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ARTICLE

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Artificial oyster reefs can facilitate the recovery of lost ecosystem function in fragmented seagrass habitat

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Abstract

Seagrasses suffer population decline when environmental stress exceeds physiological tolerance. In such instances, seagrass restoration can be successful if stressors are alleviated; however, many stressors cannot be addressed at a local scale. As such, seagrass restoration efforts often fail. In this study, we tested whether artificial oyster reefs—which are comparatively more robust to many environmental stressors—can facilitate the recovery of some lost ecosystem services in bare patches of a fragmented seagrass meadow. From 2021 to 2023, artificial reefs constructed of concrete blocks were installed annually in bare sediment patches of a nearshore estuarine eelgrass (*Zostera marina*) meadow in Prince Edward Island, Canada. In 2023, reefs were sampled to determine benthic and pelagic biodiversity, as well as abiotic environmental conditions adjacent to and away from the reefs. A total of 45 taxa were observed on the artificial reefs. Initial colonization was dominated by oyster (*Crassostrea virginica*) spat. Maximum benthic taxonomic richness was reached within one year of reef installment, and community biomass quadrupled one year thereafter, which was mostly attributable to oyster growth. Short-term monitoring of pelagic species suggested that numerous fish species actively used 2-year-old reefs for both feeding and sheltering, compared to no fishes actively using a reference bare patch; fish diversity and evenness generally increased with reef age. Reefs also appeared to modify localized water quality parameters relative to bare patches by lowering temperature and turbidity, increasing dissolved oxygen, and lowering pH. Together, these results provide support that artificial oyster reefs can facilitate the recovery of lost ecosystem services within fragmenting and declining eelgrass beds. When replacing lost or declining habitat has a low probability of success, shifting restoration efforts away from directly replacing that habitat in a 1:1 manner toward providing different, supplemental habitat comprised of foundational species that can persist will result in more effective restoration programs.

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KEYWORDS
benthic ecology, biodiversity loss, coastal restoration, ecological facilitation, estuary, marine conservation, reclamation

INTRODUCTION

The fragmentation, degradation, and loss of habitat is considered the most important threat to global biodiversity (Chase et al., 2020; Díaz et al., 2019; Pimm et al., 2014; Segan et al., 2016; Yuan et al., 2024). Habitat loss threatens thousands of species and is likely to result in extinction for many (Braun et al., 2023; Gonçalves-Souza et al., 2020; Nikolaou & Katsanevakis, 2023; Yan et al., 2021). The negative impacts of habitat loss on global biodiversity are primarily a result of lost spatial coverage, as fewer species persist and extirpation risk increases when there is less space (Chase et al., 2020; Hanski et al., 2013; He & Hubbell, 2011). Protecting existing habitat and restoring lost habitat, where possible, can offset decreases in habitat coverage and alleviate negative impacts on biodiversity (Piczak et al., 2023).

While habitat restoration activities often prioritize restoring habitat in a 1:1 manner (i.e., restoring the same foundational species and ecosystem), many habitats degrade because conditions within the localized environment no longer support their foundational species. In such cases, attempting to restore the ecosystem to its previous state is unlikely to succeed. Establishing new structural habitat comprised of foundational species that can persist in the localized environment and provide similar and/or alternative ecological services, can help functionally restore lost habitat and maintain biodiversity (Hobbs et al., 2009; Svnning et al., 2024). Herein, including alternative habitat adjacent to declining or fragmenting existing habitat can facilitate positive ecological connections between habitat types and lead to better restoration outcomes (Silliman et al., 2015). Actively restoring ecosystem function through the use of supplemental habitat that can persist, despite existing and future threats, can thus aid in the conservation of global biodiversity (Banks-Leite et al., 2020) and can help to mitigate negative effects imposed by development activities (Barrell et al., 2014). Such an approach is perhaps more likely to succeed than attempting to restore ecosystems to their previous species-specific state (Silliman et al., 2015).

In marine systems globally, seagrasses provide highly productive, three-dimensional habitat for diverse ecological communities (Terrados & Borum, 2004) and support commercial and recreational fisheries (Unsworth, Nordlund, & Cullen-Unsworth, 2018). Seagrasses also provide a wealth of other ecosystem services, including primary production, sediment stability and erosion control, air and water quality maintenance, nutrient cycling, storm protection, and carbon sequestration, among others (Lima et al., 2023; Ricart et al., 2021). Unfortunately, seagrasses are experiencing global declines in the face of myriad pressures (Capistrant-Fossa & Dunton, 2024; Dunic et al., 2021; Manca et al., 2024; Short et al., 2011; Turschwell et al., 2021; Unsworth, McKenzie, et al., 2018; Waycott et al., 2009). In this reality, conserving seagrass and its critical ecological roles is of paramount importance (Unsworth et al., 2022).

To promote seagrass conservation, a multitude of restoration programs have been attempted across the globe (Ward & Beheshti, 2023; Zhang et al., 2024); however, seagrass restoration consistently displays some of the lowest success rates among marine restoration types (Bayraktarov et al., 2016; Danovaro et al., 2025). This is particularly true for eelgrass, *Zostera marina*—the dominant and most widespread species of seagrass in the Atlantic and Pacific Oceans of the temperate northern hemisphere (Hasegawa et al., 2008). Despite advancements in methodologies (Sinclair et al., 2021; Thom et al., 2008; van Katwijk et al., 2009), eelgrass restoration projects experience high rates of failure (30%–60%) for various reasons (Eriander et al., 2016; Orth et al., 2009; Ward & Beheshti, 2023). Generally, initial stressors causing eelgrass decline are rarely alleviated prior to restoration, meaning that the environment itself is likely inhospitable to eelgrass. This is particularly true in northern temperate regions where winter conditions can impose high rates of mortality for transplanted eelgrass (Eriander et al., 2016). Facilitating the recovery of existing-but-declining eelgrass habitat through the use of supplementary habitats that provide similar ecosystem services to eelgrass but are more tolerant to stressors that eelgrass is sensitive to, may prove more successful in the long term.

Oyster beds are nearshore marine habitats that provide similar ecosystem services to eelgrass (Coen et al., 2007; Grabowski & Peterson, 2007) and often occupy adjacent or overlapping areas (DuBois et al., 2024; Valdez et al., 2017). Like eelgrass, oyster habitat restoration has a long history in the United States (Grizzle et al., 2021; Luckenbach et al., 1999). Typically, oyster restoration aims to recreate oyster habitat where it has been reduced or extirpated, or to mitigate against the contraction of existing oyster beds. Oysters are also more tolerant to

some stressors that contribute to eelgrass decline (e.g., high temperature and turbidity) and, as such, may be able to not only deal with those stressors but reduce their impact on remaining eelgrass by, for example, reducing turbulence (Wiberg et al., 2019) and turbidity (Nelson et al., 2004). Furthermore, the presence of shellfish is reported to directly benefit seagrass habitat through positive ecological facilitation (Vozzo et al., 2023). Success rates of oyster restoration projects are comparatively higher than those of seagrass by approximately 20% (Bayraktarov et al., 2016). While oysters cannot directly replace all of the ecosystem functions offered by eelgrass, both species act as ecosystem engineers providing biogenic habitat to support coastal biodiversity and contribute to localized physicochemical conditions. Oyster reefs thus have the potential to serve as a supplementary restoration technique to support lost ecosystem services in declining eelgrass beds.

The use of artificial oyster reefs as a supplemental habitat restoration method in eelgrass meadows has received little practical and research attention. Whether this technique can successfully be implemented thus remains uncertain. In the Pacific United States, one study reported approximately 99% mortality of oysters (*Ostrea lurida*) by predators from the nearby eelgrass bed (Valdez et al., 2017); however, the presence of oysters had no negative effects on the eelgrass itself (Briley et al., 2021). The efficacy of this technique on the east coast of North America, and elsewhere, remains unexplored.

The aim of this study was to determine whether artificial oyster reefs could improve epibenthic ecosystem function in bare patches of a fragmented eelgrass meadow in eastern Canada. The goals of this project were as follows:

1. Measure biodiversity and ecological succession of epibenthic communities on reefs over the course of 3 years (2021–2023).
2. Document fish use of the reefs.
3. Determine whether established (2-year-old) reefs influence surrounding abiotic conditions compared to those in bare sediment patches.

Generally, we predicted that the artificial reef structures would create biodiverse communities of epibenthic and pelagic organisms, including many nearby eelgrass residents, and enhance localized water quality parameters relative to bare patches without oyster reefs. It is important to specify here that we did not anticipate that oyster reefs would facilitate a 1:1 recovery of all species and conditions found within eelgrass meadows. As such, we did not directly compare reef endpoints to eelgrass habitat itself; rather, we interpreted the epibenthic biodiversity and environmental characteristics of the reefs relative to the lost services in bare sediment patches. The scientific objectives, methods, and monitoring approaches for this project were codeveloped with the Lennox Island First Nation, with the goal of providing the community with easily accessible tools for restoring culturally and ecologically significant habitat within their traditional territory.

METHODS

Study area

The study was conducted in nearshore shallow waters on the eastern end of Lennox Island, Prince Edward Island, Canada (46.60° N, 63.84° W; Figure 1). The site was geographically nestled within Malpeque Bay (mean semidiurnal tidal amplitude approximately 0.45 m; mean high water–low water, https://www.tides.gc.ca/en/stations/01905) in the temperate southern Gulf of St. Lawrence. The site consists of a subtidal eelgrass (*Z. marina*) meadow mosaic interspersed with large patches of bare sediment (Figure 1) and is typically ice-covered during winter. The Lennox Island First Nation is an integral collaborator in this project, and it is through its knowledge and generosity that this work was made possible.

Reef deployment

New artificial reefs were installed in bare sediment patches within the eelgrass meadow in July for three consecutive years: 18 reefs in 2021 (July 12), 16 in 2022 (July 28), and 8 in 2023 (July 25). Reefs were comprised of three-dimensional mounds of eight to ten concrete blocks (Shaw Group Ltd.; 40.6 cm × 20.3 cm × 20.3 cm L × W × H) (Figure 1). Concrete blocks were selected for use because they, as a common construction material, are readily available, are relatively inexpensive, are easy to deploy from a small boat, and are the most common substrate used in oyster restoration studies (Goelz et al., 2020). The concrete blocks comprising each reef were not arranged in any particular configuration but were installed so that there were at least three layers of bricks, with two above the sediment surface. Spatially, the reefs were deployed without a pattern, but far enough apart that they were considered independent (Figure 1); reefs from each of the 3 years overlapped in general area to avoid confounding effects of spatial placement on the interpretation of interannual differences.

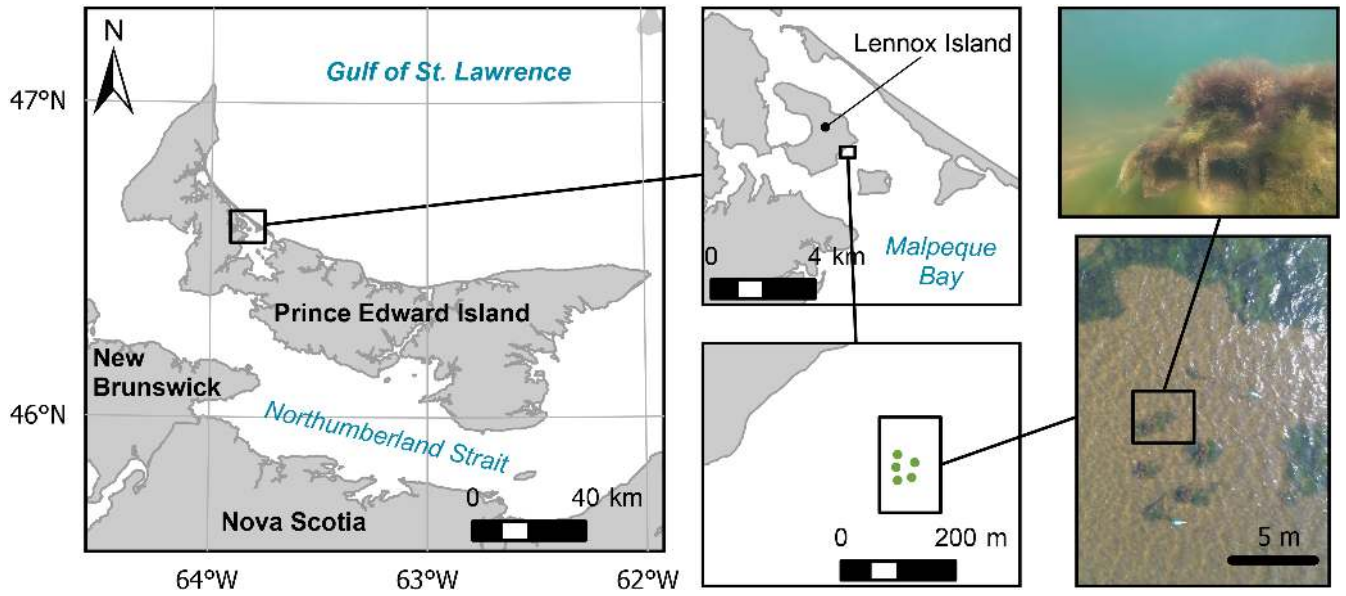


FIGURE 1 Maps of the study area near Lennox Island, PE, Canada, depicting the layout of some individual reefs deployed in 2021, and photographs of an individual reef consisting of 10 concrete blocks. Photo credit: Jeffrey Barell.

Benthic community

In October 2023, we collected three individual concrete blocks on three separate reefs from each of the three reef year classes: 2-year reefs deployed in 2021, 1-year reefs deployed in 2022, and 0-year reefs deployed earlier in 2023. The top and sides of individual blocks were visually inspected for mobile macroinvertebrates and sessile species susceptible to damage during processing (e.g., barnacles) prior to being collected, and the presence of these organisms was recorded. When possible, counts of mobile macroinvertebrates were also recorded. On the boat, any remaining large mobile species (e.g., lobster, fish, large crabs) were removed from the insides of the block and their presence was recorded prior to placing them back in the water. The block was then photographed, and the biotic contents were scraped into a sampling bag. Samples were transported in coolers to the Fisheries and Oceans Canada Regional Office in Charlottetown, PE and stored at −4°C until processing.

Individual samples were removed from the freezer and thawed prior to processing. Sample processing and organism identification was conducted by the same individual to ensure consistency in processing and identification; taxonomic guides used for organismal identification included Roff et al. (1984) and Pollock (1998). Once thawed, the total mass of the sample was taken. The sample was then separated into three different groupings: (1) larger organisms by which species was easily identifiable (hereafter 'larger organisms'); (2) smaller organisms that could not easily be identified to species (hereafter 'smaller organisms'); and (3) unidentifiable sample contents (hereafter 'unidentifiable contents'). The larger organisms were then identified to the lowest practical taxonomic level (species level where possible), and counts and mass for individual taxa were recorded when possible. For the smaller organisms, all species were combined, and the sample was homogenized (gentle mixing with a spoon for 2 min) and weighed. A subsample (10% of the smaller organism sample mass; Sebastien et al., 1988) was then obtained, the organisms were identified to the lowest practical taxonomic level as above, and counts and mass of each species/taxon were obtained; counts and mass for the smaller organisms were multiplied by 10 prior to analysis. Finally, the unidentifiable contents were weighed. It is important to note here that counts and mass were not obtainable for all individual species, as the individuals of some species (algae, colonial tunicates, and bryozoans; that is, fragile species without a robust exoskeleton) were destroyed when the bricks were scraped. For these taxa, we simply recorded the presence of species. Similarly, American lobsters (*Homarus americanus*), fish, and large mobile crabs were immediately returned to the water after being counted, and as such, we were unable to obtain biomass data for these organisms. Taxa for which counts and/or biomass data were not obtained were excluded from any analyses of count or biomass data but were included in analyses of taxonomic richness.

Fish assemblage

We monitored daytime diversity of pelagic fish species on reefs from each year class through video. GoPro HERO9 cameras were individually affixed to individual concrete

blocks (separate from reef blocks) and deployed in the field over the course of 3 days from August 22 to 24, 2023. All cameras were deployed between approximately 11:00–12:00 (mean: 11:33, max: 12:07, min: 10:57) and retrieved between approximately 12:30 and 13:00 (mean: 12:48, max: 13:07, min: 12:23), resulting in videos of 1.0–1.5 h duration (mean: 1:15, max: 1:37, min: 0:56). Deployment times were chosen to maximize sunlight and reduce shadows and glare, thus maximizing visibility of the reefs and organisms in the videos. The cameras were set to the default underwater resolution setting and were positioned facing northeast such that the sun was behind the camera. The camera angle was then adjusted to reduce glare and ensure that an individual reef was visible in the camera frame. All other settings were adjusted to maximize projected battery life prior to deployment.

Cameras were deployed to monitor reefs from each of the three year classes. To avoid physically disturbing the reefs prior to video monitoring, reef year class was inferred visually from a distance during deployment and later confirmed during camera retrieval. As such, some reef year classes were initially misidentified, resulting in uneven sample sizes for the three year classes ($n = 2$, $n = 5$, and $n = 4$ for 0-, 1-, and 2-year reefs, respectively; one camera per reef). We also deployed a single reference control camera in a bare sediment patch without any reefs. Once each camera was retrieved, the videos were downloaded and saved to an external hard drive for later processing.

Videos were later analyzed by randomly generating 24–32 individual time points (depending on length of video) within each video and examining the still frame at that time point; the first and last 5 min of the video were excluded to account for disturbance following the placement and retrieval of the camera. Any fish that were observed in the frame were identified to the lowest taxonomic unit possible and counted. The video between each analyzed frame was briefly assessed visually to ensure that the fish counted in each analyzed frame were indeed unique fish (i.e., that individual fish were not counted twice). A subjective duration of time before and after each individual frame were viewed to determine whether individuals were actively using the reef or just passively swimming by. The behavior of individuals actively using the reefs was then categorized as either feeding (actively consuming contents, such as vegetation or biological material off reef surface, on or within the reef) or sheltering (moving in and out of the reef and actively using the reef to hide). Any other significant biological events (e.g., the presence and behavior of lobsters or other mobile epibenthos) were also noted.

Environmental effects

To determine whether the artificial reefs had the capacity to influence the localized aquatic environment, we deployed a series of continuous data loggers affixed to three stands to monitor abiotic conditions that might influence biological activity: dissolved oxygen, pH, salinity, temperature, and turbidity (one logger per stand for each parameter, except temperature and pH which were both measured by the same multiparameter logger; see Appendix S1: Table S1). The three stands were strategically placed such that one stand was located directly beside a 2-year reef (hereafter termed "Reef"), while another was within the overall area of where the reefs were deployed but not directly beside a reef (hereafter termed "Inside"), and the other in a bare sediment patch well outside the general area of the reefs (reference control; hereafter termed "Outside"). Loggers were deployed for a total of 29 days, from July 26 to August 24, 2023. While the time and frequency of logging was not standardized between data loggers, the loggers provided, at minimum, one measurement per hour. Detailed information on logger models for each abiotic parameter are available in Appendix S1: Table S1.

Data analysis

Data analysis was conducted using RStudio (RStudio Team, 2020) equipped with R version 4.4.0 (R Core Team, 2024). Statistical significance was defined at $p \leq 0.05$, although marginally nonsignificant effects are discussed when appropriate. Values reported in the text are means ± standard deviation computed from raw data. For all boxplot figures, boxes represent the interquartile range (IQR) with the top and bottom bounds, respectively, representing the 75th and 25th percentiles, while top and bottom bounds of the whiskers, respectively, denote the maximum and minimum values of the data within 1.5× IQR; the thick lines within the boxes represent the median value of the data. To ensure FAIR data and code for reproducibility (Roche et al., 2022), supplementary figures and tables are provided in Appendix S1; source data and annotated R code are openly available through Mendeley Data (Clements et al., 2026; https://doi.org/10.17632/v7976rzxbv.3). With the exception of Figures 2 and 6 being generated in Microsoft Excel, all figures depicting benthic community data (Figures 3–5, 7 and 8) were generated using the 'ggplot2' package in R (Wickham, 2016).

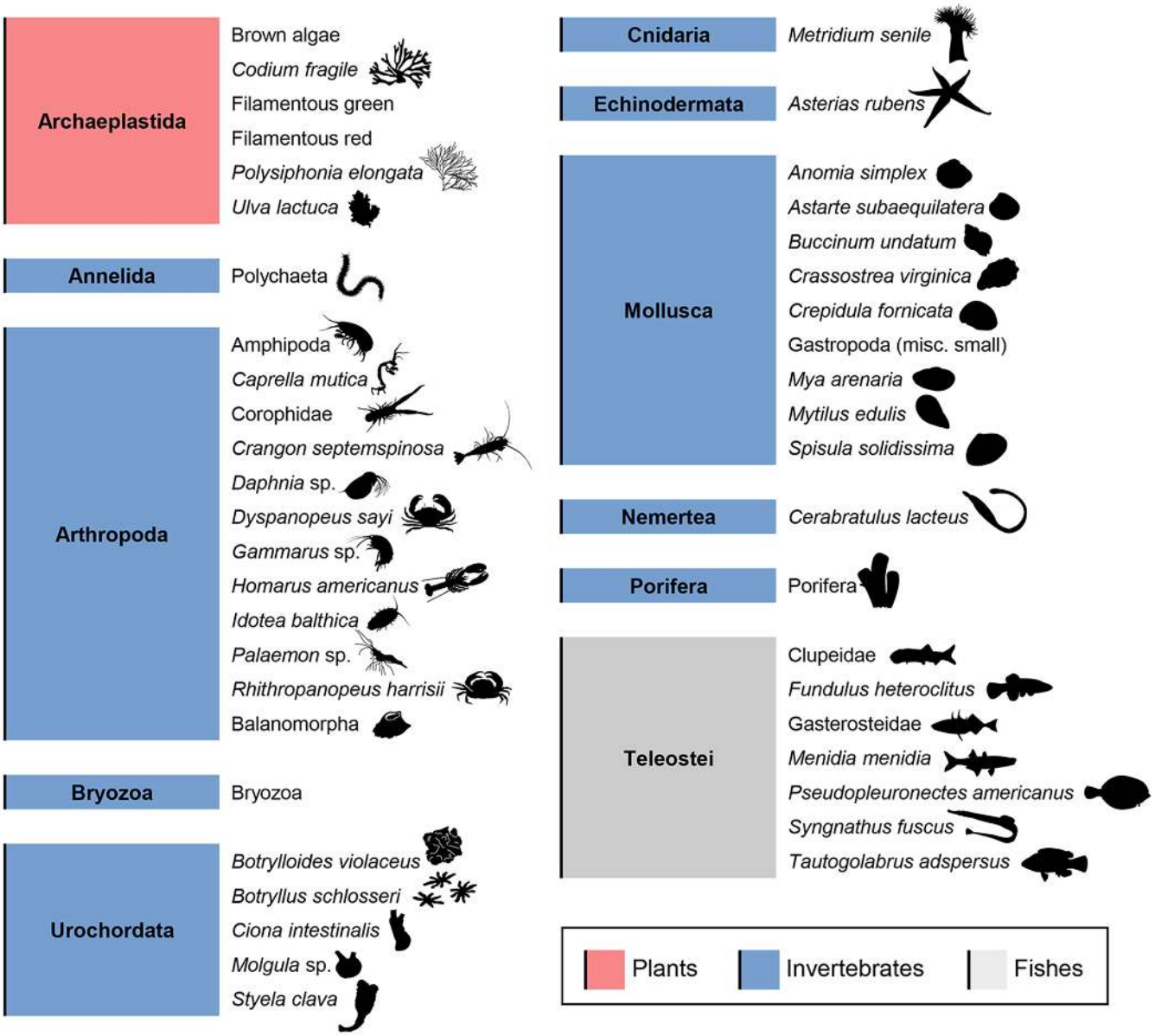


FIGURE 2 Taxonomic diversity observed on artificial reefs in this study, listed alphabetically by phylum (top–bottom, left–right). Illustration credit: Jeff C. Clements.

Benthic community

To assess successional changes in benthic species richness and whole-community biomass, we used a generalized linear modeling approach to test for differences between reef year classes. We initially built generalized linear mixed models with reef year class as a categorical fixed factor (three levels) and reef ID nested within year as a random variable; however, the mixed models for both endpoints had a singular fits, suggesting that the random variance was negligible. We thus removed the random factor and used non-mixed models instead. The model for species richness (i.e., species/taxa count) was built with a Poisson error distribution for skewed count data, while a Gamma error distribution was applied for the biomass model. Overdispersion was checked using the *check_overdispersion*() function from the 'performance' package (Lüdecke et al., 2021); data were not overdispersed (richness model dispersion ratio = 0.28; biomass model dispersion ratio = 0.64; underdispersion for the richness model was due to highly similar assemblages within reef year classes). The *Anova*() function from the 'car' package (Fox & Weisberg, 2019) was used to obtain statistical results for the effect of reef year class on each endpoint. Where significant effects of year class were detected, we subsequently used the *emmeans*() and *pairs*() functions from the 'emmeans' package (Lenth, 2024) to

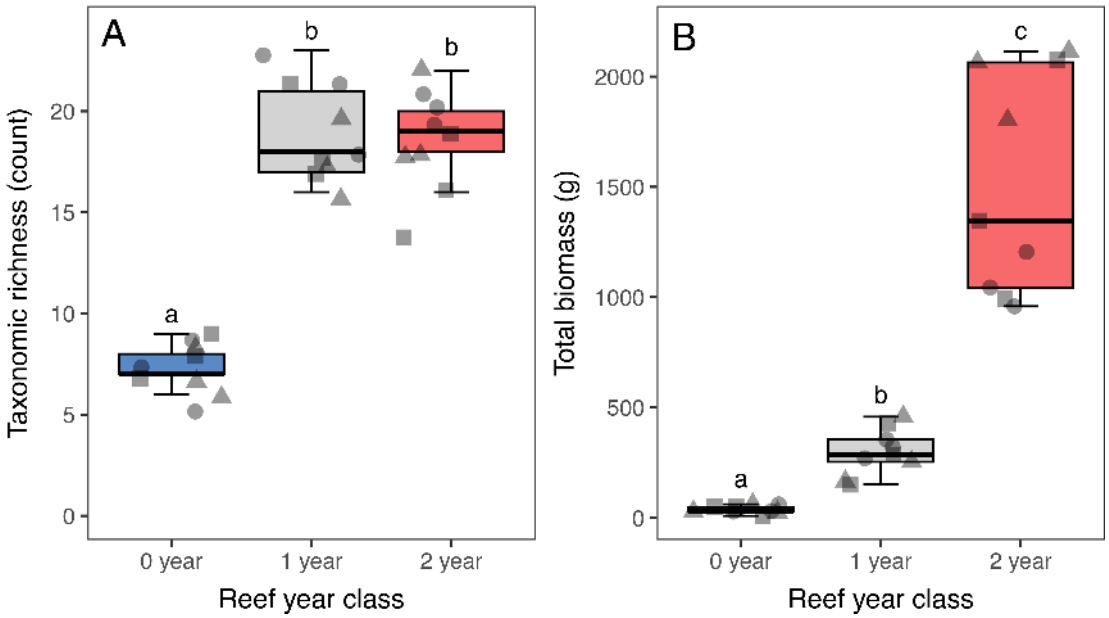


FIGURE 3 Boxplots depicting (A) taxonomic richness (taxon count) and (B) whole-community biomass for the three reef year classes. Letters above boxplots represent pairwise differences between year cases (see Appendix S1: Table S2 for full results). Note that taxonomic richness, but not biomass, includes American lobster, *Homarus americanus* (H. Milne-Edwards, 1837) (lobsters not weighed). The midline depicts the median; box limits depict the interquartile range (IQR); and whiskers represent 1.5× the IQR; data points represent individual bricks from each of the three reefs (different symbols) for a given year class.

obtain pairwise differences between year classes, applying a Holm *p*-value adjustment.

Given that the goal of the artificial reefs was to create oyster habitat that would facilitate biodiverse communities, we also honed in on successional changes in the abundance and biomass of oysters (spat and adults) across reef year classes using the same generalized linear modeling approach as above, building separate models for oyster spat and adults. Because some reef year classes contained zero counts (and thus zero biomass) on all of the concrete blocks, we added 0.1 to all count and biomass data prior to model construction. This created non-integer data for both endpoints, and we thus fit all initial models with Gamma error distributions (log-link) to account for nonlinearity in the raw data. Again, random-effects models had singular fits and nonrandom models were then applied for the abundance and biomass data, respectively; no models were overdispersed (dispersion ratios 0.30–0.78). As above, the *Anova*() function was used to obtain statistical results for the effect year class and the *emmeans*() and *pairs*() functions were used to obtain pairwise differences.

Finally, we used multivariate redundancy analysis (RDA) to determine what species were driving differences in community structure (species abundance and biomass) across year classes. This analysis was conducted on two separate datasets for each endpoint (abundance and biomass): one including the whole biological community, and another only including sessile animal species. Environmental (reef ID, brick ID, reef year class) and community (species/taxa) data were specified using the *fix*() function in R. Next, because many species/taxa had zero counts and biomass, we added 0.001 to all values, and species data were subsequently transformed using the Hellinger procedure (Legendre & Gallagher, 2001; Legendre & Legendre, 2012). We then constructed partial RDA models (with Euclidean distance) for each dataset using the *rda*() function from the 'vegan' package (Oksanen et al., 2024): one with reef year class as a sole categorical fixed factor (three levels) and another with both reef year class and reef ID nested within year class as categorical fixed factors. We then used the base *anova*() function to compare model fits via backward Akaike Information Criterion selection; model fits were not significantly different for each of the four datasets, and we thus selected the most parsimonious model (i.e., the model with reef year class as the only predictor variable). Model results (i.e., significance of reef year class) were then obtained using the base *anova*() function (999 permutations), and model fits were derived using the *RsquareAdj*() function from the 'vegan' package. Pairwise differences between the three years were obtained using the *multiconstrained*() function from the Biodiversity R package (Kindt & Coe, 2005) using the 'rda' method and Euclidean distance. It is important to note here that direct comparisons of species contributing to whole-community relative abundance trends in biplots cannot directly be compared to those contributing to

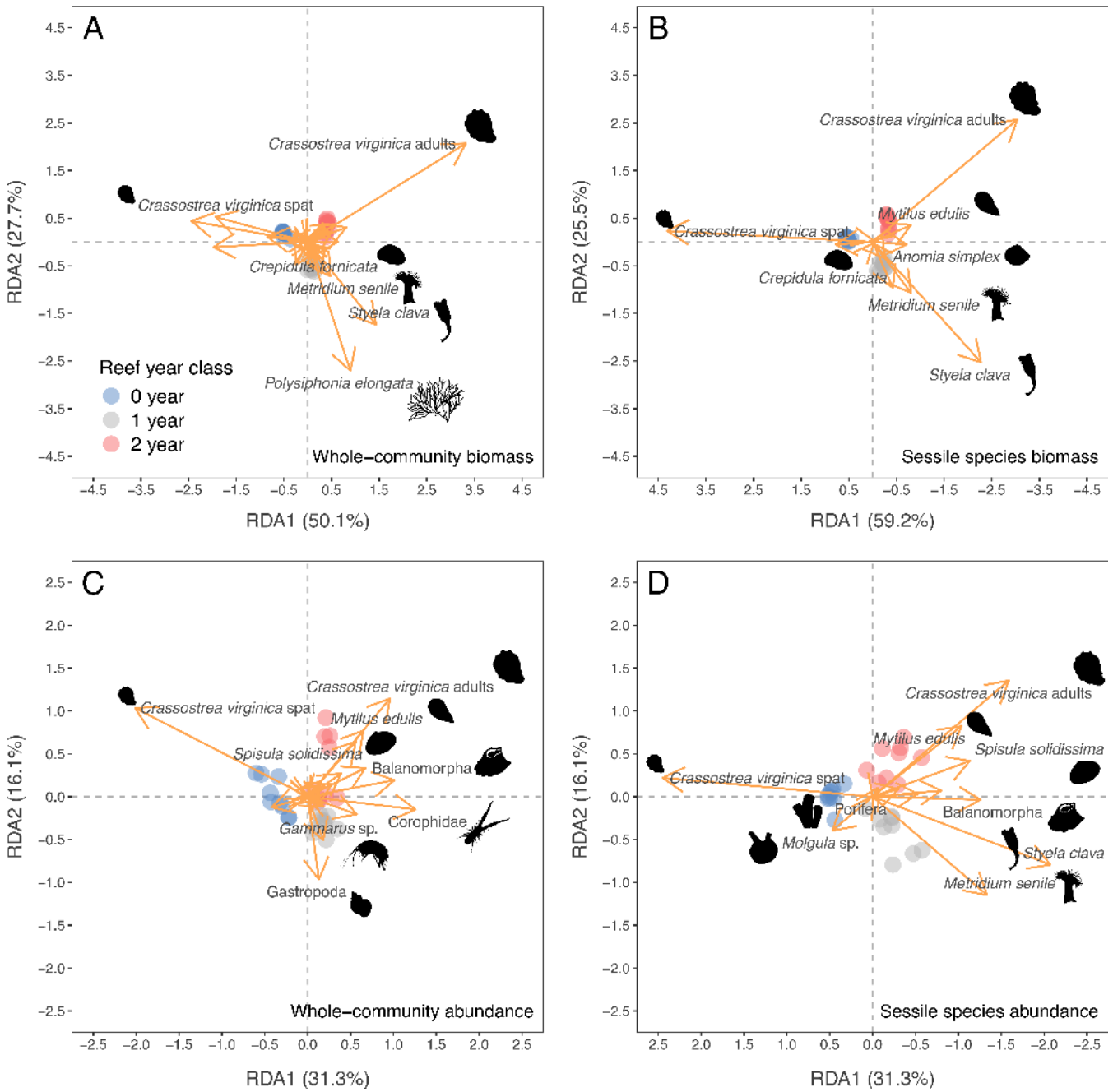


FIGURE 4 Ordination plots for each of the four datasets used in the redundancy analysis (RDA): (A) whole-community biomass, (B) sessile animal biomass, (C) whole-community abundance, and (D) sessile animal abundance. Illustration credit: Jeff C. Clements.

whole-community biomass, as some species included in the biomass dataset could not be included in the abundance dataset due to difficulties in counting individuals (marine plants, colonial tunicates, and bryozoans).

Fish assemblage

Due to the relatively low and uneven sample sizes of videos for monitoring fish biodiversity, we elected to forego formal statistical analyses and approach these data descriptively. Herein, we computed basic summary statistics for each reef year class (and the reference bare patch), including the average number of fish per reef (±SD), the total number of fish observed on reefs from each year class, the total number of fish actively interacting with reefs from each year class (i.e., feeding and/or sheltering), and the total number of fish species observed on reefs from each year class. We then pooled the data across videos to visualize the relative

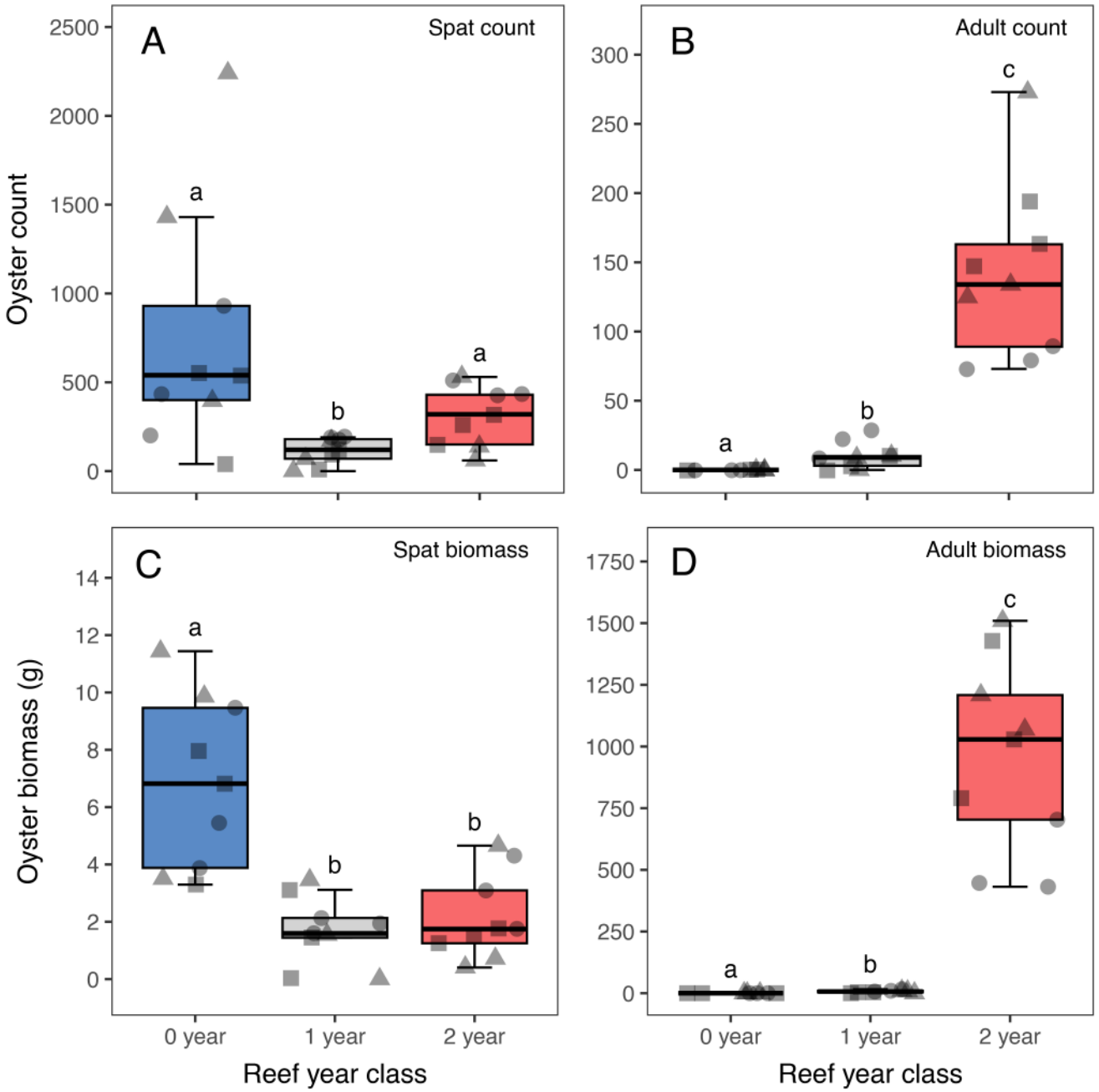


FIGURE 5 Boxplots depicting the (A, B) abundance and (C, D) biomass of (A, C) oyster spat and (B, D) adults for the three reef year classes. Letters above boxplots represent pairwise differences between year cases. The midline depicts the median; box limits depict the interquartile range (IQR); and whiskers represent 1.5× the IQR; data points represent individual bricks from each of the three reefs (different symbols) for a given year class.

percentages of species observed in the videos on each of the three reef year classes and in the reference bare patch. We also visualized the relative percentages of individuals actively using the reefs for each species (as opposed to passively swimming by the frame of the video) and for each reef year class (species pooled). Finally, for each species, we visualized the percentage of active use observations that fell into the two categories of active behaviors: feeding and sheltering.

Environmental effects

Given that the timing and frequency of recordings for each abiotic logger was not uniform, we computed hourly averages of each abiotic parameter (dissolved oxygen, pH, salinity, temperature, and turbidity) from July 26 to August 24, 2023. We also created an additional binary "time of day" variable (i.e., day vs. night), with daytime being defined as 05:00–19:00 and nighttime being

20:00–04:00, based on approximate sunrise and sunset times during the abiotic monitoring period. Linear models were then built for each abiotic parameter using the *lm*() function except for salinity and turbidity. For salinity, we simply computed the mean ± SD for the site. For turbidity, we built a generalized linear model (Gamma distributions) using the *glm*() function. The statistical models for dissolved oxygen, pH, temperature, and turbidity included the independent and interactive effects of location (fixed categorical factor with three levels: beside the reef, inside reef area, or outside reef area) and time of day (fixed categorical factor with two levels: day vs. night), as well as the independent effect of Julian date and its interaction with location, as we also anticipated abiotic parameters to vary across days and wanted to test whether reefs could influence daily fluctuations in abiotic parameters over time. To retrieve model results, we used the base *anova*() function for dissolved oxygen, pH, and temperature, and the *Anova*() function ('car' package) for turbidity. Where significant effects of location (three levels) or significant interactions were detected, we used the *emmeans*() and *pairs*() functions to obtain meaningful pairwise comparisons as above. It is important to note that the "Reef" dissolved oxygen logger malfunctioned and data were not usable; therefore, statistical comparisons for dissolved oxygen are only available for the "Inside" and "Outside" areas. In addition, the "Outside" turbidity probe failed to record data after August 13, and we therefore restricted statistical comparisons of turbidity to July 26–August 13 (19 days). Figures depicting environmental data were generated using the 'ggplot2' package in R (Wickham, 2016).

RESULTS

Reef biodiversity

Overall, a total of 45 taxa (identified to the lowest practical level) were observed on the artificial reefs deployed within bare patches of the eelgrass meadow, spanning 11 different phyla (Figure 2). Of these taxa, 29 (64%) were identified to the species level, another 4 to the genus level (73% to at least genus level), and the remaining 12 were classified at various higher levels of taxonomic resolution. Taxa included marine flora, sessile, semi-sessile, and mobile invertebrates and pelagic fishes.

Benthic community richness, biomass, and diversity

Generalized linear models revealed significant overall effects of reef year class on both benthic taxonomic richness (likelihood ratio $\chi^2 = 59.4$, df = 2, $p < 0.0001$) and biomass (likelihood ratio $\chi^2 = 308.1$, df = 2, $p < 0.0001$). As expected, taxonomic richness was lowest on 0-year reefs (7.3 ± 1.3 taxa; mean ± SD) but was significantly higher on 1-year (19.0 ± 2.3 taxa) and 2-year reefs (18.6 ± 2.5 taxa), which had similar taxon counts (Figure 3A; Appendix S1: Table S2). In contrast, whole-community biomass increased with increasing reef year class. Biomass on 1-year reefs (317.5 ± 105.3 g) was 10-fold higher than that on 0-year reefs (35.2 ± 16.9 g), while the biomass on 2-year reefs (1576.7 ± 498.4 g) was approximately 5× that of 1-year reefs (≈45× higher than 0-year reefs) (Figure 3B). All year classes were significantly different from one another with respect to biomass (Figure 3B; Appendix S1: Table S2).

RDA revealed stark dissimilarity between year classes for both abundance and biomass. When the whole community was included, models for both abundance and biomass were significant and all year classes were significantly different from one another; this was also the case when only sessile species were included (Appendix S1: Tables S3 and S4). The combination of the two RDA axes explained 77.8% of the variation for whole-community biomass, and 84.7% of the variation for sessile biomass (Figure 4A,B). For abundance, the combination of the two RDA axes explained 47.4% of the variation for both the whole community and sessile species only (Figure 4C,D).

There was clear separation between reef year classes for the whole-community biomass biplot (Figure 4A; Appendix S1: Table S4). On 0-year reefs, biomass was predominantly driven by oyster spat, as well as small gastropods, gammarids (Amphipoda), and filamentous green algae, denoting the presence of fewer, heavier species alongside oyster spat on 0-year reefs. Biomass on 1-year reefs was mostly comprised of red algae (*Polysiphonia elongata*) and clubbed tunicates (*Styela clava*), along with anemones, slipper snails, and other filamentous red algae. On 2-year reefs, whole-community biomass was almost exclusively dominated by adult oysters, with smaller but notable contributions from mussels (*Mytilus edulis*) and oyster thief (*Codium fragile*). When sessile animals were analyzed alone, biomass on 0-year reefs was dominated by sea grapes (much heavier than oyster spat), while clubbed tunicates, anemones (*Metridium senile*), and slipper snails (*Crepidula fornicata*) drove 1-year reef biomass, and adult oysters drove 2-year reef biomass (Figure 4B).

With respect to whole-community abundance, there was clear separation between the three year classes (Figure 4C; Appendix S1: Table S4). Herein, abundance on 0-year reefs was almost exclusively dominated by oyster spat, while 1-year reefs were mostly comprised

of small gastropods, gammarids (*Gammarus* sp.), and, to a lesser extent, anemones. In contrast, abundance on 2-year reefs was comprised of a more diverse assemblage of species, including multiple species of bivalves, polychaetes, barnacles (Balanomorpha), clubbed tunicates, and amphipods (Corophiidae), indicating a more diverse community structure on 2-year reefs. Notably, adult oysters had a particularly strong influence on whole-community abundance. A similar trend in abundance patterns was observed when sessile benthic animals were isolated, with 0-year reefs being dominated almost exclusively by oyster spat (and sea grapes, *Molgula* sp., to a lesser extent), 1-year reefs by anemones and clubbed tunicates, and 2-year reefs by a more diverse assemblage of bivalves and sessile slipper snails (Figure 4D).

There were other notable biological observations, mostly related to American lobsters (*Homarus americanus*) using the reefs as shelter (Appendix S1: Figure S1). For instance, during the video analysis, we observed two lobsters fighting over access to one of the reefs for shelter. We also observed one ovigerous female using one of the reefs as shelter, as well as juvenile lobsters within a couple of the reefs.

Oyster abundance and biomass

The abundance of oyster spat and adults was significantly influenced by reef year class (Appendix S1: Table S5). Spat abundance was significantly lower on 1-year reefs (113.3 ± 75.3) compared to 0-year (751.1 ± 692.0) and 2-year reefs (314.4 ± 172.0), which were only ma (Figure 5; Appendix S1: Table S6). Notably, the variation in spat abundance for 0-year reefs was also much higher than that for 1- and 2-year reefs. In contrast to spat patterns, adult abundance increased substantially over the three reef year classes, increasing slightly between 0-year (0.0 ± 0.0) and 1-year (10.1 ± 9.7) reefs, with a dramatic increase on 2-year reefs (141.9 ± 63.5); all year classes were significantly different with respect to adult abundance (Appendix S1: Table S6).

Fish diversity and behavioral use of the reefs

In total, we observed seven species of fish in the videos of the reefs, while only four species were observed in the video of the reference bare patch. With respect to reef year class, the number of fish species and the evenness of their presence on the reefs tended to increase as reef year class increased (Figure 6A). One of the species observed in the reference patch (pipefish, *Syngnathus fuscus*) was not observed on any of the reef videos.

While some individuals were simply observed passing through the video frame, the majority of individuals were observed actively engaging with the reefs. Herein, two active behaviors were observed: feeding and sheltering. With the exception of Clupeidae, which just swam by the frame, at least some individuals from all observed species showed active engagement with the reef structures, with nearly all observed individuals from some species actively using the reefs; no fish exhibited active usage (feeding or sheltering) of the bare reference patch (Figure 6B,C).

Among active users, cunner (*Tautogolabrus adspersus*) and winter flounder (*Pseudopleuronectes americanus*) used the reefs exclusively for shelter, while mummichogs (*Fundulus heteroclitus*) and sticklebacks (Gasterosteidae) were predominantly observed feeding at the reefs; however, some mummichogs and sticklebacks sheltered in the reefs (Figure 6D). Silversides (*Menidia menidia*) were observed actively using the reefs for both feeding and sheltering at more equal rates than the other four species, with one-third of active silversides using the reefs for feeding and the other two-thirds using them for shelter. Feeding was the most common behavior on 0-year and 1-year reefs, while feeding and sheltering behavior were observed in relatively equal proportions on 2-year reefs.

Environmental conditions

Abiotic conditions varied through time for each of the four environmental parameters analyzed statistically (dissolved oxygen, pH, temperature, and turbidity), as linear models revealed a significant effect of Julian date for all parameters (Appendix S1: Tables S7 and S8). General trends of decreasing pH and temperature along with increasing dissolved oxygen and turbidity were evident over the sampling period. Temporal changes were statistically consistent across stands for dissolved oxygen, pH, and temperature, as there were no significant Stand × Julian date interactions for dissolved oxygen, pH, and temperature (Figure 7A–C; Appendix S1: Table S7). There was a significant Stand × Julian date interaction for turbidity, with turbidity condition being higher at the Inside and Outside stands after August 2 (Julian date 214), but not the Reef stand (Figure 7D; Appendix S1: Table S8). Salinity was generally stable at approximately 25 (25.24 ± 0.91 psu).

There was a significant independent effect of Stand for all abiotic parameters, and significant effects of time of day were evident except for turbidity (Appendix S1:

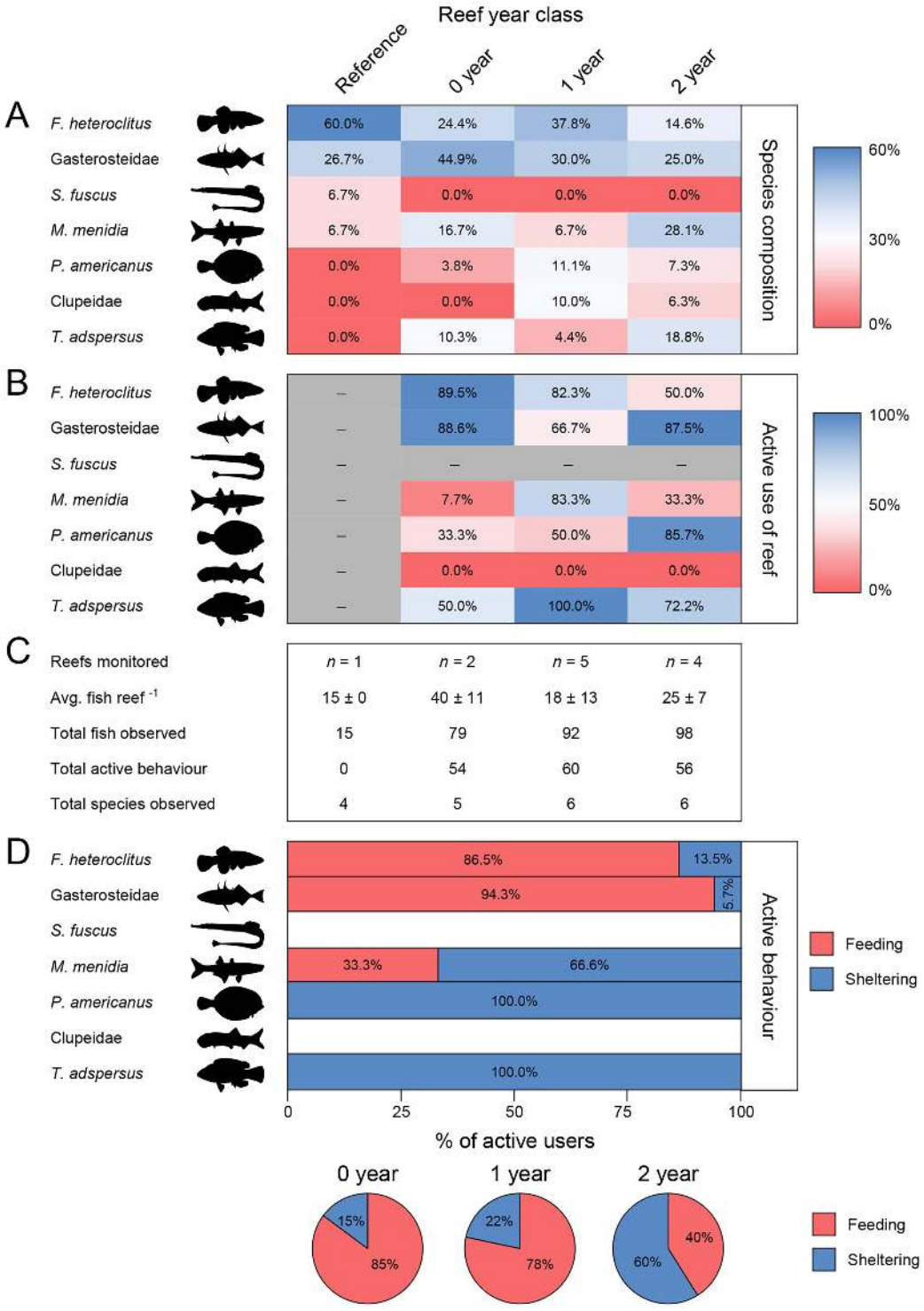


FIGURE 6 Diversity and active use of the reefs by fish species observed in the GoPro videos. (A) The relative percentage of unique individuals observed for each fish species for the three year classes and the reference footage. (B) Percentage of individuals observed actively engaging with the reef for each species. (C) Descriptive statistics regarding fish use of reefs (data are means ± SD for "Avg. fish reef^{-1}"). (D) Behavioral use of the reef by those fish that actively engaged with the reef. The bar chart shows the relative percentage of active reef users that used the reef for feeding or sheltering for each species, while the pie charts show the percentage of active users using the reefs for feeding or sheltering across the three reef year classes (species pooled). See Figure 2 for full species names. Illustration credit: Jeff C. Clements.

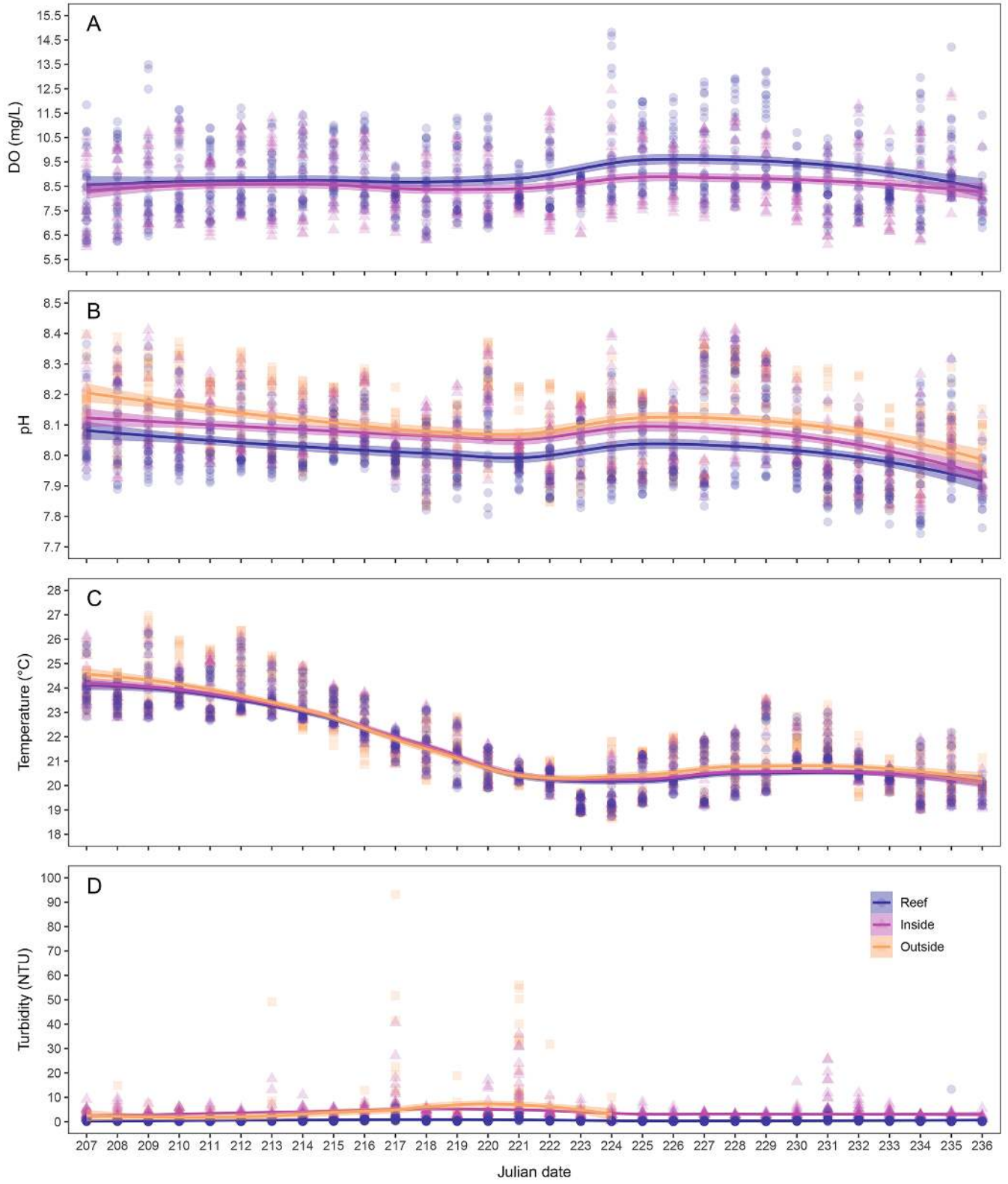


FIGURE 7 Temporal trends in abiotic conditions for each of the three stands of environmental loggers for (A) dissolved oxygen, (B) pH, (C) temperature, and (D) turbidity. Reef refers to the logger stand placed directly beside a 2-year reef; Inside refers to the logger stand placed within the area of reefs but not directly beside a reef; Outside refers to the logger stand placed in a bare patch of sediment within the eelgrass meadow but well outside the area of reefs. Each point represents an hourly average; trendlines are Loess fit ±95% confidence intervals. Actual dates: July 26–August 24, 2023.

Tables S7 and S8). There was also a significant Stand × Time of Day interaction for all four abiotic parameters.

With respect to differences between stands, dissolved oxygen conditions in the Inside stand (9.00 ± 1.52 mg/L) were significantly higher than the Outside stand (8.59 ± 1.31 mg/L) (Figure 8A; Appendix S1: Table S9; no measurements for Reef stand). Seawater pH tended to decrease with increasing proximity to the reef structures (Figure 8B), with pH values of 8.02 ± 0.12, 8.07 ± 0.12, and 8.11 ± 0.13 for the Reef, Inside, and Outside stands, respectively. Temperature conditions showed a similar trend, with the Inside (21.68 ± 1.74°C) and Reef (21.62 ± 1.70°C) stands having significantly lower temperatures than the Outside stand (21.81 ± 1.82°C) (Figure 8C). While the pH differences were perhaps biologically relevant (0.1 pH units between Reef and Outside), temperature differences were not meaningful (<0.2°C between Reef and Outside). Finally, turbidity conditions at the Reef stand (0.55 ± 0.86 NTU) were significantly lower than the Inside (3.64 ± 4.01 NTU) stand, and the Outside stand (5.13 ± 22.27 NTU) had significantly higher turbidity conditions than both the Inside and Reef stands (Figure 8D; Appendix S1: Table S9).

With respect to day-night differences, daytime dissolved oxygen was significantly higher than nighttime dissolved oxygen for the Inside stand but not the Outside stand (Figure 8E; Appendix S1: Table S10). Daytime pH and temperature conditions were significantly higher than nighttime conditions for the Reef and Inside stands, but not for the Outside stand (Figure 8F,G). For the Outside stand, daytime turbidity was significantly higher than nighttime turbidity, while there were no day-night differences in turbidity at the Reef or Inside stands.

DISCUSSION

If seagrass is lost and cannot be restored because the environment is inhospitable, many species relying on the structured, three-dimensional habitat will be lost. In such instances, providing alternative habitat comprised of foundational species that can persist in such conditions may provide an ecological lifeline for species that would otherwise be locally extirpated. In this study, we tested whether the inclusion of artificial oyster reefs in a fragmented eelgrass meadow could facilitate the recovery of lost biodiversity and ecosystem services in bare sediment patches where eelgrass is absent. Within 2 years of installation, concrete blocks successfully recruited oysters as a foundational species, promoted the proliferation of a broad diversity of benthic and pelagic species, and influenced local water quality. The increased diversity and biomass of benthic and pelagic species, relative to bare patches, suggest that artificial reefs can be successfully used as supplemental three-dimensional habitat to maintain biodiversity and ecosystem functions as eelgrass landscapes degrade.

Biotic influence of the artificial reefs

The artificial reefs promoted substantial benthic and pelagic biodiversity. Based on previous literature documenting eelgrass-associated species in this region (e.g., Coffin et al., 2018; Knysh et al., 2023; Murphy et al., 2021; Pascal et al., 2020; Schein et al., 2011), many species observed on the reefs were typical eelgrass residents, including estuarine fish, invertebrates, and macroflora. By providing hard substrate in an otherwise sandy environment, reefs also attracted various filter-feeding species, like bivalves and tunicates, which provide additional ecosystem services via water filtration (Groner et al., 2018; Smith et al., 2022). Overall, these results highlight positive interactions between two habitat types such that the incorporation of artificial oyster reefs within the fragmented eelgrass mosaic increased available habitat for many species. This positive ecological facilitation and the presence of two distinct habitat types, including species that were previously absent from the system, are likely to increase ecological resilience (Bulleri et al., 2018; Halpern et al., 2007; Silliman et al., 2015; Van den Koppel et al., 2015; Vozzo et al., 2023).

Although we observed many eelgrass residents recruiting to and using the artificial reefs, this was not the case for all eelgrass-associated species. For example, while pipefish (*Syngnathus fuscus*) were observed swimming toward eelgrass in the reference bare patch videos, we did not observe them among the reefs. This was unsurprising given the close association of pipefish with seagrass (Robbins & Ray, 1986) and occasional use of marginal habitat (Orth & Heck Jr., 1980; Roelke & Sogard, 1993; Schein et al., 2011). While conserving specific eelgrass-associated species was not the goal of this study, doing so may be the desire of other restoration projects. If so, coupling artificial oyster reefs with traditional seagrass restoration approaches may be more beneficial. The specific conservation goals of the restoration activity thus need to be defined prior to determining the appropriate restoration approach.

Seagrasses and bivalves exhibit complex interactions with the potential for both positive and negative effects depending on context (Barrell & Grant, 2015; DuBois et al., 2024; van der Heide et al., 2021). Previous research

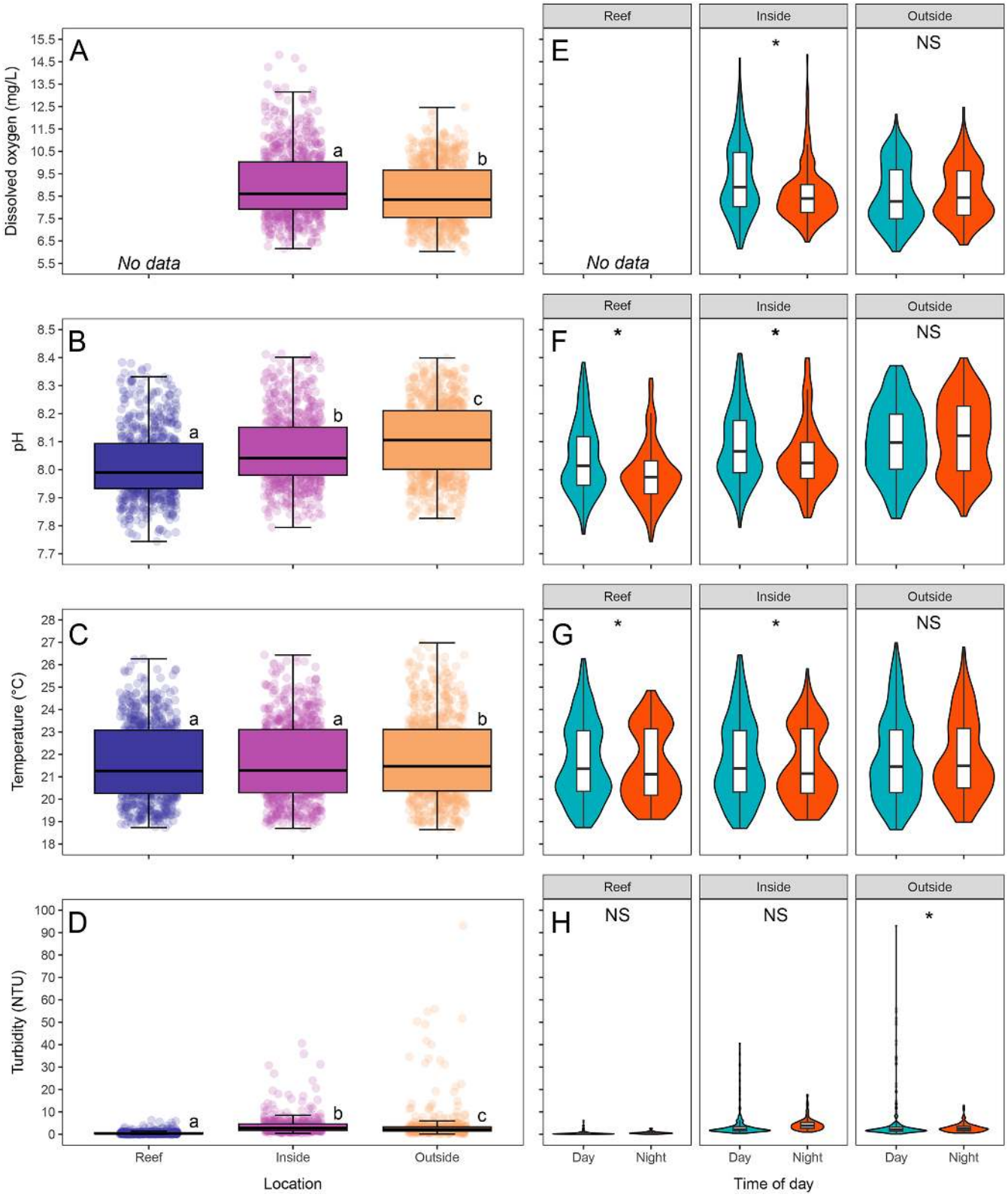


FIGURE 8 (A–D) Boxplots depicting environmental conditions across the three stands of environmental loggers and (E–H) violin plots depicting day-night differences in environmental conditions at each of the three stands for dissolved oxygen, pH, temperature, and turbidity. Letters beside boxes represent pairwise differences between stands. Asterisks above violins represent significant differences between daytime and nighttime conditions with a stand (NS, nonsignificant). For boxplots: the midline depicts the median; the box limits depict the interquartile range (IQR); the whiskers represent 1.5× IQR; each individual point represents an hourly average.

testing the efficacy of oyster reefs in eelgrass habitat reported near-complete oyster mortality due to the attraction of predators from the nearby eelgrass (Valdez et al., 2017). In contrast, we did not observe any detectable effects of predation on oyster recruitment nor establishment on the reefs in this study. The presence of oyster reefs adjacent to eelgrass beds also does not appear to have any direct negative effects on the already-present eelgrass in other regions (Briley et al., 2021). Eelgrass coexists with both wild and cultured oysters extensively in the southern Gulf of St. Lawrence (DFO, 2023). While direct effects of the reefs on surrounding eelgrass were not quantified, negative effects are unlikely given the relatively small scale of the reefs and the already patchy nature of the environment. This further suggests positive ecological interactions between the reefs and the nearby eelgrass bed. These interactions can result in facultative mutualism that improves conditions for both foundational ecosystem components, with ramifications for ecosystem structure, function, and resilience (van der Heide et al., 2021). As many of the ecosystem services provided by both seagrasses and bivalves are density-dependent and affected by spatial context, further investigation into spatial interactions at the landscape scale could offer important insights relevant to the success of habitat restoration.

Taxonomic richness on the reefs peaked after one year in this study, and species biomass increased thereafter. Furthermore, reef biodiversity was established in a natural successional pattern observed in other oyster restoration scenarios (Manley et al., 2010), with foundational species (oysters) establishing almost immediately, promoting subsequent colonization of other species and the proliferation of a lush, diverse reef. It is important to note that the timing of reef installation may play a large role in success, as we installed reefs to coincide with oyster spat settlement (Kerr, 2024). Additionally, the experimental site was selected to be near sources of oyster larvae (natural beds and aquaculture) to promote settlement and recruitment. When site selection and the timing of reef installation are carefully planned, recovery of functional biodiversity can likely be expected. Once established, these reefs would also serve as additional larval sources for other nearby areas should the expansion of artificial reefs, or the maintenance of natural reefs, be of interest.

We observed clear ecological succession and species turnover across the three reef year classes. Herein, 0-year reefs were dominated by early-settling species—predominantly oyster spat. In contrast, 1-year reefs contained more red algae, tunicates, anemones, and crepidulids, which provided habitat for mobile epibenthic invertebrates including gammarids and small gastropods. Finally, 2-year reefs saw substantial growth of adult oysters (while maintaining the presence of other filter feeders and marine macroflora), resulting in altered sediment dynamics (lower turbidity levels) and the occupancy of infaunal species such as surfclams and corophiids. This latter function of sediment deposition and habitat creation for infauna further align with ecosystem services provided by eelgrass beds (Bologna & Heck, 2000; Gintowt et al., 2025; Hasegawa et al., 2008; Tano et al., 2016; Zhang & Silliman, 2019). The hard structure of the artificial oyster reefs also provided substrate for epibenthic species that eelgrass beds do not typically harbor (e.g., *Styela clava* and *Molgula* sp., Carman et al., 2016; *Crepidula fornicata*, Wilson & Garbary, 2020), thus increasing the relative biodiversity within the fragmented eelgrass bed. Ultimately, by providing habitat for additional species to colonize and recouping ecological functions similar to eelgrass, the incorporation of artificial oyster reefs in fragmenting eelgrass systems can generate ecological facilitation between two habitat types that is likely to increase ecological resilience and lead to more successful restoration outcomes.

Environmental influence of the reefs

The observed trends in abiotic parameters at three different locations based on proximity to reefs suggested that the artificial reefs likely altered localized environmental conditions relative to a reference bare patch outside the reef area (although loggers were not replicated at each location; see Section 4.4 below). These environmental alterations were generally considered positive: loggers on the Reef and Inside stands recorded statistically lower temperatures, higher dissolved oxygen, and lower turbidity compared to the reference patch. These environmental changes are similar to those made by eelgrass beds and were most likely driven by the biological push and pull of faunal respiration and floral photosynthesis on the reefs. For example, eelgrass provides cooler temperatures for species residing within eelgrass meadows relative to outside them (Giraldo-Ospina et al., 2021), which, on the artificial reefs, was likely generated by the canopy of macroflora. Likewise, seagrass can promote increased overall dissolved oxygen through high rates of photosynthesis during the day (Aramburu et al., 2024; Hendriks et al., 2014) and can reduce turbidity through sediment stabilization and reduced water movement (but not always; see Marin-Diaz et al., 2019).

Interestingly, while day-night cycles were absent in the reference patch, conditions beside and near the reefs exhibited day-night cycles typical of those observed in eelgrass habitats. Diel cycles in eelgrass beds are largely

driven by daytime photosynthesis and nighttime respiration (Yarbo & Carlson Jr., 2008), and complex diel cycles of other variables such as animal and microbial respiration and carbon excretion (Tu et al., 2025). Such mechanisms were likely at play on the reefs given the diverse community of flora and fauna they supported. Ultimately, while the particular mechanisms leading to altered environmental conditions may not be exactly the same, the artificial reefs in this study appeared to alter surrounding abiotic conditions in ways that mirror conditions within natural eelgrass beds, corroborating findings from similar restoration activities (Smith et al., 2022).

Seawater pH gradually decreased with increasing proximity to the reefs, and a typical cycle of higher daytime pH (compared to night) was evident. These changes in pH are likely due to complex CO_2 dynamics resulting from biological respiration and photosynthesis. The lower pH near the artificial reefs aligns with a recent study that found pH conditions in microenvironments near oyster reefs to be lower than conditions away from the reef (Tomasetti et al., 2023). While studies typically report that seagrasses drive net enhancement of localized pH conditions through daytime photosynthesis (Ricart et al., 2021), others suggest that nighttime respiration can outpace daytime photosynthesis and result in net pH reduction (Pacella et al., 2018). Although pH conditions directly beside the artificial reefs (pH ≈ 8.0) were lower than those away from the reefs, they were still well above near-future ocean acidification conditions (projected pH ≈7.6–7.7; Pörtner et al., 2014) and still considered high relative to the broad range of nearshore estuarine pH conditions reported in this region (pH ≈7.3–8.2; Coffin et al., 2018; Mayrand & Benhafid, 2023). Indeed, life history exposure to low pH is thought to be one of the mechanisms by which oysters in this region appear resilient to low pH conditions (Clements et al., 2021). It is thus unlikely that the slight pH reduction near the reefs had any negative biological effects in this study, and reduced pH may have positive effects on nearby eelgrass by providing more raw inputs to photosynthesis (Groner et al., 2018). Nonetheless, practitioners wishing to employ this methodology may want to consider background pH conditions at prospective sites, and projected pH decreases attributable to the reefs, prior to selecting a site.

Applying Etuaptmumk (two-eyed seeing)

An added benefit of the artificial reef approach in this study was that it directly supported one of the key ecological priorities of Lennox Island First Nation—our Indigenous partners—in restoring culturally and ecologically significant habitat within their traditional territory. Traditional Mi'kmaq knowledge shared by Lennox Island community members speaks of once-productive oyster beds that lined the shores of the island, providing not only food security but also important cultural resources tied to harvesting practices, knowledge transmission, and community well-being. However, these oyster beds have largely disappeared over time and have struggled to naturally recover (R. Angus, personal communication; T. Bernard, personal observation). In addition to oyster restoration, the experimental reefs also provided habitat and shelter for other culturally and economically significant species, such as lobster and forage fish, contributing to both ecosystem health and the sustainability of local livelihoods. The successful establishment of oysters as a foundational species on these artificial reefs is therefore a critical step toward restoring this degraded habitat and revitalizing opportunities for Mi'kmaq stewardship, food harvesting, and cultural connection to the land and waters.

It is also important to highlight the practical and community-driven implications of the artificial reef approach for supplementing eelgrass services and nearshore habitats. The use of concrete blocks—an affordable, widely available material—allowed the Lennox Island First Nation to implement this habitat restoration method with the aid of partners, building local expertise, environmental leadership, and technical capacity within the community. Unlike traditional eelgrass restoration methods, which are often expensive, labor-intensive, and prone to failure (Eriander et al., 2016; Orth et al., 2009; Ward & Beheshti, 2023), this modular concrete block approach offers a low-cost, scalable, and resilient solution for shallow estuarine environments like those surrounding Lennox Island. Moreover, this method aligns with Indigenous stewardship principles: creating space for nature to recover, while enabling communities to directly lead restoration efforts on their own terms. Lennox Island First Nation has become a leader in this innovative approach and now holds the expertise to share these methods with other Indigenous communities across Epekwitk (Prince Edward Island), Atlantic Canada, and beyond, supporting a broader movement of Indigenous-led habitat restoration and climate adaptation.

Limitations and additional considerations

While the results of this study are generally positive and provide pertinent information for coastal restoration, it is important to explicitly recognize some limitations with the scope of this work. One such limitation relates to

spatial scale. The work presented here was intentionally conducted on a small spatial scale using a simple method that can be easily employed by few people with limited resources to promote ecological facilitation within a fragmented (but not completely lost) eelgrass meadow. As such, it is unclear how our results translate to broader spatial scales. We do not have evidence to suggest that there is a spatial limit to this method, but increasing reef size or reef expanse over a larger area could provide valuable insight. Future research may thus seek to identify spatial thresholds, as well as thresholds of eelgrass fragmentation, at which artificial oyster reefs can successfully restore lost ecosystem services. It should be noted that eelgrass coverage is highly variable in this study region (DFO, 2023), and linking changes in eelgrass coverage to the presence of artificial oyster reefs can be confounded with many other factors. Nonetheless, our data support the idea that the ecological facilitation between oyster reefs and eelgrass can yield successful restoration outcomes on localized spatial scales and provides useful insight for restoration practitioners.

Another potential limitation relates to the degree of replication for assessing fish communities and abiotic conditions in and outside of the reefs. Herein, video data were limited to daytime observations during July–August, and only a single reference bare patch was captured by video. As such, our data cannot determine the longer term interseasonal and interannual use of the reefs by fishes. Similarly, the cost-prohibitive nature of abiotic data loggers precluded proper replication of loggers in the three areas monitored, and trends in abiotic parameters were derived from a single data logger at each location. Despite these limitations in replication, however, the observed trends were predictable and generally in line with the impacts that one would expect to observe. For example, the increased fish diversity on older artificial reefs indicates increased use by more species as the reefs become more established, corroborating findings of previous research on artificial reefs (Folpp et al., 2020). Likewise, the trends in abiotic environmental parameters that we observed closer to reefs were predictable and consistent with what one would expect if the reefs were influencing localized water quality (Aramburu et al., 2024; Giraldo-Ospina et al., 2021; Hendriks et al., 2014; Marin-Diaz et al., 2019; Tomasetti et al., 2023); this is further supported by the gradient of change we observed with increasing proximity to the reefs. In addition, it is important to recognize that loggers were all calibrated and consistent with one another prior to deployment. Thus, while the lack of proper replication invites the possibility of observed trends simply reflecting natural spatiotemporal variability, this seems highly unlikely given the observed patterns.

While we saw substantial biodiversity associated with our artificial oyster reefs, it is important to recognize that these reefs provide available habitat to all species in these bays and estuaries, including aquatic invasive species. For example, *Codium fragile* and the various tunicates that we observed may not be desirable targets for habitat restoration. Similarly, while we did not observe any grazing sea urchins, invasive European green crabs (*Carcinus maenas*) were also observed on the reefs. Some of these species have the potential to interact with the surrounding eelgrass. For example, both *C. fragile* and *C. maenas* were anecdotally observed among living eelgrass at the study site, and both species are known to negatively affect eelgrass (Drouin et al., 2012; Garbary et al., 2014). In contrast, tunicates may provide beneficial filtration services that help enhance water quality for eelgrass. These invasive species are generally widespread in the region and eelgrass is already contending with their presence. As such, the presence of these species on the artificial oyster reefs is unsurprising and unavoidable, but should not detract from the net positive gain in ecosystem services provided by the reefs.

CONCLUSION

Habitat loss is the single biggest threat to global biodiversity, and restoring lost habitat is paramount to preserving that biodiversity. Unfortunately, most habitat restoration attempts seek to restore habitat like-for-like and suffer high rates of failure, in part because the environmental conditions in a given habitat no longer support the persistence of the species being restored. Consequently, resources often end up wasted without achieving the expected ecological outcomes. In this study, we provide strong evidence that artificial oyster reefs can be easily and successfully implemented as a supplemental habitat in a fragmented eelgrass landscape. Given our results, it appears that these reefs have the potential to promote ecological facilitation within declining eelgrass beds and improve biodiversity, alter water quality, and provide socioeconomic benefits to local communities. As such, we strongly suggest that restoration projects aimed at conserving biodiversity and ecological function move away from solely focusing on 1:1 habitat restoration approaches and additionally consider the use of supplemental habitat comprised of foundational species that can persist in impacted environments and enhance environmental conditions for the target species. We propose that such a philosophical shift will provide more cost-effective restoration programs and increase the likelihood of conservation success, ultimately increasing ecological resilience. As the climate changes, so too will the

makeup of its ecosystems; preserving biodiversity preserves resilience, offering a chance for flora and fauna to adapt.

AUTHOR CONTRIBUTIONS

Jeff C. Clements, Michael R. S. Coffin, and Luke A. Poirier conceived the ideas; Jeff C. Clements, Michael R. S. Coffin, Luke A. Poirier, André Nadeau, and John Davidson designed methodology; All authors contributed to data collection; Jeff C. Clements, André Nadeau, and Kyle M. Knysh analyzed the data; Jeff C. Clements, Michael R. S. Coffin, and Luke A. Poirier led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

Our study brings together local authors where the study was conducted. Given that our study was conducted on Indigenous territory, representatives from the Lennox Island First Nation and the Mi'kmaq Confederacy of Prince Edward Island (MCPEI) were regularly consulted prior to and during the project; one of the authors (TB) of this project is employed by the Lennox Island First Nation and formerly held positions with MCPEI and Fisheries and Oceans Canada during the course of the project. The COVID-19 pandemic made consultation with community members difficult during the project, which is something we plan to address in future research efforts. Nonetheless, Lennox Island Guardians were invited to visit the reefs with the lead author of the paper in 2024, and community consultation to disseminate the results of the project will be initiated upon publication. To respect the First Nations Principles of OCAP, the Lennox Island First Nation was consulted prior to, and agreed upon, the open sharing of data generated from this work. We also thank the many partners who made this work possible: Angela Douglas-Banks, Randy Angus, Dr. Scott Roloson, Jillian Hunt, staff at the Bideford Shellfish Hatchery, Dr. Barrett Kurylyk and students at Dalhousie University, Chyann Kirby and Bruce Moore. This project was funded by Fisheries and Oceans Canada.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and annotated R code (Clements et al., 2026) are available from Mendeley Data: https://doi.org/10.17632/v7976rzxbv.3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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