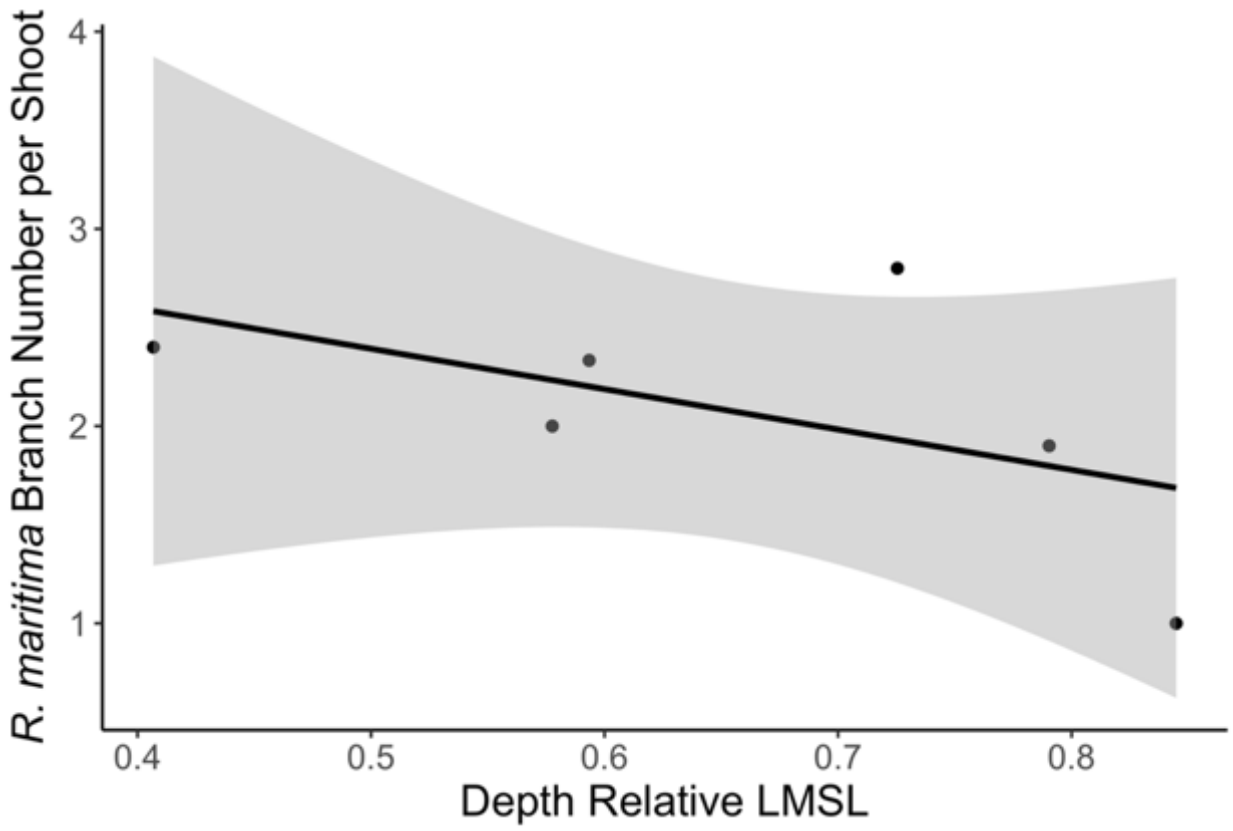

Figure S3.25: Depth relative to LMSL in m plotted on the x-axis with branch number per shoot of *R. maritima* plotted on the y-axis. The line denoted here is a LMM prediction with a 95% confidence interval. *H. wrightii* and *Z. marina* are not shown here as they had no variation in their branch number per shoot.

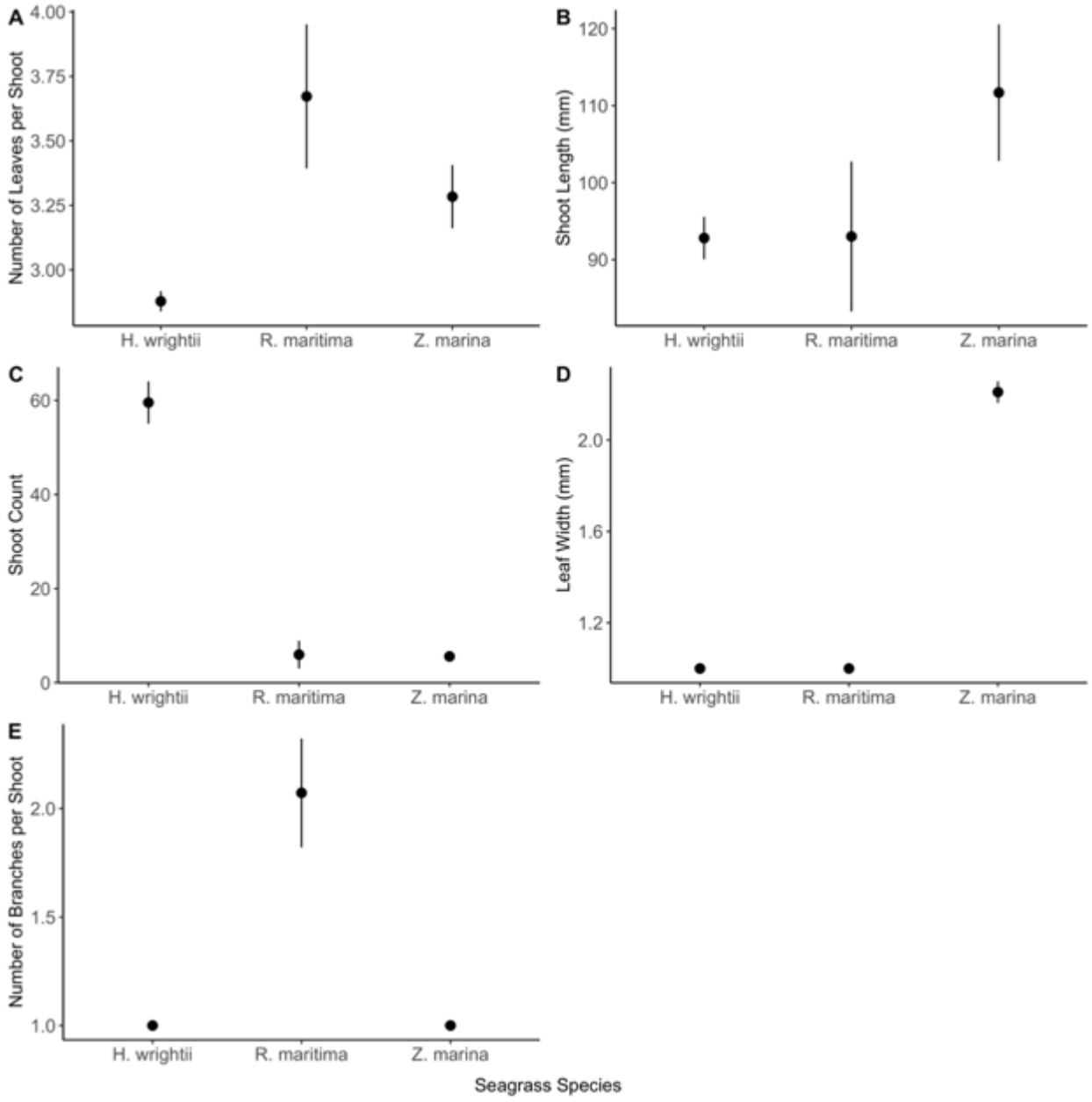

Figure S3.26: Seagrass species plotted on the x-axis with (A) number of leaves per shoot, (B) shoot length in mm, (C) shoot count per 10 cm diameter core, (D) leaf width in mm, (E) and number of branches per shoot plotted on the y-axis. Means across all beds and sampling months are plotted with error bars denoting standard error.

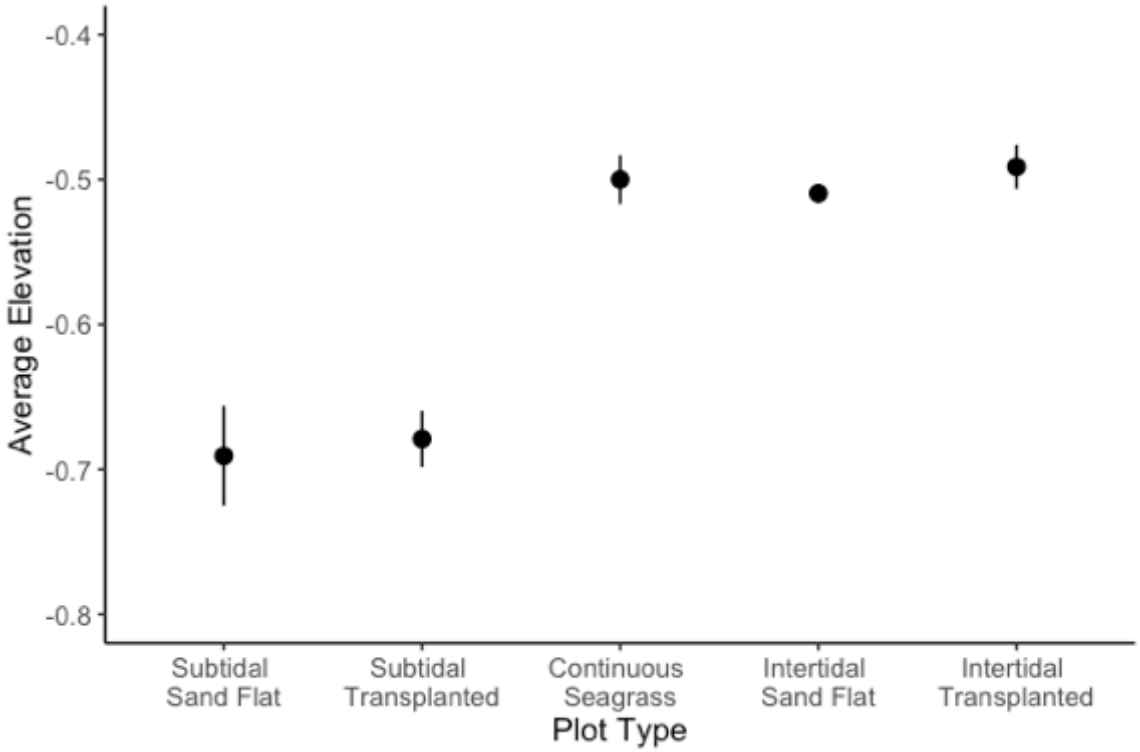

Figure S3.27: Plot type plotted on the x-axis and average elevation per plot plotted on the y-axis. Points denote average elevation and error bars denote standard error. Lower elevations indicate deeper plots.

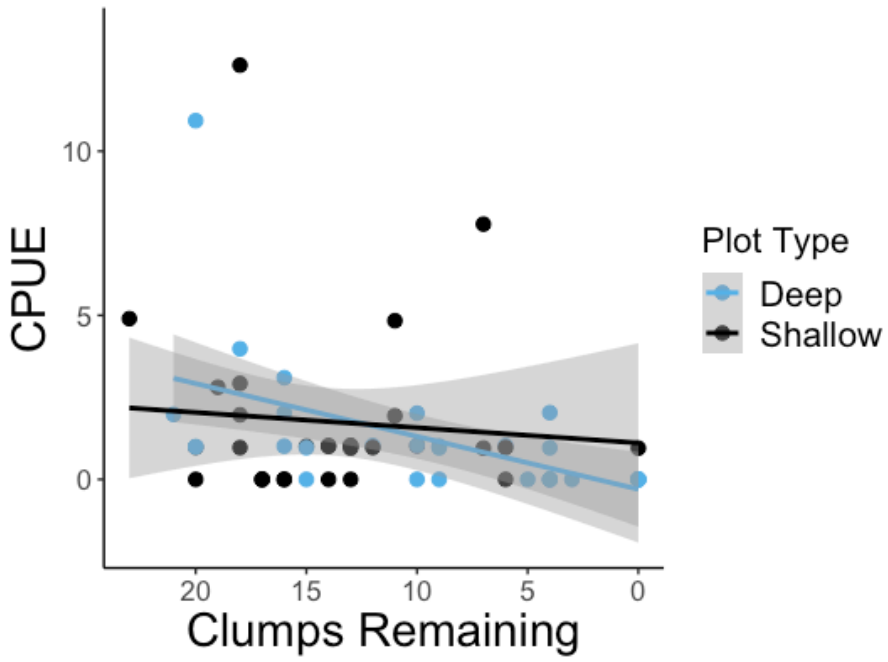

Figure S3.28: Number of clumps remaining in transplanted plots plotted on the x-axis with motile fauna CPUE from minnow traps plotted on the y-axis. Color denotes plot type with blue the deep, subtidal plots and black the shallow, intertidal plots. Lines are glm predictions with 95% confidence intervals.

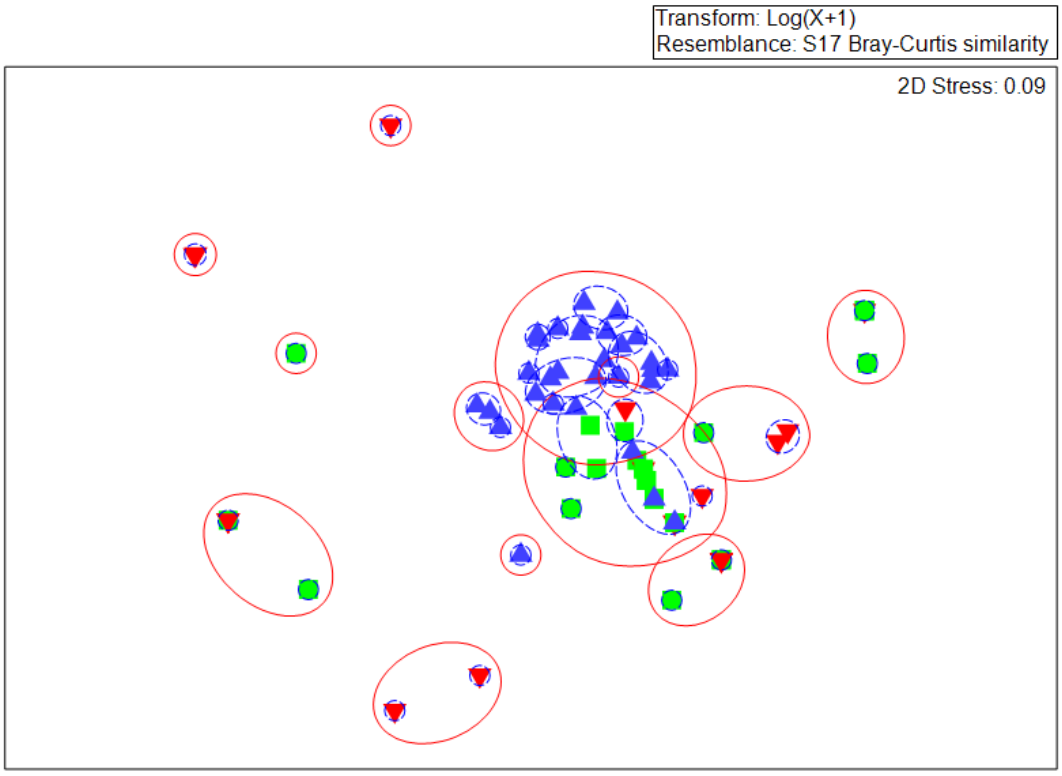

Figure S3.29: Nonmetric Multidimensional Scaling (NMDS) plot showing the minnow trap faunal communities of natural reference seagrass (blue triangle), transplanted seagrass (red triangle), and bare sand (green square) plots. 60 (red) and 80 (blue) percent similarities from cluster analysis are shown.

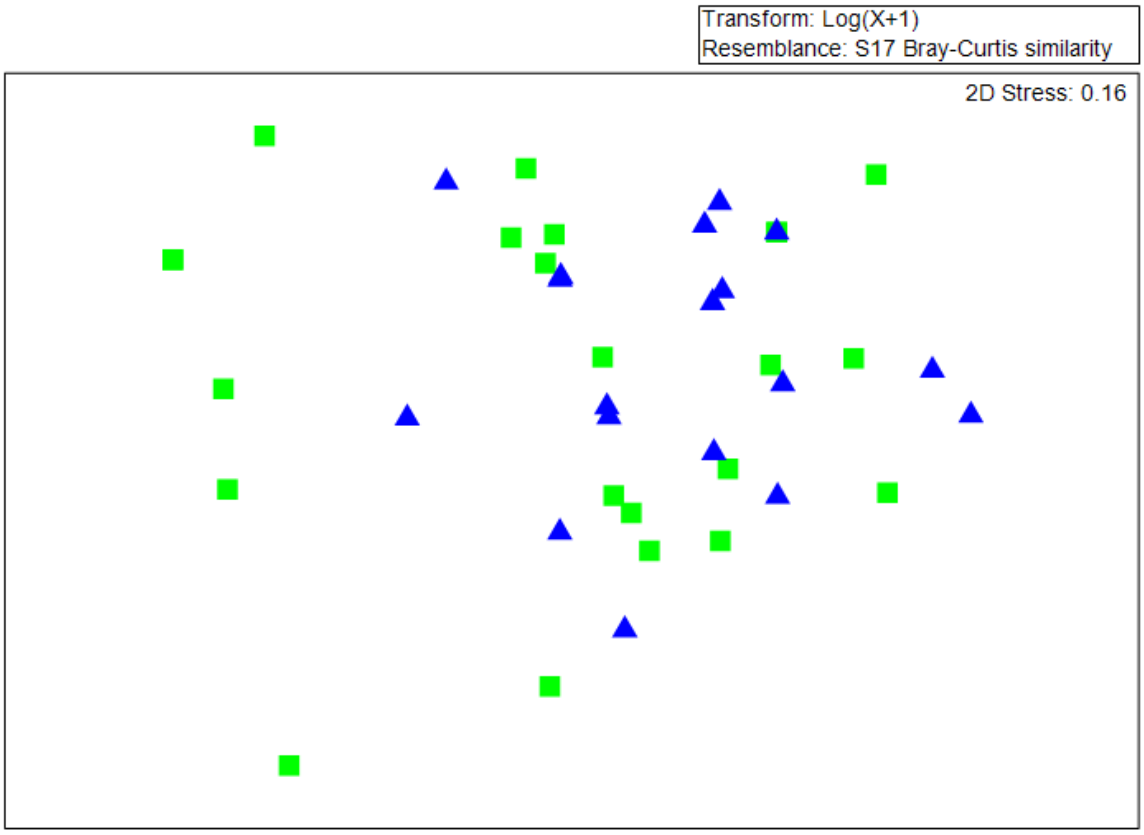

Figure S3.30: NMDS plot showing the SMURF faunal communities of intertidal bare sand (green square) and natural reference seagrass (blue triangle) plots.

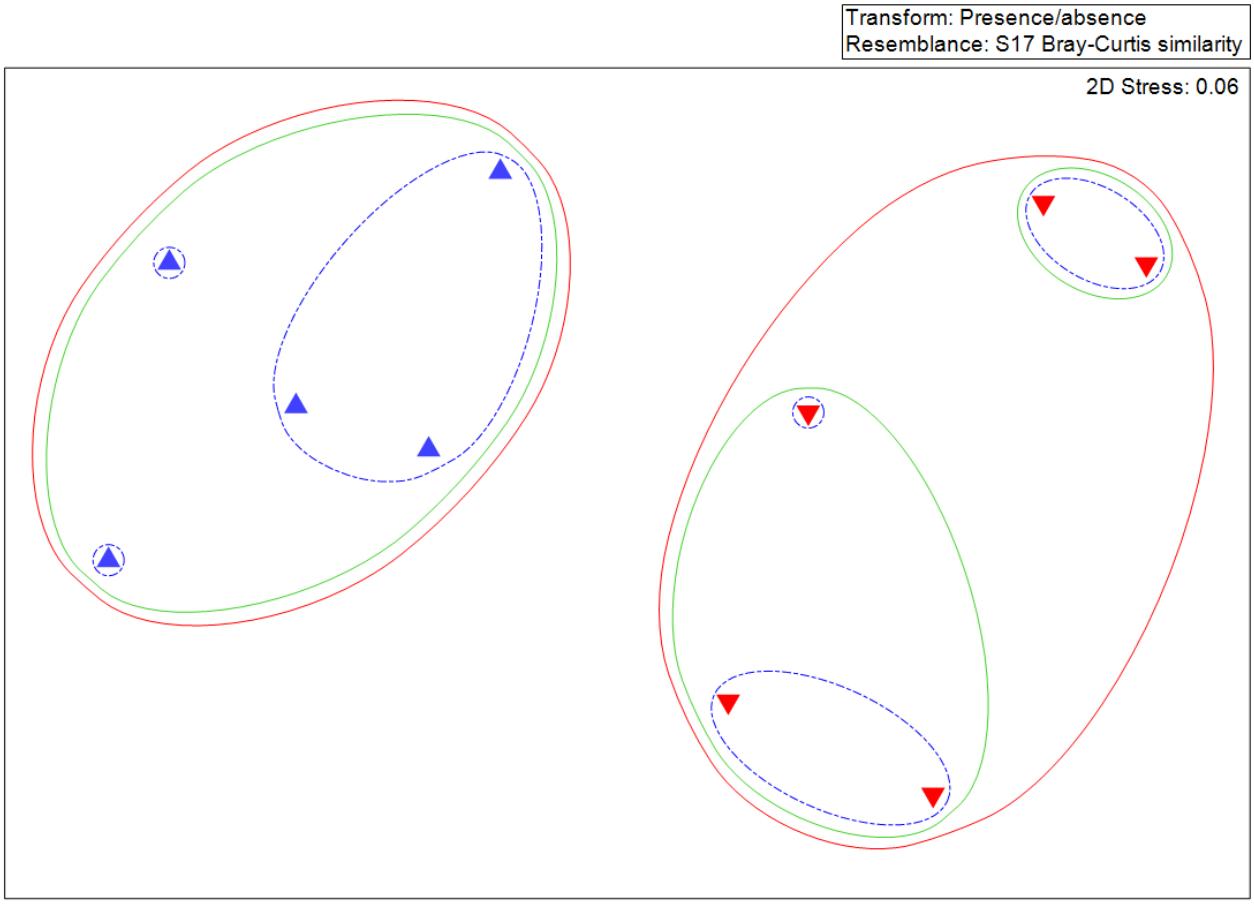

Figure S3.31: NMDS plot showing the SMURF (red triangle) and minnow trap (blue triangle) faunal communities within seagrass plots. 60 (red), 70 (green), and 80 (blue) percent similarities from cluster analysis are shown.

Supplemental Tables

Table S3.1: All fauna caught in our minnow traps across all treatment groups. Values here denote mean (standard error) across all sampled plots. Samples were standardized to 24 hours for each sampling event and totaled across dates for each plot

		Subtidal		Intertidal		
Common Name	**Scientific Name**	**Sand**	**Transplanted Seagrass**	**Sand**	**Transplanted Seagrass**	**Natural Reference Seagrass**
	Fish					
Sheepshead	*Archosargus probatocephalus*	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.2)
Silver Perch	*Bairdiella chrysoura*	0 (0)	0.32 (0.21)	0.16 (0.16)	0 (0)	0 (0)
Black Sea Bass	*Centropristis striata*	0 (0)	0 (0)	0 (0)	0 (0)	0.19 (0.19)
Spottail Pinfish	*Diplodus holbrookii*	0 (0)	0 (0)	0 (0)	0 (0)	2.41 (0.75)
Mummichog	*Fundulus heteroclitus*	0 (0)	0 (0)	0.16 (0.11)	0.38 (0.38)	1.99 (0.71)
Mojarra	*Gerreidae*	0.21 (0.21)	0 (0)	0 (0)	0.19 (0.19)	0 (0)
Feather Blenny	*Hypsoblennius hentz*	0.19 (0.19)	0.17 (0.17)	0.17 (0.17)	0.19 (0.19)	1.22 (0.38)
Pinfish	*Lagodon rhomboides*	4.09 (0.71)	6.05 (2.03)	12.6 (3.43)	7.2 (4.6)	98.34 (8.35)
Mutton Snapper	*Lutjanus analis*	0 (0)	0 (0)	0 (0)	0 (0)	0.19 (0.19)
Gray Snapper	*Lutjanus griseus*	0 (0)	0 (0)	0 (0)	0 (0)	0.77 (0.56)
Lane Snapper	*Lutjanus synagris*	0.2 (0.2)	0 (0)	0 (0)	0 (0)	0.4 (0.24)
Gag Grouper	*Mycteroperca microlepis*	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.2)
Pigfish	*Orthopristis chrysoptera*	1.17 (0.57)	0.82 (0.53)	0.66 (0.48)	0 (0)	7.75 (1.35)
Gulf Flounder	*Paralichthys albigutta*	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.2)
Planehead Filefish	*Stephanolepis hispidus*	0.41 (0.41)	0.5 (0.34)	0.16 (0.16)	0.21 (0.21)	3.23 (1.16)
Sea Robin	*Triglidae*	0 (0)	0.17 (0.17)	0 (0)	0 (0)	0 (0)
	Crab					
Blue Crab	*Callinectes sapidus*	1.16 (0.94)	0.65 (0.21)	0.82 (0.3)	0.97 (0.61)	3.17 (0.58)
Stone Crab	*Menippe mercenaria*	0 (0)	0.16 (0.16)	0.16 (0.16)	0 (0)	0 (0)
Swimming Crab	*Portunidae* spp.	0 (0)	0.17 (0.17)	0 (0)	0 (0)	0.41 (0.41)
Blotched Swimming Crab	*Portunus spinimanus*	0.8 (0.367)	0.67 (0.34)	0.33 (0.21)	0.6 (0.4)	1.38 (0.86)

Mud Crab	*Panopeidae*	0.2 (0.2)	0.49 (0.33)	0.16 (0.16)	0.4 (0.25)	1.21 (0.74)
	Shrimp					
Snapping Shrimp	*Alpheidae*	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.2)
Grass Shrimp	*Palaemonetes*	1 (0.45)	1.99 (1.23)	3.09 (2.14)	0.78 (0.78)	1.72 (1.72)
Penaeid Shrimp	*Penaeidae*	1.01 (0.56)	0.33 (0.21)	0.16 (0.16)	0.39 (0.24)	1.18 (0.19)

Table S3.2: All fauna caught in our SMURF sampling. Values denote average (standard error) across all sampled plots. Samples were standardized to 24 hours for each sampling event and totaled across dates for each plot.

Common Name	*Scientific Name*	Subtidal	Intertidal	Natural Reference Seagrass
	Fish			
Sheepshead	*Archosargus probatocephalus*	0 (0)	0 (0)	0.2 (0.2)
Skilletfish	*Gobiesox strumosus*	1.2 (0.49)	1.4 (0.4)	0.4 (0.245)
Slippery Dick	*Halichoeres bivittatus*	0.2 (0.2)	0 (0)	0 (0)
Crested Blenny	*Hypleurochilus geminatus*	7.2 (1.068)	2.6 (0.927)	1.6 (0.748)
Pinfish	*Lagodon rhomboides*	0.6 (0.4)	0.2 (0.2)	0.8 (0.374)
Snapper	*Lutjanus*	0 (0)	0 (0)	0 (0)
Gray Snapper	*Lutjanus griseus*	0.2 (0.2)	0 (0)	0.2 (0.2)
Oyster Toadfish	*Opsanus tau*	0.2 (0.2)	0.6 (0.245)	0.2 (0.2)
Planehead Filefish	*Stephanolepis hispidus*	0 (0)	0 (0)	0.4 (0.245)
	Crab			
Blue Crab	*Callinectes sapidus*	1.4 (0.4)	1.6 (0.510)	1.8 (0.583)
Say Mud Crab	*Dyspanopeus sayi*	5.6 (0.927)	3.8 (1.158)	9.2 (1.934)
Common Spider Crab	*Libinia emarginata*	0.2 (0.2)	0 (0)	0.2 (0.2)
Stone Crab	*Menippe mercenaria*	0.2 (0.2)	0.4 (0.245)	0 (0)
Atlantic Mud Crab	*Panopeus herbstii*	2.4 (1.03)	5 (1.225)	0.2 (0.2)
Blotched Swimming Crab	*Portunus spinimanus*	2.8 (1.02)	3.8 (1.715)	2 (0.316)
Harris Mud Crab	*Rhithropanopeus harrisii*	1 (0.548)	0.2 (0.2)	3.2 (0.860)
	Shrimp			
Snapping Shrimp	*Alpheidae*	0.8 (0.374)	1 (0.316)	0 (0)
Grass Shrimp	*Palaemonetes*	369 (64.908)	467 (41.057)	323.8 (15.615)

Table S3.3: All lengths/widths of fauna caught in our SMURF sampling. Values denote average length (standard error) across all sampled plots. Fish and shrimp measurements indicate total length, crab measurements indicate carapace width all in millimeters. Note: we do not include the length of the unidentified fish (SI Table 4) in this table as the fish had disintegrated and length was unable to be measured.

Common Name	Scientific Name	Subtidal	Intertidal	Natural Reference Seagrass
	Fish			
Sheepshead	*Archosargus probatocephalus*	0 (0)	0 (0)	38 (0)
Skilletfish	*Gobiesox strumosus*	15.2 (2.08)	17 (1.1)	12.5 (0.5)
Slippery Dick	*Halichoeres bivittatus*	70 (0)	0 (0)	0 (0)
Crested Blenny	*Hypleurochilus geminatus*	20.38 (1.08)	21.63 (3.11)	18.33 (3.92)
Pinfish	*Lagodon rhomboides*	41.67 (4.91)	49 (0)	45 (4.49)
Snapper	*Lutjanus*	0 (0)	0 (0)	0 (0)
Gray Snapper	*Lutjanus griseus*	55 (0)	0 (0)	40 (0)
Oyster Toadfish	*Opsanus tau*	14 (0)	39 (19.5)	79 (0)
Planehead Filefish	*Stephanolepis hispidus*	0 (0)	0 (0)	34 (8)
	Crab			
Blue Crab	*Callinectes sapidus*	39.43 (3.88)	29.36 (6.54)	33.26 (5.06)
Say Mud Crab	*Dyspanopeus sayi*	9.92 (0.45)	13.17 (1.48)	10.10 (0.55)
Common Spider Crab	*Libinia emarginata*	25 (0)	0 (0)	23 (0)
Stone Crab	*Menippe mercenaria*	8 (0)	8 (1)	0 (0)
Atlantic Mud Crab	*Panopeus herbstii*	18.29 (1.34)	18.07 (1.49)	21 (0)
Blotched Swimming Crab	*Portunus spinimanus*	25.11 (2.35)	24.48 (2.46)	33.61 (3.66)
Harris Mud Crab	*Rhithropanopeus harrisii*	11.1 (1.95)	8 (0)	8.24 (0.37)
	Shrimp			
Snapping Shrimp	*Alpheidae*	22 (1.53)	26.75 (1.03)	0 (0)
Grass Shrimp	*Palaemonetes*	23.36 (0.57)	24.48 (0.62)	24.03 (0.75)

Table S3.4: Response variable, model type, transformation, and family (for generalized linear mixed models) to determine the relationship between the fixed effect of 2019 sampling month and the random effect of seagrass site on each seagrass composition and morphology metric (response variable). LMM indicated linear mixed model and GLMM indicated generalized linear mixed model.

Response Variable	**Model Type**	**Transformation**	**Family**
Canopy Height	LMM	-	-
H. wrightii Shoot Length	GLMM	-	Gamma
R. maritima Shoot Length	GLMM	-	Gamma
Z. marina Shoot Length	LMM	-	-
H. wrightii Aboveground Biomass	LMM	-	-
R. maritima Aboveground Biomass	GLMM	-	Gamma
Z. marina Aboveground Biomass	LMM	-	-
H. wrightii + *R. maritima* Aboveground Biomass	LMM	-	-
Z. marina Leaf Width	LMM	-	-
H. wrightii Leaves per Shoot	GLMM	-	Gamma
R. maritima Leaves per Shoot	LMM	-	-
Z. marina Leaves per Shoot	LMM	-	-
R. maritima Branch Number per Shoot	GLMM	-	Gamma
Z. marina Branch Number per Shoot	LMM	-	-
Percent Dominance of *H. wrightii* + *R. maritima* by Biomass	LMM	Arcsine square root	-
H. wrightii Shoot Density	GLMM	-	Negative Binomial
R. maritima Shoot Density	GLMM	-	Negative Binomial
Z. marina Shoot Density	GLMM	-	Negative Binomial
Total Shoot Density	GLMM	-	Negative Binomial
H. wrightii + *R. maritima* Percent Cover	GLMM	Low (0) or High (1)	Binomial
Z. marina Percent Cover	GLMM	Low (0) or High (1)	Binomial

Table S3.5: Response variable, model type, transformation, and family (for generalized linear models) to determine the relationship between the fixed effect of 2020 depth relative to LMSL on each seagrass composition and morphology metric (response variable). LM indicated linear model and GLM indicated generalized linear model.

Response Variable	Model Type	Transformation	Family
Canopy Height	LM	-	-
H. wrightii Shoot Length	LM	-	-
R. maritima Shoot Length	LM	-	-
Z. marina Shoot Length	LM	-	-
H. wrightii Aboveground Biomass	LM	-	-
R. maritima Aboveground Biomass	GLM	-	Quasipoisson
Z. marina Aboveground Biomass	LM	-	-
H. wrightii + *R. maritima* Aboveground Biomass	LM	-	-
Z. marina Leaf Width	LM	-	-
H. wrightii Leaves per Shoot	LM	-	-
R. maritima Leaves per Shoot	LM	-	-
Z. marina Leaves per Shoot	LM	-	-
R. maritima Branch Number per Shoot	LM	-	-
Percent Dominance of *H. wrightii* + *R. maritima* by Biomass	LM	Arcsine square root	-
H. wrightii Shoot Density	GLM	-	Negative Binomial
R. maritima Shoot Density	GLM	-	Negative Binomial
Z. marina Shoot Density	GLM	-	Negative Binomial
Total Shoot Density	GLM	-	Negative Binomial
H. wrightii + *R. maritima* Percent Cover	GLMM	Low (0) or High (1)	Binomial
Z. marina Percent Cover	GLMM	Low (0) or High (1)	Binomial
Epibiont Load	LM	-	-

Table S3.6: Number of seagrass beds surveyed in 2019 with percent cover of *Z. marina* and *H. wrightii* for each cover category.

	0%	**0-25%**	**25-50%**	**50-75%**	**75-100%**
Z. marina	8	26	1	1	0
H. wrightii	0	10	15	11	0

Table S3.7: Results from linear mixed effect models with the random effect of site in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Response Variable	**Fixed Effect**	**Sum Sq**	**Mean Sq**	**Num DF**	**Den DF**	**F Value**	**Pr(>F)**
Canopy Height	Month	68912	12782	5	23.205	8.4544	**<0.0001**
	Percent H/R Dominance	5633.3	5633.3	1	33.969	1.4252	0.2408
Z. marina Shoot Length	Month	6662.8	1665.7	4	15.194	2.4356	*0.0920*
H. wrightii Aboveground Biomass	Month	1.0952	0.21904	5	15.632	6.1247	**0.0025**
Z. marina Aboveground Biomass	Month	0.40484	0.080968	5	17.359	8.4797	**0.0003**
H. wrightii and *R. maritima* Aboveground Biomass	Month	1.7346	0.34692	5	18.962	7.2004	**0.0006**
Z. marina Leaf Width	Month	0.44578	0.11145	4	3.9041	15.879	**0.0109**
R. maritima Number of Leaves per Shoot	Month	3.4294	1.1431	3	3.9632	0.89	0.5195
Z. marina Number of Leaves per Shoot	Month	2.8059	0.70147	4	10.947	3.3733	**0.0496**
Z. marina Number of Branches per Shoot	Month	0.2993	0.074825	4	16.381	3.9216	**0.0204**
Percent H/R Dominance	Month	0.63161	0.12632	5	23.75	5.3309	**0.002003**

Table S3.8: Tukey's Post-Hoc test to test for differences between months on the percent dominance of *H. wrightii* and *R. maritima* over *Z. marina* by aboveground biomass in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.01759	0.10035	0.175	1
June - April	0.13559	0.09869	1.374	0.7420
July - April	0.18126	0.09973	1.817	0.4533
August - April	0.27228	0.09618	2.831	*0.0526*
September - April	0.41684	0.09822	4.244	**<0.001**
June - May	0.11800	0.10469	1.127	0.8697
July - May	0.16366	0.10491	1.560	0.6241
August - May	0.25469	0.10262	2.482	0.1290
September - May	0.39925	0.09497	4.204	**<0.001**
July - June	0.04566	0.10503	0.435	0.9980
August - June	0.13669	0.10280	1.330	0.7678
September - June	0.28125	0.10089	2.788	*0.0593*
August - July	0.09102	0.09671	0.941	0.9355
September - July	0.23558	0.10283	2.291	0.1970
September - August	0.14456	0.09594	1.507	0.6589

Table S3.9: Results from generalized linear mixed effect models with the random effect of site in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Response Variable	Fixed Effect	Chisq	DF	Pr(>Chisq)
H. wrightii Percent Cover	Month	16.992	5	**0.0045**
Z. marina Percent Cover	Month	6.0526	5	0.3011
H. wrightii Shoot Length	Month	40.676	5	**<0.0001**
R. maritima Shoot Length	Month	194.57	3	**<0.0001**
R. maritima Aboveground Biomass	Month	169.68	3	**<0.0001**
H. wrightii Number of Leaves per Shoot	Month	15.9	5	**0.0071**
H. wrightii Shoot Density	Month	5.5519	5	0.3523
R. maritima Shoot Density	Month	2.3258	3	**<0.0001**
Z. marina Shoot Density	Month	32.685	5	**<0.0001**
Total Shoot Density	Month	23.531	5	**0.0003**
R. maritima Number of Branches per Shoot	Month	190.43	3	**<0.0001**

Table S3.10: Tukey's Post-Hoc test to test for differences between months on the *H. wrightii* aboveground biomass in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.11658	0.12263	0.951	0.9328
June - April	0.3708	0.12074	3.071	**0.0259**
July - April	0.59197	0.12192	4.855	**<0.001**
August - April	0.25855	0.11782	2.195	0.2396
September - April	0.08946	0.12025	0.744	0.9763
June - May	0.25422	0.12764	1.992	0.3462
July - May	0.47538	0.12789	3.717	**0.0027**
August - May	0.14197	0.12532	1.133	0.8673
September - May	-0.02713	0.11632	-0.233	0.9999
July - June	0.22117	0.12803	1.728	0.5124
August - June	-0.11225	0.12552	-0.894	0.9478
September - June	-0.28134	0.12325	-2.283	0.2004
August - July	-0.33342	0.11839	-2.816	*0.0546*
September - July	-0.50251	0.12556	-4.002	**<0.001**
September - August	-0.16909	0.11754	-1.439	0.7025

Table S3.11: Tukey's Post-Hoc test to test for differences between months on the *H. wrightii* and *R. maritima* combined aboveground biomass in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.14288	0.14115	1.012	0.9137
June - April	0.60159	0.13922	4.321	**<0.001**
July - April	0.6495	0.14041	4.626	**<0.001**
August - April	0.30145	0.13611	2.215	0.2301
September - April	0.11057	0.13877	0.797	0.9680
June - May	0.45871	0.14636	3.134	**0.0213**
July - May	0.50662	0.14662	3.455	**0.0073**
August - May	0.15857	0.14407	1.101	0.8809
September - May	-0.03231	0.13435	-0.24	0.9999
July - June	0.04791	0.14677	0.326	0.9995
August - June	-0.30014	0.14426	-2.08	0.2968
September - June	-0.49102	0.14177	-3.463	**0.0070**
August - July	-0.34805	0.13663	-2.547	0.1104
September - July	-0.53893	0.14431	-3.735	**0.0026**
September - August	-0.19089	0.13581	-1.405	0.7231

Table S3.12: Tukey's Post-Hoc test to test for differences between months on *R. maritima* aboveground biomass in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
June - May	0.72550	3.09E-04	2345	**<0.001**
July - May	-0.34030	8.30E-06	-40993	**<0.001**
August - May	-0.42730	8.30E-06	-51475	**<0.001**
July - June	-1.06600	3.09E-04	-3444	**<0.001**
August - June	-1.15300	3.09E-04	-3726	**<0.001**
August - July	-0.08701	1.01E-05	-8654	**<0.001**

Table S3.13: Tukey's Post-Hoc test to test for differences between months on the *Z. marina* aboveground biomass in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.08974	0.07105	1.263	0.8040
June - April	-0.04701	0.06667	-0.705	0.9813
July - April	-0.03562	0.07548	-0.472	0.9971
August - April	-0.20327	0.07032	-2.891	**0.0444**
September - April	-0.29921	0.067	-4.466	**<0.001**
June - May	-0.13675	0.07274	-1.88	0.4128
July - May	-0.12536	0.07753	-1.617	0.5856
August - May	-0.29301	0.07423	-3.948	**0.0011**
September - May	-0.38895	0.06722	-5.786	**<0.001**
July - June	0.01139	0.07513	0.152	1.0000
August - June	-0.15626	0.07153	-2.185	0.2435
September - June	-0.2522	0.06678	-3.777	**0.0023**
August - July	-0.16765	0.07634	-2.196	0.2383
September - July	-0.26359	0.07382	-3.571	**0.0047**
September - August	-0.09594	0.06524	-1.471	0.6816

Table S3.14: Tukey's Post-Hoc test to test for differences between months on the *H. wrightii* percent cover in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.50641	0.33741	1.501	0.6618
June - April	1.28196	0.3285	3.902	**0.0013**
July - April	1.28396	0.3342	3.842	**0.0016**
August - April	1.51436	0.31622	4.789	**<0.001**
September - April	1.22592	0.32445	3.778	**0.0022**
June - May	0.77555	0.35966	2.156	0.2571
July - May	0.77755	0.36094	2.154	0.2581
August - May	1.00795	0.34687	2.906	**0.0423**
September - May	0.71951	0.31352	2.295	0.1948
July - June	0.002	0.36148	0.006	1
August - June	0.2324	0.34808	0.668	0.9853
September - June	-0.05604	0.34035	-0.165	1.0000
August - July	0.2304	0.32042	0.719	0.9795
September - July	-0.05804	0.34802	0.167	1.0000
September - August	-0.28844	0.31535	-0.915	0.9424

Table S3.15: Tukey's Post-Hoc test to test for differences between months on the shoot density of *Z. marina* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.003855	0.287519	0.013	1
June - April	-0.696014	0.356946	-1.950	0.32393
July - April	-0.223868	0.368709	-0.607	0.98795
August - April	-1.642133	0.465188	-3.530	**0.0042**
September - April	-18.978977	3.785077	-5.014	**<0.001**
June - May	-0.699869	0.324551	-2.156	0.21886
July - May	-0.227723	0.312090	-0.730	0.97267
August - May	-1.645987	0.456165	-3.608	**0.0032**
September - May	-18.982832	3.799106	-4.997	**<0.001**
July - June	0.472146	0.367570	1.285	0.75773
August - June	-0.946119	0.434417	-2.178	0.20931
September - June	-18.282963	3.807240	-4.802	**<0.001**
August - July	-1.418265	0.495080	-2.865	**0.0376**
September - July	-18.755109	3.806350	-4.927	**<0.001**
September - August	-17.336845	3.824507	-4.533	**<0.001**

Table S3.16: Tukey's Post-Hoc test to test for differences between months on the shoot density of *R. maritima* in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	18.5057	13972.6774	0.001	1
June - April	26.259	13972.6774	0.002	1
July - April	22.9471	13972.6774	0.002	1
August - April	22.074	13972.6774	0.002	1
September - April	-2.9773	68317.0782	0	1
June - May	7.7533	1.7189	4.511	**<0.001**
July - May	4.4414	1.459	3.044	**0.0156**
August - May	3.5683	1.3781	2.589	*0.0614*
September - May	-21.483	66872.9202	0	1
July - June	-3.3119	1.0624	-3.117	**0.0126**
August - June	-4.185	1.1459	-3.652	**0.0019**
September - June	-29.2363	66872.9202	0	1
August - July	-0.8731	0.5494	-1.589	0.4998
September - July	-25.9244	66872.9202	0	1
September - August	-25.0513	66872.9202	0	1

Table S3.17: Tukey's Post-Hoc test to test for differences between months on the shoot density of all seagrass species combined in 2019. Values significant at the 0.1 level are italicized, values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.14396	0.08183	1.759	0.4904
June - April	0.28072	0.08176	3.433	**0.0078**
July - April	-0.14306	0.0909	-1.574	0.6142
August - April	-0.11672	0.08286	-1.409	0.7202
September - April	-0.35475	0.08681	-4.087	**<0.001**
June - May	0.13676	0.08737	1.565	0.6197
July - May	-0.28702	0.09489	-3.025	**0.0296**
August - Ma	-0.26068	0.08831	-2.952	**0.0371**
September - May	-0.49871	0.08423	-5.921	**<0.001**
July - June	-0.42379	0.09438	-4.49	**<0.001**
August - June	-0.39744	0.08886	-4.473	**<0.001**
September - June	-0.63547	0.0907	-7.006	**<0.001**
August - July	0.02634	0.09024	0.292	0.9997
September - July	-0.21168	0.09991	-2.119	0.2757
September - August	-0.23803	0.08842	-2.692	*0.0762*

Table S3.18: Tukey's Post-Hoc test to test for differences between months on the canopy height of the seagrass beds sampled in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	26.531	26.312	1.008	0.9149
June - April	124.894	25.879	4.826	**<0.001**
July - April	121.319	26.149	4.639	**<0.001**
August - April	117.513	25.221	4.659	**<0.001**
September - April	73.387	25.757	2.849	**0.0498**
June - May	98.362	27.445	3.584	**0.0046**
July - May	94.788	27.504	3.446	**0.0074**
August - May	90.982	26.906	3.381	**0.0093**
September - May	46.855	24.905	1.881	0.4126
July - June	-3.575	27.535	-0.13	1.0000
August - June	-7.38	26.954	-0.274	0.9998
September - June	-51.507	26.453	-1.947	0.3725
August - July	-3.806	25.36	-0.15	1.0000
September - July	-47.932	26.96	-1.778	0.4791
September - August	-44.127	25.161	-1.754	0.4950

Table S3.19: Tukey's Post-Hoc test to test for differences between months on the leaf width of *Z. marina* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.13998	0.06986	2.004	0.2592
June - April	0.29259	0.07646	3.827	**0.0012**
July - April	-0.29445	0.08336	-3.532	**0.0036**
August - April	-0.15943	0.08813	-1.809	0.3625
June - May	0.15261	0.08092	1.886	0.3195
July - May	-0.43443	0.08822	-4.924	**<0.001**
August - May	-0.2994	0.0898	-3.334	**0.0075**
July - June	-0.58704	0.09039	-6.495	**<0.001**
August - June	-0.45202	0.0864	-5.232	**<0.001**
August - July	0.13503	0.10706	1.261	0.7100

Table S20: Tukey's Post-Hoc test to test for differences between months on the number of leaves per shoot of *Z. marina* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	-0.42026	0.32171	-1.306	0.6853
June - April	0.03532	0.33277	0.106	1
July - April	-0.63962	0.35313	-1.811	0.3647
August - April	-1.13385	0.38306	-2.96	**0.0253**
June - May	0.45558	0.33639	1.354	0.6550
July - May	-0.21937	0.3572	-0.614	0.9726
August - May	-0.71359	0.38387	-1.859	0.3376
July - June	-0.67495	0.35869	-1.882	0.3251
August - June	-1.16917	0.38087	-3.07	**0.0181**
August - July	-0.49423	0.41903	-1.179	0.7616

Table S3.21: Tukey's Post-Hoc test to test for differences between months on the number of branches per shoot of *Z. marina* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	-0.2783	0.08736	-3.186	**0.0124**
June - April	-0.2783	0.08736	-3.186	**0.0124**
July - April	-0.2783	0.09266	-3.004	**0.0223**
August - April	-0.2783	0.10090	-2.759	**0.0456**
June - May	9.78E-07	0.08736	0	1
July - May	-2.55E-06	0.09266	0	1
August - May	6.51E-06	0.10090	0	1
July - June	-3.53E-06	0.09266	0	1
August - June	5.53E-06	0.10090	0	1
August - July	9.06E-06	0.10550	0	1

Table S3.22: Tukey's Post-Hoc test to test for differences between months on the shoot length of *R. maritima* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
June - May	0.28370	0.2398	1.183	0.5846
July - May	0.23460	0.2398	0.978	0.7201
August - May	-0.59550	0.2398	-2.483	**0.0459**
July - June	-0.04906	0.1517	-0.323	0.9854
August - June	-0.87920	0.1517	-5.797	**<0.001**
August - July	-0.83010	5.11E-05	-16258.609	**<0.001**

Table S3.23: Tukey's Post-Hoc test to test for differences between months on number of branches per shoot of *R. maritima* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
June - May	0.0256666	0.3258176	0.079	0.9998
July - May	0.3693133	0.3258176	1.133	0.6180
August - May	-0.5245045	0.3258176	-1.61	0.3172
July - June	0.3436468	0.2060652	1.668	0.2868
August - June	-0.5501711	0.2060652	-2.67	**0.0273**
August - July	-0.8938179	0.0000742	-12045.807	**<0.001**

Table S3.24: Tukey's Post-Hoc test to test for differences between months on the shoot length of *H. wrightii* in 2019. Values significant at the 0.1 level are italicized and values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.21112	0.07708	2.739	*0.0667*
June - April	0.2726	0.07898	3.452	**0.0073**
July - April	0.62275	0.07494	8.31	**<0.001**
August - April	0.44865	0.07216	6.218	**<0.001**
September - April	0.30391	0.07337	4.142	**<0.001**
June - May	0.06147	0.08997	0.683	0.9836
July - May	0.41163	0.08185	5.029	**<0.001**
August - May	0.23752	0.07898	3.007	**0.0311**
September - May	0.09279	0.071	1.307	0.7789
July - June	0.35016	0.08495	4.122	**<0.001**
August - June	0.17605	0.0855	2.059	0.3061
September - June	0.03132	0.08334	0.376	0.9990
August - July	-0.17411	0.07339	-2.372	0.1640
September - July	-0.31884	0.0782	-4.077	**<0.001**
September - August	-0.14473	0.07104	-2.037	0.3181

Table S3.25: Tukey's Post-Hoc test to test for differences between months on the number of leaves per shoot of *H. wrightii* in 2019. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Standard Error	Z value	Pr(>|z|)
May - April	0.034141	0.047529	0.718	0.9790
June - April	0.185322	0.045072	4.112	**<0.001**
July - April	0.108773	0.050755	2.143	0.2602
August - April	0.106345	0.043794	2.428	0.1433
September - April	0.135931	0.044211	3.075	**0.0249**
June - May	0.151181	0.052445	2.883	**0.0446**
July - May	0.074632	0.061363	1.216	0.8248
August - May	0.072204	0.051141	1.412	0.7141
September - May	0.10179	0.045396	2.242	0.2139
July - June	-0.076548	0.049926	-1.533	0.6365
August - June	-0.078977	0.046479	-1.699	0.5256
September - June	-0.049391	0.046103	-1.071	0.8898
August - July	-0.002429	0.046528	-0.052	1
September - July	0.027158	0.052218	0.52	0.9952
September - August	0.029586	0.043863	0.675	0.9842

Table S3.26: Results from ANOVA on morphology metrics between seagrass species in 2019. Values significant at the 0.05 level are bolded.

Response Variable	Fixed Effect	DF	F	Pr(>F)
Number of Leaves per Shoot	Seagrass Species	2, 65	53.18	**<0.001**
Shoot Length	Seagrass Species	2, 65	7.189	**0.0015**
Shoot Density	Seagrass Species	2, 105	257.3	**<0.001**
Leaf Width	Seagrass Species	2, 65	123.1	**<0.001**
Branch Number per Shoot	Seagrass Species	2, 65	117.9	**<0.001**

Table S3.27: Tukey's Post-Hoc test to test for differences between seagrass species on the measured morphology values of the three seagrass species in 2019. Values significant at the 0.05 level are bolded.

Response Variable	Contrast	Estimate	Standard Error	t value	Pr(>|t|)
Number of Leaves per Shoot	*H. wrightii* - *Z. marina*	-1.0243	0.1682	-6.089	**<0.001**
	R. maritima - *Z. marina*	1.1359	0.2371	4.791	**<0.001**
	R. maritima - *H. wrightii*	2.1602	0.2222	9.721	**<0.001**
Shoot Length	*H. wrightii* - *Z. marina*	-1.109	0.07379	-15.03	**<0.001**
	R. maritima - *Z. marina*	-1.109	0.10400	-10.66	**<0.001**
	R. maritima - *H. wrightii*	2.44E-15	0.09747	0	1
Shoot Density	*H. wrightii* - *Z. marina*	52.6343	2.6755	19.67	**<0.001**
	R. maritima - *Z. marina*	0.1343	2.6755	0.05	0.9990
	R. maritima - *H. wrightii*	-52.500	2.6755	-19.62	**<0.001**
Leaf Width	*H. wrightii* - *Z. marina*	-1.109	0.07379	-15.03	**<0.001**
	R. maritima - *Z. marina*	-1.109	0.10400	-10.66	**<0.001**
	R. maritima - *H. wrightii*	2.44E-15	0.09747	0	1
Branch Number per Shoot	*H. wrightii* - *Z. marina*	-0.063	0.11502	-0.55	0.8450
	R. maritima - *Z. marina*	2.19396	0.16211	13.53	**<0.001**
	R. maritima - *H. wrightii*	2.25722	0.15194	14.86	**<0.001**

Table S3.28: Number of seagrass beds surveyed in 2020 with percent cover of *Z. marina* and *H. wrightii* for each cover category.

	0%	0-25%	25-50%	50-75%	75-100%
Z. marina	6	6	4	2	0
H. wrightii	1	0	8	9	0

Table S3.29: Results from linear models in 2020. Values significant at the 0.1 level are italicized and values significant at the 0.05 level are bolded.

Response Variable	Fixed Effect	DF	Sum Sq	Mean Sq	F Value	Pr(>F)
Canopy Height	Depth	1, 16	9691	9691.4	4.3705	*0.0529*
	Percent H/R Dominance	1, 16	15915	15915.2	8.704	**0.0094**
H. wrightii Shoot Length	Depth	1, 15	525.72	525.72	5.124	**0.0389**
R. maritima Shoot Length	Depth	1, 4	794.13	794.13	1.5506	0.2810
Z. marina Shoot Length	Depth	1, 13	779.1	779.12	0.643	0.4370
H. wrightii Aboveground Biomass	Depth	1, 16	0.01432	0.014315	0.3795	0.5465
Z. marina Aboveground Biomass	Depth	1, 16	0.0018	0.001802	0.0263	0.8731
H. wrightii and *R. maritima* Aboveground Biomass	Depth	1, 16	0.04458	0.044575	0.9724	0.3388
Z. marina Leaf Width	Depth	1, 13	0.03246	0.032456	0.9819	0.3398
H. wrightii Number of Leaves per Shoot	Depth	1, 15	0.03896	0.038956	1.53	0.2351
R. maritima Number of Leaves per Shoot	Depth	1, 4	0.00743	0.00743	0.0127	0.9156
Z. marina Number of Leaves per Shoot	Depth	1, 13	0.19588	0.19588	0.8623	0.3700
R. maritima Number of Branches per Shoot	Depth	1, 4	0.54728	0.54728	1.6306	0.2707
Percent H/R Dominance	Depth	1, 16	0.00041	0.000407	0.0028	0.9582
Epibiont Load	Depth	1, 16	0.18362	0.18363	1.31	0.2692

Table S3.30: Results from generalized linear models in 2020. Values significant at the 0.05 level are bolded.

Response Variable	Fixed Effect	DF	F	Pr(>F)
R. maritima Aboveground Biomass	Depth	1, 16	1.0875	0.3125
H. wrightii Shoot Density	Depth	1, 16	11.41	**0.0007**
R. maritima Shoot Density	Depth	1, 16	0.7452	0.4008
Z. marina Shoot Density	Depth	1, 16	0.1324	0.716
Total Shoot Density	Depth	1, 16	0.3633	0.5467

Table S3.31: Results from generalized linear models in 2020.

Response Variable	Fixed Effect	DF	Pr(>Chi)
H. wrightii Percent Cover	Depth	1, 16	0.7323
Z. marina Percent Cover	Depth	1, 16	0.6591

Table S3.32: Results from ANOVA on morphology metrics between seagrass species in 2020. Values significant at the 0.1 level are italicized and values significant at the 0.05 level are bolded.

Response Variable	Fixed Effect	DF	F	Pr(>F)
Number of Leaves per Shoot	Seagrass Species	2, 35	9.332	**0.0006**
Shoot Length	Seagrass Species	2, 35	2.628	*0.0865*
Shoot Density	Seagrass Species	2, 51	96.35	**<0.001**
Leaf Width	Seagrass Species	2, 35	503.1	**<0.001**
Branch Number per Shoot	Seagrass Species	2, 35	53.79	**<0.001**

Table S3.33: Tukey's Post-Hoc test to test for differences between seagrass species on the measured morphology values of the three seagrass species in 2020. Values significant at the 0.05 level are bolded.

Response Variable	Contrast	Estimate	Standard Error	t value	Pr(>|t|)
Number of Leaves per Shoot	*H. wrightii* - *Z. marina*	-0.4055	0.1456	-2.785	**0.0221**
	R. maritima - *Z. marina*	0.3885	0.1985	1.957	0.1358
	R. maritima - *H. wrightii*	0.794	0.1952	4.068	**<0.001**
Shoot Density	*H. wrightii* - *Z. marina*	53.9528	4.4723	12.064	**<0.001**
	R. maritima - *Z. marina*	0.3769	4.4723	0.084	0.9960
	R. maritima - *H. wrightii*	-53.576	4.4723	-11.979	**<0.001**
Leaf Width	*H. wrightii* - *Z. marina*	-1.210	0.04071	-29.72	**<0.001**
	R. maritima - *Z. marina*	-1.210	0.05551	-21.79	**<0.001**
	R. maritima - *H. wrightii*	-2.22E-16	0.05457	0	1
Branch Number per Shoot	*H. wrightii* - *Z. marina*	4.68E-17	0.08232	0	1
	R. maritima - *Z. marina*	1.072	0.11220	9.553	**<0.001**
	R. maritima - *H. wrightii*	1.072	0.11030	9.717	**<0.001**

Table S3.34: Results from ANOVA to test for differences in depth between intertidal and subtidal depth categories. Values significant at the 0.05 level are bolded.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Elevation Category	1	0.219483	0.219483	114.61	**<0.0001**
Residuals	25	0.047876	0.001915		

Table S3.35: Mean (standard error) of the depth relative to LMSL of all plot types in the manipulative field experiment

Plot Type	Depth (m)
Intertidal Transplanted Seagrass	0.39 (0.02)
Intertidal Natural Reference Seagrass	0.40 (0.02)
Intertidal Bare Sand	0.41 (0.01)
Subtidal Transplanted Seagrass	0.58 (0.02)
Subtidal Bare Sand	0.59 (0.03)

Table S3.36: Results from ANOVA to test for differences in depth within intertidal plot categories (natural reference seagrass, transplanted seagrass, bare sand).

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Habitat Category	2	0.0009123	0.00045615	0.5132	0.6102
Residuals	13	0.0115542	0.00088879		

Table S3.37: Statistical table of ANOVA results to test for differences in depth within subtidal plot categories (transplanted seagrass, bare sand).

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Habitat Category	1	0.000376	0.0003761	0.0966	0.7630
Residuals	9	0.035034	0.0038926		

Table 3.38: Statistical table of ANOVA results to test for differences in initial shoot length between subtidal and intertidal transplanted plots.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Depth Category	1	51.503	51.503	1.376	0.2745
Residuals	8	299.424	37.428		

Table S3.39: Results of linear mixed effect model to test for the effect of date, plot type, and their interaction on the number of clumps remaining with plot number as a random effect. Significant values at the 0.05 level are bolded

	Estimate	Std. Error	DF	t value	Pr(>|t|)
Plot Type	-911.7	266.9	92.13	-3.416	**0.0009**
Date	-0.15	0.01	91.83	-15.046	**<0.0001**
Plot Type x Date	0.05	0.01	92.14	3.425	**0.0009**

Table S3.40: Results of linear mixed effect model to test for the effect of date on the number of clumps remaining with plot number as a random effect. Significant values at the 0.05 level are bolded.

	Estimate	Std. Error	DF	t value	Pr(>|t|)
Date	-0.04784	0.01025	38.99985	-4.666	**<0.0001**

Table S3.41: Results of ANOVA to test for differences between minnow trap catch across plot types. Significant values at the 0.05 level are bolded.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Plot Type	4	1065.6	266.401	170.34	**<0.0001**
Residuals	22	34.41	1.564		

Table S3.42: Tukey post-hoc test to test for differences in minnow trap CPUE between plot types. Values significant at the 0.05 level are bolded.

Contrast	Estimate	Std. Error	t value	Pr(>|t|)
Subtidal Transplanted – Subtidal Bare	0.2937	0.7572	0.388	0.995
Natural Reference Seagrass – Subtidal Bare	16.5643	0.7909	20.943	**<0.0001**
Intertidal Bare – Subtidal Bare	1.1698	0.7572	1.545	0.546
Intertidal Transplanted – Subtidal Bare	0.1266	0.7909	0.16	1
Natural Reference Seagrass – Subtidal Transplanted	16.2706	0.7572	21.486	**<0.0001**
Intertidal Bare – Subtidal Transplanted	0.876	0.722	1.213	0.744
Intertidal Transplanted – Subtidal Transplanted	-0.1671	0.7572	-0.221	0.999
Intertidal Bare – Natural Reference Seagrass	-15.3946	0.7572	-20.33	**<0.0001**
Intertidal Transplanted – Natural Reference Seagrass	-16.4377	0.7909	-20.783	**<0.0001**
Intertidal Transplanted – Intertidal Bare	-1.0432	0.7572	-1.378	0.647

Table S3.43: Statistical table from generalized linear model for CPUE by clumps remaining. Values significant at the 0.1 level are italicized, significant values at the 0.05 level are bolded.

	DF	Deviance	Residual DF	Residual Deviance	F	Pr(>F)
Clumps Remaining	1	27.2367	59	131.68	9.68	**0.002909**
Elevation Category	1	0.1716	58	131.51	0.061	0.805817
Interaction	1	8.8819	57	122.63	3.1567	0.*080954*

Table S3.44: PERMANOVA table of results for comparison of communities from all intertidal minnow trap plots (natural reference seagrass, transplanted seagrass, bare sand). Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations. Values significant at the 0.05 level are bolded

Source	DF	SS	MS	Pseudo-F	P(perm)	Unique perms
Date	5	19041	3808.3	2.3942	**0.0008**	9905
Transplantation Category	2	30749	15374	6.0887	**0.0001**	9948
Plot (Transplantation Category)	14	37168	2654.8	1.6691	**0.0085**	9871
Date * Transplantation Category	10	36771	3677.1	2.3117	**0.0001**	9884

Table S3.45: PERMDISP table of results for plot type (natural reference seagrass, transplanted seagrass, bare sand) on the comparison of all communities of intertidal minnow trap plots with 999 permutations. Values significant at the 0.05 level are bolded.

F	DF1	DF2	P(perm)
17.178	2	73	**<0.001**
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Seagrass	30	28.923	1.8682
Transplanted	20	56.524	3.6091
Bare Sand	26	44.262	4.3164

Table S3.46: PERMDISP on sampling date on the comparison of all communities of intertidal minnow trap plots with 999 permutations.

F	DF1	DF2	P(perm)
1.1097	5	70	0.64
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
6/17/21	15	41.395	4.2247
6/30/21	16	40.832	4.8406
7/12/21	12	44.747	5.0791
7/29/21	11	50.926	5.1592
8/10/21	12	43.785	4.4203
9/6/21	10	53.2	3.7402

Table S3.47: Pairwise PERMANOVA comparing pairs of levels of the factor transplantation category across dates of all communities from intertidal minnow trap plots. Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations. Values significant at the 0.1 level are italicized, significant values at the 0.05 level are bolded.

Within level '6/17/21' of factor 'Date'			
Groups	**t**	**P(perm)**	**Unique perms**
Natural Reference Seagrass, Transplanted Seagrass	2.0427	**0.0077**	126
Natural Reference Seagrass, Bare Sand	1.8609	**0.0439**	126
Transplanted Seagrass, Bare Sand	0.63315	0.8914	126
Within level '6/30/21' of factor 'Date'			
Groups	**t**	**P(perm)**	**Unique perms**
Natural Reference Seagrass, Transplanted Seagrass	2.1579	**0.0073**	91
Natural Reference Seagrass, Bare Sand	1.6875	**0.0367**	582
Transplanted Seagrass, Bare Sand	1.08	0.3593	162
Within level '7/12/21' of factor 'Date'			
Groups	**t**	**P(perm)**	**Unique perms**
Natural Reference Seagrass, Transplanted Seagrass	2.4151	**0.0161**	41
Natural Reference Seagrass, Bare Sand	1.6268	**0.0087**	126
Transplanted Seagrass, Bare Sand	0.93154	0.4874	18
Within level '7/29/21' of factor 'Date'			
Groups	**t**	**P(perm)**	**Unique perms**
Natural Reference Seagrass, Transplanted Seagrass	2.1317	**0.0173**	56
Natural Reference Seagrass, Bare Sand	2.9969	**0.0177**	56
Transplanted Seagrass, Bare Sand	1.6844	0.1013	4
Within level '8/10/21' of factor 'Date'			
Groups	**t**	**P(perm)**	**Unique perms**
Natural Reference Seagrass, Transplanted Seagrass	2.5831	**0.0466**	16
Natural Reference Seagrass, Bare Sand	1.598	*0.069*	126
Transplanted Seagrass, Bare Sand	0.92361	0.2446	8
Within level '9/6/21' of factor 'Date'			
Groups	**t**	**P(perm)**	**Unique perms**
Natural Reference Seagrass, Transplanted Seagrass	1.5764	*0.0534*	56

Natural Reference Seagrass, Bare Sand	4.1943	**0.0439**	16
Transplanted Seagrass, Bare Sand	1.0954	0.4072	3

Table S3.48: SIMPER analysis on the comparison of communities from minnow trap sampling of intertidal transplanted seagrass, bare sand, and natural reference seagrass plots.

Group Natural Reference Seagrass
Average similarity: 58.98

Species	**Avg Abund**	**Avg sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lagodon rhomboides	2.62	46.51	3.95	78.86	78.86

Group Transplanted Seagrass
Average similarity: 21.63

Species	**Avg Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lagodon rhomboides	0.59	18.15	0.6	83.93	83.93

Group Bare Sand
Average similarity: 38.97

Species	**Avg Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lagodon rhomboides	1.08	35.92	0.99	92.17	92.17

Groups Natural Reference Seagrass & Transplanted Seagrass
Average dissimilarity = 77.16

Species	**Natural Seagrass Avg Abund**	**Transplanted Seagrass Avg Abund**	**Avg Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lagodon rhomboides	2.62	0.59	36.42	2.19	47.2	47.2
Orthopritis chrysoptera	0.65	0	9.71	1.09	12.59	59.79
Callinectes sapidus	0.34	0.12	6.1	0.87	7.9	67.69
Stephanolepis hispidus	0.32	0.03	4.71	0.74	6.1	73.79

Groups Natural Reference Seagrass & Bare Sand
Average dissimilarity = 62.46

Species	**Natural Seagrass Avg Abund**	**Bare Sand Avg Abund**	**Avg Diss**	**Diss/SD**	**Contrib%**	**Cum.%**

Lagodon rhomboides	2.62	1.08	26.22	1.61	41.97	41.97
Orthopritis chrysoptera	0.65	0.1	9.1	1.11	14.58	56.55
Callinectes sapidus	0.34	0.13	5.54	0.84	8.87	65.42
Stephanolepis hispidus	0.32	0.03	4.24	0.75	6.79	72.21
Groups Transplanted Seagrass and Bare Sand Average dissimilarity = 71.36						
Species	**Transplanted Seagrass Avg Abund**	**Bare Sand Avg Abund**	**Avg Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lagodon rhomboides	0.59	1.08	34.89	1.45	48.9	48.9
Callinectes sapidus	0.12	0.13	9.63	0.59	13.5	62.39
Portunus spinimanus	0.1	0.08	7.28	0.51	10.2	72.59

Table S3.49: PERMANOVA table of results for comparison of communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots on the first sampling date: June 17, 2021. Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations.

Source	DF	SS	MS	Pseudo-F	P(perm)	Unique perms
Transplantation category	1	2477.7	2477.7	1.2326	0.3173	9953
Depth	1	3564.9	3564.9	1.7735	0.1475	9947
Transplantation category * Depth	1	3004.9	3004.9	1.4949	0.2256	9957

Table S3.50: PERMDISP table of results for transplantation category on the comparison of all communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots on the first sampling date (6/17/21) with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
2.4767	1	15	0.238
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Transplanted Seagrass	8	47.026	6.78
Bare Sand	9	32.407	6.3551

Table S3.51: PERMDISP table of results for depth category on the comparison of all communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots on the first sampling date (6/17/21) with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
1.1357	1	15	0.463
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Subtidal	7	31.928	7.9689
Intertidal	10	42.397	6.0492

Table S3.52: PERMANOVA table of results for comparison of communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots on the last sampling date (9/6/21). Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations.

Source	**DF**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Transplantation Category	1	3833.3	3833.3	0.92	0.5112	5051
Depth	1	7833.3	7833.3	1.88	0.1167	5102
Transplantation Category * Depth	1	3166.7	3166.7	0.76	0.6032	2210

Table S3.53: PERMDISP table of results for transplantation category on the comparison of all communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots on the last sampling date (9/6/21) with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
8.0637 e-14	1	8	1
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Bare Sand	5	59.395	4.2481
Transplanted Seagrass	5	59.395	4.2481

Table S3.54: PERMDISP table of results for depth category on the comparison of all communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots on the last sampling date (9/6/21) with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
0.93251	1	8	0.518
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Intertidal	5	49.629	9.1782
Subtidal	5	59.395	4.2481

Table S3.55: PERMANOVA table of results for comparison of communities coming from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots. Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations.

Source	**DF**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Transplantation Category	1	785.82	785.82	0.46111	0.7458	9957
Depth	1	944.47	944.47	0.55421	0.6733	9967
Transplantation Category * Depth	1	1330.5	1330.5	0.78075	0.5304	9961

Table S3.56: PERMDISP table of results for transplantation category on the comparison of all communities from minnow trap sampling of intertidal and subtidal transplanted and bare sand plots with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
0.83291	1	21	0.464
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Transplanted Seagrass	11	39.466	3.7309
Bare Sand	12	35.025	3.1655

Table S3.57: PERMDISP table of results for depth category on the comparison of all communities from minnow trap sampling of intertidal and subtidal transplanted seagrass and bare sand plots with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
0.04161	1	21	0.871
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Subtidal	11	35.824	4.2635
Intertidal	12	36.996	3.8698

Table S3.58: PERMANOVA table of results for comparison of communities from SMURF sampling of intertidal bare sand and natural reference seagrass plots. Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations. Values significant at the 0.05 level are bolded.

Source	**DF**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Date	4	10226	2556.5	1.3387	0.2068	9932
Plot Type	1	4439.7	4439.7	2.9655	**0.0216**	8213
Plot # (Plot Type)	8	11267	1408.3	0.73745	0.7978	9927
Date * Plot Type	3	6842.8	2280.9	1.1944	0.3097	9933

Table S3.59: PERMDISP table of results for plot category on the comparison of all communities from SMURF sampling of intertidal bare sand and natural reference seagrass plots with 999 permutations. Values significant at the 0.05 level are bolded.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
8.2527	1	39	**0.021**
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Bare Sand	23	45.578	3.034
Natural Reference Seagrass	18	34.142	2.2745

Table S3.60: PERMDISP table of results for sampling date on the comparison of all communities from SMURF sampling of intertidal bare sand and natural reference seagrass plots with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
2.3689	4	36	0.134
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
6/17/21	10	36.039	4.2562
7/12/21	10	27.286	2.9757
8/10/21	10	39.578	5.712
9/6/21	5	50.649	6.1508
10/4/21	6	42.446	8.022

Table S3.61: SIMPER analysis table of results for the comparison of communities from SMURF sampling of intertidal bare sand and natural reference seagrass plots.

Group Bare Sand
Average similarity: 35.84

Species	Avg Abund	Avg sim	Sim/SD	Contrib%	Cum.%
Panopeidae	0.96	22.21	0.97	61.97	61.97
Portunus spinimanus	0.43	7.47	0.43	20.83	82.8

Group Natural Reference Seagrass
Average similarity: 51.15

Species	Avg Abund	Avg Sim	Sim/SD	Contrib%	Cum.%
Panopeidae	1.46	42.9	2.86	83.87	83.87

Groups Bare Sand & Natural Reference Seagrass
Average dissimilarity = 58.37

Species	Bare Sand Avg Abund	Seagrass Avg Abund	Avg Diss	Diss/SD	Contrib%	Cum.%
Panopeidae	0.96	1.46	18.08	1.08	30.98	30.98
Portunus spinimanus	0.43	0.31	11.11	0.93	19.03	50.01
Callinectes sapidus	0.22	0.31	7.83	0.85	13.41	63.42
Blenniiformes	0.32	0.24	7.68	0.85	13.15	76.57

Table S3.62: PERMANOVA table of results for comparison of communities from SMURF sampling of intertidal and subtidal bare sand plots. Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Date	4	13029	3257.4	1.551	0.114	9920
Depth	1	212.2	212.2	0.1377	0.7607	9633
Plot(Depth)	8	11887	1485.9	0.70751	0.8022	9918
Date * Depth	4	5860.7	1465.2	0.69764	0.7354	9927

Table S3.63: PERMDISP table of results for plot depth on the comparison of all communities from SMURF sampling of intertidal and subtidal bare sand plots with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
2.3624	1	41	0.182
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Intertidal	23	45.578	3.034
Subtidal	20	39.038	2.9395

Table S3.64: PERMDISP table of results for sampling date on the comparison of communities from SMURF sampling of intertidal and subtidal bare sand plots with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
1.7653	4	38	0.276
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
6/17/21	10	34.111	5.421
7/12/21	10	31.975	3.3776
8/10/21	9	42.813	6.3526
9/6/21	9	45.987	4.9079
10/4/21	5	29.405	5.3105

Table S3.65: PERMANOVA table of results for comparison of communities from SMURF and minnow trap sampling of natural reference seagrass plots. Type III (partial) sum of squares, unrestricted permutation of raw data with 9999 permutations. Values significant at the 0.05 level are bolded.

Source	**DF**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique Perms**
Gear Type	1	5397.9	5397.9	12.54	**0.0088**	126

Table S3.66: PERMDISP table of results for gear type on the comparison of communities from SMURF and minnow trap sampling of natural reference seagrass plots with 999 permutations. Values significant at the 0.1 level are italicized.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
3.1444	1	8	*0.089*
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Minnow Trap	5	13.518	3.0865
SMURF	5	20.897	2.7909

Table S3.67: SIMPER analysis table of results for the comparison of communities from SMURF and minnow trap sampling of natural reference seagrass plots.

Group Minnow Trap
Average similarity: 77.92

Species	Avg Abund	Avg Sim	Sim/SD	Contrib%	Cum.%
Callinectes sapidus	1	12.08	7.66	15.5	15.5
Orthopristis chrysoptera	1	12.08	7.66	15.5	31.01
Lagodon rhomboides	1	12.08	7.66	15.5	46.51
Diplodus holbrookii	1	12.08	7.66	15.5	62.01
Blenniiformes	0.8	7.39	1.14	9.49	71.5

Group SMURF
Average similarity: 67.98

Species	Avg Abund	Avg Sim	Sim/SD	Contrib%	Cum.%
Portunus spinimanus	1	18.68	4.21	27.48	27.48
Callinectes sapidus	1	18.68	4.21	27.48	54.96
Panopeidae	1	18.68	4.21	27.48	82.45

Groups Minnow Trap & SMURF
Average dissimilarity = 51.26

Species	Minnow Trap Avg Abund	SMURF Avg Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Orthopristis chrysoptera	1	0	7.39	5.05	14.42	14.42
Diplodus holbrookii	1	0	7.39	5.05	14.42	28.83
Fundulus heteroclitus	0.8	0	5.62	1.84	10.96	39.79
Portunus spinimanus	0.4	1	4.7	1.14	9.16	48.95
Stephanolepis hispidus	0.8	0.4	4.06	1.05	7.92	56.87
Lutjanus	0.6	0.2	4.03	1.07	7.86	64.73
Blenniiformes	0.8	0.6	3.55	0.84	6.92	71.64

Table S3.68: PERMANOVA table of results for comparison of communities from SMURF and minnow trap sampling of intertidal and subtidal bare sand plots. Type III (partial) sum of squares, permutation of residuals under a reduced model with 9999 permutations. Values significant at the 0.05 level are bolded.

Source	DF	SS	MS	Pseudo-F	P(perm)	Unique Perms
Gear Type	1	18300	18300	17.942	**0.0001**	9958
Depth	1	592.28	592.28	0.58067	0.6384	9956
Type * Depth	1	512.48	512.48	0.50244	0.6802	9968

Table S3.69: PERMDISP table of results for gear type on the comparison of communities from SMURF and minnow trap sampling of intertidal and subtidal bare sand plots with 999 permutations. Values significant at the 0.05 level are bolded.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
18.221	1	19	**<0.001**
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Minnow Trap	11	35.119	2.4339
SMURF	10	18.321	3.144

Table S3.70: PERMDISP table of results for depth on the comparison of communities from SMURF and minnow trap sampling of intertidal and subtidal bare sand plots with 999 permutations.

DEVIATIONS FROM CENTROID			
F	**DF1**	**DF2**	**P(perm)**
0.013362	1	19	0.91
MEANS AND STANDARD ERRORS			
Group	**Size**	**Average**	**SE**
Subtidal	9	40.117	4.7829
Intertidal	12	39.449	3.4981

Table S3.71: SIMPER analysis table of results for the comparison of communities from SMURF and minnow trap sampling of intertidal and subtidal bare sand plots.

Group Minnow Trap
Average similarity: 49.52

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Lagodon rhomboides	1	30.02	3.03	60.63	60.63
Callinectes sapidus	0.55	7.26	0.58	14.66	75.3

Group SMURF
Average similarity: 71.69

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeidae	1	18.73	5.8	26.12	26.12
Blenniiformes	0.9	15.18	1.84	21.17	47.29
Portunus spinimanus	0.9	14.5	1.86	20.23	67.52
Callinectes sapidus	0.8	10.84	1.23	15.12	82.64

Groups Minnow Trap & SMURF
Average dissimilarity = 69.39

Species	Minnow Trap Av.Abund	SMURF Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeidae	0.18	1	9.69	1.83	13.96	13.96
Blenniiformes	0.18	0.9	9.18	1.58	13.23	27.19
Lagodon rhomboides	1	0.3	8.44	1.42	12.16	39.35
Gobiesox strumosus	0	0.7	7.79	1.38	11.23	50.59
Portunus spinimanus	0.45	0.9	6.55	1.01	9.43	60.02
Callinectes sapidus	0.55	0.8	5.62	0.9	8.09	68.11
Orthopristis chrysoptera	0.45	0	4.9	0.87	7.06	75.17

Table S3.72: Results of generalized linear model for squid pop consumption at the one-hour check comparing intertidal and subtidal transplanted seagrass and bare sand plots. Values significant the 0.05 level are bolded.

	DF	Deviance	Residual Df	Residual Deviance	F	Pr(>F)
Transplantation Category	1	0.51288	20	5.2095	2.8538	0.1084
Elevation Category	1	1.35747	19	3.852	7.5534	**0.01322**
Interaction	1	0.16275	18	3.6892	0.9056	0.3589

Table S3.73: Results of generalized linear model for squid pop consumption at the one-hour check comparing all intertidal habitats (bare sand, transplanted seagrass, and natural reference seagrass). Values significant the 0.1 level are italicized.

	DF	Deviance	Residual DF	Residual Deviance	F	Pr(>F)
Habitat Category	2	0.82193	13	1.9224	2.9727	*0.08647*

Table S3.74: Results of generalized linear model for squid pop consumption at the two-hour check comparing intertidal and subtidal transplanted seagrass and bare sand plots. Values significant the 0.1 level are italicized and values significant at the 0.05 level are bolded.

	DF	Deviance	Residual DF	Residual Deviance	F	Pr(>F)
Transplantation Category	1	0.52946	20	3.8989	3.786	0.*06747*
Elevation Category	1	0.3131	19	3.5858	2.2389	0.1519
Interaction	1	0.69975	18	2.886	5.0037	**0.03819**

Table S3.75: Tukey post-hoc results to test for differences between treatments at the two-hour check comparing intertidal and subtidal transplanted and bare sand plots. Values significant at the 0.1 level are italicized, significant values at the 0.05 level are bolded.

Comparison	Estimate	Std. Error	z value	Pr(>|z|)
Intertidal Transplanted – Subtidal Transplanted	-1.2683	0.5033	-2.52	*0.0564*
Subtidal Bare Sand – Subtidal Transplanted	-0.1454	0.5456	-0.267	0.9934
Intertidal Bare Sand – Subtidal Transplanted	0.2744	0.556	0.494	0.9604
Subtidal Bare Sand – Intertidal Transplanted	1.1229	0.518	2.168	0.132
Intertidal Bare Sand – Intertidal Transplanted	1.5427	0.529	2.916	**0.0183**
Intertidal Bare Sand – Subtidal Bare Sand	0.4199	0.5694	0.737	0.8817

Table S3.76: Results of generalized linear model for squid pop consumption at the two-hour check comparing all intertidal habitats (bare sand, transplanted seagrass, and natural reference seagrass). Values significant the 0.05 level are bolded.

	DF	Deviance	Residual DF	Residual Deviance	F	Pr(>F)
Habitat Category	2	1.401	13	2.3261	4.6107	**0.03066**

Table S3.77: Tukey post-hoc results to test for differences between treatments at the two-hour check comparing all intertidal habitats. Values significant at the 0.1 level are italicized and values significant at the 0.05 level are bolded.

Comparison	Estimate	Std. Error	z value	Pr(>|z|)
Bare Sand – Transplanted	0.31667	0.10436	3.034	**0.0242**
Natural Reference Seagrass - Transplanted	0.25	0.109	2.294	*0.0922*
Natural Reference Seagrass - Bare Sand	-0.06667	0.10436	-0.639	0.8017

Appendix A: IACUC Approval Letters

The following IACUC protocol approvals were issued for the research in this dissertation:

- AUP #D358: "Evaluating How Foundation Species Diversity Affects Community Composition." The attached approval letter was issued by ECU IACUC in 2019, the first year of the author's research. IACUC reapproved this protocol through the conclusion of the author's work in 2023.

- AUP #D374: "Assessing Faunal Habitat Choice Within Seagrass Beds Across a Depth Gradient." The attached approval letter was issued by ECU IACUC in 2021, prior to the beginning of the author's habitat preference experiment. This approval continued through the conclusion of the author's work in 2023

- ID #87157: "Assessing faunal habitat choice within seagrass beds across a depth gradient." The attached approved application was issued by UNC IACUC in 2021, prior to the beginning of the author's habitat preference experiment. This approval continued through the conclusion of the author's work in 2023.

- AUP #D371: "Assessing Faunal Community Composition in Newly Restored Seagrass Beds Across a Depth Gradient." The attached approval letter was issued by ECU IACUC in 2021, prior to the beginning of the author's transplantation experiment. This approval continued through the conclusion of the author's work in 2023.

ECU

Animal Care and Use Committee
212 Ed Warren Life Sciences Building | East Carolina University | Greenville, NC 27834-4354
252-744-2436 office | 252-744-2355 fax

July 2, 2019

Rachel Gittman, Ph.D.
Department of Biology
Howell Science Complex
East Carolina University

Dear Dr. Gittman:

Your Animal Use Protocol entitled, "Evaluating How Foundation Species Diversity Affects Community Composition" (AUP #D358) was reviewed by this institution's Animal Care and Use Committee on July 2, 2019. The following action was taken by the Committee:

"Approved as submitted"

A copy is enclosed for your laboratory files. Please be reminded that all animal procedures must be conducted as described in the approved Animal Use Protocol. Modifications of these procedures cannot be performed without prior approval of the ACUC. The Animal Welfare Act and Public Health Service Guidelines require the ACUC to suspend activities not in accordance with approved procedures and report such activities to the responsible University Official (Vice Chancellor for Health Sciences or Vice Chancellor for Academic Affairs) and appropriate federal Agencies. **Please ensure that all personnel associated with this protocol have access to this approved copy of the AUP and are familiar with its contents.**

Sincerely yours,

Susan McRae, Ph.D.
Chair, Animal Care and Use Committee

SM/jd

Enclosure

EAST CAROLINA UNIVERSITY
ANIMAL USE PROTOCOL (AUP) FORM
LATEST REVISION APRIL, 2017

Project Title:

Evaluating How Foundation Species Diversity Affects Community Composition

	Principal Investigator	Secondary Contact
Name	Dr. Rachel Gittman	Stacy Trackenberg
Dept.	Biology	Biology
Office Ph #	252-328-9986	Click here to enter text.
Cell Ph #	804-691-0645	973-886-1242
Pager #	Click here to enter text.	Click here to enter text.
Home Ph #	804-691-0645	Click here to enter text.
Email	Gittmanr17@ecu.edu	Trackenbergs18@students.ecu.edu

For IACUC Use Only

AUP # D358			
New/Renewal New 6/24/19			
Full Review/Date	DR/Date		
Approval Date 7/2/19			
Study Type population / ecosystems			
Pain/Distress Category C			
Surgery	Survival	Multiple	
Prolonged Restraint			
Food/Fluid Regulation			
Other			
Hazard Approval/Dates	Rad	IBC	EHS
OHP Enrollment			
Mandatory Training			
Amendments Approved			

Animal Care and Use Committee
003 Ed Warren Life Sciences Building | East Carolina University | Greenville NC 27834 – 4354
252-744-2436 office | 252-744-2355 fax

August 23, 2021

Rachel Gittman, MD
Department of Biology, ECU

Dear Dr. Gittman:

Your Animal Use Protocol entitled, " Assessing Faunal Habitat Choice Within Seagrass Beds Across a Depth Gradient " (AUP #D374) was reviewed by this institution's Animal Care and Use Committee on 08/23/2021. The following action was taken by the Committee:

"Approved as submitted"

****Please contact Aaron Hinkle prior to any hazard use****

A copy of the protocols is enclosed for your laboratory files. Please be reminded that all animal procedures must be conducted as described in the approved Animal Use Protocol. Modifications of these procedures cannot be performed without prior approval of the ACUC. The Animal Welfare Act and Public Health Service Guidelines require the ACUC to suspend activities not in accordance with approved procedures and report such activities to the responsible University Official (Vice Chancellor for Health Sciences or Vice Chancellor for Academic Affairs) and appropriate federal Agencies. **Please ensure that all personnel associated with this protocol have access to this approved copy of the AUP/Amendment and are familiar with its contents.**

Sincerely yours,

Susan McRae, Ph.D.
Chair, Animal Care and Use Committee

SM/GD

enclosure

EAST CAROLINA UNIVERSITY
ANIMAL USE PROTOCOL (AUP) FORM
LATEST REVISION APRIL, 2017

Project Title:

Assessing Faunal Habitat Choice Within Seagrass Beds Across a Depth Gradient

	Principal Investigator	Secondary Contact
Name	Dr. Rachel Gittman	Stacy Trackenberg
Dept.	Biology	Biology
Office Ph #	252-328-9986	Click here to enter text.
Cell Ph #	252-732-6520	973-886-1242
Pager #	Click here to enter text.	Click here to enter text.
Home Ph #		Click here to enter text.
Email	Gittmanr17@ecu.edu	Trackenbergs18@students.ecu.edu

For IACUC Use Only

AUP #	D374		
New/Renewal	New		
Full Review/Date 7/26/2021			
Approval Date	8/23/2021		
Study Type	Biodiversity		
Pain/Distress Category	C		
Surgery			
Prolonged Restraint			
Food/Fluid Regulation			
Other			
Hazard Approval/Dates	Rad	IBC	EHS 7/27/2021
OHP Enrollment			
Mandatory Training			
Amendments Approved			

Application to Use Live Vertebrate Animals

PI: **Joel Fodrie**
Dept: **Institute For Marine Sciences-OLD**
IACUC ID: **21-197.0** **Web ID: 87157**

Title:	**Assessing faunal habitat choice within seagrass beds across a depth gradient**
Species:	**Fish ()**
Application Type:	**New Application**
Multiple Species	**No**
Total Animal Number:	**120 (Non-DCM - Caught in Wild)**
Core Facility/ Service Provider:	**No**

IACUC Use Only

IACUC ID:	21-197.0-A
Renewal Date:	07/31/2022
Expiration Date:	07/31/2024

- ☐ 1.1 Are there confidential or potentially patentable issues?
- ☑ 1.2 Will you be working with **a non-UNC collaborator** or providing services to **a non-UNC group** as part of the studies outlined in this animal care protocol?

  -or-

  Will **DCM Veterinary Services** be providing anesthetic, surgical, or research procedural support for the studies outlined in this animal care application?
- ☐ 1.3 Will you be using the services of a UNC Core Facility or will procedures be performed under the protocol of another UNC PI?
- ☑ 3.1 Will animals be housed or used in any DCM, investigator laboratory, or other space?
- ☑ 3.2 Will live animals be removed from a DCM Housing Facility or an IACUC-approved Investigator-maintained Housing Space and taken to another location for temporary holding and/or manipulation?
- ☑ 3.3 Will animals be housed long-term in an Investigator space? (Satellite Facility: an investigator-maintained, non- DCM facility where animals are housed on a long-term basis and are cared for by the principal investigator's laboratory personnel.)
- ☑ 3.4 Are study animals now or have they ever been free-ranging wildlife?
- ☐ 5.1 Will animals be bred as part of this study?
- ☐ 5.2 Will animals be used in terminal surgical procedures (non-survival surgery)?
- ☐ 5.3 Will animals undergo a surgical procedure from which they recover (survival surgery)?
- ☐ 5.4 Will tumors be induced in study animals or may they form spontaneously?
- ☑ 5.5 Will behavioral and/or conditioning experiments be conducted?
- ☐ 5.6 Will conscious animals be physically restrained?
- ☐ 5.7 Will animals experience weight loss as a result of this study?
- ☐ 5.8 Will tissues be collected from live or dead animals?
- ☐ 5.9 Will blood or body fluids be collected from live or dead animals?
- ☐ 6.1 Will food and/or fluid be restricted?
- ☐ 8. Are you requesting an exception to established regulation or IACUC policy?
- ☐ 9. Will animals be used for mouse ascites production?
- ☐ 10. Will animals be immunized or used for antibody (non-ascites) production?
- ☐ 11.1 Will animals be treated with chemical, pharmacologic, toxicologic, biologic, or radioactive agents (not anesthetics/analgesics)?
- ☐ 11.2 Will this protocol require the use of experimental/investigational drugs or drug dosages that will not be described in other sections of the protocol?
- ☐ 11.3 Will live animals be treated with non-pharmaceutical grade compounds, including experimental, investigational and novel compounds, analgesics, anesthetics and euthanasia agents?
- ☐ 13. Are Biological Hazards used? (includes use of biological agents, human blood, tissue, body fluids, infectious agents etc.)
- ☐ 14. Are Chemical Hazards used?*
- ☐ 15. Are Radioactive Hazards used?*
- ☐ Are transgenic animals created, including knockins (excluding knockouts), using/use of recombinant DNA/synthetic nucleic acids, siRNA, or viral vectors during this study in animals or in tissue culture to eventually be placed in animals(Schedule G)?
- ☐ Are transgenic animals, including knockins (excluding knockouts) used or purchased from a vendor or acquired from a collaborator/another scientist (Schedule H) in this study?

Submission History for New Application:

08/19/2021 - Complete 08/18/2021 - Revised

Date Approved: 08/18/2021

Animal Care and Use Committee
003 Ed Warren Life Sciences Building | East Carolina University | Greenville NC 27834 - 4354
252-744-2436 office | 252-744-2355 fax

March 8, 2021

Rachel Gittman, Ph.D.
Department of Biology, ECU

Dear Dr. Gittman:

Your Animal Use Protocol entitled, "Assessing Faunal Community Composition in Newly Restored Seagrass Beds Across a Depth Gradient" (AUP #D371) was reviewed by this institution's Animal Care and Use Committee on 03/08/2021. The following action was taken by the Committee:

"Approved as submitted"

****Please contact Aaron Hinkle prior to any hazard use****

A copy of the protocols is enclosed for your laboratory files. Please be reminded that all animal procedures must be conducted as described in the approved Animal Use Protocol. Modifications of these procedures cannot be performed without prior approval of the ACUC. The Animal Welfare Act and Public Health Service Guidelines require the ACUC to suspend activities not in accordance with approved procedures and report such activities to the responsible University Official (Vice Chancellor for Health Sciences or Vice Chancellor for Academic Affairs) and appropriate federal Agencies. **Please ensure that all personnel associated with this protocol have access to this approved copy of the AUP/Amendment and are familiar with its contents.**

Sincerely yours,

Susan McRae, Ph.D.
Chair, Animal Care and Use Committee

SM/GD

enclosure

EAST CAROLINA UNIVERSITY
ANIMAL USE PROTOCOL (AUP) FORM
LATEST REVISION APRIL, 2017

Project Title:

Assessing Faunal Community Composition in Newly Restored Seagrass Beds Across a Depth Gradient

	Principal Investigator	Secondary Contact
Name	Dr. Rachel Gittman	Stacy Trackenberg
Dept.	Biology	Biology
Office Ph #	252-328-9986	Click here to enter text.
Cell Ph #	252-732-6520	973-886-1242
Pager #	Click here to enter text.	Click here to enter text.
Home Ph #		Click here to enter text.
Email	Gittmanr17@ecu.edu	Trackenbergs18@students.ecu.edu

For IACUC Use Only

AUP #	D371		
New/Renewal	New		
Full Review/Date 02/22/2021	DR/Date		
Approval Date	3/8/2021		
Study Type	Biodiversity		
Pain/Distress Category	D		
Surgery	Survival	Multiple	
Prolonged Restraint			
Food/Fluid Regulation			
Other			
Hazard Approval/Dates	Rad	IBC	EHS 3/8/2021
OHP Enrollment			
Mandatory Training			
Amendments Approved			

Appendix B: Collection Permits

The following collection permits were issued for the research in this dissertation:

- Field collections were authorized by the North Carolina Division of Marine Fisheries (Scientific or Educational Permit #706671. The attached copy of this permit is from 2019, the first year of the author's research. This permit was reauthorized by DMF every year through the conclusion of the author's work in 2023.

- Field collections were authorized by the North Carolina Division of Marine Fisheries (Scientific or Educational Permit #706481). The attached copy of this permit is from 2019, the first year of the author's research. This permit was reauthorized by DMF every year through the conclusion of the author's work in 2023.

- Field collections were authorized by the North Carolina Division of Marine Fisheries (Scientific or Educational Permit #1627488). The attached copy of this permit is from 2019, the first year of the author's research. This permit was reauthorized by DMF every year through the conclusion of the author's work in 2023.

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706671

Permit Number : 706671 **NC Residency :** **Sales Outlet :** DMF Morehead City Office
Permit Year : 2019 **Qualifying Product :** **Terminal Number :** JRLEWIS1

Effective Date/Time 01/31/2019 16:36 **Fee :** 0.00
Expiration Date/Time : 12/31/2019 23:59 **Status :** Active
Issue Date/Time : 01/31/2019 16:36 **Status Date :** 01/31/2019

Permit Holder : **660357** **EAST CAROLINA UNIVERSITY (HARGITTAI)** **Business Type:**

Physical Address : DEPT. OF BIOLOGY MAIL STOP 551,
HOWELL SCIENCE COMPLEX,
GREENVILLE, NC, 27858-4353
United States
County : Pitt

Mailing Address : DEPT. OF BIOLOGY MAIL STOP 551,
HOWELL SCIENCE COMPLEX,
GREENVILLE, NC, 27858-4353
United States
County : Pitt

Race : **Eyes :** **Weight :**
Gender : **Date of Birth :** **Hair :** **Height :** **ft.** **Inches**

Home Phone : **Primary Residence :** NC **Prior Names :**
Business Phone : (252) 328-6355 **Secondary Residence :**
Fax : (252) 328-4178
Ids : **E-Mail :**

Business Agent : **1066638** **HARGITTAI, PAL TIBOR**

Physical Address : 213 GLORIA STREET,
GREENVILLE, NC, 27858
United States
County : Pitt

Mailing Address :
County :

Race : Other **Eyes :** Brown **Weight :** 160
Gender : Male **Date of Birth** 05/13/1951 **Hair :** Brown **Height :** 5 **ft.** 10 **Inches**

Home Phone : (252) 756-7691 **Primary Residence :** **Prior Names :**
Business Phone : (252) 328-6355 **Secondary Residence :**
Fax : (252) 328-4178
Ids : **E-Mail :** HARGITTAIP@ECU.EDU

Contact Information

Contact Person	Contact Person DOB	Contact Person Telephone #
PAL TIBOR HARGITTAI	05/13/1951	(252) 756-7691

Purpose of Collection

- [X] **Research**
- [X] **Teaching Specimens**
- [X] **Educational Display (Aquariums)**
- [ ] **Other (specify)**

Collectors

ParticipantId	Name	DOB	Contact Phone
	DR. ROGER RULIFSON	**11/13/1951**	**(252) 328-6718**
	DR. JOSEPH J. LUCZKOVICH	**07/06/1956**	**(252) 328-9402**
	DR. MARK SPRAGUE	**02/19/1966**	**(252) 328-1862**
	DR. JEFFREY MCKINNON	**11/30/1962**	**(252) 328-5258**
	ALLISON STEWART MULLIGAN	**03/30/1990**	**(336) 339-6809**
	LAURA BISHOP	**10/23/1993**	**(336) 456-9884**
	CHUCK BANGLEY	**03/19/1984**	**(401) 824-0782**
	HILDE ZENIL	**04/22/1985**	**(321) 750-7860**
	HENRY RAAB	**11/20/1988**	**(609) 287-4797**
	SHELBY WHITE	**06/02/1992**	**(252) 339-7192**
	RYAN MACKENZIE	**06/02/1992**	**(252) 474-9938**
	CAPTAIN ERIC DIADDORIO	**12/05/1968**	**(252) 328-4121**
	TYLER PEACOCK	**07/18/1989**	**(252) 328-4121**
	AARON KELLY	**08/14/1974**	**(252) 441-6575**
	CECILIA SUSANA KRAHFORST	**10/21/1982**	**(252) 917-7210**
	MIKE IZAACK	**12/22/1995**	**(919) 628-2571**
	CORI JOHANNA SPEIGHTS	**01/31/1992**	**(903) 390-2914**
	JILLIAN OSBORN	**12/12/1988**	**(704) 232-5172**

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706671

Permit Number :	706671	**NC Residency :**		**Sales Outlet :**	DMF Morehead City Office
Permit Year :	2019	**Qualifying Product :**		**Terminal Number :**	JRLEWIS1
Effective Date/Time	01/31/2019 16:36			**Fee :**	0.00
Expiration Date/Time :	12/31/2019 23:59	**Status :**	Active		
Issue Date/Time :	01/31/2019 16:36	**Status Date :**	01/31/2019		

DR. APRIL BLAKESLEE	**04/16/1976**	**(443) 366-4555**
CHRISTOPHER MOORE	**10/05/1982**	**(336) 577-6204**
DR. REBECCA ASCH	**05/03/1978**	**(617) 697-8375**
WILLIAM CHRISTOPHER THAXTON	**10/03/1994**	**(252) 286-8691**
HILDE SPEIGHT ZENIL	**04/22/1985**	**(321) 750-7860**
DR. ENRIQUE REYES	**12/19/1960**	**(252) 328-5778**
LINDSAY DAVENPORT	**07/30/1994**	**(336) 501-0225**
DR. PATRICK HARRIS	**03/16/1959**	**(252) 737-2082**
ALEX HUYNH	**04/20/1996**	**(980) 875-1835**
KETURAH KOVLEVEW	**04/24/1996**	**(919) 633-4700**
JASMINE SPENCER	**05/08/1998**	**(252) 495-2706**
ADAM VOIGT	**12/02/1994**	**(919) 381-0088**
STEVEN MEYER	**12/10/1995**	**(678) 654-3006**
JORDAN PATE SMITH	**05/09/1991**	**(252) 367-1832**
JOHN JACOBSON CLARK	**04/08/1997**	**(252) 717-2728**
DR. RACHEL KELLY GITTMAN	**08/06/1984**	**(804) 691-0645**
DR. MICHAEL SCOTT BREWER	**04/10/1983**	**(252) 328-1833**
DR. ERIN KIRBY FIELD	**08/31/1983**	**(860) 575-9639**
BRIAN BARTLETT	**04/15/1987**	**(516) 721-7131**
CHEOUITA NICOLE BROOKS	**07/23/1994**	**(336) 620-1715**
CODY EDWARD GARRISON	**09/23/1988**	**(434) 390-2704**
ALES HUYNH	**04/20/1996**	**(980) 875-1835**
TIMOTHY LEE	**07/31/1987**	**(201) 657-7590**
JONATHON SHERMAN, II	**11/10/1994**	**(252) 481-3105**
KATE WALKER	**06/11/1984**	**(907) 717-0762**
COREY WINKLER	**01/08/1997**	**(828) 773-4863**
JAVAN BAILEY	**01/22/1991**	**(360) 477-6929**
SIERRA WACHALA	**05/24/1996**	**(217) 552-6096**
ESRA GOKTURK	**12/24/1993**	**(572) 205-2167**
CHRISTOPHER BAILLIE	**10/09/1987**	**(919) 270-9303**
SARAH DONAHER	**10/05/1995**	**(704) 562-2326**
NOAH GWYNN	**06/26/1997**	**(336) 264-8412**
TYLER PEACOCK	**07/18/1989**	**(252) 362-4444**
KYRA PRICE	**07/01/1997**	**(704) 249-6553**
KYLE SWANSON	**06/18/1994**	**(303) 483-3062**

Restriction Information

Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time:	End Time:		
Comments:	**GEARS OR METHODS: GILL NET; TRAWL; BEACH SEINE; DREDGE; CAST NET; POUND NET; ROTENONE (CONTAINED); FYKE NET; HOOK AND LINE**		
Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time:	End Time:		
Comments:	**WATERBODIES: ALL COASTAL WATERS IN NORTH CAROLINA**		
Restriction Type : **RESTRICT FROM**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time:	End Time:		
Comments:	**NO NIGHT OR POLLUTED AREA SHELLFISHING.**		
Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time:	End Time:		
Comments:	**THIS SEAP PERMIT DOES NOT AUTHORIZE INTERACTIONS WITH ENDANGERED OR THREATENED SPECIES**		

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706671

Permit Number :	706671	**NC Residency :**		**Sales Outlet :**	DMF Morehead City Office
Permit Year :	2019	**Qualifying Product :**		**Terminal Number :**	JRLEWIS1
Effective Date/Time	01/31/2019 16:36			**Fee :**	0.00
Expiration Date/Time :	12/31/2019 23:59	**Status :**	Active		
Issue Date/Time :	01/31/2019 16:36	**Status Date :**	01/31/2019		

Request To Sell? **Authorized to Sell?**

Issued By: Kathy Rawls **Issued Date:** 1/31/2019

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706481

Permit Number : 706481 **NC Residency :** **Sales Outlet :** DMF Morehead City Office
Permit Year : 2019 **Qualifying Product :** **Terminal Number :** JRLEWIS1

Effective Date/Time 02/01/2019 15:55 **Fee :** 0.00
Expiration Date/Time : 12/31/2019 23:59 **Status :** Active
Issue Date/Time : 02/01/2019 15:55 **Status Date :** 02/01/2019

Permit Holder : 729210 **UNC INSTITUTE OF MARINE SCIENCES** **Business Type:**

Physical Address : 3431 ARENDELL STREET,
MOREHEAD CITY, NC, 28557
United States
County : Carteret

Mailing Address :

County :

Race :
Gender :

Date of Birth :

Eyes :
Hair :

Weight :
Height : ft. Inches

Home Phone :
Business Phone : (252) 726-6841
Fax : (252) 726-2420
Ids :

Primary Residence : NC
Secondary Residence :

Prior Names :

E-Mail :

Business Agent : 1176346 **FODRIE, FREDRICK JOEL**

Physical Address : 1156 STRAITS RD,
SMYRNA, NC, 28579
United States
County : Carteret

Mailing Address :

County :

Race : Caucasian
Gender : Male

Date of Birth 12/21/1976

Eyes : Hazel
Hair : Brown

Weight :
Height : 6 ft. 4 Inches

Home Phone :
Business Phone : (252) 726-6841
Fax :
Ids :

Primary Residence : NC
Secondary Residence :

Prior Names :

E-Mail : jfodrie@unc.edu

Contact Information

Contact Person	Contact Person DOB	Contact Person Telephone #
FREDRICK JOEL FODRIE	12/21/1976	

Purpose of Collection

- [X] **Research**
- [X] **Teaching Specimens**
- [ ] **Educational Display (Aquariums)**
- [ ] **Other (specify)**

Collectors

ParticipantId	Name	DOB	Contact Phone
	DR. CHARLES H. PETERSON (PETE)	**02/18/1946**	**(252) 726-6841**
	DR. NEILS LINDQUIST	**01/01/1959**	**(252) 726-6841**
	ABIGAIL PORAY	**07/15/1981**	**(252) 726-6841**
	CHRISTINE VOSS	**05/09/1960**	**(252) 726-6841**
	JEREMY BRADDY	**09/05/1979**	**(252) 726-6841**
	HOWARD MENDLOVITZ	**08/08/1968**	**(252) 726-6841**
	MEREDITH BURKE	**04/08/1992**	**(252) 726-6841**
	DR. JOHN BRUNO	**10/13/1965**	**(252) 726-6841**
	STACY DAVIS	**07/19/1963**	**(252) 726-6841**
	PHILLIP HERBST	**07/09/1987**	**(252) 726-6841**
	DR. MIKE PIEHLER	**07/05/1968**	**(252) 726-6841**
	SUZANNE THOMPSON	**03/04/1962**	**(252) 726-6841**
	JOEL FODRIE	**12/21/1976**	**(252) 726-6841**
	TONY WHIPPLE	**04/19/1963**	**(252) 726-6841**
	J IPOCK	**07/21/1956**	**(252) 726-6841**
	PATRICK BARRETT	**12/31/1991**	**(252) 726-6841**
	ALEXANDER REQUARTH	**09/20/1995**	**(252) 726-6841**
	HANNAH AICHELMAN	**06/10/1992**	**(252) 726-6841**
	DENENE BLACKWOOD	**09/22/1967**	**(252) 726-6841**

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706481

Permit Number :	706481	**NC Residency :**		**Sales Outlet :**	DMF Morehead City Office
Permit Year :	2019	**Qualifying Product :**		**Terminal Number :**	JRLEWIS1
Effective Date/Time	02/01/2019 15:55			**Fee :**	0.00
Expiration Date/Time :	12/31/2019 23:59	**Status :**	Active		
Issue Date/Time :	02/01/2019 15:55	**Status Date :**	02/01/2019		

KARL CASTILLO	**12/11/1969**	**(252) 726-6841**
STEPHEN FEGLEY	**03/14/1955**	**(252) 726-6841**
WAYNE FLUELLEN	**11/06/1965**	**(252) 726-6841**
BRETT FROLICH	**04/04/1979**	**(252) 726-6841**
MATTHEW KENWORTHY	**04/30/1983**	**(252) 726-6841**
CHRIS MARTENS	**01/11/1946**	**(252) 726-6841**
RACHEL NOBLE	**11/04/1969**	**(252) 726-6841**
JOE PURIFOY	**01/20/1953**	**(252) 726-6841**
REBECCA GAESSER	**05/25/1993**	**(252) 726-6841**
SARAH DONAHER	**10/05/1995**	**(252) 726-6841**
OWEN MULVEY-MCFERRON	**12/21/1994**	**(252) 726-6841**
LEWIS NAISBETT-JONES	**05/04/1993**	**(252) 726-6841**
MATTHEW PRICE	**09/25/1989**	**(252) 726-6841**
RACHEL CANTY	**01/10/1994**	**(252) 726-6841**
MARY CONROY	**07/26/1993**	**(252) 726-6841**
MARIANNA MILLER	**12/12/1995**	**(252) 726-6841**
ANDREW MCMAINS	**02/07/1995**	**(252) 726-6841**
JONATHAN LUCAS	**06/19/1985**	**(252) 726-6841**
CHRIS BAILLIE	**10/09/1987**	**(252) 726-6841**
JEF PLUMLEE	**12/28/1984**	**(252) 726-6841**
ZOFIA KNOREK	**11/02/1994**	**(252) 726-6841**
THOMAS KIFFNEY	**12/13/1994**	**(252) 726-6841**
STEVEN KENT BROADHURST	**10/14/1966**	**(252) 726-6841**

Restriction Information

Restriction Type : **RESTRICT TO** | Gear Code : | Gear Quantity : | Gear Units : | Species Group : | Species Quantity : | Species Size : | Species Units : | Water Body :
Time :
Start Time: End Time:
Comments: **GEARS OR METHODS: 16 FT TRAWL, FYKE, TRAPS (CRABS / MINNOW), SEINE, LONG LINE (SHARKS), SCIENTIFIC GILL NET**

Restriction Type : **RESTRICT TO** | Gear Code : | Gear Quantity : | Gear Units : | Species Group : | Species Quantity : | Species Size : | Species Units : | Water Body :
Time :
Start Time: End Time:
Comments: **NEW CONTACT PERSON: JOEL FODRIE, JFODRIE@UNC.EDU, 252-726-6841, EXT. 149**

Restriction Type : **RESTRICT TO** | Gear Code : | Gear Quantity : | Gear Units : | Species Group : | Species Quantity : | Species Size : | Species Units : | Water Body :
Time :
Start Time: End Time:
Comments: **SPECIES: SHARKS, ESTUARINE FISHERIES, DECAPOD CRUSTACEANS AND BIVALVES**

Restriction Type : **RESTRICT TO** | Gear Code : | Gear Quantity : | Gear Units : | Species Group : | Species Quantity : | Species Size : | Species Units : | Water Body :
Time :
Start Time: End Time:
Comments: **NO COLLECTION OF OYSTERS, CLAMS OR MUSSELS IN CLOSED SHELLFISH WATERS (PROHIBITED OR CONDITIONALLY CLOSED). NO COLLECTION OF BIVALVES AT NIGHT**

Restriction Type : **RESTRICT FROM** | Gear Code : | Gear Quantity : | Gear Units : | Species Group : | Species Quantity : | Species Size : | Species Units : | Water Body :
Time :
Start Time: End Time:
Comments: **THIS SEAP DOES NOT AUTHORIZE INTERACTIONS WITH ENDANGERED AND/OR THREATENED SPECIES.**

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706481

Permit Number :	706481	**NC Residency :**		**Sales Outlet :**	DMF Morehead City Office
Permit Year :	2019	**Qualifying Product :**		**Terminal Number :**	JRLEWIS1
Effective Date/Time	02/01/2019 15:55			**Fee :**	0.00
Expiration Date/Time :	12/31/2019 23:59	**Status :**	Active		
Issue Date/Time :	02/01/2019 15:55	**Status Date :**	02/01/2019		

Request To Sell? **Authorized to Sell?**

Issued By: Kathy Rawls **Issued Date:** 2/1/2019

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 1627488

Permit Number : 1627488 **NC Residency :** **Sales Outlet :** DMF Morehead City Office
Permit Year : 2019 **Qualifying Product :** **Terminal Number :** JRLEWIS1

Effective Date/Time 02/01/2019 16:04 **Fee :** 0.00
Expiration Date/Time : 12/31/2019 23:59 **Status :** Active
Issue Date/Time : 02/01/2019 16:04 **Status Date :** 02/01/2019

Permit Holder : 729210 **UNC INSTITUTE OF MARINE SCIENCES** **Business Type:**

Physical Address : 3431 ARENDELL STREET,
MOREHEAD CITY, NC, 28557
United States
County : Carteret

Mailing Address :

County :

Race :
Gender :
Date of Birth :
Eyes :
Hair :
Weight :
Height : ft. Inches

Home Phone :
Business Phone : (252) 726-6841
Fax : (252) 726-2420
Ids :
Primary Residence : NC
Secondary Residence :
Prior Names :
E-Mail :

Business Agent : 1176346 **FODRIE, FREDRICK JOEL**

Physical Address : 1156 STRAITS RD,
SMYRNA, NC, 28579
United States
County : Carteret

Mailing Address :

County :

Race : Caucasian
Gender : Male
Date of Birth 12/21/1976
Eyes : Hazel
Hair : Brown
Weight :
Height : 6 ft. 4 Inches

Home Phone :
Business Phone : (252) 726-6841
Fax :
Ids :
Primary Residence : NC
Secondary Residence :
Prior Names :
E-Mail : jfodrie@unc.edu

Contact Information

Contact Person	Contact Person DOB	Contact Person Telephone #
FREDRICK JOEL FODRIE	12/21/1976	

Purpose of Collection

- [X] **Research**
- [X] **Teaching Specimens**
- [ ] **Educational Display (Aquariums)**
- [ ] **Other (specify)**

Collectors

ParticipantId	Name	DOB	Contact Phone
	CLAUDE LEWIS	**08/19/1954**	**(252) 726-6841**
	CHRISTOPHER COOK	**02/06/1991**	**(252) 726-6841**
	JOHN STEPHENS	**08/26/1990**	**(252) 726-6841**
	JOHN ROGER BROTHERS	**06/08/1989**	**(252) 726-6841**
	AVERY PAXTON	**03/18/1989**	**(252) 726-6841**
	MARTIN BENAVIDES	**06/27/1986**	**(252) 726-6841**
	SHELBY ZEIGLER	**02/20/1991**	**(252) 726-6841**
	COLLEEN BOVE	**01/23/1992**	**(252) 726-6841**
	KELSEY JESSER	**10/30/1988**	**(252) 726-6841**
	JUSTIN BAUMANN	**04/16/1989**	**(252) 726-6841**
	MOLLY BOST	**12/11/1990**	**(252) 726-6841**
	DAVID CESSNA	**08/01/1960**	**(252) 726-6841**
	RACHEL GITTMAN	**08/06/1984**	**(252) 726-6841**
	CORI LOPAZANSKI	**05/02/1994**	**(252) 726-6841**
	JIM MORLEY	**06/08/1977**	**(252) 726-6841**
	TESSA PFEIFFER	**10/03/1992**	**(252) 726-6841**
	JP RIPPE	**03/20/1991**	**(252) 726-6841**
	ADAM ROK	**06/21/1994**	**(252) 726-6841**
	CARTER SMITH	**05/16/1987**	**(252) 726-6841**

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 1627488

Permit Number :	1627488	**NC Residency :**		**Sales Outlet :**	DMF Morehead City Office
Permit Year :	2019	**Qualifying Product :**		**Terminal Number :**	JRLEWIS1
Effective Date/Time	02/01/2019 16:04			**Fee :**	0.00
Expiration Date/Time :	12/31/2019 23:59	**Status :**	Active		
Issue Date/Time :	02/01/2019 16:04	**Status Date :**	02/01/2019		

ADAM TYLER	**08/18/1974**	**(252) 726-6841**
TIM WAHL	**01/11/1994**	**(252) 726-6841**
AMY YARNALL	**06/18/1993**	**(252) 726-6841**

Restriction Information

Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time: End Time:			
Comments: **GEARS AND MEHTODS: 16 FT TRAWL, FYKE, TRAPS (CRAB / MINNOW), SEINE, LONG LINE (SHARKS), SCIENTIFIC GILL NET**			
Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time: End Time:			
Comments: **SEE PERMIT #706481 FOR MORE INFORMATION OR ADDITIONAL COLLECTORS**			
Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time: End Time:			
Comments: **SPECIES: SHARKS, ESTUARINE FISHES, DECAPOD, CRUSTACEANS AND BIVALVES,**			
Restriction Type : **RESTRICT TO**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size :	
Time :		Species Units :	
Start Time: End Time:			
Comments: **NO COLLECTION OF OYSTERS, CLAMS OR MUSSELS IN CLOSED SHELLFISH WATERS (PROHIBITED AND CONDITIONALLY CLOSED) NO COLLECTION OF BIVALVES AT NIGHT**			
Restriction Type : **RESTRICT FROM**	Gear Code :	Species Group :	Water Body :
	Gear Quantity :	Species Quantity :	
	Gear Units :	Species Size ;	
Time :		Species Units :	
Start Time: End Time:			
Comments: **THIS SEAP DOES NOT AUTHORIZE INTERACTIONS WITH ENDANGERED AND/OR THREATENED SPECIES.**			

Request To Sell? **Authorized to Sell?**

Issued By: Kathy Rawls **Issued Date:** 2/1/2019

ROY COOPER
Governor
DIONNE DELLI-GATTI
Secretary
KATHY B. RAWLS
Director

Appendix C: Sanctuary Proclamation

To: Stacy Trackenberg
From: Tina Moore
Cc: Kathy Rawls and Rachel Gittman
Date: May 11, 2021
Subject: RS-4-2021 research sanctuary for East Carolina University

Proclamation RS-4-2021 was issued on May 11, 2021 with an effective date of 12:01 a.m., May 14, 2021 for the protection of research on the restoration of submerged aquatic vegetation. Research sanctuary requestor, Stacy Trackenberg, will be responsible for the marking and signage requirements of the area to ensure that Division of Marine Fisheries (DMF) Marine Patrol officers can enforce no fishing gear or the taking of shellfish within the boundaries set out in the proclamation for one year. Site visits to the sanctuaries by DMF staff may occur to determine that the specific locations, marking, and signage is maintained. Marking requirements include:

- Mark corners with small poles or PVC Pipe
- Signage on each pole should, at a minimum, say "Research Sanctuary", the name of the "requestor" and the division phone number (800-682-2632).

The locations of the poles for the research sanctuary were identified as:

Corner 1	34° 43.4495'N	076° 34.8327'W
Corner 2	34° 43.4308'N	076° 34.7643'W
Corner 3	34° 43.4089'N	076° 34.7688'W
Croner 4	34° 43.4217'N	076° 34.8284'W

Marking of the areas can begin on May 14, 2021.

The proclamation is in effect through 11:59 P.M., May 13, 2022 and will be considered terminated after that date. All sites must be cleared of poles, signs or material by the requestor unless permitted by Division of Coastal Management by this date. It is requested that the Research Sanctuary requestor contact Tina Moore at Tina.Moore@ncdenr.gov or by phone 252-808-8082 when the poles, signs and materials are removed from the site.