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Effects of seagrass restoration on coastal fish abundance and diversity

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Abstract

Restoration is accelerating to reverse global declines of key habitats and recover lost ecosystem functions, particularly in coastal ecosystems. However, there is high uncertainty about the long-term capacity of restored ecosystems to provide habitat and increase biodiversity and the degree to which these ecosystem services are mediated by spatial and temporal environmental variability. We addressed these gaps by sampling fishes biannually for 5–7 years (2012–2018) at 16 sites inside and outside a rapidly expanding restored seagrass meadow in coastal Virginia (USA). Despite substantial among-year variation in abundance and species composition, seine catches in restored seagrass beds were consistently larger (6.4 times more fish, $p < 0.001$) and more speciose (2.6 times greater species richness, $p < 0.001$; 3.1 times greater Hill–Shannon diversity, $p = 0.03$) than seine catches in adjacent unvegetated areas. Catches were particularly larger during summer than autumn ($p < 0.01$). Structural equation modeling revealed that depth and water residence time interacted to control seagrass presence, leading to higher fish abundance and richness in shallow, well-flushed areas that supported seagrass. Together, our results indicate that seagrass restoration yields large and consistent benefits for many coastal fishes, but that restoration and its benefits are sensitive to the dynamic seascapes in which restoration is conducted. Consideration of how seascape-scale environmental variability affects the success of habitat restoration and subsequent ecosystem function will improve restoration outcomes and the provisioning of ecosystem services.

KEYWORDS
biodiversity, community ecology, eelgrass Zostera marina, foundation species, long-term ecological research, nursery habitat, restoration, seagrass

Efectos de la restauración de pastos marinos sobre la abundancia y diversidad de peces costeros

Resumen: La restauración ecológica está acelerándose para revertir la declinación mundial de hábitats importantes y para recuperar las funciones ambientales perdidas, particularmente en los ecosistemas costeros. Sin embargo, hay una gran incertidumbre en cuanto a la capacidad a largo plazo que tienen los ecosistemas restaurados de proporcionar hábitats e incrementar la biodiversidad y el grado al que estos servicios ambientales están mediados por la variabilidad ambiental espacial y temporal. Abordamos estos vacíos mediante el muestreo bianual de peces durante 5-7 años (2012-2018) en 16 sitios dentro y fuera de una pradera restaurada de pastos marinos con expansión acelerada en la costa de Virginia (E.U.A.). A pesar de la variación sustancial anual en abundancia y composición de especies, la captura de cerco en los lechos de pastos marinos restaurados fue mayor (6.4

veces más peces, *p*< 0.001) y con más especies (2.6 veces mayor riqueza de especies, *p*< 0.001; 3.1 veces mayor diversidad Hill-Shannon, *p*= 0.03) que la captura de cerco en las áreas aledañas sin vegetación. En particular, las capturas fueron mayores durante el verano que durante el otoño (*p* < 0.01). Los modelos de ecuaciones estructurales revelaron que la profundidad y el tiempo de residencia acuática interactúan para controlar la presencia de los pastos marinos, lo que resulta en una mayor abundancia y riqueza de peces en áreas someras con buena circulación que fomentan los pastos marinos. En conjunto, nuestros resultados indican que la restauración de los pastos marinos produce grandes beneficios constantes para muchos peces costeros, pero también que la restauración y sus beneficios son sensibles a la dinámica marina en la que se realiza la restauración. Si se considera cómo la variabilidad ambiental a escala de paisaje afecta el éxito de la restauración del hábitat y la función ambiental subsecuente, entonces mejorarán los resultados de restauración y el suministro de servicios ambientales.

INTRODUCTION

Human activities have led to global degradation of ecosystem structure and function over the past century (Ellison et al., 2005; Barbier et al., 2011). In response, habitat restoration has increasingly been investigated as a tool for combating these declines (Guan et al., 2019), although there remains uncertainty about the long-term capacity of restored ecosystems to consistently provide ecosystem services, such as habitat provisioning (Lamb, 2018). Restored ecosystems may fail to enhance and sustain ecosystem services due to site-specific environmental constraints that limit restoration success or the suitability of restored areas for associated fauna (Raposa & Talley, 2012; England & Wilkes, 2018). For example, the direction (positive, negative, zero) and magnitude of effects of salt marsh restoration on nekton are highly variable and site-dependent at a regional scale due to local-scale environmental variability and anthropogenic impacts (Raposa & Talley, 2012). Similarly, although river restorations have been successful in reinstating physical functioning to degraded waterways, these improvements are not always associated with the rehabilitation of associated macroinvertebrate communities subject to local- and catchment-scale environmental variability (Leps et al., 2016; England & Wilkes, 2018). Evaluating how spatial and temporal variation affects communities in restored habitats is critical to maximizing the success of restorations and the ecosystem services they provide.

Following declines of seagrass meadows in shallow coastal ecosystems worldwide (Dunic et al., 2021), restoration efforts have increased to restore these areas and their associated ecosystem services (Duarte et al., 2020; Orth et al., 2020). Although numerous studies show the benefits of seagrass for fish and fisheries (e.g., Gilby et al., 2018; Unsworth et al., 2019; Orth et al., 2020), there is still uncertainty about how spatial environmental variability directly and indirectly mediate the capacity of restored meadows to yield more numerous and diverse fish assemblages. Moreover, it is unclear how the enhancement of fish communities through the restoration of seagrass meadows varies over longer time scales because almost all studies that compare habitat provisioning with restored meadows and reference areas have been <5 years in duration (e.g., Fonseca et al., 1996; Sheridan et al., 2003; Sheridan, 2004). Fish populations are highly variable over space and time (Auth et al., 2020), so positive trends in fish abundance or diversity associated with seagrass restoration may be overwhelmed by seasonal, interannual, and spatial variability in relation to environmental conditions, such as nearshore oceanography (Shanks, 2020). Quantifying the spatial and temporal variability in the enhancement of fish communities by restored seagrass meadows informs restoration and is especially urgent as climate change intensifies a variety of factors that may have direct and indirect effects on coastal fishes, including ocean warming, sea-level rise, and storm disturbance (Ummenhofer & Meehl, 2017; Castorani et al., 2018; von Biela et al., 2019; Aoki et al., 2020a).

Seagrass restoration may be particularly beneficial to juvenile fishes because meadows commonly function as nursery habitat (Heck et al., 2003; Lefcheck et al., 2019) that offer shelter from predation (Hindell et al., 2002; Smith et al., 2011) and enhance food availability (Nakamura & Sano, 2005; Alfaro, 2006). Numerous coastal fishes recruit to seagrass meadows as larvae and remain in or near meadows until maturity (Rooker et al., 1998; ASMFC, 2010; Faletti et al., 2019). Seasonal recruitment results in distinct assemblages of juvenile fishes inhabiting meadows throughout the year (Rooker et al., 1998; Sobocinski et al., 2013). Overlaid on these seasonal patterns are typically large year-to-year variations in recruitment and community composition due to variability in climate drivers, currents, and lower trophic-level production, among other factors (Wood, 2000; Woodland et al., 2021; Schonfeld et al., 2022). Further, in seagrass meadows, the distributions and diversities of fishes and mobile invertebrates vary spatially in response to meadow attributes (Yeager et al., 2011, 2016; Cheng et al., 2022) that are mediated by environmental context. For example, the density and patchiness of seagrass meadows are affected by wave

exposure, current speed, and water depth (Fonseca & Bell, 1998; Carr et al., 2010, Uhrin & Turner, 2018), and these meadow characteristics contribute to the structure of associated fish communities (Yeager et al., 2011, 2016). However, studies have rarely considered the direct and indirect effects of the abiotic conditions associated with the seagrass niche on fish communities explicitly (e.g., Giacomazzo et al., 2020).

To address these gaps, we determined how seagrass restoration affects fish abundance and diversity; the extent to which this effect varies among seasons, years, and locations; and the direct and indirect effects of spatial variation in abiotic conditions on the distribution of seagrass and the fish community. We carried out a long-term and spatially replicated study (5−7 years at 16 sites) to characterize fish community dynamics across a rapidly expanding restored seagrass meadow in coastal Virginia (USA).

METHODS

Study system

We conducted our investigation in a network of coastal bays along the Atlantic coastline of Virginia which is under study by the Virginia Coast Reserve Long Term Ecological Research project. The bays are shallow (1–2 m below mean sea level [MSL]) and punctuated by deep inlets connecting them to the Atlantic Ocean (McGlathery et al., 2001; Oreska et al., 2021). Salinities are euhaline (typically >30 PSU) due to limited freshwater inputs from the Delmarva Peninsula bordering the western margin of the bays (Oreska et al., 2021), and low nutrient loading from the coastal watersheds results in general oligotrophy and consistently high water quality (McGlathery et al., 2001; Anderson et al., 2010). These factors combine to provide an estimated >100 km^2 of habitat for the dominant species of seagrass in the coastal bays, eelgrass (*Zostera marina*) (Oreska et al., 2021).

Seagrass was extirpated from the coastal bays in the 1930s due to wasting disease and hurricane disturbance. The discovery of a small patch of naturally occurring seagrass spurred the creation of a large-scale, seed-based restoration program that since 1999 has deposited >75 million seeds across the coastal bays (Orth et al., 2012, 2020). The total area restored now exceeds 36 km^2, and the meadows have contributed to improvements in water quality, carbon and nitrogen sequestration, and finfish and epifaunal invertebrate biomass and diversity (Lefcheck et al., 2017; Aoki et al., 2020b; Oreska et al., 2020; Orth et al., 2020).

We focused on 2 restored bays: South Bay (median depth = 0.85 m below MSL) and Hog Island Bay (median depth = 1 m below MSL). The 2 bays have similar tidal ranges, 1.32 m in South Bay and 1.24 m in Hog Island Bay (McGlathery et al., 2012). Aerial surveys (Moore et al., 2009) show that seagrass cover expanded 83% in South Bay (from 10.7 km^2 to 19.6 km^2) and 80% in Hog Island Bay (1.8 km^2 to 3.3 km^2) from the start to end of our study (2012−2018). We sampled fish at each of 16 fixed locations (sites): 4 vegetated sites in the South Bay meadow and 4 nearby unvegetated sites outside the

meadow and 4 vegetated sites in the Hog Bay meadow and 4 nearby unvegetated sites (Figure 1).

Within the 2 bays, we used observations of seagrass presence at fish sampling sites to evaluate relationships among abiotic drivers, seagrass, and the fish community. Because the initial sampling design established a total of 8 sites inside and 8 sites outside the meadows, we assumed that seagrass was present or absent at these sites until noted otherwise during field sampling. When unvegetated sites were overtaken by seagrass or seagrass was lost from vegetated sites, we assumed these altered states persisted at each site until another change was noted (see Appendix S1 for seagrass presence through time).

Fish sampling

To examine the effects of seagrass restoration on fish communities over time, we sampled fish at each site once or twice per year with beach seines (7.6 m wide × 1.8 m tall; 1.5 m deep pocket with 6.4 mm mesh) pulled along 25-m transects in the summer (May or June) and autumn (September or October) from 2012 through 2018. Researchers stopped sampling at the 4 initially unvegetated sites in South Bay after 2015 when sites were colonized by seagrass, although seining occurred once more at these sites during the autumn of 2017. We counted, measured (total length), and identified fish to the lowest possible taxon in the field prior to release. All seine pulls occurred during the day and within 3 h of low tide for logistical reasons ($n = 204$).

Catch data were analyzed in terms of catch per unit effort (CPUE), richness per seine haul, and diversity per seine haul as Hill–Shannon diversity (*D*) (Hill, 1973). Hill–Shannon diversity can be interpreted as an index of mean rarity, where a seine haul containing many species in low abundance (i.e., many rare species) would have a larger *D* than a seine haul with few species in high abundance:

$$D = \exp\left(-\sum_{i=1}^{S} p_i \ln\left(p_i\right)\right), \qquad (1)$$

where p_i is the proportion of individuals belonging to species i and S is the number of species (Roswell et al., 2021).

All fish sampling methods have some degree of bias. Our sampling method likely represents a conservative estimate of the effect of seagrass restoration on fish communities because the capture efficiency of beach seines is generally lower in structured habitat relative to unstructured habitats (Connolly, 1994; Jenkins & Sutherland, 1997). Benthic fishes in seagrass meadows may avoid capture in seine nets because they are positioned deeper in the vegetation (Connolly, 1994). The strength of undersampling varies among species; for instance, fish associated with the upper seagrass canopy and middle of the water column are sampled in seines more efficiently than seafloor-associated species that may avoid the net capture area (Jenkins & Sutherland, 1997). Therefore, reduced capture efficiency in the seagrass meadow likely resulted in our data underestimating fish densities for segments of the fish community.
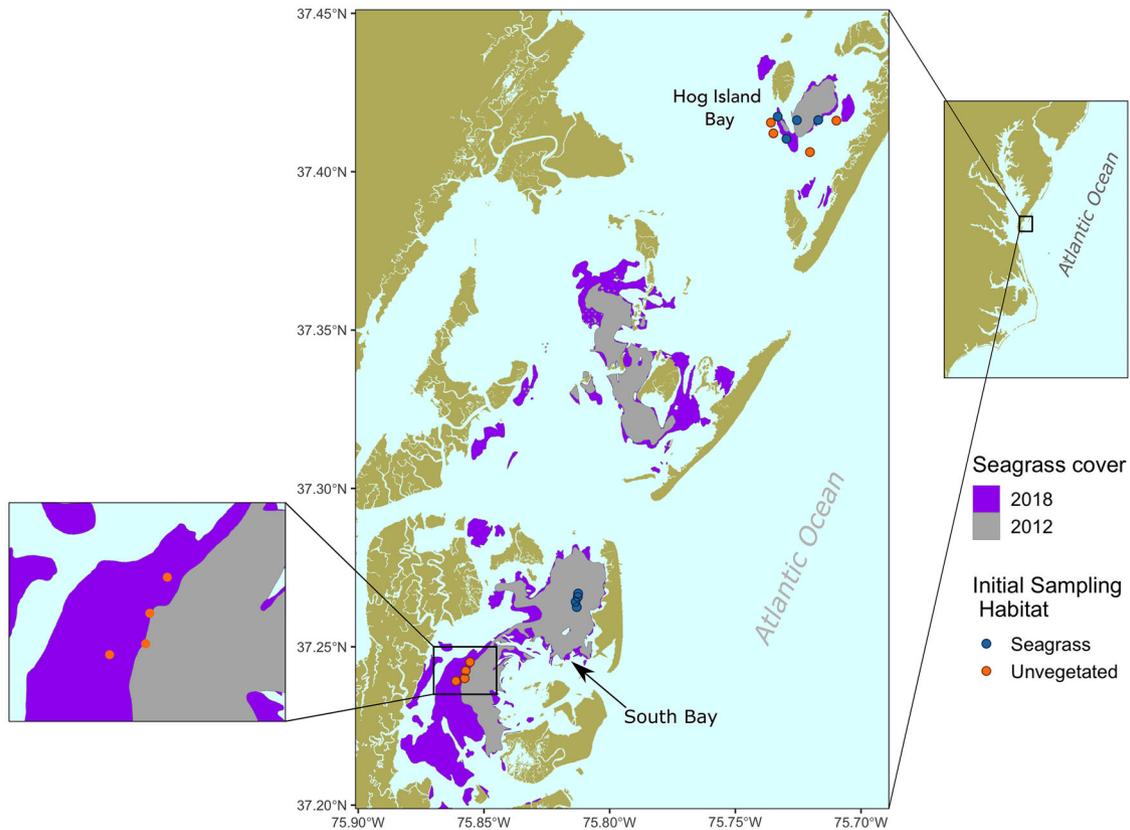
FIGURE 1 Fish sampling sites in Hog Island and South Bay seagrass meadows in the Virginia Coast Reserve (VCR) along the Atlantic coast of Virginia (USA) (gray, extent of seagrass in 2012; purple, extent of seagrass in 2018; points, sampling sites; colored points, presence [blue] and absence [orange] of seagrass at sampling sites when fish surveys began in 2012). Some sites that were initially unvegetated became vegetated during the study period (e.g., bottom left inset).

Abiotic variables

To address our third goal of determining the influence of spatial variation in abiotic conditions on seagrass and the fish community, we modeled the effects of wind fetch, water residence time, and bathymetry on seagrass presence and absence, fish CPUE, and fish species richness. Specifically, we used piecewise structural equation models (SEMs) (described below) to test the hypotheses that wind fetch, water residence times, and depth have direct effects on seagrass occurrence, which in turn mediates indirect effects between these environmental variables and fish community responses. An SEM is a class of modeling technique that allows for testing hypotheses about causal relationships in a multivariate system (Huber, 2014).

Spatial niche modeling in the Virginia coastal bays shows that wind fetch and water residence times are important predictors of seagrass recruitment and survival, respectively (Oreska et al., 2020). We included bathymetry in SEMs because water depth constrains seagrass growth through light limitation in turbid waters (McGlathery et al., 2012; Aoki et al., 2020a) and because desiccation, temperature stress, and wave disturbance cause mortality in shallow zones (Marsh et al., 1986; Boese et al., 2005; Castorani et al., 2014). We also tested the hypothesis that water residence times directly affect fish abundance and richness because sites closer to inlets may be more suitable for fishes due

to the higher stability of abiotic conditions associated with more frequent tidal flushing (Martino & Able, 2003).

We created the wind fetch predictor by averaging wind fetch lengths within 150 m of seine sampling sites from raster layers of fetch calculated across the coastal bays for the summers of 2014 and 2015 (Kremer & Reidenbach, 2021). Fetch was calculated as the maximum distance wind may travel unobstructed over water in a constant direction and was weighted by observed wind directions from a nearby meteorological station. Despite variability in fetch from 2014 to 2015 due to changes in wind direction, fetch lengths at sampling sites were highly correlated ($R^2 = 0.97$), so we assumed that the average fetch length across years was representative of site-specific fetch lengths over the study period. We followed a similar approach to estimate water residence times, which were developed with a 3-dimensional numerical coastal circulation model (Safak et al., 2015). Here, residence time refers to the amount of time a Lagrangian particle, released during high tide, spends at a particular location in the coastal bays before leaving through a tidal inlet (Safak et al., 2015; data from Wiberg et al., 2015). Variability in residence times in the inlet bays—where our seining sites were located—is largely mediated by distance to the bay inlet, bay geometry, and tidal phase (Safak et al., 2015), factors that do not show large interannual variation on the timescale of our study. Therefore, we assumed that the residence times used here were

broadly representative of residence times over the study period. We extracted depths within 150 m of each site with bathymetric maps of the Virginia coastal bays (Richardson et al., 2014; Barnes & Wiberg, 2020).

Statistical analyses

We used generalized linear mixed models (GLMMs) to quantify the effects of seagrass (inside vs. outside meadows) and season (summer vs. autumn) on fish CPUE, richness, and Hill–Shannon diversity. We also evaluated whether the meadow where sampling occurred mediated changes in the fish community by modeling the interactions between meadow location (Hog Island or South Bay) and abundance, richness, and diversity, with sampling sites and years treated as random intercepts (Zuur et al., 2009). Hill–Shannon diversities had a high frequency of 1 s due to seine hauls in which 0 or 1 species of fish were caught, so we subtracted 1 from calculated catch diversities to model the data as zero-inflated (Zuur et al., 2009) and modeled non-zero Hill Shannon diversities with the gamma distribution with log link. We used a negative binomial distribution with log link in community- and species-level models of CPUE and a Poisson distribution with log link to model richness. When comparing the catches of multiple species across habitats or seasons, we adjusted p values according to Benjamini and Hochberg (1995). We used a residual simulation approach to confirm that fitted model residuals met expectations of dispersion, zero inflation, the abundance of outliers, and residual normality with the DHARMa package (Hartig, 2017). We fit GLMMs with the glmmTMB package in R (Brooks et al., 2017).

We applied permutational multivariate analysis of variance with distance matrices (PERMANOVA) to the fish catch data to test the hypothesis that fish community composition differs between meadow locations (South Bay vs. Hog Island Bay) and sampling area (inside vs. outside meadows) (Anderson, 2005). We log transformed catches according to ln(CPUE + 1) for CPUE > 0 in the community matrix and then converted the catch matrix to Bray-Curtis dissimilarities for hypothesis testing. We included sampling area, meadow location, season, and year as model covariates and blocked permutations in sampling sites ($n = 5000$). We used the R package vegan for these analyses (Oksanen et al., 2020).

We used piecewise SEMs to evaluate the strengths of relationships among direct and indirect predictors of CPUE and species richness. We used piecewise SEMs because they provided for the inclusion of hierarchical data structures and non-Gaussian response distributions in evaluating model paths (Lefcheck, 2016). For SEMs of CPUE and richness, we created path diagrams encoding hypothesized relationships among seagrass presence, physical variables (fetch, residence time, and depth), and fish community variables (CPUE, richness) (see "Physical Variables"). All covariates in SEMs were scaled and centered prior to model fitting.

We used Fisher's C to determine whether the proposed model structures were appropriate given the data and that no important paths were excluded (Shipley, 2000; Lefcheck, 2016), in which large p values derived from Fisher's C ($p > 0.05$) indicated a well-fitting model. We modeled the probability of seagrass occurrence with a binomial GLMM with a logit-link and modeled CPUE and richness with negative binomial and Poisson GLMMs with log links, respectively. We found standardized path coefficients for the binomial GLMM submodel with the latent-theoretical approach and for the Poisson and negative binomial models with the observation-empirical approach (Grace et al., 2018). We fitted piecewise SEMs with R package piecewiseSEM and mixed models with lme4 (Bates et al., 2015; Lefcheck, 2016). The data and code used in this manuscript are available for review at https://figshare.com/s/026cbd6a330592a425cd.

RESULTS

Total fish CPUE and diversity

On average, total fish CPUE was 6.4 times greater inside than outside seagrass meadows (Wald $\chi_1^2 = 59.14$, $p < 0.001$). Likewise, estimates of Hill–Shannon diversity were 3.1 times greater ($\chi_1^2 = 4.68$, $p = 0.03$), and estimates of species richness were 2.6 times greater ($\chi_1^2 = 38.67$, $p < 0.001$) inside than outside seagrass meadows (Figures 2a, c, & e). We also found that CPUE, diversity, and species richness were consistently elevated in the seagrass meadow relative to outside the meadow regardless of whether samples were collected in Hog Island or South Bay. However, the interaction model for species richness showed that richness was significantly higher overall in South Bay compared with Hog Island Bay ($\chi_1^2 = 5.39$, $p = 0.02$). Summary tables for community-level statistical models are available in Appendices S2 and S3.

Community composition

Fish community composition differed between vegetated and unvegetated areas (SS = 4.61, pseudo $F = 15.84$, $p = 0.02$). Inside of seagrass meadows, pipefish (*Syngnathus* spp.; $n = 610$) and silver perch (*Bairdiella chrysoura*; $n = 486$) were the most common taxa. Outside of seagrass meadows, anchovies (*Anchoa* spp.; $n = 210$) and Atlantic silversides (*Menidia menidia*; $n = 78$) were most common (Figures 3 & 4). Together with pinfish (*Lagodon rhomboides*) and spot (*Leiostomus xanthurus*), these 6 taxa accounted for 91.8% of the total catch. Twenty-eight additional taxa comprised the remaining 8.2% of catch (see Appendix S4 for complete list). Of the 2664 fish collected over the 2012−2018 sampling period, 86.7% were collected in seagrass (Figure 3a). Significant ($p < 0.05$) species-level differences in CPUE inside and outside seagrass were also evident in 4 of the 6 most common taxa. Species-specific pairwise comparisons showed that 11.7 times more pinfish, 57 times more pipefish, 24.8 times more silver perch, and 14 times more spot were collected inside versus outside seagrass (all $p_{adj.} < 0.01$) (Figure 4b). Despite increased richness in the South Bay
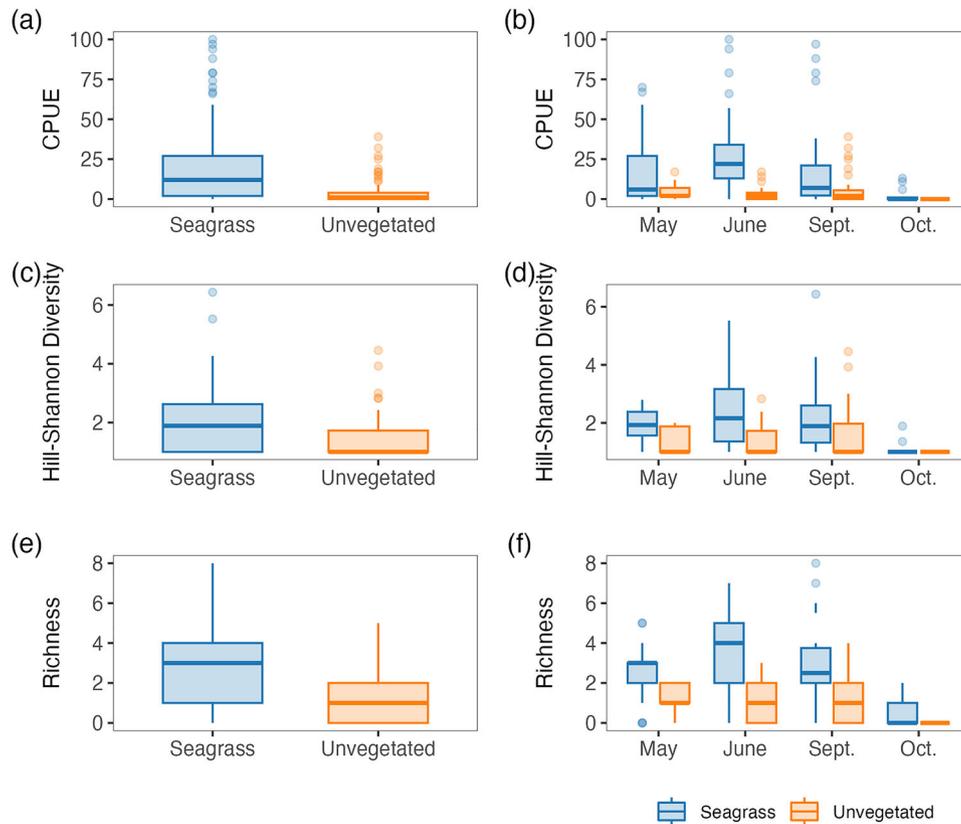
FIGURE 2 In seagrass and unvegetated sampling sites in Hog Island and South Bays (a and b) fish catch per unit effort (CPUE), (c & d) Hill–Shannon species diversity, and (e and f) species richness (a, c, & e) across all sampling months and (b, d, & f) specific to each sampling month (bold lines, median; boxes, interquartile range; whiskers, interquartile range; points, outliers [>1.5 times interquartile range]). All years of data are included (May, 28 sites; June, 72; September, 80; October, 24).

meadow, we did not detect any differences in community composition between the 2 meadows ($p = 0.3$).

Fish lengths

The lengths of collected fishes ranged from 2.5 mm (Gobiidae) to 400 mm (bluespotted cornetfish [*Fistularia commersonii*]). Lengths of the majority of Atlantic silverside, pinfish, silver perch, and spot were below respective lengths at maturity as indicated in the literature (Stevenson, 1958 [anchovy]; Fay et al., 1983 [Atlantic silverside]; Ripley and Foran, 2006 [pipefish]; Ohs et al., 2011 [pinfish]; Grammer et al., 2009 [silver perch]; ASMFC, 2010 [spot]), suggesting that the majority of collected fish were juveniles or postlarvae (Figure 5).

Season and interannual variation in fish communities

Pairwise comparisons showed that CPUE during the summer months significantly exceeded those in the autumn (Wald $\chi_1^2 = 7.45$, $p < 0.01$), and catch data suggested this effect was mostly due to a decline in October CPUE rather than September (Figure 2a). In contrast, D was not significantly different between seasons ($p = 0.8$), although species-level models of

catch across sampling seasons revealed strong within-year patterns in catch composition. Within the top 6 most collected taxa, pipefish, pinfish, and spot were significantly more abundant in the summer rather than autumn months (all $p_{adj.} < 0.001$) (Figure 4a).

Species-specific catches also varied greatly among years. For example, pinfish made up 69% of catch during June 2015, but they were absent from collections in June 2016. Similar patterns emerged for catches of silver perch, which were absent from May 2017 collections but made up 69% of catch in May 2018. Pipefish were the only taxa present across all years and sampling months, whereas Atlantic silversides were present in all sampling years and months except for October of 2018.

Seascape-scale environmental drivers

Fisher's C indicated that no paths were missing from SEMs modeling CPUE ($C = 0.9$, $p = 0.9$, df = 4) (Figure 6), but identified a missing path in the richness SEM between depth and richness that we updated the model to include ($C = 1.04$, $p = 0.6$, df = 2). The best fitting submodel of seagrass presence included an interaction between depth and residence time ($\beta_{unstd.} = -3.13$ [SE 1.24], $p = 0.01$) (unstd., unstandardized) with a significant main effect of depth ($\beta_{unstd.} = -2.55$ [1.0], $p = 0.01$), indicating that seagrass presence was more likely
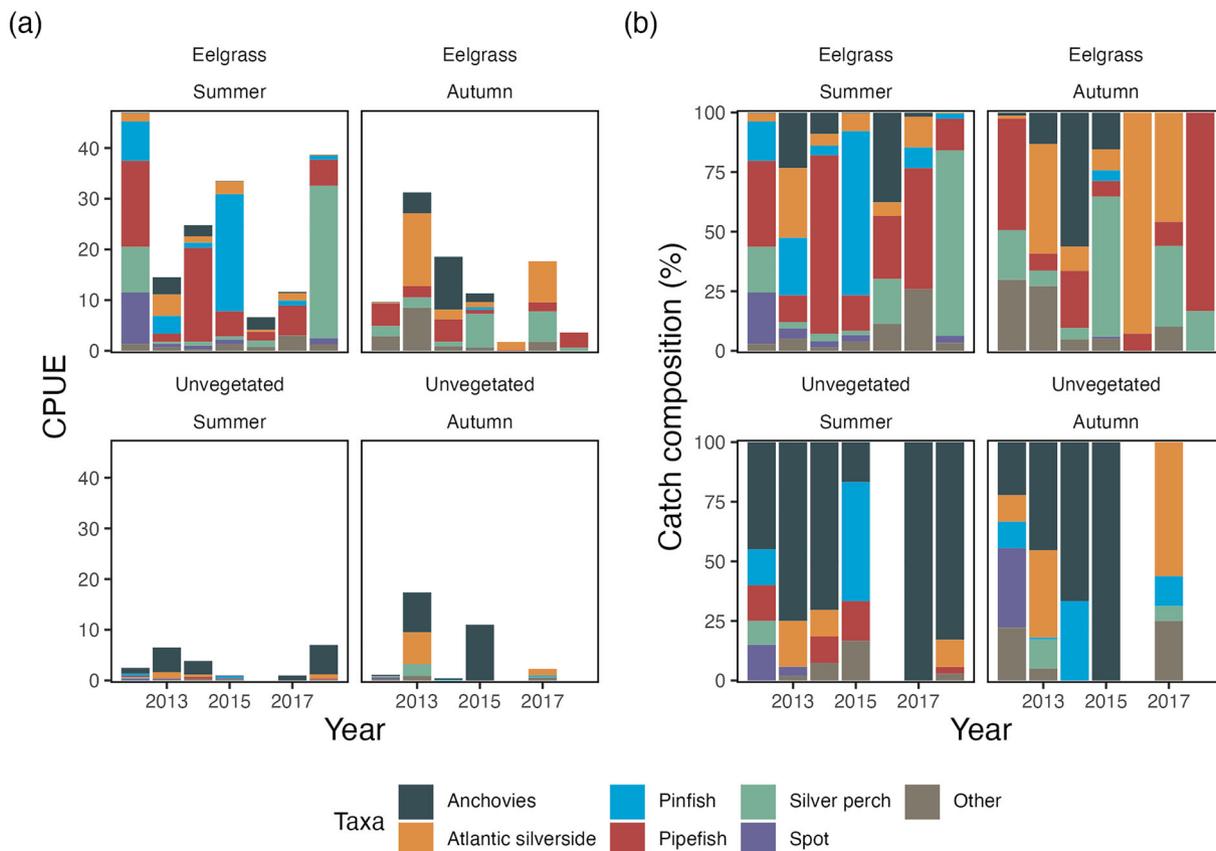
FIGURE 3 Fish catch per unit effort (CPUE) of the 6 most common taxa and all other taxa in the summer (May and June) and autumn (September and October) inside and outside restored seagrass meadows: (a) total and (b) percent contribution of taxa to aggregate CPUE (empty bars, year-season-habitat combination in which sampling occurred but no fish were captured).
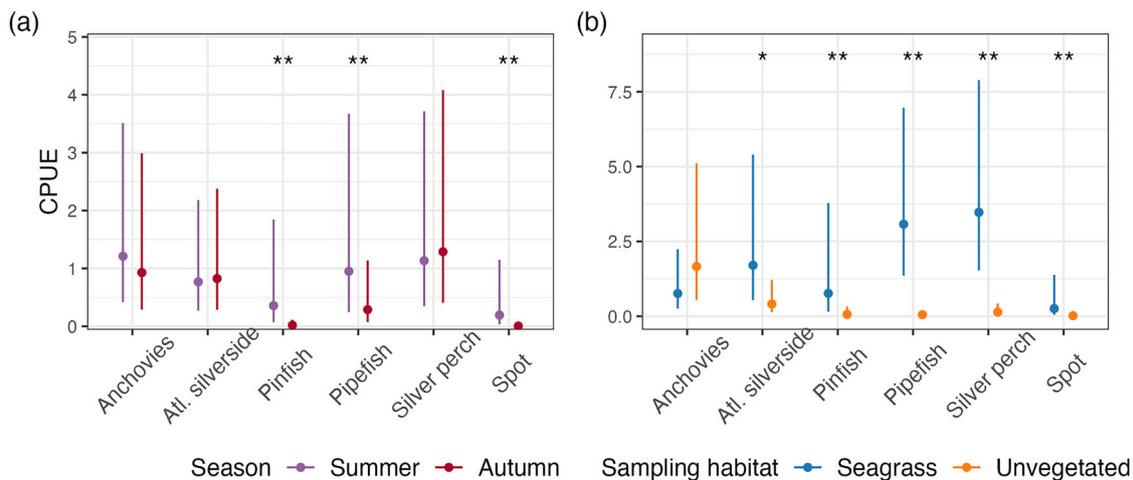
FIGURE 4 Predicted catch per unit effort (CPUE) for the 6 most commonly collected taxa in (a) summer and autumn months and (b) inside and outside seagrass areas (points, marginal means; bars, 95% confidence intervals; asterisks, significant differences [*, $p < 0.1$; **, $p < 0.05$] in mean CPUE between seasons or area type after adjusting for multiple comparisons).

in shallow areas, particularly when those shallower areas were more frequently flushed.

In the CPUE SEM, seagrass presence was the most important contributor to CPUE ($\beta_{unstd.} = 1.82$ [SE 0.23], $p < 0.001$),

whereas residence time did not influence catch. However, in the richness SEMs, seagrass presence ($\beta_{unstd.} = 0.83$ [0.13], $p < 0.001$), residence time ($\beta_{unstd.} = -0.11$ [0.05], $p = 0.03$), and depth ($\beta_{unstd.} = -0.17$ [0.07], $p = 0.01$) were each significant
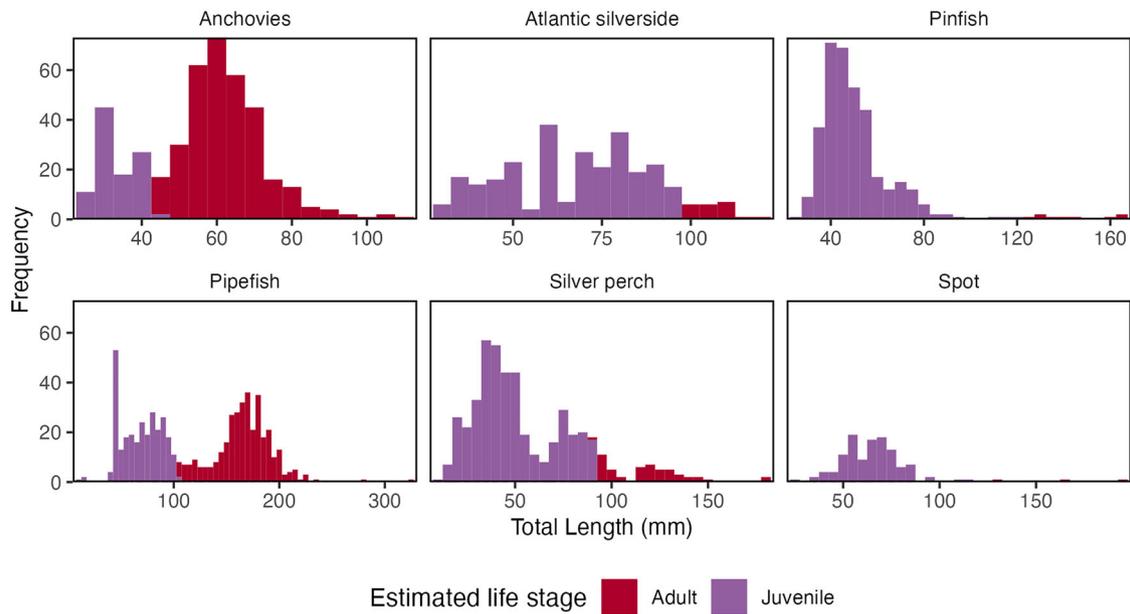
FIGURE 5 Fish length frequencies for the 6 most common taxa in seine collections segregated into estimated life stages based on available estimates of lengths at maturity (purple vs. red). Life stage splits are reported as total lengths at maturity except for pipefish and silver perch, for which length-length conversions were unavailable and reported as standard lengths at maturity. The pipefish length at maturity is the minimum of reported lengths for mature *Syngnathus floridae* females (Ripley & Foran, 2006). For anchovies, length at maturity for the highly abundant bay anchovy (*Anchoa mitchilli*) is shown. These data represent lengths measured during all sampling periods and locations inside and outside seagrass.
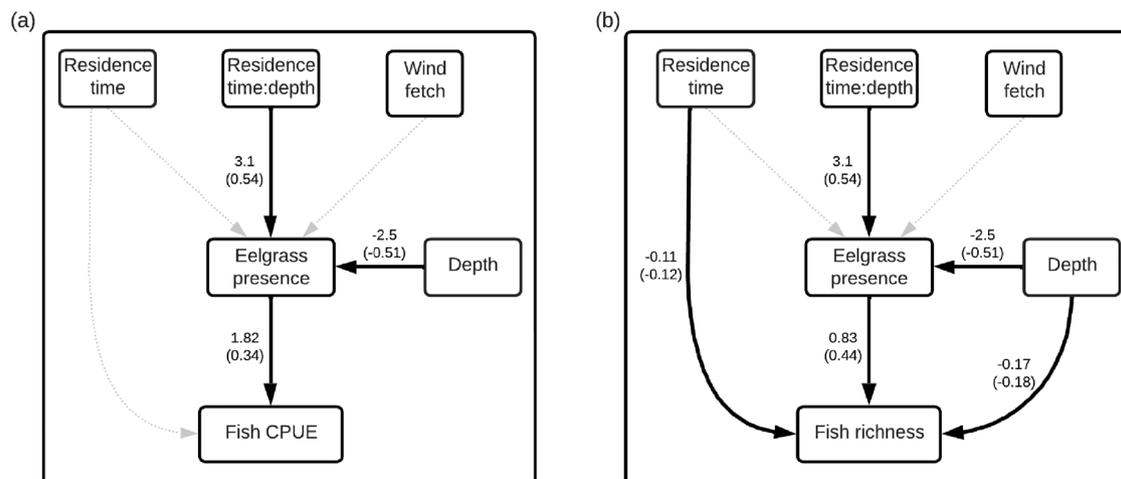

FIGURE 6 Path coefficients for (a) community-level fish catch per unit effort (CPUE) and (b) taxa richness (black, significant at $p < 0.05$; gray, nonsignificant paths; values next to black lines, unstandardized coefficients [$\beta_{unstd.}$] for which $p < 0.05$; values in parentheses, standardized coefficients [$\beta_{std.}$]; residence time:depth, interaction between residence time and depth).

contributors to richness. Standardized coefficients for the richness submodel showed that seagrass presence had a larger influence on mean richness ($\beta_{std.} = 0.44$) (std., standardized) than residence time ($\beta_{std.} = -0.12$) or depth ($\beta_{std.} = -0.18$).

DISCUSSION

Using a spatially replicated, multiyear seine survey, we found that restored seagrass meadows were associated with large gains

in fish abundance and diversity relative to adjacent unvegetated areas. Catches in restored meadows were 6.4 times more abundant and 3.1 times more diverse; substantial differences in community composition were attributable to the presence of seagrass and seasonal patterns in abundance. The seine method we used undersamples fishes that closely associate with the seafloor, where they may avoid the net capture area (Connolly, 1994; Jenkins & Sutherland, 1997). Therefore, our assessment of the benefits of seagrass restoration for the abundance and diversity of juvenile fishes is likely an underestimate.

Patterns of enhanced abundance and richness were stable through space and time despite environmental variability across seagrass meadows and seasonal-to-interannual variability in species composition. The SEM results showed that seagrass presence was influenced by coastal hydrodynamics and bathymetry. Deeper areas with longer residence times (less frequent flushing) were less likely to have seagrass, and an absence of seagrass was associated with less diverse and abundant catches. By considering the environmental constraints limiting restoration success and the provisioning of ecosystem services by restored habitats, practitioners may better optimize site selection during the initial phases of restoration and reduce the risk of restoring habitats that fail to meet benchmarks for recovering lost ecosystem functions. For instance, our results from coastal Virginia indicate that the success of seagrass restoration and the associated benefits for fish production and diversity is maximized at shallow, frequently flushed sites. Optimal site selection guidelines for other regions will differ with variation in the relationships between environmental conditions and seagrass restoration success and the associated direct and indirect effects on fishes.

Our findings showed that fish were more numerous in the restored seagrass meadows than outside them, supporting short-term studies documenting higher densities of fishes in seagrass meadows relative to unvegetated areas (Orth & Heck, 1980; Heck et al., 1989; Arrivillaga & Baltz, 1999; Gilby et al., 2018). Importantly, these patterns held over long periods (5−7 years) despite spatial, between-year, and within-year variability in community composition. Catches were largest during the summer months when new and recently recruited fishes could be found in high densities. For example, pinfish (*L. rhomboides*) recruit to seagrass meadows from offshore spawning grounds in the winter and spring months (Faletti et al., 2019). Likewise, the most abundant taxa in our collections, pipefish (*Syngnathus* spp.), migrate from offshore into estuaries during the spring and summer where spawning and brooding of eggs occurs (Campbell & Able, 1998). We also documented spot (*L. xanthurus*) in higher abundance in seagrass meadows during the summer months, which aligns with the timing of spot larval migration from offshore into nearshore nurseries (spring to early summer in the Mid-Atlantic) (ASMFC, 2010).

Silver perch (*B. chrysoura*) were also collected in higher abundance in the meadow, although catches were similar across seasons, aligning with previous work from the northern Gulf of Mexico identifying silver perch as permanent residents of estuaries with a peak spawning period between mid-March and June (Grammer et al., 2009). Similarly, there was a weakly significant, positive effect of meadow presence on Atlantic silverside abundance ($p_{\text{adj.}} = 0.06$), and silverside catches did not differ between seasons. Within the U.S. mid-Atlantic region, juvenile and adult Atlantic silverside are found in coastal areas in high abundance in all seasons except winter, when migration to deeper or offshore waters occurs (Fay et al., 1983). Our results and the life histories of these species suggest that silver perch and Atlantic silverside may contribute less to seasonal differences in community composition than other species inhabiting the meadows.

Length-frequency distributions for these common fishes suggest that the majority of collected Atlantic silverside, pinfish, silver perch, and spot were juveniles; fish lengths also tended to be smaller during the summer months than in the autumn (Appendix S5). This interpretation was less well-supported for pipefish, possibly because 2 species of pipefish with distinct length frequencies—*Syngnathus fuscus* and *Syngnathus floridae* (Ripley & Foran, 2006)—are found in this region, and we only identified pipefish to genus. Given increases in water temperatures in the Mid-Atlantic that favor the more southerly distributed *S. floridae* (Sobocinski et al., 2013), understanding of the relative abundance dynamics of these species in the restored meadows may provide insights into the responses of seagrass-associated fish communities to climate change. Although our findings suggest that the restored meadows act as preferred habitat for juvenile fishes over nearby unvegetated areas, the vegetated-versus-unvegetated dichotomy oversimplifies the complexity of fish movement patterns in the meadow and broader seascape mosaic (Nagelkerken et al., 2015; Litvin et al., 2018). The coastal bay seascape is composed of a variety of structured habitats used by fishes in addition to seagrass meadows, including intertidal marshes, oyster reefs, and hydrodynamically and bathymetrically complex areas, such as oceanic inlets, channels, and tidal creeks. The proximity of these habitats to seagrass meadows and the capacity of fishes to move between habitat patches influences fish abundance and biodiversity patterns (Yeager et al., 2016; Gilby et al., 2018). Expanding these analyses to consider interactions between restored meadows and features of the seascape more broadly would further refine understanding of how environmental context shapes ecosystem services associated with seagrass restoration.

The SEM analyses showed how seascape-scale environmental covariates affected fish–habitat relationships indirectly by influencing seagrass distributions. Depth negatively affected the probability of seagrass occurrence, indicating a lower likelihood of seagrass presence in deeper areas, where deep, turbid water restricts seagrass growth through light limitation (Carr et al., 2010; Aoki et al., 2020a). Further, we identified an interaction effect of depth and water residence time on the probability of seagrass occurrence, indicating a greater likelihood of seagrass presence in shallower areas, especially those with frequent tidal flushing. Frequently flushed areas tend to have larger sediment grain sizes that are favorable for seagrass growth (Koch, 2001; Wiberg et al., 2015) and may be less susceptible to the disturbance effects of marine heatwaves through more frequent exchange with the cooler coastal ocean (Aoki et al., 2021, Berger et al., 2020).

Although we found that depth and an interaction between depth and residence time mediated seagrass presence and habitat provisioning for juvenile fishes, our analyses were limited because we considered only seagrass presence in the immediate vicinity of sampling sites. Seagrass-associated fish communities will also organize along gradients of seagrass patchiness and areal coverage (Yeager et al., 2011, 2016; McCloskey & Unsworth, 2015). In the species richness SEM, depth had a direct negative effect on species richness, indicating a greater diversity of fishes at shallower sites. This could be due to

correlations between depth and unmeasured characteristics of the meadow, such as meadow area, patchiness, or shoot density (Aoki et al., 2020a; Belgrad et al., 2021). For example, in the shallower and more frequently flushed South Bay meadow, average seagrass shoot densities were 4.4 times greater than in Hog Island Bay during the study period (365 vs. 84 shoots/m^2) (McGlathery 2017; Aoki et al., 2020a) (Appendix S6). Alternatively, physical properties of the water column that scale with depth, such as light availability or water temperature (Aoki et al., 2020a), may alter local suitability and subsequent community structure (Belgrad et al., 2021).

Catches at sites with shorter water residence times (more frequent tidal flushing) tended to be more species rich, a pattern largely due to high richness in the South Bay meadow where residence times were approximately 3 h. Comparatively, residence times at all other sites exceeded 20 h (Appendix S7). Beyond the consistent presence of seagrass in South Bay, this finding may be due to higher stability in environmental conditions afforded by more frequent flushing by the coastal ocean (Martino & Able, 2003), which has been hypothesized to mitigate the negative effects of marine heatwaves on seagrass (Aoki et al., 2021). Alternatively, more frequent water exchange with the coastal ocean may simply introduce more larvae into the meadow, where the presence of dense structured habitat (Grol et al., 2011) and an abundance of food (Lefcheck et al., 2017) could improve survivorship of recruits and lead to a more diverse species assemblage relative to Hog Island Bay.

Through long-term study, we discovered a diverse and abundant coastal fish community that is highly dynamic over space and time yet is consistently enhanced by restored seagrass. Such increases in abundance and diversity add to the numerous ecosystem services shown to recover with large-scale seagrass restoration (Orth et al., 2020). Continued long-term study may further contextualize how local to regional scale environmental variation mediates the benefits of seagrass restoration for fish production and biodiversity. The acceleration of marine habitat restoration in recent decades (Duarte et al., 2020) should serve as motivation for new studies to evaluate the functional services of restored habitats, advise restoration planning, and inform policies that incentivize restoration (e.g., Smith & Castorani, 2023). For example, the seagrass restoration we studied will soon be the first of its kind to enter a blue carbon market with payments for ecosystem services, which involves a spatial accounting of carbon sequestered by the restored meadow (Oreska et al., 2021; Shilland et al., 2021). Understanding how ecosystem services beyond carbon sequestration, such as provisioning habitat and supporting biodiversity, could contribute to such markets is nascent, but interest in these services is growing (Shilland et al., 2021).

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OPEN RESEARCH BADGES

This article has earned Open Data badges. Data is available at https://figshare.com/s/026cbd6a330592a425cd.

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SUPPORTING INFORMATION

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