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Meta-analysis reveals drivers of restoration success for oysters and reef community

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Abstract

Restoration aims to reverse the global declines of foundation species, but it is unclear how project attributes, the physical setting, and antecedent conditions affect restoration success. In coastal seas worldwide, oyster reef restoration is increasing to counter historical habitat destruction and associated declines in fisheries production and biodiversity. Yet, restoration outcomes are highly variable and the factors that enhance oyster production and nekton abundance and diversity on restored reefs are unresolved. To quantify the drivers of oyster restoration success, we used meta-analysis to synthesize data from 158 restored reefs paired with unstructured habitats along the United States Gulf and Atlantic coasts. The average recovery of oyster production was 65% greater in subtidal (vs. intertidal) zones, 173% greater in polyhaline (vs. mesohaline) environments and increased with tidal range, demonstrating that physical conditions can strongly influence the restoration success of foundation species. Additionally, restoration increased the relative abundance and richness of nektonic fishes and invertebrates over time as reefs aged (at least 8 years post-construction). Thus, the restoration benefits for provisioning habitat and enhancing biodiversity accrue over time, highlighting that restoration projects need multiple years to maximize ecosystem functions. Furthermore, long-term monitoring of restored and control sites is needed to assess restoration outcomes and associated drivers. Last, our work reveals data constraints for several potential drivers of restoration outcomes, including reef construction material, reef dimensions, harvest pressure and disease prevalence. More experimental and observational studies are needed to target these factors and measure them with consistent methods across studies. Our findings indicate that the assisted recovery of foundation species yields several enhancements to ecosystem services, but such benefits are mediated by time and environmental conditions.

KEYWORDS
biodiversity, eastern oyster *Crassostrea virginica*, fisheries, foundation species, habitat provisioning, nekton, oyster reefs, restoration

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INTRODUCTION

Anthropogenic degradation has caused worldwide declines of foundation species (Ellison et al., 2005). These valuable organisms provide the underlying structure of entire ecosystems, and losses of foundation species prompt associated declines of the diverse faunal communities that benefit from habitat creation (Ellison, 2019; Ellison & Degrassi, 2017). Restoration promises to counter these declines, yet outcomes vary among projects and the drivers of such variability are often unknown (Suding, 2011). Understanding the drivers of restoration outcomes is needed to optimize restoration design, set appropriate goals, and develop monitoring programs. With the increase in restoration projects in recent decades and projected expansion during the UN Decade of Restoration (2021–2030) (Cooke et al., 2019), we have gained enough empirical studies of restoration outcomes to systematically quantify the drivers of restoration success through data synthesis (Cooke et al., 2019; Wortley et al., 2013).

The loss of 85% of global oyster populations due to overfishing and disease is one of the most staggering reductions of foundation species worldwide (Beck et al., 2011). To reverse these declines, coastal restoration projects add hard substrate (e.g., shell, concrete) to the seafloor to support oyster recruitment from existing populations and/or transplant live oysters to enhance larval supply in recruitment-limited areas (Brumbaugh & Coen, 2009; Lipcius et al., 2008). Restoration projects were historically designed to increase oyster production alone, but efforts have recently shifted to optimize other ecosystem services, such as habitat provisioning for a diversity of ecologically and economically important free-swimming fishes and invertebrates (nekton) that live and feed on oyster reefs (Grabowski et al., 2012). Oyster restoration projects have increased exponentially since the 1990s (Duarte et al., 2020), despite mixed outcomes and a limited understanding of the drivers of restoration success (Geraldi et al., 2013; Kennedy et al., 2011; Powers et al., 2009; Schulte et al., 2009; Smith et al., 2005). Given the wide range of project outcomes, standardized evaluation across studies is needed to assess what factors promote the enhancement of oyster production and nekton abundance and diversity on restored reefs.

Restoration outcomes can vary predictably based on the restoration attributes (e.g., project size or age), the physical setting (e.g., habitat type, elevation, climate), and the antecedent conditions (e.g., prior disturbance regime) (Atkinson et al., 2022; Crouzeilles et al., 2016; Jones et al., 2018). Oyster restoration projects differ in restored reef area, height, age, and construction material, but it is unknown how these factors influence oyster production and nekton abundance and diversity. Extrapolating from studies of other foundation studies, oyster and nekton production may be expected to increase with restoration area (van Katwijk et al., 2015) or with reef age (Atkinson et al., 2022; Crouzeilles et al., 2016; Hollweg et al., 2020). However, a recent meta-analysis did not find strong, consistent effects of restored reef area, age, or vertical relief on juvenile fish recruitment (Davenport et al., 2021). We build on this work by examining additional drivers of restoration outcomes, including tidal zone, salinity, and tidal range, and investigating responses by both oysters and nekton (juveniles and adults). Oysters are restored in diverse physical conditions, as oysters can tolerate a range of temperature, salinity, and inundation regimes (−2–41°C, 0–42.5 PSU; Byers et al., 2015; Shumway, 1996). The physical setting for restoration may affect oyster production and nekton abundance and diversity. For instance, salinity can alter oyster susceptibility to predators or pathogens and inundation regimes can influence larval supply, food availability, and sedimentation (Fodrie et al., 2014). Last, restoration outcomes may vary based on a region's history of oyster harvest or disease. Thus, restoration attributes, the physical setting of restoration, and antecedent conditions may influence the success of oyster restoration, but the relative importance of these potential drivers is unclear.

In a recent meta-analysis of ecosystem services associated with restoration of the eastern oyster, *Crassostrea virginica*, we discovered that restored reefs (artificial reefs created to establish habitat resembling a natural reef) enhanced oyster production by 21-fold and increased nekton abundance and richness (no. of taxa) by 34%–99% relative to unstructured habitats that represented restoration starting points or undesired endpoints (Smith, Cheng, & Castorani, 2022). Yet, outcomes from individual studies were highly variable (Smith, Cheng, & Castorani, 2022). Here, we assessed the factors influencing oyster restoration success. We combined data on oyster production and the abundance and diversity of nektonic fishes and macroinvertebrates with metadata of restoration attributes (e.g., reef area, age, construction material), the physical setting of restoration (e.g., tidal zone, salinity, tidal range), and antecedent conditions (e.g., reef harvest status, disease prevalence). Where data were robust, we quantified the contributions of these potential drivers to the enhanced oyster production and nekton abundance and diversity associated with restoration. Our findings indicate that physical setting plays a strong role in the restoration-driven recovery of foundation species and that the habitat provisioning benefits of restoration accrue over time.

METHODS

Rationale

To understand the drivers of increased oyster production and nekton abundance and diversity with oyster restoration, we used meta-analysis to compare these metrics of restoration success with metadata on restoration attributes, physical setting, and the antecedent conditions of restoration (where available). Restoration attributes included reef area (m^2), height above bottom (m), age (years), construction material (e.g., shell, live oysters, concrete, limestone, rock, etc.), and reef type (fringe vs. patch). Aspects of the physical setting included tidal zone (intertidal vs. subtidal), salinity (mesohaline: 5–18 PSU vs. polyhaline: 18–35 PSU), water depth (m), and tidal range (m). Harvest pressure of the restored reef (open vs. restricted vs. closed) represented the antecedent conditions. At the publication level, we documented binary responses to assess whether studies reported on disease prevalence, proximity to adjacent habitats, predation pressure, or metapopulation dynamics (Appendix S2: Figure S3). We also indicated whether each paper experimentally manipulated or observed variation in oyster restoration attributes; if so, we documented what aspect of oyster restoration was manipulated or varied (e.g., construction material, reef area, reef height, reef slope, tidal zone, etc., or a combination of these factors; Appendix S2: Figure S5). Several of these potential predictor variables were eventually dropped from analyses due to a lack of data (see *Statistical analyses*).

Oyster production included all measures of oyster abundance (i.e., density, count, percent cover, biomass) given for any oyster size (spat, juveniles, adults, total oysters). Habitat provisioning responses included measures of nekton abundance and richness (no. of taxa). We categorized responses as “aggregate abundance” if the authors reported measures grouped across multiple taxa groups (e.g., “total nekton,” “total fish,” “total macroinvertebrates”). In addition, we categorized abundance measures reported for individual taxa as “taxon abundance” and classified taxa by order and family using the *taxize* package (Chamberlain & Szöcs, 2013) to extract taxonomic hierarchies in R 4.1.2, which we used for all analyses (R Core Team, 2022). If both density and count were reported for the same response, we recorded only density.

Literature search and inclusion criteria

We followed Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) standards for meta-analysis reporting (Appendix S1: Figure S1, Table S1; Moher et al., 2009). As described in detail in Smith, Cheng, and Castorani (2022), we identified candidate publications with two search strings run in Web of Science using the Science Core Collection (search date: 17 October 2019) and Google Scholar for 2019–2020 (search date: 26 January 2020; Appendix S1). We identified additional papers from in-text citations, Google Scholar search-term alerts, existing reviews (Davenport et al., 2021; La Peyre et al., 2019; zu Ermgassen et al., 2016), and communications with published authors. For inclusion, publications had to contain an experimental or observational field study of the eastern oyster, *Crassostrea virginica*, that measured oyster production or nekton abundance or diversity (as defined above) on both a restored reef and a paired, unstructured habitat. We screened the title, keywords, and abstracts of 1121 candidate publications and identified 53 for inclusion (Appendix S1: Figure S1, Table S2).

Data extraction

For each publication, we extracted means (or sums), sample sizes, and standard deviations (when reported) for each response measured on restored reefs and their paired unstructured habitats. If the authors did not explicitly match a restored reef with an unstructured habitat, we chose the closest unstructured habitat to approximate local abiotic conditions. If a response was measured repeatedly over time for the habitat pairs, we used data only from the final measurement to maximize time since the construction of the restored reef. When the same response variable was reported for multiple habitats in a study and as a spatial average (e.g., across restored reefs), we used the individual responses for each habitat. We extracted data from figures with the *metaDigitise* package (Pick et al., 2019) and collected data from publication text and tables.

Calculating effect sizes

We measured the proportional change of oyster production and nekton abundance and diversity on restored oyster reefs relative to unstructured habitats using the log response ratio (LRR = ln[Value on restored reef/Value on unstructured habitat]; Koricheva et al., 2013). An LRR of zero indicates equivalency between restored and unstructured habitats; positive and negative values indicate greater and lesser responses, respectively, on restored reefs relative to unstructured habitats. We used LRR because estimates of variation were not available for many studies. We removed effect sizes where the values in restored and unstructured habitats were both zero (Koricheva et al., 2013). To avoid undefined values in cases where one of the responses was zero, for both responses we added the minimum detectable value likely for the sampling method (e.g., a count of 1 for no. of individuals per quadrat; Poore et al., 2012). Data are provided in the Environmental Data Initiative (Smith et al., 2023).

Statistical analyses

To assess the suitability of potential predictors of restoration success for inclusion in the meta-analysis, we examined LRR sample sizes, distributions, the frequency of missing metadata, and collinearity among predictors for each response (i.e., oyster production, nekton aggregate abundance, nekton taxon abundance, nekton richness; Appendix S2: Figures S1–S4). Construction material, reef type, region, and harvest pressure were too unbalanced to include in any of the models (Appendix S2: Figure S2). We also excluded water depth, reef height, reef area, and oyster density on restored reefs due to high frequencies of missing data and discrepancies in data collection methods and reporting across studies (Appendix S2: Figure S1). Few studies reported information related to disease, proximity to adjacent habitats, metapopulation dynamics or predation pressure, so we could not include these factors in the models (Appendix S2: Figure S3). Hence, the predictor variables with sufficient data were tidal zone (subtidal vs. intertidal), salinity (mesohaline vs. polyhaline), tidal range (meters), and reef age (years since construction).

For each response, we included these balanced, data-rich predictors in a linear mixed effects model (LMM) fitted with the *glmmTMB* package (Brooks et al., 2017). To account for within-study correlation and differences in sampling gear efficiency, all models also included a random intercept term that combined publication and sampling method. The model for nekton taxon abundance also included taxa order as a random intercept to account for variation by taxonomic group. To assess the contributions of functional groups to patterns of nekton taxon abundance, we also subset the taxon abundance responses and fit separate models for fish and macroinvertebrates, which also included taxa order and taxa family, respectively, as a random intercept. We tested all models for predictor multicollinearity with the performance package (Lüdecke et al., 2021) and ensured that model residuals met assumptions of normality and heterogeneity using the *DHARMa* package (Hartig, 2019). We removed outliers for reef age based on Cook's distance.

To assess the potential for publication bias to over-represent significant findings, we used a "drop-one" approach to assess whether any study exerted undue influence (as in Lefcheck et al., 2019). We examined funnel plots of effect sizes versus sample size for asymmetry (Møller & Jennions, 2001) and calculated the Rosenthal's fail-safe number to indicate the number of nonsignificant, unpublished studies required to remove a significant overall effect size (Rosenthal, 1979; Appendix S3: Figure S1). These analyses indicated that our findings were robust to publication bias. Within-study variance was low for all responses (Appendix S3: Figure S2).

RESULTS

Restored reef attributes

We collected 1571 effect sizes from 158 pairs of restored reefs and unstructured habitat pairs from 53 studies (45 peer-reviewed papers, four theses, and four reports). Restored reefs included in the analysis were constructed from 1958 to 2017 and were sampled from 1 day to 14 years post-construction (median = 1.5 years). Reefs ranged in area from <0.5 to 230,000 m^2 (median = 96 m^2) and varied in height from 0.05 to 1.2 m (median = 0.25 m). Patch and fringing reefs were constructed from various materials, including shell, concrete, limestone, and live oysters. Paired habitats included intertidal and subtidal areas of mesohaline and polyhaline coastal waters, encompassing microtidal and mesotidal ranges (0.1–3.0 m; median = 0.4 m) and a variety of water depths (0.4–5 m, median = 1.7 m).

Measures of oyster production (80 effects, 16 papers), nekton aggregate abundance (151 effects, 33 papers), nekton taxon abundance (1250 effects, 34 papers), and nekton richness (90 effects, 24 papers) were widely distributed across the United States Gulf and Atlantic coasts (Figure 1). For all four of these response variables, restored reefs outperformed paired unstructured habitats on average (mean LRR > 0; Figure 1), as we have shown previously (Smith, Cheng, & Castorani, 2022). However, individual LRRs were highly variable among studies (ranging from −4 to 8), demonstrating large variation in restoration success (Figure 1).

Drivers of oyster production

Tidal zone, salinity, and tidal range altered oyster production on restored reefs relative to unstructured habitats (Appendix S2: Table S1). The relative effect of restoration

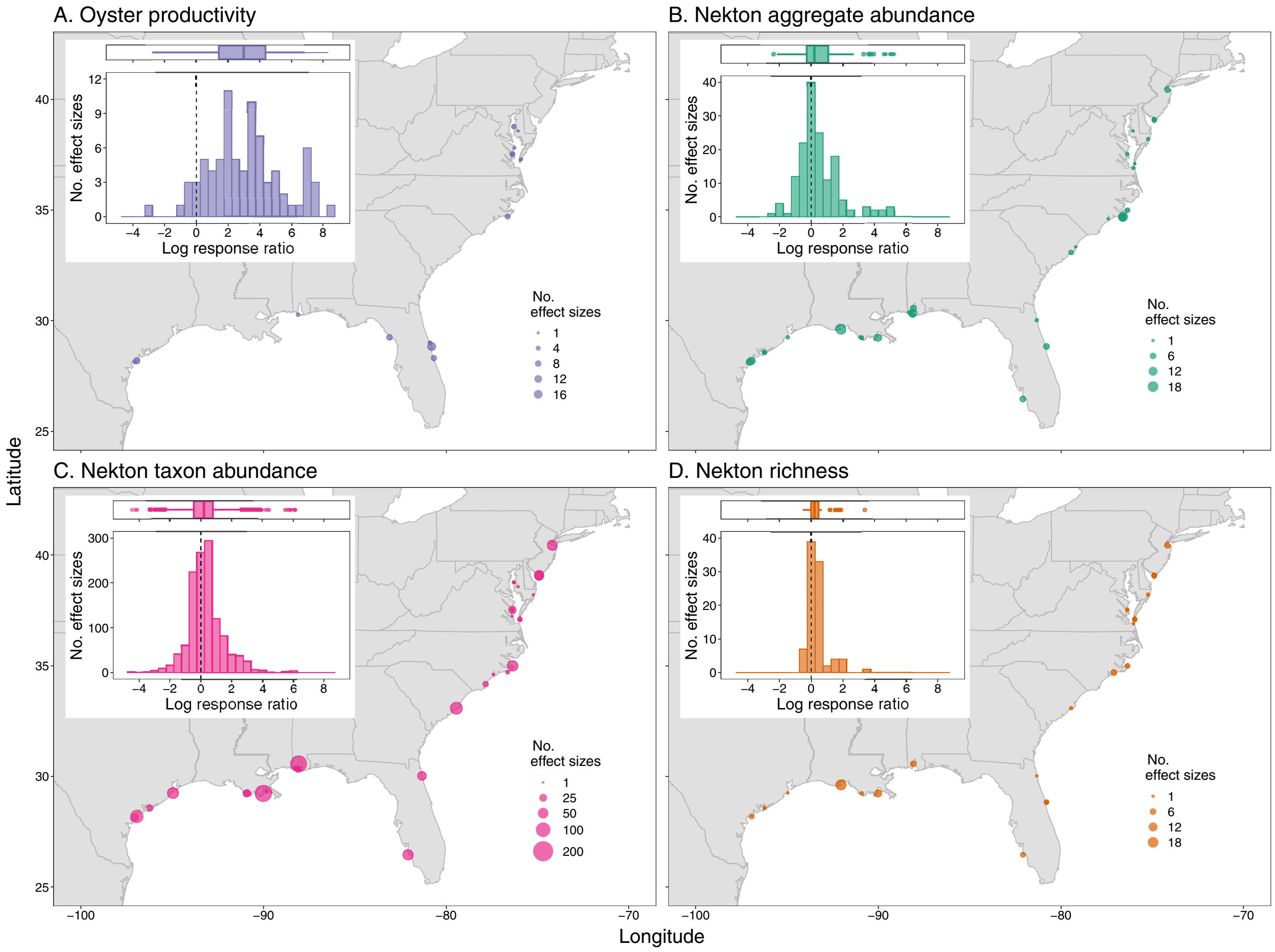

FIGURE 1 The 1571 effect sizes (collected from 53 papers) included measures of (A) oyster production, (B) nekton aggregate abundance, (C) nekton taxon abundance, and (D) nekton richness that were widely distributed across the United States Gulf and Atlantic coasts. Points indicate the locations of suitable studies; larger points indicate more effect sizes. All responses had log response ratios (LRRs) that ranged from negative to positive values, illustrating variability in restoration success across studies. Positive LRRs (above the dashed line at zero) in histograms indicate greater responses on restored reefs relative to unstructured habitats (i.e., relative enhancement of oyster production), whereas negative LRRs indicate lesser responses on restored reefs relative to unstructured habitats. Boxplots above histograms show median LRRs (bold lines) and interquartile ranges (boxes) with outliers greater than 1.5 × IQR (whiskers). Median LRR values for all responses were >0.

on oyster production was estimated to be 65% greater in subtidal habitats (mean predicted LRR, $\text{LRR} = 6.1$ for subtidal vs. 3.7 for intertidal; $p = 0.012$; Figure 2A) and 173% greater in polyhaline habitats ($\text{LRR} = 3.7$ for polyhaline vs. 1.3 for mesohaline; $p = 0.014$; Figure 2B). The relative effect of restoration on oyster production increased with tidal range by an estimated 2.5 predicted LRR units per meter ($p = 0.032$; Figure 2C), corresponding to a predicted LRR increase of 3.5 units when comparing lowest and highest tidal ranges (0.1 vs. 1.5 m). Oyster production also showed a marginally significant positive trend with restoration age ($p < 0.10$; Figure 2D), increasing by an estimated 0.11 LRR units/year and corresponding to a predicted LRR increase of 1.5 units over 14 years.

Drivers of nekton abundance and diversity

None of the included predictors had a detectable effect on nekton aggregate abundance on restored reefs relative to unstructured habitats ($p \geq 0.47$; Figure 2E–H). However, nekton taxon abundance ($p = 0.0004$; Figure 2L) and nekton taxa richness ($p = 0.006$, Figure 2P) on restored reefs relative to unstructured habitats increased with restoration age. Nekton taxon abundance increased

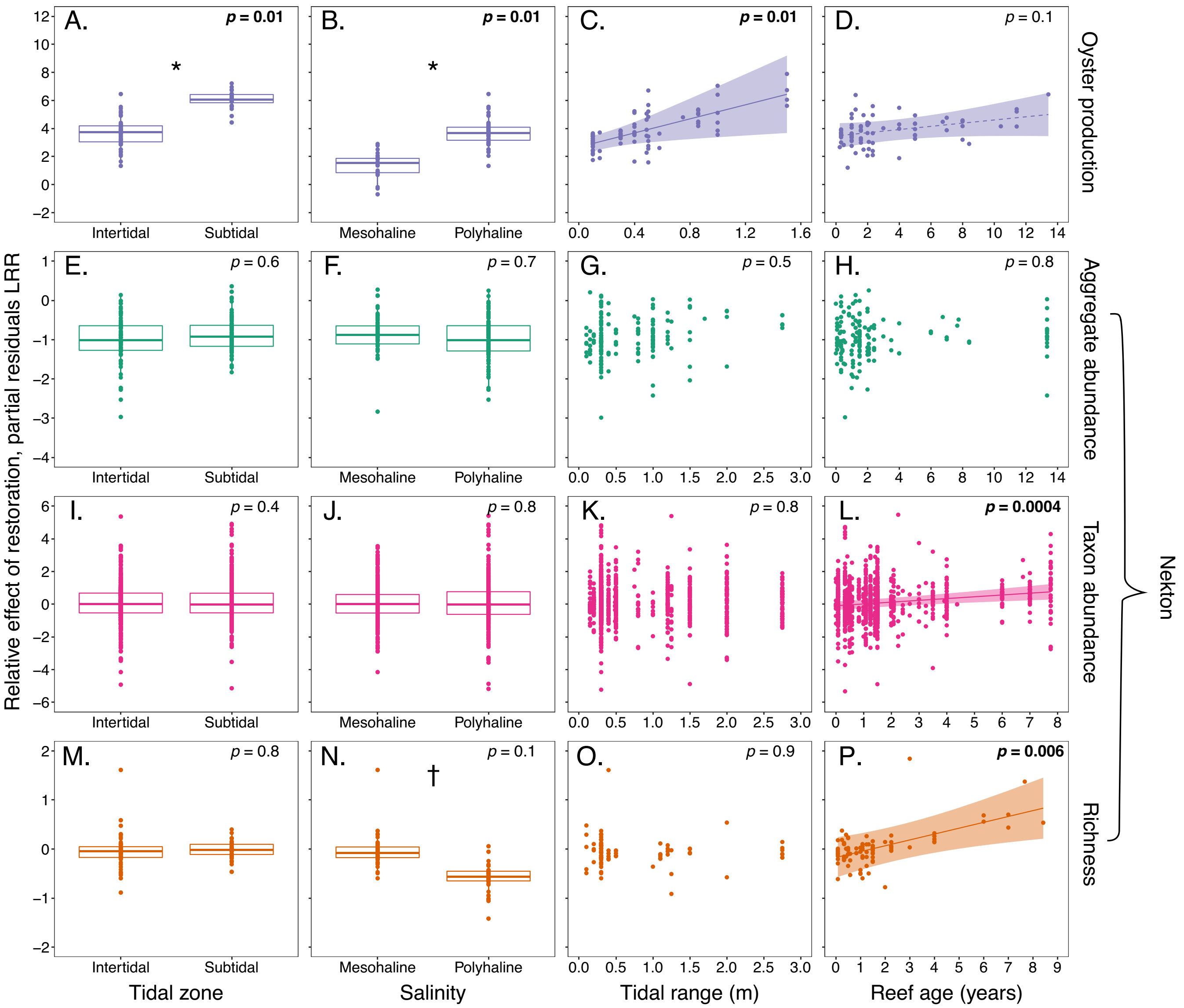

FIGURE 2 Partial residual plots from mixed effects models indicate that tidal zone, salinity, and tidal range influenced (A–D) oyster production, with enhanced oyster production in subtidal, polyhaline environments, and at larger tidal ranges on restored reefs relative to unstructured habitats. (E–H) None of the included drivers significantly influenced nekton aggregate abundance on restored reefs relative to unstructured habitats. Restored reef age was positively related to (I–L) nekton taxon abundance and (M–P) nekton richness, indicating enhanced nekton taxon abundance and richness on restored reefs relative to unstructured habitats with increasing years since restored reef construction. Partial residuals of the log response ratios report the effect of each predictor after accounting for the variation explained by other predictors included in the model (indicated by points) and should be interpreted in relative, not absolute, terms. Asterisks and bold *p*-values indicate significant model predictors ($p \leq 0.05$); daggers indicate marginally significant predictors ($p \leq 0.1$). Lines indicate the model-estimated fit (solid lines: $p \leq 0.05$, dashed lines: $p \leq 0.1$) and shading represents 95% CIs. Boxplots as in Figure 1.

by an estimated 0.11 LRR units/year, corresponding to a predicted LRR increase of 0.9 units over 8 years. Nekton richness increased by an estimated 0.12 LRR units/year, corresponding to a predicted LRR increase of 1.0 units over 9 years. Enhanced taxon abundance on older restored reefs was primarily driven by fish, rather than macroinvertebrates (Appendix S2: Table S2, Figure S6). Fish abundance on restored reefs relative to unstructured habitats increased by an estimated 0.13 LRR units/year with restoration age ($p < 0.0001$), corresponding to a predicted LRR increase of 1.0 units over 8 years. There was no effect of the included predictors on macroinvertebrate abundance (Appendix S2: Table S2, Figure S6).

Tidal zone, salinity, and tidal range had no detectable effects on nekton taxon abundance (Figure 2I–K) or nekton taxa richness (Figure 2M–O) on restored reefs relative to unstructured habitats ($p \geq 0.44$), aside from a marginal increase in nekton richness on restored reefs in mesohaline (vs. polyhaline) environments ($p = 0.1$, Figure 2N).

DISCUSSION

We quantified how physical setting and restored reef attributes influence the effects of oyster reef restoration on oyster production and nekton abundance and diversity. Synthesizing data from 158 pairs of restored reefs and unstructured habitats along 3500 km of the United States coastline, we found that nekton abundance and richness on restored reefs relative to unstructured habitats increased with restoration age (Figure 2L,P). Likewise, modest increases over time in relative oyster production suggest that restoration projects may enhance benefits to foundation species over time (Figure 2D). These two findings strengthen the evidence that habitat restoration projects need several years to maximize ecosystem service benefits (Smith, Lusk, & Castorani, 2022). Restoration enhanced oyster production most strongly in locations with subtidal reefs, saltier water (polyhaline), and large tidal ranges (Figure 2A–C). Although effects were most pronounced in these environments, we stress that restoration still improved oyster production over unstructured habitats in 93% of cases (LRR > 0 for 74 out of 80 effect sizes; Figure 1A). Surprisingly, the effects of the tidal zone, salinity, and tidal range on oyster recovery did not extend to reef nekton (Figure 2E–G, I–K, M–O), suggesting that other, unexplored factors are driving differences in restoration benefits for fishes and mobile invertebrates. Indeed, many of the expected drivers of oyster restoration success—including restored reef construction material, height, size, harvest status, and disease prevalence—were too unbalanced, data poor, or inconsistently measured across studies to include in our statistical analysis (Appendix S2: Figures S1–S3); these potential drivers warrant additional study and future experiments designed to explicitly test their effects.

Our finding that restoration benefits foundation species and their associated biodiversity over time demonstrates the value of long-term monitoring of restoration projects. More broadly, these results add to a growing understanding of the large-scale drivers of success in the restoration of foundation species. Our work supports the findings of prior syntheses in terrestrial, aquatic, and marine systems that found ecosystem functioning increases with the age of foundation species restorations (Atkinson et al., 2022; Barral et al., 2015; Crouzeilles et al., 2016; Hollweg et al., 2020; Miller et al., 2010, but see Ren et al., 2016; Shimamoto et al., 2018).

Physical setting drives enhanced oyster production

Oysters can tolerate a range of physical conditions (Shumway, 1996) and oyster production is, on average, greatly enhanced by restoration (Figure 1; Smith, Cheng, & Castorani, 2022). Yet, the effect of restoration on oyster production (relative to unstructured habitats) was highly variable across studies (Figure 1A). We found that three aspects of the physical setting—tidal zone, salinity, and tidal range—altered oyster production on restored reefs relative to unstructured habitats. Although alternative explanations are possible, we found no potentially confounding factors (e.g., construction material, reef age, geographic location) that consistently covaried with tidal height, salinity, or tidal range.

Specifically, we found that the effect of restoration on oyster production was enhanced by 65% on subtidal reefs relative to intertidal reefs (Figure 2A). In the context of restored oyster reefs, these results indicated that, on average, the advantages of subtidal environments, which include enhanced larval delivery, longer feeding time and lessened desiccation or temperature stress (Bishop & Peterson, 2006; Lenihan, 1999), were likely to outweigh the detrimental effects of subtidal habitats, such as heightened predation, biofouling, disease, and sedimentation (Fodrie et al., 2014; Johnson & Smee, 2014; Powers et al., 2009). However, it is important to note that, on average, oyster production on restored intertidal reefs still outperformed paired unstructured habitats (mean LRR > 0; Appendix S2: Figure S4), indicating that intertidal zones are also good restoration sites, particularly in areas where predation, disease, sedimentation or other factors limit subtidal restoration efforts. Indeed, assessing local conditions relative to where reefs naturally occur can indicate the best locations to restore reefs in a given estuary.

Oyster production on restored reefs relative to unstructured habitats was 173% greater on polyhaline reefs relative to mesohaline reefs (Figure 2B). These results demonstrated that, on average, the positive effects of greater salinities, such as increased oyster feeding and growth rates (Casas et al., 2018; Lowe et al., 2017), outweighed the increased predation pressure and disease prevalence that are also associated with more saline environments (La Peyre et al., 2006; Pusack et al., 2019). Our study provides some of the first synthesis of salinity effects for oyster reefs that are either consistently polyhaline or mesohaline; much of the understanding of salinity effects on oyster reefs occurs in the context of short-term salinity disturbances (e.g., freshwater pulses; Kimbro et al., 2017; Marshall et al., 2019; Pusack et al., 2019). As with the tidal zone, oyster production on restored mesohaline reefs still outperformed paired unstructured habitats (mean LRR > 0; Appendix S2: Figure S4), indicating that more brackish sites are also generally suitable for restoration. Guidance for restoration sites within a given estuary can be gained by assessing where reefs naturally occur relative to the salinity regime.

The effect of restoration on oyster production relative to unstructured habitats also increased with tidal range (Figure 2C). Regions with greater tidal amplitudes have more net water delivery per unit of time. Associated increases in seston and oxygen fluxes, enhanced larval delivery, and reduced sedimentation could all contribute to greater oyster production with restoration at higher tidal ranges (Byers et al., 2015; Grizzle, 1990). Indeed, a prior study of oyster production across a latitudinal gradient found peak oyster growth and recruitment in regions with the greatest tidal ranges, which was associated with increased inundation depth and higher flow velocity (Byers et al., 2015). Increased inundation depth was the strongest driver of enhanced oyster production across latitude, accounting for more variation in oyster biomass and recruitment than temperature, salinity, oyster reef slope, or reef vertical relief (Byers et al., 2015). Together with the tidal zone, the tidal range is likely to help determine the inundation conditions of oyster restoration; for optimal growth, oyster reefs should be inundated at least 50% of the time (Morris et al., 2021).

We also found a marginally significant increase in oyster production on restored reefs relative to unstructured habitats with increasing restoration age (Figure 2D). As oyster reefs mature, they produce shell that facilitates larval recruitment and builds the reef over time via positive feedback (Lenihan, 1999). The positive relationship between oyster production and restored reef age supports prior literature, as restored oyster reefs placed in ideal physical conditions can grow rapidly (Dillon et al., 2015; Rezek et al., 2017; Walles et al., 2016), reaching the oyster density and biomass of natural reefs within ~6 years of restoration (Smith, Lusk, & Castorani, 2022).

Nekton abundance and richness increase with reef age

We found that the abundance and richness of free-swimming fish and invertebrate taxa on restored reefs relative to unstructured habitats also increased with reef age (Figure 2L,P). These effects were detectable even within the relatively short timescale of the data in our analysis (8–9 years after restoration). In theory, ecosystem services associated with restoration projects are expected to increase rapidly following restoration initiation (Suding, 2011). As described above, restored oyster reefs can quickly accumulate oyster biomass, creating habitat and food for other species in a relatively brief period of time. Fisheries production is expected to scale with oyster biomass (Grabowski et al., 2012; Peterson et al., 2003; zu Ermgassen et al., 2012, 2016); as restored reefs mature and gain more oysters, they create additional structure that can support greater densities of ecologically and economically important nekton taxa (Gilby et al., 2021; Rezek et al., 2017; Smith, Lusk, & Castorani, 2022). Moreover, theory predicts that biodiversity should increase over time through the accumulation of stochastic colonization events (Hanski, 1999; MacArthur & Wilson, 1967); our findings for restored oyster reefs are consistent with this idea.

These results support the findings from other syntheses on foundation species restoration showing that community abundance and diversity increase with restoration age in salt marshes (Baumann et al., 2020; Hollweg et al., 2020), freshwater streams (Miller et al., 2010), forests (Crouzeilles et al., 2016), and terrestrial habitats (Atkinson et al., 2022). However, syntheses in agroecosystems (Barral et al., 2015), grasslands (Ren et al., 2016), wetlands (Meli et al., 2014), and tropical forests (Shimamoto et al., 2018) found no effect of restoration age on community richness or other ecosystem services. These disparate findings could be due to differences in expected recovery timelines relative to the timing of data collection, the degree of initial degradation, or the extent of restorative actions, among other factors. More research is needed to generate a unified theory on timelines for restoration benefits.

Nekton *taxon* abundance (i.e., responses reported for distinct taxa) was positively correlated with restoration age, but this trend did not extend to nekton *aggregate* abundance (i.e., responses reported as "total nekton," "total fish," "total macroinvertebrates"). This apparent discrepancy may be explained by the fact that nekton responses to oyster reef restoration vary strongly among taxonomic groups (Smith, Cheng, & Castorani, 2022). In our previous meta-analysis, we found that restoration greatly enhanced some species, including many known associates of oyster reefs (e.g., toadfishes, mullets, stone crabs, mud crabs, swimming crabs, snapping shrimps, penaeid shrimps), but had no effect on others (e.g., catfishes, flatfishes, forage fishes, spider crabs, phyllodocid worms, neogastropod snails; Smith, Cheng, & Castorani, 2022). Our analysis for nekton taxon abundance accounted for this variation by including the taxonomic group as a random intercept, but we could not account for the taxonomic group in the aggregate taxon response. Rather, pooling faunal abundance data across multiple taxonomic groups may have masked the potential variables that influence restoration effects, explaining our null results for this response variable. Indeed, a recent synthesis of the drivers of juvenile fish recruitment on restored oyster reefs only found the effects of restoration when accounting for fish order (Davenport et al., 2021). Similarly, in our study, we found that the pattern of increasing nekton taxon abundance with restored reef age was driven primarily by fish, not by macroinvertebrates (Appendix S2: Table S2, Figure S6). Thus, our work highlights the importance of accounting for differences in taxonomic responses when assessing restoration outcomes. Aggregating across groups can conceal individual responses to restoration for both common and rare taxa that may be targeted for recovery.

Future directions

Our study quantified how tidal zone, salinity, tidal range, and reef age influence the effect of restoration on oyster production and the abundance and diversity of nekton with restoration. However, data constraints limited our ability to examine other potential drivers of variation in restoration outcomes. We collected data for many potential predictors of restoration success, including aspects of other reef attributes (i.e., restored reef construction material, height, area), aspects of the physical setting (i.e., water depth, proximity to adjacent habitats, predation pressure, population connectivity), and antecedent conditions (i.e., harvest status, disease prevalence). However, we could not analyze these factors because few studies explicitly manipulated or observed their variation (Appendix S2: Figure S5), they were too unbalanced, or they were measured in incomparable ways across studies (Appendix S2: Figures S1–S3). In fact, we could not even include the most commonly manipulated predictor, reef construction material, due to inconsistencies in the type of materials used across studies. Another limitation of our meta-analysis was that few studies measured intertidal versus subtidal reefs or mesohaline versus polyhaline reefs within the same system (but see Brown et al., 2013; Kenworthy, 2019; La Peyre et al., 2013, 2014; Pierson & Eggleston, 2014; Powers et al., 2009). Such constraints highlight the need to explicitly design experiments and observational studies that target these variables and measure them with consistent methods within and across studies.

Conclusions and implications for practice

Our meta-analysis demonstrates that physical setting and reef age are important contributors to enhanced oyster production and nekton abundance and diversity on restored reefs relative to unstructured areas. We identified multiple physical variables as strong drivers of increased oyster production on restored reefs, suggesting that physical setting is vital to the restoration success of foundation species that create and maintain ecosystems. Furthermore, the important role of restoration age in increasing oyster production, nekton taxon abundance, and nekton richness on restored reefs indicated that many of the benefits of oyster restoration take several years to accrue. Given that most oyster restoration projects are monitored in short time frames (<2 years; Bayraktarov et al., 2016; Smith, Cheng, & Castorani, 2022), our work highlights the importance of funding and monitoring restoration projects for extended time periods (Cusser et al., 2021; Rastetter et al., 2021). Furthermore, reporting on successful conservation project outcomes is more common than for "failed" or less effective projects (Catalano et al., 2019). The influence of such potential bias is unknown, but our synthesis of the drivers of oyster restoration outcomes was strengthened by including data from restorations with varying degrees of success. Reporting restoration failures in the peer-reviewed literature is essential to inform the conditions that support desired restoration outcomes.

Our progress in identifying predictors of oyster restoration outcomes brings us closer to designing projects that are optimized for specific ecosystem services. In practice, managers are already altering oyster restoration approaches to accentuate different services (Fitzsimons et al., 2019). For example, restored reefs are built taller or from harder substrates such as concrete or rock to increase shoreline protection, shell reefs are used in substrate-limited areas to enhance habitat provisioning, and live oysters are added in areas with poorer water quality to boost water filtration capacity. Our work indicates the importance of physical setting and reef age to enhance the ecosystem services of oyster production and habitat provisioning, but more work is needed to identify drivers for other services, such as nutrient cycling, water filtration, and shoreline protection. In our prior meta-analysis, we found that these ecosystem services were particularly data sparse and required more studies to quantify the drivers of variation among projects (Smith, Cheng, & Castorani, 2022).

This study focuses on drivers of restoration success for eastern oysters because data were extremely limited for other species (Smith, Cheng, & Castorani, 2022). Because most ecological studies and restoration projects have targeted eastern oysters, many international oyster restoration efforts are modeled after successful projects with this species (Fitzsimons et al., 2019; zu Ermgassen et al., 2020). We expect that oyster species with common life history traits would respond similarly to the predictors included in our analysis. For example, other oyster species used in oyster restoration projects have comparable salinity tolerances to eastern oysters (Nell & Holliday, 1988), so we would tentatively expect to find similar increases in oyster production in polyhaline areas relative to mesohaline ones. With the continued expansion of oyster restoration projects worldwide, we recommend that studies include control habitats in their design (unstructured habitats representing restoration starting points/undesired endpoints or natural reference habitats representing desired restoration endpoints) and also explicitly manipulate or measure variation in the potential drivers of restoration outcomes to support future global syntheses of oyster restoration success.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Smith et al., 2023) are available in the Environmental Data Initiative (EDI) Data Portal at https://doi.org/10.6073/pasta/30c4fc18cabc79f6ee4d20c8d3800277. The list of literature used for our meta-analysis was obtained from Web of Science and Google Scholar using the search terms described in Appendix S1: Section S1, and the complete list of publications included in the meta-analysis can be found in Appendix S1: Table S3.

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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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