ECOLOGY

Oyster reef restoration fails to recoup global historic ecosystem losses despite substantial biodiversity gain

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Human activities have led to degradation of ecosystems globally. The lost ecosystem functions and services accumulate from the time of disturbance to the full recovery of the ecosystem and can be quantified as a "recovery debt," providing a valuable tool to develop better restoration practices that accelerate recovery and limit losses. Here, we quantified the recovery of faunal biodiversity and abundance toward a predisturbed state following structural restoration of oyster habitats globally. We found that while restoration initiates a rapid increase in biodiversity and abundance of reef-associated species within 2 years, recovery rate then decreases substantially, leaving a global shortfall in recovery of 35% below a predisturbed state. While efficient restoration methods boost recovery and minimize recovery shortfalls, the time to full recovery is yet to be quantified. Therefore, potential future coastal development should weigh up not only the instantaneous damage to ecosystem functions but also the potential for generational loss of services.

INTRODUCTION

Exploitation and disturbance of ecosystems in the Anthropocene has led to severe degradation of natural biomes and loss of biodiversity (*1*–*3*). Consequently, investment in conservation and restoration efforts has increased worldwide (*4*–*7*), especially as a strategy to restore ecosystem services (*8*). While the cost-benefit ratio of restoration is often justified as ecosystem recovery that yields sufficient benefits to human prosperity (*9*), recovery of ecosystems back to a reference state in terms of biodiversity and ecosystem functions and services (*10*) often takes decades (*11*–*13*). Where damaged ecosystems provide reduced function or support reduced biodiversity relative to the historical "natural state" (reference/pristine condition), there is an accumulation of the lost ecosystem functions and services between the initiation of habitat damage and "full recovery" to a reference state. These lost functions and services accumulate over time and can be quantified a "recovery debt" (Fig. 1) (*13*). While this debt in lost services has been estimated in ecosystems that largely only require natural regeneration following the removal of persistent disturbances (*13*), the recovery pathway, time to full recovery, and accumulated debt of lost services in marine habitats that require active intervention, including structural restoration, remain undetermined (Fig. 1).

A major part of the accumulated debt in recovering ecosystems can be considered as services foregone, ecosystem services that would have existed had there not been damage (*14*). While many ecosystems will slowly recover functions once an impact is removed, actions that increase the rate of system recovery (e.g., habitat restoration) will theoretically increase both the rate of recovery and the potential for an ecosystem to recover to its maximum capacity, minimize the services foregone, and thus reduce the accrual of lost services. Therefore, using the best-performing restoration methods to rapidly boost recovery of ecosystems may minimize the accumulated recovery debt and at least partially offset the ongoing damage associated with current activities (e.g., coastal development).

Oyster habitats are one of the most anthropogenically affected coastal habitats worldwide. At least 85% of oyster habitats have been lost globally, predominantly as a consequence of not only historical overharvest using destructive fishing practices but also because of more recent effects of coastal urbanization, including declining water quality and introduced diseases (*15*, *16*). Destructive dredge harvest removed not only live oysters and their biological functions but also the remnant dead oyster shells that provide structural complexity (vertical relief and size) and substrate for oyster settlement (*15*). Hence, only a handful of sites remain globally where oyster habitats exist in their natural state. Given the biogenic reef-building nature of oyster habitats and a life history that leaves them vulnerable to Allee effects, natural recovery is unlikely given the loss of structural habitat that is essential for oyster settlement. Therefore, intensive restoration efforts of oyster habitats have led to large capital investment in various methods, all aiming to increase the spatial area of oyster habitat, their functioning, and their ecosystem services (*17*–*23*).

Restoration of oyster habitats typically includes remediation of environmental conditions, substrate provision, and/or restocking with juvenile and/or adult oysters (*24*). Key considerations in substrate provision are the type of material used (e.g., recycled shell versus artificial materials such as concrete blocks) and its spatial arrangement (*25*). While oyster habitats naturally accrete on oyster shell, the availability of oyster shells (from aquaculture or shell recycling programs) is generally limited, such that different substrate types have been tested as an alternative in oyster habitat restoration. Furthermore, although a range of factors associated with the spatial arrangement of substrate (e.g., patch size and fragmentation) can influence oyster establishment and ecosystem service provision (*25*), vertical relief is considered particularly important as it can influence oyster habitat growth by determining water flow and dissolved

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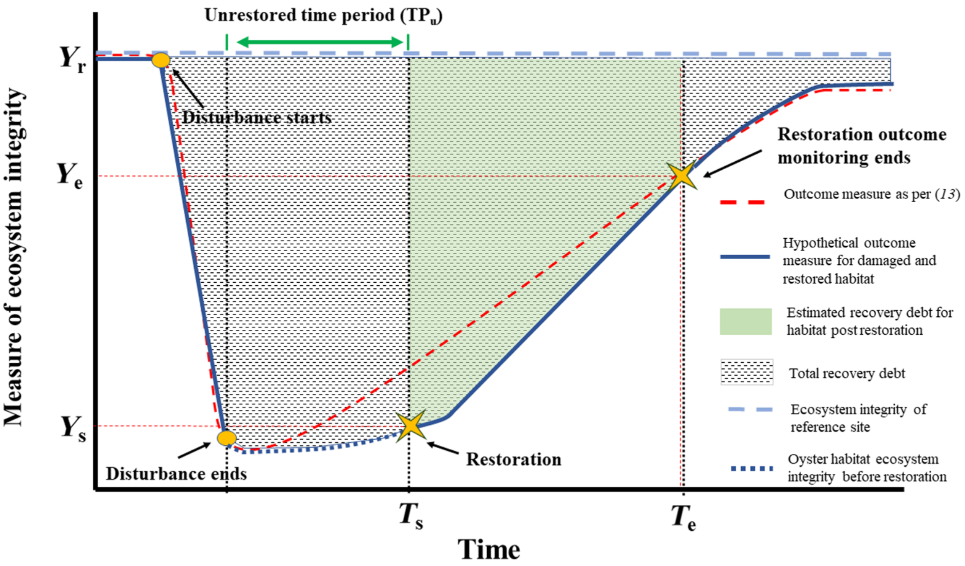

Fig. 1. Theoretical diagram of general recovery debt (red dashed line) and recovery debt specific to restored habitats (dark blue lines). TP$_u$ reflects the ecosystem integrity in the absence of restoration efforts. Y_s and T_s represent ecosystem integrity outcome measure and the time when measurement started. Y_e and T_e represent ecosystem integrity outcome measure and time when measurement ended. The position of T_e on the graph is project specific and may be influenced by factors such as funding and recovery objectives but, to date, has generally been before full recovery. Ideally, monitoring should be continued until after full recovery. The pale blue dashed line (Y_r) represents the ecosystem integrity outcome measure of a reference site. The dark blue dotted line represents ecosystem integrity of unrestored oyster habitats. This line is lower than the theoretical line of Moreno-Mateos *et al.* (*13*) because of the integral nature of the physical structure of oyster habitat, which takes more time to regenerate without restoration. In contrast, the model of Moreno-Mateos *et al.* (*13*) assumes that recovery rate is not limited by the absence of the physical structure provided by habitat-forming species. Note that time (*x* axis) is not to scale, and the unrestored time period (TP$_u$) from when disturbance stopped to restoration could be 20- to 50-fold longer than the postrestoration period; in some cases, TP$_u$ can be more than 100 years. The figure was modified and fully redrawn following the model proposed by Moreno-Mateos *et al.* (*13*).

oxygen concentrations and reduce smothering from the accumulation of sediment.

The exploitation and removal of oyster habitats largely took place during, or before, the 19th century (*26*–*29*). While scarce documentation exists, which depicts the pristine or preimpact condition of oyster reefs, it is widely accepted that our current understanding is hampered by a shifted baseline. Therefore, without extensive historical knowledge, the rate at which loss of function and services will reduce following structural restoration of oyster habitats (i.e., recovery toward an undamaged state; Fig. 1) can currently only be assessed relative to remnant habitats (Table 1) or perhaps modeling of the key services that would have been provided by historical reefs. However, assessment of the current recovery can be used to identify the extent to which restoration efforts can mitigate contemporary damage (e.g., with coastal development) and to improve the incorporation of recovery debt into restoration planning, in environmental offsets, and in mitigation measures. For example, identification of methods that increase the rate of recovery and more rapidly reduce recovery debt could be used to improve restoration and recovery efficiency. While oyster habitat restoration tends to yield positive results in terms of recovery toward a reference state, the effectiveness of different methods of restoration in terms of maximum habitat recovery remains unclear. Here, we calculated the recovery debt, or the annual rate at which lost ecosystem functions and services accumulate [see (*13*)], for restored oyster habitat globally (from the beginning of restoration instead of from the start of historical degradation, which is unknown) and undertook a meta-analysis of oyster habitat restoration worldwide to (i) calculate restoration-associated recovery of biodiversity and abundance of resident and transient fish and invertebrates in oyster habitats and (ii) identify the methods for oyster habitat restoration that most successfully increased the rate of recovery and reduced the accumulation of lost services. Overall, we demonstrate that restoration is effective at mitigating damage to oyster habitat ecosystems, rapidly increasing both diversity and abundance of reef-associated species, but full recovery of resorted systems is still to be realized, and there is still a global shortfall in functions and services.

RESULTS

Oyster habitat recovery after restoration

The analysis of monitoring data for 20 restored oyster habitats, obtained over an average of 4 years after restoration (Fig. 2, A and B), revealed that the restored habitats had an annual average of 36.08% (±5.58 SE) lower species diversity of fish and invertebrates than remnant habitats. While four restoration sites recovered well in terms of diversity within 3 to 4 years after restoration [estimated percentage recovery debt per annum (RDr) < 10%], all remaining sites had a recovery debt of >20% (Fig. 2). Total abundance of fish and invertebrates recovered better than diversity, having a mean recovery debt of 24.37% per annum (±9.28 SE), over an average monitoring period of 3 years. In contrast to diversity, fish and invertebrate abundance at 5 of 20 restored habitats had fully offset the recovery debt (negative recovery debt) after 2.5 years, suggesting complete recovery and even higher fish and invertebrate abundance compared to remnant habitats. It must be noted, however, that abundance does not account for shifts in relative abundance among species compared to remnant habitats and does not discriminate between attraction and production.

Table 1. Definitions of the key terminologies used in the study.

Term	Definition
Oyster habitat	A patch of oysters large enough to form a three-dimensional complex habitat. Similar terminology used in the literature includes "oyster bed," "oyster ecosystem," or "oyster reef."
Recovery debt	Accumulated loss of ecosystem structure and functions between the point of habitat damage and "full recovery" to a reference state. In the context of oyster habitat restoration, we adapted the calculation of recovery debt from the point of first restoration as opposed to historical degradation, which is largely unquantified.
Restored habitat	An oyster habitat patch that has been actively restored, for example, by the addition of a substrate (e.g., oyster shell, limestone, and concrete) and/or the provision of live oysters
Remnant habitat	Oyster habitats that have not been destroyed or degraded (e.g., by extraction of oysters) and have persisted over centuries or those that have historically been damaged but have since fully recovered through natural processes. These habitats are used as a reference habitat for calculating the services that have been lost and the recovery debt of restored reefs.
Unrestored habitat	An area where oysters historically were present but are presently degraded and are not being restored. These habitats are generally areas of bare sediment where oyster reefs previously existed.

Over the longer term, neither diversity nor abundance showed a consistent relationship between estimated recovery debt and time (years) since the implementation of structural restoration ($r^2 = 0.029$, $P = 0.458$ and $r^2 = 0.057$, $P = 0.315$, respectively; Fig. 2). However, during the first 4 years, there was a substantial decrease in recovery debt in terms of species diversity (slope = −22.849, $r^2 = 0.4962$, $P = 0.0054$). Annual recovery rates were high in the first 2 to 4 years but then decreased (Fig. 3). Overall, with a few exceptions, restored oyster habitats tended to recover toward a reference state (percentage recovery rate = 27.05 ± 4.07 SE and 90.16 ± 32.16 SE for diversity and abundance, respectively; Fig. 3); because no studies observed full recovery (matching reference habitats) within their monitoring period (up to 10 years), there was no clear indication as to when, or whether, the habitats would reach full recovery.

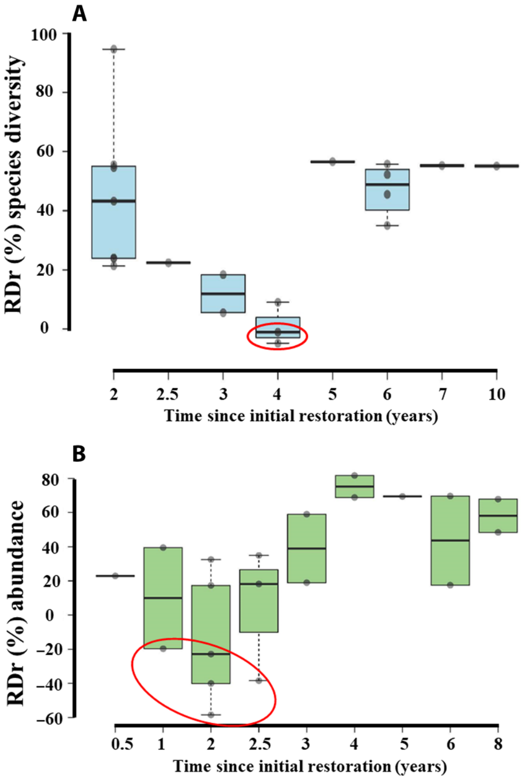

Fig. 2. Oyster habitat accumulated recovery debt per annum as a function of time since restoration. (**A** and **B**) Recovery debt calculated from diversity (A) and abundance (B) (*n* = 20 sites for each). Accumulated debt declines initially with rapid recovery following restoration but then begins to increase as recovery slows and debt begins to accumulate again. Black dots represent estimated recovery debt data points. Black lines represent median recovery debt. Box limits represent the 25th and 75th percentiles. Note the different scales of each graph. Negative recovery debt values represent recovery of outcome measures (species diversity or abundance) above that of the reference habitat. Red circles represent data points extracted from studies that used limestone, oyster shell, or a combination of both as substrate for habitat building (*48*–*51*).

Difference in diversity and abundance between restored and unrestored habitats

The calculated effect sizes [log response ratio (lnRR)] indicated that compared to unrestored habitats [areas that have been left in a degraded state for decades (generally as bare sediment)], restored habitats had an overall greater nekton abundance (δ = 1.117 ± 0.309, $P < 0.001$) (see table S1 for all meta-analysis results). Invertebrate abundance displayed a larger effect size between restored and unrestored habitats than fish abundance (93.5% increase for fish and 532.2% increase for invertebrates), although both were significant (invertebrates: δ = 0.273 ± 0.264, $P < 0.042$; fish δ = 1.294 ± 0.48, $P < 0.001$; Fig. 4, A and B). The effect size for abundance was greatest in the first year of habitat restoration and overall displayed a negative relationship with time ($Q = 7.76$, df = 1, $P = 0.005$; Fig. 4C), suggesting that recovery slowed following an initial period of rapid response. However, while the rate of increase in abundance declined over time (Fig. 3), abundance remained consistently higher in restored habitats relative to unrestored sites (Fig. 4C).

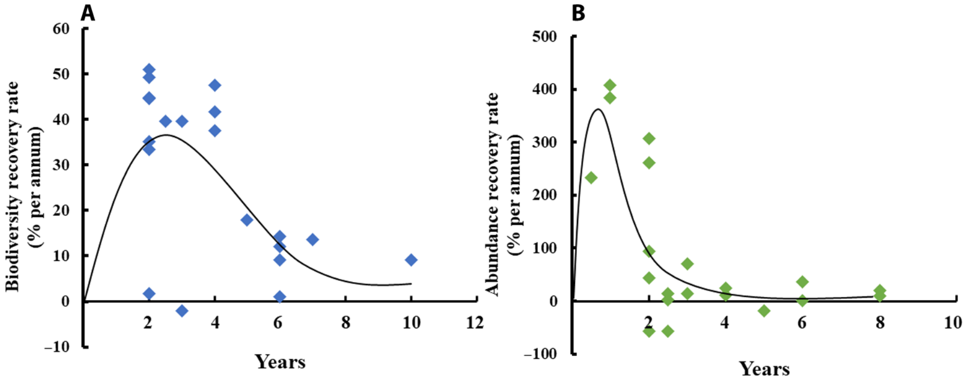

Fig. 3. Oyster habitat recovery rates against time of monitoring. (**A** and **B**) Calculated recovery rate using fish and invertebrate diversity (A) and abundance (B). Note the different scales for diversity and abundance, indicating that abundance recovers more rapidly than diversity. The black lines represent a smoothed quadratic model with intercept set at 0. Recovery rates are calculated in relation to a reference remnant site.

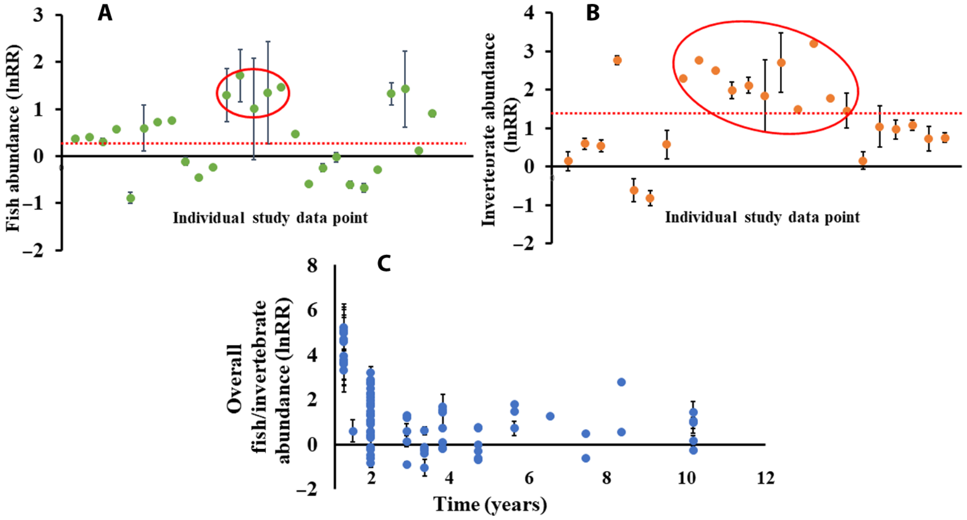

Fig. 4. Inverted forest plots representing the effect size for increase or decrease in transient and resident fish and invertebrate relative to unrestored habitats. (**A** and **B**) Change in fish (A) and invertebrate (B) abundance in restored oyster habitats compared to bare sediment. Data points, effect sizes (lnRR). *X* axes in graphs (A) and (B) only represent distribution of data points. Red dotted lines represent the overall mean effect size. Red circles represent data points extracted from studies that used limestone, oyster shell, or both as substrate for habitat building (*48*–*51*). (**C**) Overall abundance of oyster habitat–associated fauna remains higher than that of bare sediment over time. Error bars, 95% confidence interval (CI). Data points without visible error bars are due to very small CI.

Oyster habitat restoration method

Overall, more oysters were recruited to oyster shells than 15 alternate substrata (of which limestone, concrete, and granite were most common) (δ = −0.472 ± 0.203, $P < 0.001$; Fig. 5A). Of the alternate substrata, recruitment was most similar between limestone and oyster shells, with no significant difference between the two (δ = 0.120 ± 0.256, $P = 0.356$; Fig. 5A). Recruitment to granite was slightly less than to oyster shells (7 of 12 studies), but that difference was not significant (δ = −0.206 ± 0.657, $P = 0.540$). However, fewer recruits (approximately −37% compared to oyster shell) settled on concrete structures (δ = −0.788 ± 0.372, $P < 0.001$; Fig. 5A).

Vertical relief influenced the density of live oysters, whereby oyster habitats of more than 20 cm above the sediment had ~84% higher live oyster density than unrestored bare sediment (δ = 1.771 ± 0.474, $P < 0.001$; Fig. 5B), while oyster habitats with a vertical relief of <20 cm did not support higher oyster densities than unrestored bare sediment (δ = 0.34 ± 1.391, $P < 0.631$). When all datasets were included (including potential outliers; see below), no linear relationship was found between relief and oyster density, with increased vertical relief above 20 cm not contributing to substantially more recruitment ($Q = 0.0715$, df = 1, $P = 0.789$; Fig. 5B). However, when the two potential outlying data points at 0.8 and 1 m were removed, a significant positive linear relationship was observed between vertical relief (up to 50 cm) and oyster density ($Q = 14.225$, df = 1, $P < 0.001$).

DISCUSSION

Historical exploitation has left most ecosystems formed by oysters in a severely degraded state for decades to centuries (*15*). Our analyses focus on the rate at which ecosystem functions and services recover following restoration, showing that the damage to coastal habitats can take more time to recover than might be anticipated

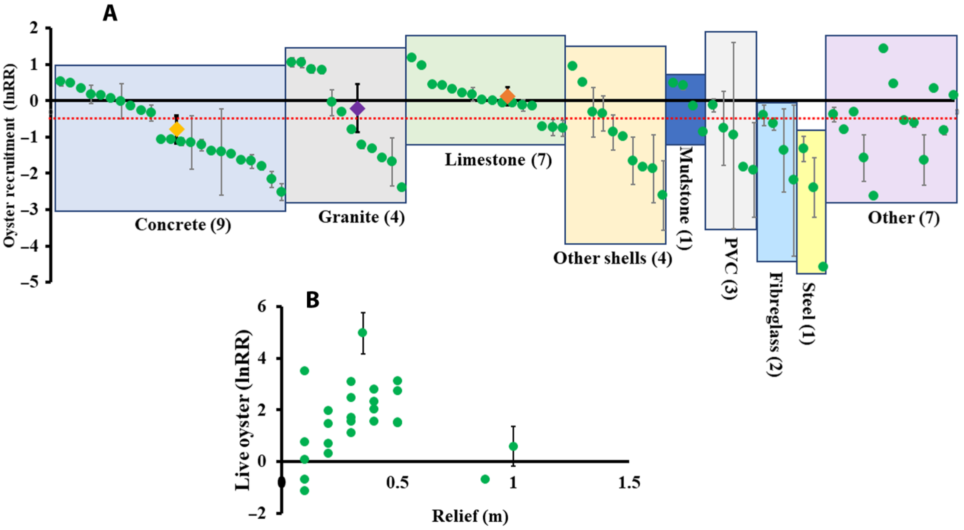

Fig. 5. Inverted forest plot representing difference in overall oyster settlement and oyster density. (**A** and **B**) Oyster settlement on alternative substrata compared to oyster shell (A) and change in live oyster density on oyster habitats as a function of vertical relief above the sediment (B). Data points, effect size (lnRR). LnRR was calculated from (A) oyster recruitment on other substrates compared to oyster shells and (B) live oyster density on reefs that were above 10 cm in height compared to those that were less than 10 cm in height above the substrate. (Error bars, 95% CI.) Data points without visible error bars are due to very small CI. Yellow, purple, and orange diamonds represent the mean effect sizes for concrete, granite, and limestone, respectively. The red dotted line represents the overall mean effect size for all alternative substrata compared to using oyster shells. Numbers in parentheses represent the number of papers from which the data points were taken. PVC, polyvinyl chloride.

[e.g., (*30*, *31*)]. We found that, immediately following restoration, recovery debt (using changes in diversity/abundance values) decreased across all the locations assessed globally (Fig. 2), concomitant with rapid colonization of biota (Fig. 3), an important result given the increasing investment of resources in oyster habitat restoration worldwide. However, the decrease in recovery debt is not maintained through time, and following a rapid initial recovery of faunal assemblages associated with the restored habitat, reducing the lost services, there is a gradual increase in annual accrual of debt as recovery slows (Figs. 2 and (3). This shift likely reflects the stabilization of communities, where an initial rapid accumulation of biodiversity of early successional species is followed by establishment of competitively dominant taxa that stabilize the assemblage structure and exclude some species. An initial increase in species abundance/diversity followed by subsequent community turnover and change in species interactions is a trend of recovery through time observed in many terrestrial and aquatic ecosystems (*32*–*34*). Ecosystem complexity is attained following buildup of species abundance and richness, community turnover, and meta-community interactions (*11*–*13*). Therefore, while restoration can be effective in rapidly reducing the rate at which lost services accrue following destruction of coastal habitats, focusing the monitoring on the initial years following restoration will overestimate the trajectory toward recovering to historical levels or an unaffected reference habitat. It is important, however, to consider what restoration projects regard as their recovery objective (e.g., a simple increase in abundance of live oysters or reef-associated species), how they justify the monitoring period (e.g., based on funding or whether the recovery objective is met), and to what extent the recovery objective is met within that monitoring time frame.

The recovery in diversity of organisms (both fish and invertebrates) associated with oyster reefs was slower than that of their abundance (~36 and ~24% recovery debt for diversity and abundance, respectively). This differs from the previous estimates from most ecosystems, whereby the overall recovery in diversity is generally faster than that of abundance (*13*). The trajectory of recovery in abundance and diversity tend to differ in ecosystems depending on the type of restoration practice (active versus passive restoration; examples below) by driving either rapid abundance of opportunistic colonizers or slow progression in community turnover (*35*). For example, in the terrestrial realm, active landscape restoration (e.g., tree planting) tends to increase faunal abundance faster than diversity because of the sudden change in habitat structure, which can be rapidly exploited by few species [e.g., forest specialists (*34*, *35*)]. On the other hand, similar barren landscapes undergoing passive recovery, where the stressor is removed but no active intervention is undertaken, will experience progressive community turnover from an open-field community to a forest species–dominated community as the habitat setting gradually changes (*35*). Comparable trends have been recorded in active mangrove restoration, where abundance of algivorous fish species peak after restoration, but overall fish diversity remains low (*36*). Therefore, while there are as yet no formal comparisons among different ecosystems for how passive and active restoration affects the rate of recovery, especially of lost services, our results suggest that active restoration will provide more rapid increase in abundance of species in systems when habitat-forming species are key for substrate provision.

It is likely that attraction of mobile fauna from adjacent habitats to the more structurally complex restored habitats, rather than purely enhanced recruitment, accounts for some of this rapid increase in faunal abundance (*37*, *38*). Twenty-five percent of the restored sites that we assessed gained greater abundance than their reference sites (remnant habitats). This could be a result of the added structural complexity of the substrate within otherwise relatively simple mudflats, which will provide multiple resources and attract fauna from a broad area. Alternatively, as the remnant habitats themselves are likely to have experienced some extent of change since industrial overfishing began in the 19th century, the higher abundance on restored sites is likely to be, at least partly, reflective of somewhat disturbed remnant habitats and a shift in our perception of the "natural" baseline. Unfortunately, the multigenerational exploitation and damage of marine systems mean that we have lost most of the undisturbed reference habitats (*39*). Anecdotally, many of the "remnant habitats" are actually reefs formed from other human activities such as abandoned benthic oyster farm infrastructure or even discarded rock ballast from early trade, making it largely impossible to quantify the degree of this past impact; effectively, we cannot recreate the true historical baseline. It is important to note, however, that our estimates only consider locations where nominally undisturbed remnant habitats were available for comparison with restored habitats, yet these locations form a very small proportion of the areas where oyster habitats would have been historically found worldwide (*15*). In addition, the short duration of most monitoring programs (2 to 6 years) means that it is not possible to quantify the time to full recovery toward the faunal abundance and diversity seen in reference habitats. Nonetheless, the estimated recovery debt during this initial 2 to 6 years, and the trend for slowing recovery over time, suggests that complete recovery for both abundance and diversity of reef-associated fauna will require >10 years (Fig. 6). Our study focused only on metrics of community structure and not on complex ecological processes (e.g., community or metacommunity interactions) that may take even longer to recover (*12*).

Irrespective of the accrued recovery debt, restoration efforts rapidly increase habitat function relative to unrestored sites. Restoration contributes to approximately double the abundance of fish and more than fivefold the abundance of invertebrates to coastal ecosystems over unrestored habitats. These increases are promising in terms of recouping ecosystem services such as fisheries (*22*, *38*, *40*). For example, multiple assessments of the increase in habitat provisioning and nekton abundances show that restoration provides multiple prospects for fisheries (*22*, *41*–*43*). Nonetheless, the general temporal progression of ecosystem recovery toward climax community composition through compositional turnover (*44*), community and meta-community interactions, and broader ecosystem resilience and stability have to be accounted for when managing ecosystem recovery (*2*, *12*, *41*).

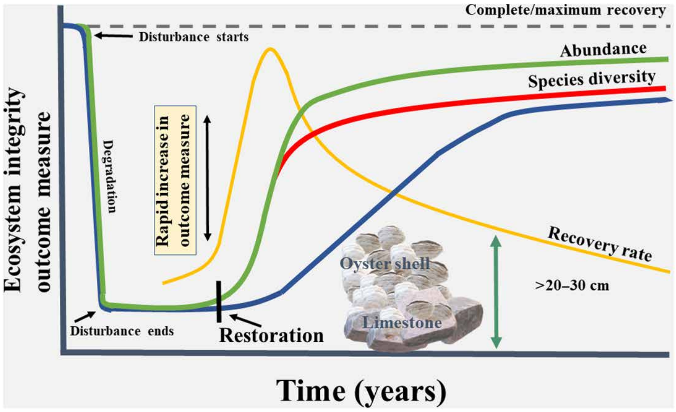

Fig. 6. Model of oyster habitat recovery following disturbance and subsequent restoration. Trends are based on analysis of change in overall recovery of oyster habitat (blue line), cumulative species diversity (red line), and cumulative abundance (green line) of associated species. Note the initial rapid recovery rates after restoration (yellow line), which then declines over time.

In this sense, complementing active restoration with adequate time and protection for the habitat to mature will further benefit recovery (*45*).

While oyster habitat restoration is generally beneficial in terms of increased oyster density and oyster habitat–associated biodiversity, not all restoration methods performed equally. First, we found that oyster shell was the best substrate for habitat building in terms of oyster recruitment. However, oyster shells are not readily available in bulk for large-scale restoration, may have biosecurity risks if not adequately weathered before use, may not provide sufficiently stable structure in wave-swept areas, and have high monetary costs (*46*). We also advise caution with the use of other types of shells, as there is preliminary evidence that brittle or thin shells may break down rapidly and not form the structure that is key for oyster recruitment and survival [e.g., the use of surf clam shell in Harris Creek, Chesapeake Bay (*47*)]. As an alternative substrate when oyster shell is limited, limestone performed almost as well in terms of oyster recruitment. On the basis of our analysis, the best-performing restoration projects that fully recouped the recovery debt (negative debt; e.g., *Crassostrea virginica* reefs in the United States) were all constructed with either limestone, oyster shell, or a mix of both (see red circles denoting data points from these studies in Figs. 2 and 4) (*48*–*51*). Second, our finding that live oyster density is maximized on habitats with structure of more than 20 to 30 cm above the sediment reinforces current restoration practices that provide vertical relief (*52*, *53*). It is important to note, however, that we were unable to partition the effects of vertical relief from that of different substrate types because few studies manipulated these two variables independently. Irrespective of this, habitats with higher relief are more likely to avoid smothering of oysters by sedimentation and elevate oysters above seasonally hypoxic bottom waters, thereby increasing survival of juveniles and adults (*52*, *54*). However, the maximum relief of habitats above the sediment will be defined by water depth and tidal range, especially for intertidal habitats. These intertidal habitats will expand laterally, gaining surface area rather than height, while subtidal habitats have the potential for both lateral and vertical growth. In addition, oyster reefs that are above 50 cm have likely grown on layers of dead oysters that provide the vertical relief, but the density of live oyster on these taller reefs may not necessarily be greater than shorter reefs because surface area has not changed, as shown in the data. Alternatively, there could be a threshold effect whereby raising oysters above the hypoxic zone and area of shifting sediment enhances oyster settlement and density, but once above this zone, there is little added benefit in greater vertical relief. Irrespective of whether restoration is inter- or subtidal, however, we demonstrate that the greatest success is achieved when the restoration substrate is sufficiently above the sediment, providing refined guidance for restoration planning.

Overall, we demonstrate that active restoration of oyster habitats provides enormous benefits to the recovery of associated faunal diversity and abundance (Fig. 4). Our measurement of recovery debt after restoration highlights that recovery of degraded oyster habitats to a reference state is a long-term process and will also benefit from elimination of any external disturbance (e.g., protection from oyster harvest). In addition, ecosystems require time to develop a stable and resilient community structure following active restoration. For example, the biological assemblages and biogeochemical processes in restored wetlands only recover to 74% after at least 50 years, while that of lakes and coastal and coastal ecosystems recover to 24 and 34% after 16 and 12 years, respectively (*12*). In comparison, we calculated 27 to 90% recovery of biodiversity/abundance with 2 to 4 years in oyster habitats. On the basis of other systems, however, none of the studies used here monitored recovery of oyster reefs over sufficiently long periods to capture recovery of either the measured parameters or more complex ecological processes. Nonetheless, implementing appropriate restoration methods has the potential to boost recovery rate, improve overall outcomes, and maximize return for effort. It must be noted, however, that monitoring of restored oyster habitats is currently done for <5 years after restoration in most cases, capturing the initial boost in recovery but not the subsequent progressive change in community composition that remains integral to regaining full ecosystem complexity (*12*). Refining our understanding of the capacity of restored habitats to recover full functions and services will require longer-term monitoring, even more so in areas where remnant reefs are not present to provide a reference, as maximum recovery in these habitats will only likely be indicated by long-term maintenance of ecosystem complexity and stability. Overall, by integrating an estimation of oyster habitat recovery with an assessment of the most effective restoration methods, we show that, globally, biodiversity and abundance benefit immensely from oyster habitat restoration, but the full recovery of system structure, functions, and services will be on decadal scales.

MATERIALS AND METHODS

Literature search

Our analysis followed the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) and the CEE (Collaboration for Environmental Evidence) guidelines. We aggregated studies targeting oyster habitat restoration using the search terms [("oyster reef" OR "oyster habitat" OR "oyster bed") AND ("restoration" OR "recovery" OR "rehabilitation" OR "substrate" OR "relief" OR "biodiversity" OR "species richness" OR "abundance" OR "living shoreline" OR "community" OR "epifauna" OR "nekton")] from three databases: Google Scholar, Scopus, and Web of Science. Study identification was terminated on 29 September 2021 (range, 1970 to 29 September 2021), and only peer-reviewed journal articles and dissertations were included in our study. In addition, we used species abundance and diversity for recovery debt and rate calculations, as few papers documented how other parameters (e.g., filtration and wave attenuation) changed after restoration compared to a remnant site (low sample size). Our initial literature search yielded 12,128 papers. After removal of duplicates and studies that were out of context, 1374 papers remained (primary screening). We then screened these papers to identify those that were specifically relevant to oyster restoration projects. The majority of studies (~73%) and sites focusing on oyster habitat restoration were situated in the east coast of North America (figs. S1 and S2).

Selection criteria

We removed duplicate papers and manually screened the titles and abstracts of each study to select studies that explicitly targeted oyster habitat restoration. We included all papers that studied one or more of the following:

1) A measure of the resident or transient fish and invertebrates sampled in restored and remnant habitats [e.g., abundance, density, catch per unit effort (CPUE), species richness, and diversity].
2) A measure of the resident or transient fish and invertebrates sampled in restored oyster habitats and degraded habitat (commonly represented as bare sediment).
3) A measure of oyster density in relation to oyster habitat vertical relief.
4) A measure of recruitment on oyster shell and other substrata for restoration.

To be extracted and used in our analysis, studies had to report data as either mean or median with a measure of variance (e.g., SD or range) in tables or figures or provide the full dataset from which mean and SD could be calculated. In case a study reported data from multiple sites, each site was used as an individual data point. If a study reported two metrics that were of interest (e.g., diversity and abundance or fish abundance and invertebrate abundance), then each metric was analyzed separately and as appropriate for our analysis. We only included data that were directly relevant to oyster habitat performance, excluding anything that could indirectly come from the influence of other types of habitats (e.g., adjacent marsh or mangroves). For example, if a study reported a metric from a control site, an oyster-only site, and an oyster and seagrass site, then we only use the data from the control and oyster-only sites. When studies reported data over shorter time intervals than yearly (e.g., monthly), we calculated a pooled annual mean and SD including each data point in our estimation to capture the whole range of response (*55*). Data meeting the selection criteria were identified in 70 papers spanning sites worldwide (table S2) (*30*, *31*, *41*, *42*, *48*–*53*, *62*–*120*). From these papers, a total of 232 data points were retrieved to estimate recovery debt in terms of biological diversity (n = 20 data points) and transient and resident fish and invertebrate abundance (n = 20), to analyze difference in fish and invertebrate abundance between restored and unrestored habitats (n = 76), to estimate the influence of different substrates on oyster recruitment (n = 90), and to estimate the influence of vertical relief on oyster density (n = 26). Data for analysis were extracted from figures using PlotDigitizer for windows or from tables and text.

Calculating recovery debt and recovery rate

Recovery debt was calculated following (*13*). Briefly, we screened all studies that reported an outcome metric that was either species richness, diversity index, species density, or species abundances. Here, we used overall organism diversity or abundance (combining fish and invertebrates) linked to reef restoration to obtain the best estimate of overall recovery debt for each reef. For recovery rate and debt calculations, we only used data from studies that included the outcome metrics (e.g., abundance and diversity metrics) from before restoration and after restoration (no matter the time after restoration) at the restoration and a reference remnant site. Recovery debt in terms of diversity (including metrics representing the number of species using a site, e.g., species richness and diversity) and abundance (including metrics representing an estimate of the number of individuals within a site, e.g., abundances, CPUE, and density) was then separately calculated using the following equations

$$\mathrm{RD} = X_r T - [(1/r) \times (X_e - X_s)] \tag{1}$$

$$\mathrm{RDt} = X_r - [(1/rT) \times (X_e - X_s)] \tag{2}$$

$$\mathrm{RDr}(\%) = 100 \times (X_r/\mathrm{RDt}) \tag{3}$$

where RD is the estimated graphical area of recovery debt (Fig. 1) for the time period where monitoring took place, RDt is the estimation of recovery debt per annum, and RDr(%) is the estimated percentage recovery debt per annum. X_r is the outcome metric of the reference site (either in a predisturbance state or a current undisturbed reference site), X_e is the outcome metric (e.g., abundance or diversity) after restoration (at time $t = T$), X_s is the outcome metric before restoration (at time $t = 0$), and r is a constant ($[1/T] \times \text{Ln}\,[X_e/X_s]$). In the case where either X_e or X_s were zero, we replaced zero by a value in the same order of magnitude as X_s or X_e in the median magnitude (e.g., 0.5, 5, and 50) [see (*13*)]. Recovery rate per annum was calculated following the study of Jones *et al.* (*11*) using the following equation

$$\text{Recovery rate} = 100 \times (X_e - X_s)/(X_r - X_s)/\text{Time}$$

Estimating difference between restored and unrestored habitats

To (i) estimate the difference in fish or invertebrate diversity and abundance between restored and unrestored habitats at various time points after restoration, (ii) to assess differences in oyster recruitment between shell and alternate substrata, and (iii) to test for the influence of relief on oyster density (by comparing adult oyster density at different reef relief), we calculated the effect size of response variables (spat density, oyster density, diversity, or abundances) by using means, SD, and sample sizes extracted from studies. We used lnRR as effect size because of its capacity to detect true effects (expected value of the log-proportional change between two independent and normally distributed populations) and robustness to small sample sizes (*56*, *57*). LnRR was calculated using the following equation

$$lnRR = \ln(\text{Mean}_E/\text{Mean}_C)$$

where Mean_E is the mean of experimental measure (e.g., number of spat on alternate substrate or adult oyster density on reef over 10 cm above sediment) and Mean_C treatment is the control measure (e.g., number of spat on shell or adult oyster density on reef below 10 cm on sediment). If one of the measures was zero, to avoid computational error, we used a correction proportional to the reciprocal of the value of the contrasting measure (e.g., value = N, reciprocal = $1/N$). When variance was reported as SE, we calculated SD as

$$\text{SD} = \text{SE} \times \sqrt{N}$$

where N is the sample size. When median and ranges were reported, means and SD were calculated as per Hozo *et al.* (*58*) with the following equations

$$\text{Mean} = (a + 2m + b)/4$$

where a is the lower range, b is the upper range, and m is the median

$$\text{SD} = (1/12)\left\{(a - 2m + b)^2/4 + (b - a)^2\right\}$$

for $N < 15$, where a is the lower range, b is the upper range, and m is the median and

$$\text{SD} = \text{Range}/4$$

for $N > 15$. Before formal statistical analyses, we tested for publication bias using a Rosenberg fail-safe test, Egger's regression test, and trimfill method. Publication bias arises if studies with nonsignificant effects are not published (*59*) and are thus excluded in analysis, thereby influencing results and interpretation. The Rosenberg fail-safe test calculates the number of studies with nonsignificant effects (effect size of zero) that would be required to change the results of the meta-analysis from significant to nonsignificant (*59*). The Rosenberg fail-safe numbers calculated in our analysis were larger than $5n + 10$, where n is the number of studies included in the analysis (*59*), and observed significance was lower than 0.05. The Egger's regression tests were used to estimate asymmetry in funnel plots, and any asymmetry was adjusted using the trimfill method. For all data, either the regression tests resulted in significance values above 0.05 or the trimfill method did not change the mean effect size estimations (figs. S3 to S5). Therefore, publication bias was unlikely to affect our results. Following publication bias tests, we used a weighed random-effects model (restricted maximum likelihood) to undertake our meta-analyses, including heterogeneity test (Q) that indicates the percentage variation between studies due to heterogeneity (i.e., differences in outcomes between different studies; also denoted as I^2) rather than chance (*60*). We then performed meta-regressions using mixed-effects models to analyze variation in effect sizes (e.g., relationship between nekton abundance effect sizes and time after restoration). All calculation of effect sizes, publication bias tests, meta-analysis, and meta-regressions were performed on Meta-Essentials 1.5 (*61*) and OpenMEE, which is an open-source software specifically designed for meta-analysis in ecology and evolutionary biology and based on the "metafor" and "ape" packages for R (*60*).

SUPPLEMENTARY MATERIALS

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