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LETTER

Restored oyster reefs match multiple functions of natural reefs within a decade

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[Correction added on 26 May 2022 after first online publication: an error was made in unit conversion of oyster counts/lengths to oyster biomass and reported biomass results in units of 0.25 m2 instead of units of 1 m2.]

Abstract

Global declines of foundation species have reduced ecological function at population, community, and ecosystem levels. Restoration of foundation species promises to counter such losses, despite unknown recovery timelines, undefined benchmarks, and uncertainty about whether restored ecosystems approximate natural ones. Here, we demonstrate through a 15-year large-scale experiment in coastal Virginia, USA, that restored oyster reefs can quickly recover multiple ecological functions and match natural reefs. Specifically, abundances of oysters and a key crab mesopredator on restored reefs equaled reference reefs in approximately 6 years, indicating that restoration can initiate rapid, sustained recovery of foundation species and associated consumers. As reefs matured and accrued biomass, they became more temporally stable, suggesting that restoration can increase resilience and may stabilize those ecosystem processes that scale with foundation species biomass. Together, these results demonstrate that restoration can catalyze rapid recovery of imperiled coastal foundation species, reclaim lost community interactions, and help reverse decades of degradation.

KEYWORDS
community ecology, ecosystem function, foundation species, restoration, temporal stability

1 | INTRODUCTION

Loss of foundation species and their associated ecological functions epitomizes environmental degradation in the Anthropocene (Ellison et al., 2005). As we enter the United Nations Decade on Ecosystem Restoration (2021–2030), restoration promises to hasten the recovery of many vanishing ecosystems (Cooke et al., 2019). However, assessment of restoration outcomes is limited by unknown recovery timelines, undefined performance metrics, and uncertainty about whether restored systems can approximate natural ones (Suding, 2011; Cooke et al., 2019).

These challenges are particularly acute when restoring coastal foundation species, such as oysters. Oysters historically provided the foundation of many temperate coastlines worldwide, and valuable ecosystem services, including fisheries production and water filtration, scale with oyster biomass (Grabowski et al., 2012; zu Ermgassen et al., 2012, 2015). However, overfishing and disease caused catastrophic oyster declines and associated losses of ecosystem services (Kirby, 2004). To reverse oyster declines and recover lost ecosystem services, oyster restoration projects have increased exponentially since 1990 (Duarte et al., 2020) as governments and nonprofits have widely funded restoration projects (e.g., US RESTORE Act: \$133.3 M; Gulf Coast Ecosystem Restoration Council, 2019; America Recovery and Reinvestment Act of 2009: \$167 M; Samone et al., 2017; Australia's *Reef Builder* project: \$20 M; The Nature Conservancy Australia, 2020).

Despite these investments, oyster restoration has mixed evidence of success (Smith et al., 2005; Powers et al., 2009; Schulte et al., 2009; Kennedy et al., 2011; Geraldi et al., 2013), and evaluation of restoration outcomes is hindered by undefined goals and success criteria, insufficient replication, and short monitoring timelines (Kennedy et al., 2011). Few studies simultaneously measure comparable reference sites, especially over the sustained durations (>10 years) required to establish baselines and evaluate continued restoration success (Suding, 2011). Indeed, current oyster restoration monitoring recommendations are based on short-term studies that compare restored and natural reefs (usually 2 years or less; not exceeding 6 years), but do not capture long-term restoration outcomes (Dillon et al., 2015; Bayraktarov et al., 2016; Walles et al., 2016; Rezek et al., 2017). Therefore, it is unclear whether restored reefs can approximate the functions of natural reefs and how much time is needed for recovery.

Here, we help address these gaps with a distinctively long-term (15 years), large-scale (70 reefs) experiment to assess the extent to which restored reefs can match some of the ecological functions of natural reefs and determine how quickly managers can anticipate recovery of these functions following restoration. Ecological functions include population, community, and ecosystem processes (Akçakaya et al., 2019). At a population level, high-biomass oyster reefs produce shell that facilitates recruitment and sustains population growth (Lenihan, 1999). At the community level, reefs provide habitat and food for nekton species (La Peyre et al., 2019). Lastly, oysters and other foundation species can buffer temporal variability of ecosystem-level processes by stabilizing local abiotic conditions (Ellison et al., 2005; Lamy et al., 2020). Our study demonstrates that restoration initiates rapid and sustained recovery of oyster biomass, mesopredator abundance, and ecosystem stability over time. These results demonstrate one of the fastest recovery timelines for a restored coastal foundation species and support the continued and expanded use of restoration to recover lost ecological functions.

2 | METHODS

2.1 | Study system

We focused our investigation on intertidal reefs formed by the Eastern oyster *Crassostrea virginica*, which is commonly targeted for restoration along the US Gulf and Atlantic coasts (1768 projects, 5199 ha restored, \$299,999/ha on average) (Bersoza Hernández et al., 2018; Duarte et al., 2020). Our experiment was located along the Atlantic coast of the Eastern Shore of Virginia, USA, in the Virginia Coast Reserve (VCR; Figure 1a; Fig. S1), where severe overharvesting and disease decimated reefs in the 1900s, mirroring declines in the nearby Chesapeake Bay (Schulte, 2017). Despite these losses, some remnant reefs naturally recovered in the early 2000s to develop the pronounced vertical structure and multiple oyster size classes that represent the desired endpoint of restoration efforts (Figure 1). Choosing references to serve as restoration targets is challenging in degraded systems where population baselines have shifted and historical population levels may be unattainable (Suding, 2011). Although these natural reefs cover only a margin of their historic extent and biomass, they represent the upper end of oyster densities measured in the United States since the collapse of wild commercial oyster fisheries (~1600–2200 oysters per m^2; Luckenbach et al., 2005; Milbrandt et al., 2015; Blomberg et al., 2018), suggesting that these natural reefs are suitable references for a historically degraded system. Nearly every year since 2003, The Nature Conservancy and Virginia Marine Resource Commission have constructed intertidal oyster reefs in the VCR to create 54 restored reefs at 16 sites (Figure 1 and Table S1; 0.02–1.06 ha). At eight of these sites, 35 restored reefs are colocated with a natural reference reef present within 2 km (Figure 1 and Table S1; 0.004–0.84 ha).

2.2 | Data collection and restoration performance metrics

To assess the performance of restored oyster reefs relative to reference reefs, and determine recovery timelines, we quantified multiple ecological functions: density, biomass, and shell height of live adult oysters; density of mud crab mesopredators; and temporal stability of oyster biomass. We sampled reefs from 2005 to 2019, sampling within their first 3 years of construction, and then opportunistically sampling each reef every 3–4 years afterward (mean no. of sampling events $\pm$ SD: 5.6 $\pm$ 2.8, $n = 1$–12; Tables S2 and S3). Sampling frequency of each reef varied by year and season (Tables S2 and S3).

During each sampling event, we collected 0.0625 m^2 quadrat excavations (15–30 cm) from each reef (mean no. of quadrats per reef $\pm$ SD: 3.21 $\pm$ 0.96, n = 1–8; Tables S2 and S3). In 2005–2006, we used a 0.25 m^2 quadrat, and we subsequently converted all data to units per m^2. We deconstructed each excavation and counted all live oysters and measured shell height (mm). We estimated oyster biomass by developing a height-biomass relationship for live oysters (Figure S2, $Biomass = 1.76 \times 10^{-5} \times Height^{2.41}$).

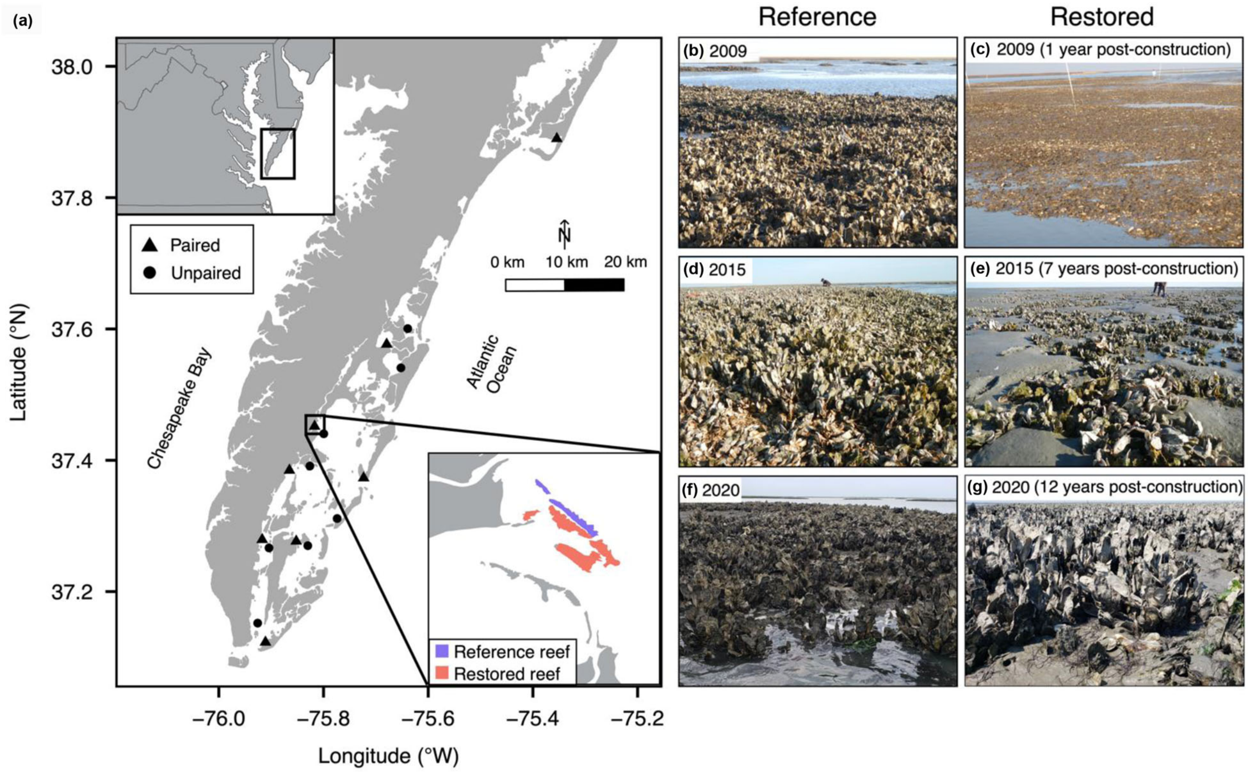

FIGURE 1 Study system and experimental design. (a) We measured reef attributes for 15 years (2005–2019) at 70 restored and reference reefs at 16 sites in coastal Virginia, USA. Triangles mark sites containing paired restored reefs ($n = 35$) and reference reefs ($n = 11$). Circles represent unpaired sites containing either restored or reference reefs. Paired sites encompass at least one restored reef (red in inset) and an associated reference reef (blue in inset). (b–g) Examples of a paired restored reef (HC6) and its associated reference reef (HC2_R; Table S1) over the study period from 2009 to 2020 show that the reference reef maintained vertical structure and multiple oyster age classes over time, as oyster populations on the restored reef increased from 1 to 12 years post construction. Photos: B. Lusk

We categorized oysters >25 mm as adult and excluded spat oysters with lengths ≤25 mm due to variability in sampling season.

As one indicator of community effects of restoration, in each quadrat we counted Xanthid mud crabs, which are fast-growing, ubiquitous mesopredators that prey on oysters, shelter from predators in reef interstices, and comprise an important trophic link to higher order consumers (White & Wilson, 1996; Grabowski et al., 2020).

Lastly, we calculated the temporal stability of adult oyster biomass and examined how it changed with restored reef maturity (see Section 2.3).

2.3 | Data analysis

To examine how adult oyster attributes (abundance, biomass, size) and crab abundance on restored reefs and reference reefs varied with years since construction, we subset the data to include only restored reefs with paired reference reefs as described above. We further subset the data to only include sampling events where we sampled the restored reef within the same seasonal recruitment period as its paired reference reef for that year (one recruitment season per year, May to September). We then averaged adult oyster and crab attributes across quadrats for each reef and sampling event in the subset dataset. For each variable, we calculated the difference between paired restored and reference reefs. We calculated years since construction for each sampling event based on the number of recruitment seasons that each reef experienced at the time of sampling. We adjusted "years since construction" to account for the sampling date relative to whether a reef was constructed in the fall after the recruitment season ($n = 11$), or during the spring or summer ($n = 43$), when reefs were available to oyster recruits. Examining the difference between restored and reference reefs as a function of year since construction accounted for the fact that restored reefs were constructed during different years.

We used linear mixed models (LMMs) to relate differences in adult oyster abundance, adult oyster biomass, and mud crab abundance to years since construction (with site as a random intercept for all models to account for non-independence among reefs by site) (Zuur et al., 2009). We related differences in oyster size to years since construction using generalized additive mixed models (GAMMs) because residuals from linear models indicated nonlinearity (Zuur et al., 2009). We examined the relationship between adult oyster and crab abundance using zero-inflated negative binomial generalized LMMs (GLMMs; with quadrats nested in reef identity as a random intercept; Zuur et al., 2009). Sample autocorrelation function analysis and semivariograms showed no evidence of temporal or spatial autocorrelation (Zuur et al., 2009).

To examine how adult oyster biomass affects temporal stability of adult oyster biomass, we calculated temporal stability as the inverse of the coefficient of variation (1/CV) in oyster biomass across all sampling dates for each monitored reef sampled three or more times (n = 63 reefs, including restored reefs without paired references and vice versa) (Ives & Carpenter, 2007). We averaged across quadrats for each sampling event prior to calculating stability. We used ordinary least squares regression to explain temporal stability as a function of mean oyster biomass.

To assess how temporal stability of adult oyster biomass varied between reference reefs and restored reefs of different maturities, we grouped the time series of each restored reef into two parts to represent developing reefs (0–6 years since construction) and mature reefs (7–15 years since construction). We chose this breakpoint based on when restored reefs approximate the measured population and community attributes of reference reefs (~ 6 years; see Section 3). We calculated stability as described above for time series with three or more sampling events. To examine the sensitivity of our results to the duration over which we calculated stability, we repeated our analyses using sites sampled over timespans of 3–7 years (Figure S5). We used analysis of variance to quantify the effect of reef type (reference reef, developing restored reef, mature restored reef) on temporal stability and compared pairwise differences in temporal stability among reef types using Tukey's post hoc tests (details in Supplementary Material).

3 | RESULTS

Although adult oyster abundance and biomass on restored reefs initially underperformed reference reefs, these attributes increased over time on restored reefs relative to reference reefs by 160.4 oysters/m^2/year (Figure 2a; $F_{1,90} = 45.3$, $p < 0.001$, $R^2 = 0.63$; Figure S3a) and 43.1 g ash free dry mass (AFDM)/m^2/year (Figure 2b; $F_{1,90} = 32.4$, $p < 0.001$, $R^2 = 0.43$; Figure S3b), respectively. Restored reefs matched reference reefs in oyster abundance after 6.0 years (95% confidence interval = 3.1–9.3 years) and matched oyster biomass after 5.7 years (3.6–8.3 years). For the remainder of the study, restored reefs equaled or slightly exceeded oyster abundance and biomass on reference reefs. Oyster size matched reference reefs more quickly, increasing sharply over the first 3 years and then saturating (Figure 2c; $F_5 = 18.5$, $p < 0.001$, $R^2 = 0.57$; Appendix 2: Figure S3c), as anticipated from prior estimates of individual oyster growth rates (Southworth et al., 2010). After 2.5 years (2.0–3.0 years), there was no difference in the shell height of adult oysters on paired restored and reference reefs; oyster size remained equivalent between restored and reference reefs as reefs aged. Size frequency distributions on restored reefs also approximated reference reefs within 3 years (Figure S4).

Abundances of Xanthid mud crabs on restored reefs mirrored trends in oyster abundance and biomass, increasing with years since construction by 16.2 crabs/m^2/year to match or exceed reference reefs after 6.2 years (4.6–8.2 years) (Figure 3a; $F_{1,90} = 47.4$, $p < 0.001$, $R^2 = 0.45$; Figure S3d). Moreover, crab abundance was positively correlated with adult oyster abundance across both restored and reference reefs (Figure 3b; $\chi^2_1 = 127.1$, $p < 0.001$, $R^2 = 0.30$).

Increases in adult oyster biomass enhanced the temporal stability of adult oyster biomass (Figure 4a; $F_{1,61} = 9.4$, $p = 0.003$, $R^2 = 0.13$). Although we found large variation in oyster reef temporal stability, reefs with the greatest biomass (527.5 g AFDW/m^2) were on average nearly three times more temporally stable than those with the lowest biomass (8.4 g AFDW/m^2) over the study's duration; this trend was robust to outliers and the minimum duration for which we calculated temporal stability (3–7 years; $p < 0.05$; $R^2 = 0.13$–0.22; Figure S5). Furthermore, mature restored reefs (7–15 years postconstruction) approximated the temporal stability of reference reefs, whereas developing reefs (0–6 years postconstruction) were on average 30% less temporally stable than reference reefs (Figure 4b; $F_{2,70} = 7.1$, $p = 0.002$).

4 | DISCUSSION

Restoration initiated rapid and sustained oyster reef recovery. Adult oyster abundance and biomass on restored reefs matched populations on natural reference reefs within 6 years. Furthermore, the presence of both spat (<25 mm height) and market-size adults (>75 mm height) on restored reefs within 3 years indicates that restored reefs rapidly attracted oyster recruits and produced broodstock (Baggett et al., 2015). Development of multiple oyster size classes at high densities indicates that restored reefs met common criteria for restoration success (Powers et al., 2009; Schulte et al., 2009; La Peyre et al., 2014). In our region, most restored-reference pairs were closed to harvest (Table S1), which may have helped promote

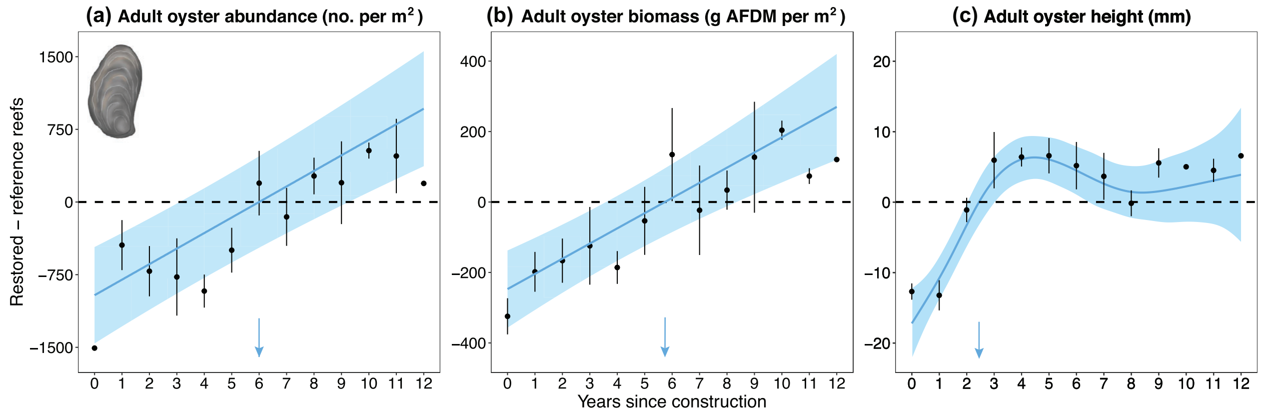

FIGURE 2 Changes in adult oyster abundance, biomass, and size with time since construction. Restored reefs matched reference reefs for adult oyster (a) abundance (no./m^2), (b) biomass (g ash free dry mass/m^2), and (c) shell height (mm) as years since construction increased. The horizontal dashed line at zero indicates equivalent performance between paired restored and reference reefs. Positive values indicate overperformance and negative values indicate underperformance of restored reefs relative to paired reference reefs. Reefs reached equivalency after approximately 6.0 years for abundance, 5.7 years for biomass, and 2.5 years for shell height (indicated by arrows, where the marginal mean trend line intersects zero). Points and error bars indicate mean ± standard error of paired differences. Lines represent the estimated marginal mean trends ($p < 0.001$) and shading indicates 95% confidence intervals for the model fixed effects. Illustration: T.L. Rogers

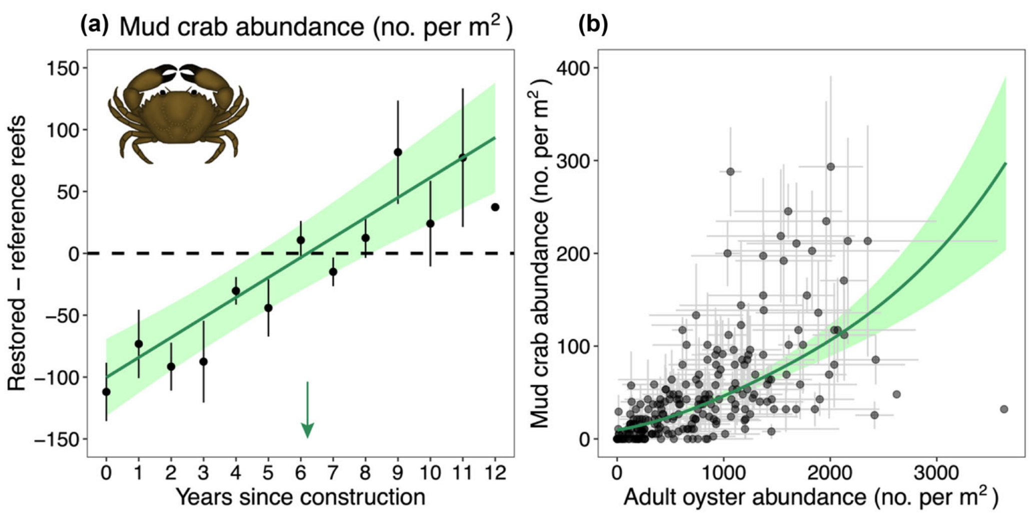

FIGURE 3 Changes in mud crab abundance with time since construction and as a function of adult oyster abundance. Restored reefs matched reference reefs for (a) mud crab abundance (no./m^2) at 6.2 years postconstruction. Arrows, points, lines, and shading as in Figure 2. (b) Mud crab abundance (no./m^2) was positively associated with adult oyster abundance (no./m^2) across restored and reference reef pairs. In panel b, points represent the mean abundances ± standard error of each reef sampling event. Illustration: T.L. Rogers

oyster recovery (Powers et al., 2009; Schulte et al., 2009). Moreover, deploying hard substrate (shell cultch) was sufficient to support recruitment from existing larval sources. In contrast, in recruitment-limited systems, oyster recovery will likely be slower without transplanting broodstock (Fitzsimons et al., 2019).

Abundances of mud crabs—the most common mesopredator in our system—on restored reefs matched reference reefs within 6 years, mirroring the recovery timelines for adult oyster density and biomass. Crabs colonized restored reefs as adult oyster abundance increased, probably because restored reefs rapidly provided habitat and food (White & Wilson, 1996; Grabowski et al., 2020). Indeed, mud crab abundance was positively correlated with adult oyster abundance, highlighting the link between oyster density and mesopredator production. Although we did not directly measure other fisheries species, previously documented trophic cascades reveal that mud crabs are consumed by other ecologically and commercially important nekton species that feed on

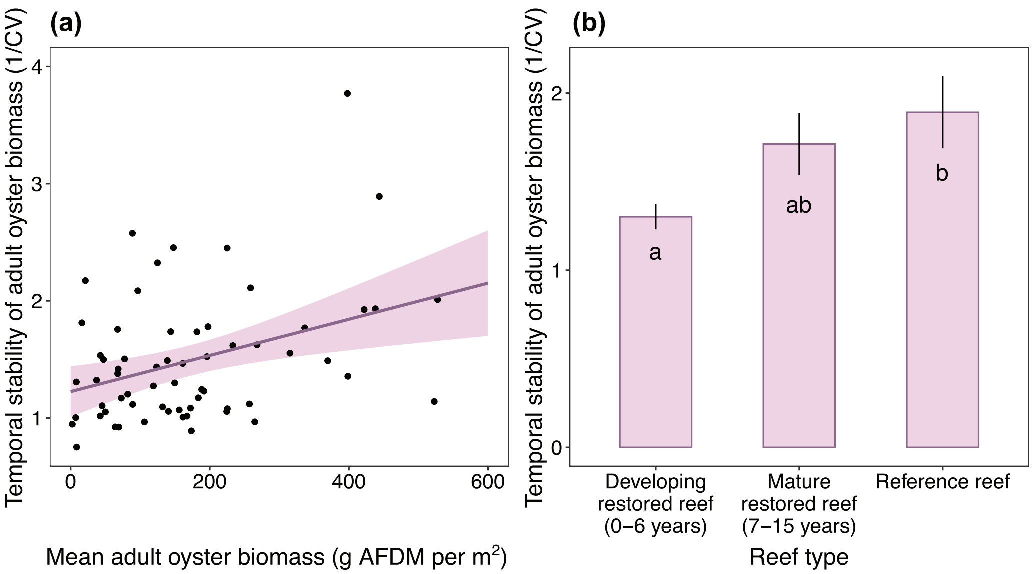

FIGURE 4 Effects of restoration on the temporal stability of adult oyster biomass. (a) The temporal stability of adult oyster biomass ($1/CV = \mu/\sigma$) increased with mean adult oyster biomass (g AFDM per m^2) on restored and reference reefs monitored three or more times during the study ($n = 56$ reefs). Line and shading as in Figure 2. (b) Mean temporal stability on restored reefs was lower than reference reefs during development (0–6 years, $n = 47$ reefs), but mature restored reefs (7–15 years, $n = 11$ reefs) matched the stability of reference reefs ($n = 15$ reefs). Error bars indicate standard error. Letters indicate significant differences among groups in post hoc analysis ($p < 0.05$)

oyster reefs (White & Wilson, 1996; Grabowski et al., 2020). Furthermore, higher trophic species that do not directly consume mud crabs have been previously shown to increase with oyster biomass (zu Ermgassen et al., 2015; La Peyre et al., 2019). Our finding that mud crab populations rapidly rebounded in tandem with oyster populations suggests that restoring oysters could quickly recover such community interactions, although reef-associated species that are slower to colonize or grow will likely require longer recovery trajectories.

Increases in adult oyster biomass enhanced the temporal stability of adult oyster biomass, which could indicate stability of other reef ecosystem functions, as processes such as water filtration or fisheries production scale with oyster biomass (Grabowski et al., 2012; zu Ermgassen et al., 2012, 2015). Increased stability of foundation species biomass can also improve ecosystem recovery from disturbance (Ives & Carpenter, 2007; Lamy et al., 2020). Together with our finding that adult oyster biomass builds quickly on restored reefs (Figure 2b), the fact that enhanced temporal stability increased with adult oyster biomass could suggest that restoration can increase overall ecosystem stability and enhance resilience. Indeed, mature restored reefs approximated the temporal stability of reference reefs, in contrast to developing restored reefs, which were less stable than reference reefs. The temporal stability of restored populations is not yet widely used to evaluate restoration success, but our results suggest that it could be a valuable metric for restoration practitioners.

Overall, our results show that restored reefs can match multiple ecological functions of reference reefs within a decade. Relative to other coastal foundation species, the recovery timeline that we identify for oysters is similar to kelps and fast-growing seagrasses (<10 years), but rapid relative to slow-growing seagrasses (10–30 years), salt marshes (5–20 years), mangroves (10–20 years), and reef-building corals (>30 years) (Alongi, 2008; Borja et al., 2010; Roman & Burdick, 2012; Duarte et al., 2020). Together, these results add to growing evidence that marine systems typically regain ecological functions more quickly than aquatic or terrestrial systems, which can take 20–60 years to recover from disturbance (Jones & Schmitz, 2009). Our findings build on previous shorter-term studies of restored reef development (1- to 6-year duration) to increase confidence that the observed trends in recovery are sustained, and not due to natural variability or transient dynamics (Dillon et al., 2015; Walles et al., 2016; Rezek et al., 2017). Thus, our study supports the continued and expanded use of oyster restoration projects to promote long-term recovery of oyster reefs and their valuable ecological functions.

Importantly, our results indicate the general time frame in which managers can anticipate oyster restoration success (6–10 years). However, the median duration of oyster restoration projects is only 2 years (Bayraktarov et al., 2016), and our work highlights the need to extend monitoring timelines beyond currently recommended short-term (1–2 years) and mid-term (4–6 years) measurements (Baggett et al., 2015) to effectively evaluate restoration outcomes. Indeed, if we had monitored populations for less than 6 years—as in most studies of oyster recovery—we would have failed to detect restored reef recovery relative to natural reefs. Sustained long-term monitoring is essential to separate directional trends from temporal variability, describe the rate and shape of recovery trajectories, and forecast restoration success (Suding, 2011). Thus, scientists and practitioners should consider trade-offs between duration and frequency when allocating limited resources for monitoring programs. Clarifying the expected recovery timeline for oyster restoration can improve the timing of restoration goal setting and inform when managers can reliably measure restoration progress, plan fundraising efforts, or implement adaptive management.

Providing longer-term estimates of oyster recovery can improve accuracy in valuating ecosystem services. Estimating the value of ecosystem services and the associated return on investment with restoration is based largely on short-term studies (Grabowski et al., 2012). Yet, we find that—for the ecological functions we measured—there is a 6-year lag before restored reefs approximate natural reefs. Such lags in functionality should be incorporated into valuation of ecosystem services associated with restoration projects. These results also highlight that the benefits of oyster restoration may not be fully realized when projects are monitored on short-term or mid-term time frames. Furthermore, oyster restoration can enhance additional ecological functions not measured in our study, including biodiversity (Dillon et al., 2015; Rezek et al., 2017), biogeochemical cycling (Kellogg et al., 2013), and shoreline protection (La Peyre et al., 2015), although we are currently more data-limited about how closely these functions scale with oyster biomass. The relative recovery timelines for these distinct ecological functions are not well resolved and warrant future comparison, especially given known divergence in recovery timelines for different ecosystem functions in other restored systems (Roman & Burdick, 2012).

In conclusion, our work demonstrates that restoration of foundation species can catalyze rapid recovery of degraded foundation species and their associated fauna, while increasing the temporal stability of ecosystems. Restored systems rarely show complete recovery of ecological functions (Benayas et al., 2009; Suding, 2011; Jones et al., 2018), and widespread degradation of natural systems means that we must compare restored systems to reference populations whose baseline levels have already shifted relative to historic levels. Despite these challenges, we found that restored oyster reefs matched multiple functions of natural oyster reefs at a rapid pace relative to other restored ecosystems (Kirby, 2004; Borja et al., 2010; Jones et al., 2018). Yet, the capacity to detect this pattern and refine recovery timelines was only possible with sustained measurements at both restored and reference sites, underscoring the necessity of funding long-term studies (>10 years) of restoration outcomes that include appropriate controls.

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SUPPORTING INFORMATION

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