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ARTICLE

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Lessons learned from over thirty years of eelgrass restoration on the US West Coast

Melissa Ward[1] | **Kathryn Beheshti**[2]

[1]San Diego State University, Coastal Marine Institute, San Diego, California, USA

[2]University of California, Santa Barbara, Marine Science Institute, Santa Barbara, California, USA

Correspondence
Melissa Ward
Email: windwardsciences@gmail.com

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Abstract

Seagrass habitats, which provide essential ecosystem functions such as water quality improvement, biodiversity support, ocean acidification amelioration, and sediment carbon storage, are declining worldwide. Eelgrass (*Zostera marina*) habitats along the contiguous US West Coast are threatened by conflicting human uses and global change, resulting in significant protections of and efforts to restore areas where habitat is extant or degraded. Despite a history of eelgrass restoration in this region spanning nearly 60 years, very little work has been published on the subject. Here, we review all available literature on eelgrass restoration projects conducted in California, Oregon, and Washington. Of the 82 restoration projects included in this analysis, which were conducted from 1989 to 2020, only 6 were published in peer-reviewed journals. Thus, despite the precedent for conducting restoration, a lack of data availability makes assessing regional success, drivers of failure, and best practices extremely difficult. From this synthesis, we find that the majority of restoration projects (73%) have been conducted for mitigation (compliance) purposes, contributing to the lack of peer-reviewed literature on the subject. We find that while eelgrass mitigation policies serve to maintain eelgrass structure and regional acreages, they do not facilitate assessments of habitat function or incentivize advancements in regional best practices. We also find that when we could evaluate project outcomes, 32.3%–59.6% of restoration plots were unsuccessful by the end of the project, but this percentage is highly dependent on how success is defined. According to restoration practitioners, failure was likely to result from environmental factors such as light, nutrients, or macroalgal blooms, but was occasionally due to logistical factors such as restoration method or approach. From this work, we recommend a standardized, evidence-based approach to restoration, improved data sharing practices, and careful consideration of existing eelgrass mitigation practices. As marine habitat restoration enters a new global stage, backed by public and private investment, burgeoning carbon markets, and global biodiversity initiatives, it

Kathryn Beheshti and Melissa Ward contributed equally to this study.

is essential to learn from past work to understand and improve seagrass conservation and restoration success.

KEYWORDS
mitigation, restoration, seagrass

INTRODUCTION

Seagrass habitats are valued across the globe for a wide variety of ecosystem functions, providing critical habitat for commercially and ecologically important species, driving biogeochemical cycles, attenuating wave action, and improving water quality (Short et al., 2011). In recent decades, seagrass habitats have gained additional attention for their ability to mitigate climate change impacts, serving to ameliorate ocean acidification and sequester carbon in underlying sediments (Hejnowicz et al., 2015; Ricart et al., 2021). Nonetheless, seagrass habitat is declining worldwide, largely due to human activity (Short et al., 2011; Waycott et al., 2009). This global loss, despite the myriad of documented ecosystem functions, is apparent in many coastal ecosystems, leading to the United Nations' call for a "Decade on Restoration" (Saunders et al., 2020; United Nations Environment Agency, 2019). The development of domestic greenhouse gas inventories and carbon offset markets has also spurred increased public and private interest and investment in coastal habitat restoration, including seagrass meadows, given these habitats' high potential carbon value (Buelow et al., 2022; California Natural Resources Agency [CNRA], 2022; Oregon Global Warming Commission, 2021; WDFW, 2022). With this context in mind, understanding successes, failures, and lessons learned from past seagrass restoration projects is of global importance to guide a future of effective seagrass recovery and management (Strachan et al., 2022; Tan et al., 2020).

Along the US West Coast, eelgrass (*Zostera marina*), the dominant seagrass species in the region, is continually affected by human activities such as dredging, dyking, eutrophication, and pollution (Merrifield et al., 2011). These acute stressors are compounded by the current and future impacts of wasting disease (Aoki et al., 2022; Renn, 1936), degraded water quality (Hauxwell et al., 2001; McGlathery et al., 2007), invasive species (Howard et al., 2019), erosion (Walter et al., 2020), and sedimentation (Mills & Fonseca, 2003), all of which can intensify with climate change, particularly ocean warming and increasing intensity and frequency of storms and associated runoff (Lefcheck et al., 2017; Rasmussen, 1977).

Eelgrass habitat throughout the United States is protected under multiple federal and state policies including the Clean Water Act and the Magnuson-Stevens Conservation and Management Act (NMFS, 2007). In California, avoidance or minimization of impacts to eelgrass is required by the California Eelgrass Mitigation Policy, or CEMP, which stipulates that if impacts cannot be avoided, compensatory mitigation must take place to account for loss of eelgrass habitat function (Bernstein et al., 2011). Although Oregon and Washington do not have formal eelgrass policies analogous to the CEMP, in-kind mitigation for eelgrass impacts is often typically required through implementation of other state policies (ODSL, 2019; WDFW, 2014). The majority of eelgrass mitigation projects are concentrated around populated, urban areas, where coastal development has degraded much of the existing eelgrass habitat. While mitigation protections are integral to eelgrass persistence across the West Coast, they are only applied to direct, acute human-derived impacts, not indirect impacts or stressors, such as wasting disease or warming sea surface temperatures. Thus, seagrass losses from extreme events (Aoki et al., 2022; Hauxwell et al., 2001; Walter et al., 2020) often go unmitigated, presenting a unique challenge for managers and policymakers interested in protecting a coastal system vulnerable to global change. Nonetheless, eelgrass restoration does occur through avenues other than mitigation. For example, natural resources agencies, nonprofits, and other agencies across the West Coast and beyond also participate in eelgrass restoration, providing a valuable service in contexts where mitigation is not applicable (Barth et al., 2018; California Ocean Protection Council, 2020; Nielsen et al., 2018; Washington Marine Resources Council, 2017).

The United States has a long history of seagrass restoration relative to many other global locales. To our knowledge, the earliest documented US eelgrass restoration project was conducted in the 1940s (Addy, 1947; Fonseca, 2011) and the earliest US West Coast project in 1964 within Puget Sound, Washington (Phillips, 1974). This history has been facilitated in part by long-standing federal policy recommending protection of seagrass (NMFS, 2007). In many other regions, however, seagrass restoration efforts are nascent and can learn from regions with longer restoration histories. For example, the United Kingdom's first seagrass restoration projects were implemented in 2019, even though they have lost up to 92% of historical seagrass extent (Gamble et al., 2021; Green et al., 2021).

Yet despite the rich history of US seagrass restoration, there are few syntheses in the primary literature that evaluate success and glean lessons learned from these efforts, representing a real loss toward global advancement of seagrass restoration (but see Fonseca, 2011; van Katwijk et al., 2016). Even fewer syntheses include data from the US West Coast, and of those that do, almost none are published in the peer-reviewed literature (but see Thom et al., 2012), and none consider the West Coast region as a whole (see non-peer-reviewed reports Merkel & Associates, 1998; Thom, 1990; Thom et al., 2008, 2012). Given the high number of projects from the contiguous US West Coast and the clear need and demand for seagrass restoration, synthesizing and analyzing this region's rich seagrass restoration history serve as an opportunity to take stock of its efforts for the first time, while also advancing global seagrass restoration.

The lack of comprehensive documentation of regional eelgrass restoration makes it extremely challenging to learn from previous efforts to improve restoration outcomes. Rather, much of the collective knowledge on restoration resides exclusively with practitioners within the region. Exemplifying this issue, it remains unclear whether restoration efforts have led to long-term region-wide increases in eelgrass habitat, despite the 60-year long history along the West Coast. From existing regional white papers, early data suggested that restoration had limited success (Merkel & Associates, 1998; Stamey, 2004; Thom, 1990), a finding reflected in a global peer-reviewed synthesis of seagrass restoration success (van Katwijk et al., 2016), and that regional mitigation efforts may even have resulted in a net loss of habitat (Fonseca et al., 1998). These early, unpublished West Coast syntheses were written at a time when the majority of reviewed projects were failing and practitioners rarely assessed functional equivalency, resulting in the identification of key recommendations to advance eelgrass restoration best practices (Thom et al., 2008). Recommendations included conducting comprehensive site suitability assessments and experimental transplanting, especially when eelgrass was not present at potential restoration sites, and quantifying whether restored and reference sites were performing similar functions. In each of these efforts, reporting authors were challenged in their ability to compare project outcomes due to inconsistent definitions of success, inconsistent monitoring plans, and a lack of data availability. One early synthesis report makes clear the immediate need for a "clearinghouse" of eelgrass restoration and monitoring results and standardization of monitoring techniques (Thom, 1990). Yet nearly two decades later, a second report by Thom et al. (2008) identified nearly identical needs—a review of existing projects, lessons learned, and recommendations for standardization. Despite this long history of defining explicit needs and the passage of over 30 years since Thom (1990)'s call for data coalescence, we still lack peer-reviewed literature that comprehensively reviews the subject. The few examples that do exist in the primary literature are limited in their geographic scope or are not comprehensive in their project inclusion, often excluding mitigation data despite the fact that this drives much of the region's eelgrass restoration (see Thom et al., 2012, 2018 for reviews within the US Pacific Northwest and van Katwijk et al., 2009, 2016 for global reviews).

To address this need and build upon previous synthesis reports, we comprehensively review and synthesize eelgrass restoration projects from 82 projects across California, Oregon, and Washington. To our knowledge, this is the most comprehensive effort within the region to date, including decades of data unpublished in the peer-reviewed literature from mitigation, compliance-based, and nonmitigation projects spanning these states. Through this regional synthesis, we (1) summarize applied restoration approaches and attributes (e.g., planting methodologies, mitigation ratios, monitoring plans), (2) define and evaluate restoration success, and (3) derive lessons learned from these efforts to improve future seagrass restoration.

METHODS

Literature and database

To evaluate eelgrass restoration along the California, Oregon, and Washington coasts, hereafter "West Coast," we extracted data from a variety of sources including technical reports or other gray literature, raw data, and peer-reviewed articles. Peer-reviewed articles were included based on a Web of Science search using the terms (*seagrass* OR *eelgrass* OR *submerged aquatic vegetation*) AND (*restoration* OR *transplant*) AND (*California* OR *Oregon* OR *Washington* OR *west coast*). Given the low number of peer-reviewed articles detailing eelgrass restoration in the region, the majority of restoration data come from non-peer-reviewed reports and raw data identified by regional practitioners. To find these reports and raw data, we contacted a list of eelgrass restoration practitioners across the West Coast including any other practitioners our initial contact list recommended, and accepted restoration data that they or their agencies conducted. Although mitigation projects represent a large portion of the eelgrass restoration conducted along the West Coast (Olsen et al., 2014), these data are often proprietary or not publicly available, leading to challenges in finding such data. One previous effort by NOAA to coalesce eelgrass mitigation data in California led to a high relative availability of California mitigation projects, found on the site EcoAtlas (Eelgrass Survey GIS Data, 2019, accessed 2019-11-14). Data from all mitigation reports in the EcoAtlas repository were extracted for analysis.

For raw data to be included, data needed to be sent directly from the project manager or data collector, to ensure data quality prior to inclusion. Incongruencies in reported data were resolved through communications with the project contact or report author. Where incongruencies could not be resolved, data were flagged and excluded from analysis. Additionally, to be considered for quantitative analyses, projects needed to report either the transplanted shoot density and at least one subsequent monitored shoot density or the transplanted areal coverage and at least one subsequently monitored areal coverage. See the data repository for a list of all included projects and their metadata. Additionally, the literature search process revealed some projects with no available data that were therefore excluded from all analyses; these projects are included in Appendix S1: Table S1.

Numerous additional variables were extracted from each project and are detailed in Appendix S1: Table S3. Of note, data regarding the restoration technique and each consecutive monitoring period for each plot were extracted. These included spatial and structural attributes of the planted area as well as these same data from any reference meadows, when available. The primary spatial and structural variables collected included plot area and shoot density. Additional attributes such as canopy height or percent cover were also extracted, if collected and reported. However, the low prevalence of these metrics prevented their use in robust analyses, and as such, restoration success was evaluated from areal coverage and shoot density metrics alone. Additional information aside from structural and spatial project attributes was also noted for each project, including any collection of environmental variables (e.g., temperature, dissolved oxygen, depth) or ecosystem functions (e.g., habitat provisioning, species richness, carbon burial). Available numerical data on these metrics were not extracted given how few projects collected these data; however, it was noted which were collected for each project. All analogous data from co-monitored reference meadows were also extracted.

Data processing

For each project, all data from each plot (regardless of the defined plot size) were extracted in an effort to include the finest spatial resolution possible, rather than losing information by averaging or summing across plots. For passive restoration projects ($n = 4$), the plot size was defined as the area monitored for eelgrass return, and was typically defined by practitioners (e.g., the area over which debris was removed). In these projects, the "starting shoot density" (analogous to the transplanted shoot density in active restorations) was input as the average shoot density in this area immediately post-restoration (e.g., upon removal of debris). If no eelgrass was present, this was input as "0." Passive restorations were therefore removed from statistics reporting average transplant density. Monitored shoot densities were input as the average shoot densities measured within the plot at each monitoring period. Similarly, for the area of passive restoration projects, the starting area was defined as the area restored that contained eelgrass. If no eelgrass was present, this was input as "0," in an effort to capture areal expansion in the same way as active restoration projects. The subsequent monitored area was likewise input as the total area with eelgrass present at each monitoring period.

Evaluating success

There are many ways a restoration project can be deemed "successful," and how it is defined can vary widely across projects (Zedler, 2007). In mitigation projects, there are typically rigid definitions of success based around meeting predefined shoot density and areal coverage criteria (e.g., the CEMP generally defines success as achieving an areal mitigation ratio of 1.2:1, 100% coverage, and 85% density relative to the reference meadows after 5 years, with unique stipulations throughout the monitoring period and some geographic variability in requirements) (NMFS, 2014). Other projects compare ecosystem attributes related to ecosystem functioning, diversity, and vegetative structure to reference sites (Beheshti et al., 2022; Orth et al., 2020; Ruiz-Jaen & Aide, 2005). To evaluate restoration success across all projects, we used four definitions of success:

1. Practitioner-defined shoot density success
2. Practitioner-defined areal coverage success
3. Shoot density in the last monitoring period ≥ transplanted shoot density
4. Plot area in the last monitoring period ≥ transplanted plot area

Defining our own metrics (definitions 3 and 4) allowed us to assess success across projects that may have had varying practitioner-defined success metrics (see Table 3). Unfortunately, too few projects conducted analyses of ecosystem functions altered via restoration for us to assess restoration success based on such outcomes (see Table 1 for "ecosystem function" definition). Ecosystem functions were therefore excluded from formal analyses of success.

TABLE 1 Within the database, we defined the terms below and extracted data accordingly.

Extracted variable	Definition
Project	Each report, publication, or dataset typically included restoration efforts that were initiated on a single transplant date or during a single transplant season. In these cases, this was defined as a single project. However, some reports detail restoration efforts spanning numerous years. In these cases, projects were considered distinct in each transplant year (or for passive projects, each year where the site was "created").
Plot	A unique plot within a project was defined by the practitioner or report—creating large variation in plot sizes within the database. For example, a mitigation project may restore a relatively large area (e.g., 100 m^2) and consider this a single plot, monitoring the total area and the average shoot density within it during each monitoring period. On the other hand, other projects may have relatively small plots (e.g., 0.5 m^2), transplanting many more of these plots and monitoring each separately within a larger area.
Mitigation project	Any project conducted for compliance purposes due to expected or previous loss of eelgrass, with predefined target mitigation criteria, typically for areal coverage and/or shoot density.
Non-mitigation project	All other projects not categorized as mitigation projects were defined as nonmitigation projects. These projects were conducted for a variety of reasons (e.g., experimental purposes or to meet management targets).
Passive restoration project	Projects where no seeding or transplanting occurred. Instead, passive projects altered site conditions to promote natural recruitment or expansion of eelgrass. For example, debris removal, altering substrate, or sediment removal/additions to create suitable depth zones qualify as passive restorations.
Active restoration project	Use of any direct transplant methods displayed in Figure 3, Appendix S1: Table S2, including seeding techniques.
Ecosystem function	Processes supported by eelgrass, including habitat provisioning (including biodiversity metrics), pH amelioration, carbon sequestration, wave attenuation, and improved water quality.

We also extracted practitioner-defined reasons for suspected eelgrass loss or failure directly from reports and peer-review publications for each of the 82 reviewed projects. To identify broad patterns of eelgrass loss or project failure, certain contributing factors were combined, when appropriate. Specifically, bioturbation and herbivory were pooled under "species interactions"; phytoplankton blooms and macroalgae under "algal blooms"; and currents and tidal flow under "hydrodynamics." Projects that cited transplant density or technique as potential reasons of loss or failure fell under the "method" category. All other suspected drivers are listed as reported and summarized at the project level with many projects citing more than one potential driver.

Temporal trends in shoot density

We also evaluated the effect of initial transplant density on post-restoration shoot densities to test the question "does transplanting at higher shoot densities lead to greater shoot densities 6, 12, or 24 months following restoration?" Specifically, we used a generalized linear model with a gamma distribution and a log link function, with plot transplant density and transplant season as fixed effects, including their interaction (Bates et al., 2015). This model was applied three times, on post-restoration shoot densities measured at projects' 6-, 12-, and 24-month monitoring periods. These monitoring periods were selected given they are the most common and those recommended by the mitigation policies (i.e., monitoring restoration 6 months after transplant, and annually thereafter). However, due to weather and other logistical constraints, these monitoring times can vary slightly (i.e., a project may aim to monitor at the 12-month mark, but in reality, monitor at the 11- or 13-month mark). Greater flexibility in these monitoring windows often expanded as projects progressed. As such, we accepted a 3-month range ($\pm$1 month) within the 6- and 12-month monitoring period, and a 5-month range ($\pm$2 months) at the 24-month monitoring period. To understand how differences in shoot densities between restored and reference plots (Δ shoot density = reference shoot density − restored shoot density, at time t) varied over time, we used a linear mixed model with monitoring time (month after transplant) as a fixed effect and project as a random effect (Bates et al., 2015). This model was applied to all data where restoration plots were explicitly co-monitored with a reference meadow. To visualize data, we fit a loess regression (95% CI) to shoot densities over time in both the restored and co-monitored reference meadows.

RESULTS

Regional restoration attributes

We identified 117 total restoration projects (Appendix S1: Table S1), 82 of which were included for analysis in this study. Included projects restored a total of 557 individual restoration plots across California, Oregon, and Washington, with significantly more data available from Southern California (Figure 1; see Table 1 for how "plot" is defined). Transplant densities applied across active transplant projects ranged from 1 to 137 shoots/m^2, with an average of 28 $\pm$ 4.8. Split by mitigation and nonmitigation projects, the average shoot densities were 17 $\pm$ 3.4 and 54 $\pm$ 11, respectively (Table 2; mean $\pm$ SE). Of the 557 plots monitored across all 82 projects, data on transplant area were available from 521 of these plots, reporting a total transplant area of 85.5 ha. Due to the lack of areal coverage monitoring data beyond the initial transplanting, we are unable to report total restored acreage. Of the 82 projects, 57 co-monitored restoration plots with at least one reference meadow, with a smaller proportion of nonmitigation projects monitoring a reference than mitigation projects (Table 2). Of the plots that reported transplant season ($n = 500$), initial planting typically occurred in summer (41%) and spring (34.6%; with 3.2% planting across both seasons), followed by winter (18.4%) and fall (2.8%). Sixty of the 82 projects were conducted for mitigation purposes, while 22 were conducted for nonmitigation purposes. Project data come from technical reports or other gray literature ($n = 34$), raw data ($n = 11$), and peer-reviewed articles ($n = 6$). Four projects were passive restoration projects, while 78 were conducted through actively seeding or transplanting shoots (Figure 1C).

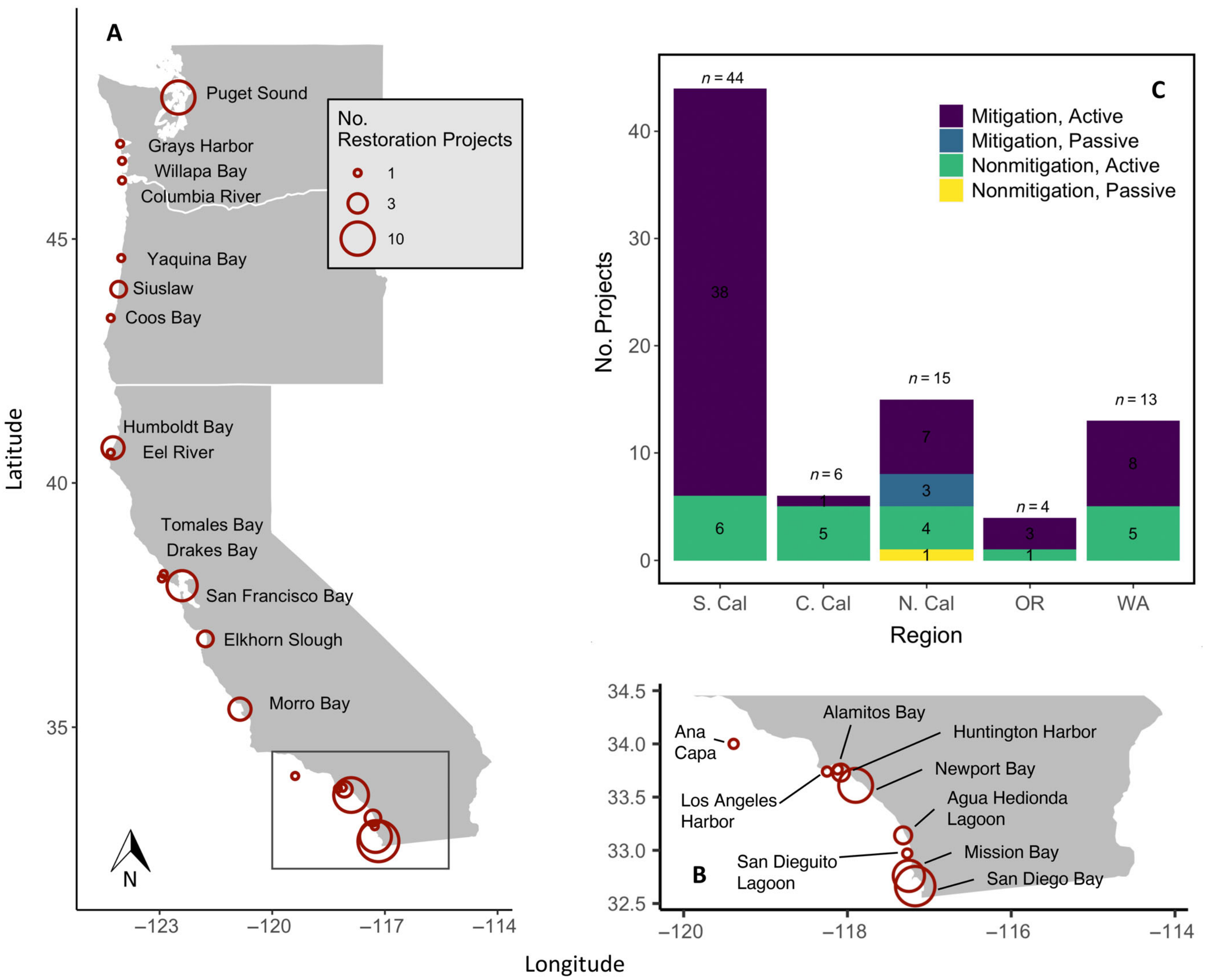

FIGURE 1 (A, B) Maps of reviewed projects extending from San Diego, California, to Puget Sound, Washington, with a high concentration of projects within Southern California. Circle sizes are scaled by the number of projects in any given locale. (C) Type and number of projects reviewed in each region. California was split into three regions, southern ($n = 44$), central ($n = 6$), and northern ($n = 15$). The majority of projects were active (e.g., transplanting or seeding) mitigation projects, followed by active, nonmitigation projects. Passive mitigation and passive nonmitigation projects were less common, with data only found for northern California.

TABLE 2 Summary of reviewed mitigation ($n = 60$) and nonmitigation projects ($n = 22$).

Project type	Transplant area (ha)	Project length (years)	Transplant density (shoots/m^2)[a]	Applied mitigation ratio	No. projects (n)	No. projects with a reference (n)
Mitigation	84.39	4.47 ± 0.74	16.54 ± 3.38	2.95 ± 0.42	60	45
Nonmitigation	1.09	1.51 ± 0.39	53.62 ± 10.16	NA	22	12

Note: Reported is the total transplant area (summed across all plots), average project length (which includes post-transplant monitoring), transplant density, and applied mitigation ratio for the 82 reviewed projects.
[a]Passive restoration projects were removed from averages of transplant density.

TABLE 3 Proportion (%) of plots meeting four definitions of success.

Defined success criteria	Practitioner-defined shoot density success	Practitioner-defined areal coverage success	Shoot density in the last monitoring period ≥ transplanted shoot density	Plot area in the last monitoring period ≥ transplanted plot area
Plots meeting criteria (%)	20.1	18.0	47.4	14.4
n	112	100	264	80
Plots failing to meet criteria (%)	14.5	17.6	22.6	21.2
n	81	98	126	118
Plots in which criteria could not be evaluated (%)	65.4	64.4	30.0	64.4
n	364	359	167	359

Note: Counts (total number of plots) are shown in parentheses. Criteria could not be evaluated (row 3) if the practitioner did not define success, or if no data were available.

Commonly applied methodologies

Practitioners employed a wide variety of restoration methods across the included projects. The most commonly used methods were variations on bare root transplant techniques, followed by seeding, plugs, transplanting eelgrass remotely with frames (TERFS), or unanchored shoot techniques (Figure 2; Appendix S1: Table S2). Within the category of bare root transplants, the popsicle stick ($n = 31$) and garden staple ($n = 16$) methods were the two most commonly used transplanting techniques, followed by the rebar stake method ($n = 6$; Figure 2). A full description of eelgrass transplant methods can be viewed in Appendix S1: Table S2 and Figure S1.

Evaluating success

When practitioners defined and evaluated success (i.e., excluding plots where criteria could not be evaluated), 51%–58% of restoration projects succeeded by the final monitoring period. However, practitioner-defined success could not be evaluated in the majority of projects (65.4%) because practitioners either did not define project success or failed to evaluate defined success (Table 3). If success was defined as greater shoot densities or areal coverage compared with the initial transplant by the final monitoring period, we see that 67.7% and 40.4% of plots succeeded, respectively. Areal coverage data beyond transplant dates were sparse (final monitoring areas were unreported in 64.4% of projects), making this metric more challenging to evaluate. Data on functional success (e.g., return of a target ecosystem function) were too sparse to evaluate. Specifically, only 18 of the 82 projects evaluated recovery of any ecosystem functions, the vast majority of which were biological functions. Of projects that did measure ecosystem functions, metrics, methodologies, and reporting were highly variable, making cross-comparisons difficult, particularly given the low sample size.

Temporal trends in shoot density

Of the 82 projects included, a subset of them monitored shoot densities 6 ($n = 42$), 12 ($n = 57$), and 24 months ($n = 42$) after transplanting. We found a significant effect of transplanted shoot density on the monitored shoot densities 6 months following transplantation

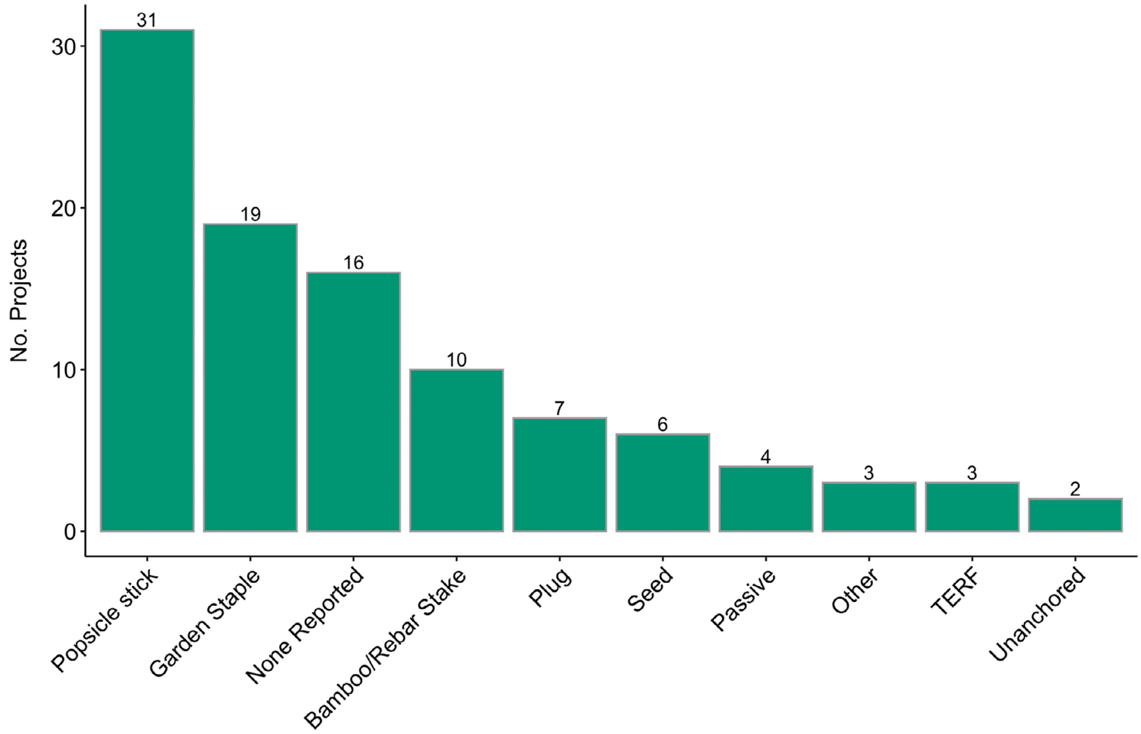

FIGURE 2 Summary of applied restoration methods for both mitigation and nonmitigation projects. The popsicle stick method was the most commonly used transplanting technique ($n = 31$), followed by the garden staple method ($n = 19$). All projects that did not report transplant technique were mitigation projects. If a project used more than one method, both were tallied here. See Appendix S1: Figure S1 for a more comprehensive overview of the methods shown above. TERF, transplanting eelgrass remotely with frames.

(t value = 8.4, $p \leq 0.01$, df = 215, $r^2 = 14.1\%$; Figure 3A). However, 1 and 2 years following transplantation, initial transplant density was no longer significantly positively associated with an increase in plot density ($p \geq 0.05$, $r^2 < 1\%$; Figure 3B,C). We failed to detect an effect of season, or the interaction between season and transplant shoot density, on monitored shoot densities at 6, 12, or 24 months following restoration. Relatedly, there was a significant effect of time on "Δ shoot density" (reference shoot density – restored shoot density) (linear mixed effects model; $p \leq 0.01$, $t = -6.2$, df = 406), and we see that while restored shoot densities begin lower than reference meadows, they ultimately converge around comparable densities (Figure 3D).

Drivers of eelgrass loss

Suspected reasons for restored eelgrass loss or project failure were cited in reports and were based on practitioner observations during transplantation or monitoring. We found that the majority of cited factors were physical ($n = 86$), while the rest were either biological ($n = 30$) or logistical ($n = 8$). Thirty-six projects either showed no signs of eelgrass loss or failed to report potential drivers of observed losses. Algal blooms were the highest cited factor of eelgrass loss ($n = 16$), followed by sedimentation ($n = 14$) and light limitation ($n = 12$) (Figure 4; Appendix S1: Table S4). Although many of these factors (e.g., eutrophication and macroalgae, light limitation and turbidity) can be interrelated, we lacked additional data needed to group cited reasons of failure by mechanism, given none of the factors were quantitatively attributed to project failure or eelgrass loss. Instead, we highlight observations from practitioners who spend numerous hours in their restoration sites and in the system under study. This expert knowledge should not be discounted as these data allude to probable mechanisms of eelgrass decline and can serve to inform future quantitative, mechanistic work.

DISCUSSION

Characteristics of US West Coast seagrass restoration

Here, we document results of projects with available data from over 30 years of eelgrass restoration along the West Coast (1989–2020). Given the long restoration history and the apparent lack of associated literature, the included 82 projects represent only a portion of the total

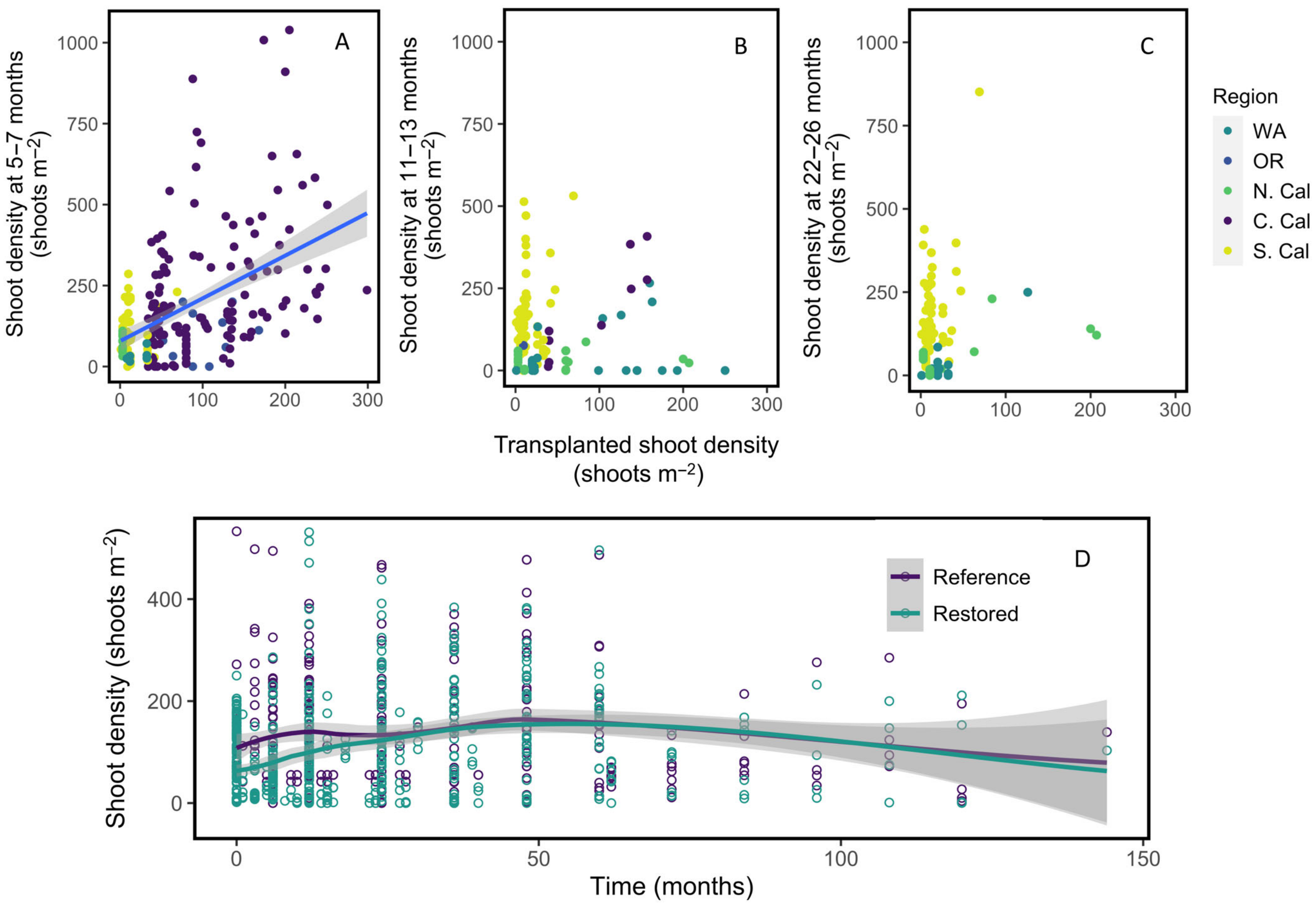

FIGURE 3 Shoot densities over time. (A–C) The shoot densities in restoration plots between 5–7 months, 11–13 months, and 22–26 months after transplant against the initial transplant densities. (D) All restoration plot shoot densities over time that had corresponding reference meadow monitoring, along with these associated reference meadow densities. Shoot densities of "0" indicate a monitored density of 0; no point is displayed for plots that did not measure shoot density.

restoration conducted along the West Coast. Available data indicate a disproportionately high concentration of projects located in Southern California (Figure 1). Although a lot of eelgrass restoration occurs in Southern California for mitigation given the degree of urbanization and associated impacts, it is unlikely that this imbalance is entirely reflective of more restoration occurring here relative to other studies regions. One potential contributor is that a high number of Southern California mitigation reports were available from a single source (Eelgrass Survey GIS Data, 2019, accessed 2019-11-14), whereas no singular database or data synthesis efforts could be found for other regions, making data availability extremely challenging. Despite challenges in acquiring data, we can glean important trends and lessons to inform future restoration efforts from the data that are available.

From these projects, we report a total transplanted area of approximately 85.5 ha (Table 2). It is probable that of the projects that succeeded, transplanted plots expanded, and the total area restored is larger than this value. However, the lack of areal monitoring data makes this value impossible to discern. Nonetheless, the total acreage planted and the relatively small total size of each project demonstrate the small scale at which restoration has been conducted to date. Comparisons to eelgrass coverage and restoration goals in other locales can add perspective to this acreage. For example, San Francisco Bay, CA, holds around 1200 ha of existing seagrass, and the state has goals to restore an additional 405 ha by 2025 (California Ocean Protection Council, 2020). Similarly, Washington set a target to increase seagrass abundance by 20% by 2020 (Thom et al., 2018). Given the small size of past restoration projects, reaching these habitat goals will likely require a large amount of natural expansion, adding credence to the need for simultaneous improvements to habitat quality (e.g., water quality) (van Katwijk et al., 2016). Moreover, given larger scale projects may be more likely to survive, this small-scale approach could be contributing to the rates of failure observed here (van Katwijk et al., 2009, 2016).

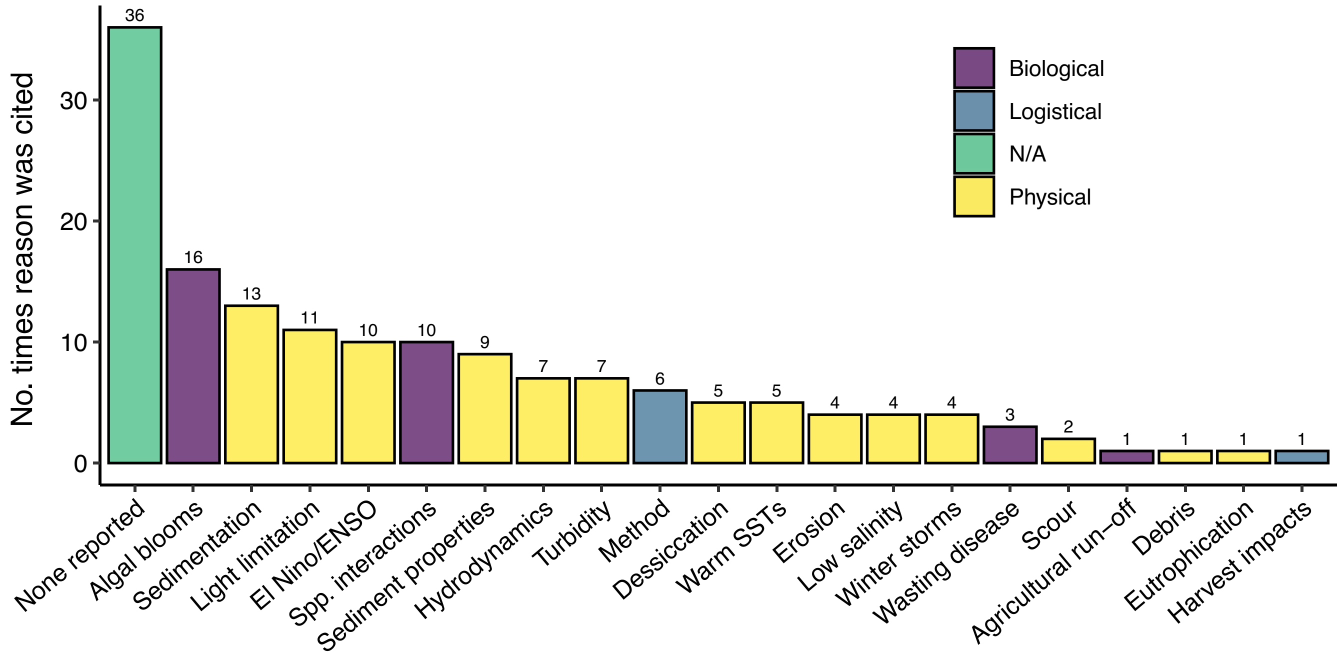

FIGURE 4 Cited reasons for restoration failure: biological factors, logistical factors, physical factors, and those with no reported reasons (N/A). ENSO, El Nino southern oscillation; SST, sea surface temperature.

Seeding, which has been successfully used in other regions but is underutilized along the West Coast, could also aid in reaching these goals while minimizing harvest impacts to natural meadows (Orth et al., 2020; Reynolds et al., 2016; van Katwijk et al., 2021). However, West Coast large-scale restoration via seeding is not currently scalable, requiring further development of the appropriate infrastructure for seagrass mariculture to supply the seed needed for this approach (van Katwijk et al., 2021).

Site conditions and logistical constraints likely dictate a practitioner's selected restoration method (Appendix S1: Figure S1). Of the reviewed projects, 31 used the popsicle stick method, most commonly in mitigation projects ($n = 26$). Garden staple transplanting was the second most applied method, used almost equally in both mitigation ($n = 9$) and nonmitigation ($n = 10$) projects (Figure 2). Although a full analysis of the benefits and drawbacks of each method is beyond the scope of this review, these two methods are likely commonly applied due to their low cost and their speed and efficiency when transplanting, among other considerations. For further information on selecting an appropriate restoration method, see Appendix S1: Figure S1 (Boyer & Wyllie-Echeverria, 2010; Campbell, 2002; Gann et al., 2019).

Defining and evaluating success

Determining the proportion of successful restoration projects was highly dependent on the metrics (structural or functional) used to evaluate success—a phenomenon well discussed in the study by Zedler (2007). For example, when practitioners defined and evaluated success, we see that 51%–58% of restoration projects succeeded by the final monitoring period, but when shoot density and areal coverage metrics were defined herein, 40%–68% of projects were successful (Table 3). This emphasizes the importance of clearly defining success before project commencement to ensure that the correct monitoring is conducted to enable evaluation of restoration outcomes. Both shoot density and areal coverage (the most common monitoring metrics) are valuable, yet have their limitations. Areal coverage can indicate habitat contraction or expansion, but remains insensitive to meadow structure, whereas shoot density can be used to evaluate production and other important functions but provides no information on meadow extent.

Partly driven by the assumption that structure begets function (Dobson et al., 1997), the vast majority of restoration projects here and within the literature exclusively evaluate structural attributes (but see Beheshti et al., 2022; Lewis & Henkel, 2016; Orth et al., 2020). Specifically, monitoring has focused on the shoot density and areal coverage (and occasionally percent cover) of restored habitats, assuming that structural recovery is synonymous with functional recovery (McCune et al., 2020; NMFS, 2014). However, the near-complete lack of evaluation of ecosystem functions gained by restoration makes this paradigm difficult to assess. Of the 82 studies reviewed, only 18 measured one or more ecosystem functions. Prior studies suggest that biological functions (e.g., habitat provisioning, biodiversity) are quicker to recover post-restoration compared with some biogeochemical functions (carbon sequestration, pH amelioration) (Beheshti et al., 2022; Lewis & Henkel, 2016). The paucity of studies investigating functional recovery and the high spatial and temporal variability of ecosystem functioning within systems limits the use of structural attributes as proxies for functional recovery. Often, the motivation for restoration is to return lost or degraded functions and services, in which case the functions and services of interest should be measured directly at least until the body of literature grows and we have more regionally explicit examples to support the use of structural attributes as proxies for function. As governments and resource managers across the globe make commitments to recover multiple ecosystem benefits and meet sustainable development goals via restoration, understanding these relationships is essential.

Temporal trends in shoot density

Projects transplanting at higher relative densities can lead to greater "success" after 6 months, when success is defined as densities above transplant densities (Figure 3A). However, we find that after one and two years, high initial transplant density no longer translate into significantly elevated shoot densities (Figure 3B,C). This suggests that high transplant densities may not enhance the likelihood of plot survivorship beyond 6 months, or that density dependence is contributing to natural thinning or convergence of transplanted plots toward reference meadow shoot densities over time. Previous work testing the effects of shoot density in mesocosm and in situ environments demonstrates a significant positive effect between transplant density and subsequent survivorship and shoot density (Worm & Reusch, 2000; Zhang et al., 2022). However, these studies do not evaluate effects beyond 7 months. The data in the review presented here suggest agreement with previous work, but also indicate that if monitoring continued, these effects may be lost (Figure 3). More broadly, across the entire dataset, we see that the shoot densities in restored plots ultimately converge around shoot densities in accompanying reference meadows over time, despite the fact the starting shoot densities were typically well below those in reference meadows (Figure 3D).

These findings hold management relevance, demonstrating the value of post-restoration monitoring beyond 6 months in order to inform best practices for future restoration success. They suggest that the additional effort, project costs, and potential impacts to donor meadows required to inflate transplant densities early in the project timeline may not be the most effective use of resources, particularly for larger scale projects. This may in part explain the large variation in transplant shoot densities, whereby nonmitigation transplant densities were nearly three times higher than those of mitigation projects, given mitigation projects often have stringent time, budgets, and personnel constraints (Table 2). In some cases, mitigation reports cite anecdotal evidence of this apparent limited utility of transplanting at higher relative shoot densities, given plots will likely converge on natural densities over time. However, with so few of these reports published or publicly available, it is unclear whether this finding has been quantitatively demonstrated, disseminated, or received broad acceptance in order to enable its consideration in future restoration projects by other practitioners within the region and beyond (but see Duarte et al., 2013 for mention of this potential).

Although there was no significant effect of transplant season on subsequent shoot densities, additional data may elucidate relationships between the two. There are trade-offs to planting in certain seasons over others. For example, attempting to optimize transplant growth by restoring when eelgrass is most productive (spring–summer) (Orth & Moore, 1986; Zhang et al., 2016) may coincide with other seasonal stressors (ephemeral macroalgal blooms, warm water events, mid-day low tides, etc.). We recommend future syntheses explore this question more directly, with the aim of including region-specific seasonal environmental factors into eelgrass restoration best practices. Understanding seasonal stressors and how they interact with restoration outcomes also offers an opportunity for practitioners to test different restoration designs (e.g., transplanting intertidally vs. subtidally, trimming shoots, positioning plots with consideration of flow direction) and methods (e.g., favoring a technique that best secures the shoot to the substrate) considered most appropriate for the chosen transplanting season.

Drivers of restoration failure

A global review of seagrass restoration projects found that, when considering long-term survival (≥23 months) of transplants, 63% of restorations fail (van Katwijk et al., 2016). The failure rate of the 82 West Coast eelgrass (*Z. marina*) restorations reviewed in this synthesis was 32.3%–59.6%, depending on how failure was defined. While failure can be driven by restoration practices (e.g., methodology, scale), our data show that more often practitioners attribute failure to environmental conditions (i.e., water quality, hydrology) that could inhibit transplant or seedling survival (Figure 4) and/or inhibit natural recruitment (Oreska et al., 2021; van Katwijk et al., 2016). Restoration outcomes are heavily dependent on factors that foster or interfere with known growth requirements of eelgrass (Thom et al., 2012). Practitioners here indicate that algal blooms, sedimentation, and light are the highest likely drivers of loss—factors that also interact directly with many of the other stated drivers (e.g., turbidity, winter storms). The literature on the subject directly supports these findings, with cases of eelgrass loss in the region directly attributed to each of these (Lefcheck et al., 2017; Waycott et al., 2009). On the other hand, ENSO index was also indicated as a likely driver of loss, but there is very little evidence to ascertain its impact on eelgrass survival. It has been previously suggested to impact southern eelgrass populations (Johnson et al., 2003) and hypothesized to impact more northern populations but with some direct literature contradiction to this concept (Shelton et al., 2017; Walter et al., 2020). Clearly, there may be spatial variation in environmental factors that drive restoration success. For example, some recommend elevated nutrients to facilitate eelgrass propagation in restoration (Carroll et al., 2008; Unsworth et al., 2022), while past work and practitioners here cite elevated nutrients as drivers of loss, often driving algal blooms and eutrophication (Boyer & Wyllie-Echeverria, 2010; Hughes et al., 2013; Merrifield et al., 2011). Despite these differences, building understanding of the drivers of eelgrass survival and restoration success will be essential in a future of rapid environmental change. This can ultimately bolster restoration success rates, help meet existing habitat goals, and improve modeling efforts to include seagrass meadows in regional climate projections (California Natural Resources Agency [CNRA], 2022).

Strengths and weaknesses of restoration via mitigation

Mitigation projects have their own set of unique challenges in success evaluation. As mentioned above, the vast majority of projects only measure eelgrass structure, assuming an accompanying return of ecosystem functions. Based on this assumption, California's eelgrass mitigation policy calls for no net loss of eelgrass or eelgrass function, yet they do not require explicit monitoring of functions (NMFS, 2014). Given the relatively long monitoring duration of eelgrass mitigation projects (Table 2), it is likely that by project completion, many ecosystem functions have indeed returned, and the costs required to monitor a long list of ecosystem functions could be prohibitive. Few studies rigorously evaluate whether biological functions (i.e., biodiversity, nursery function) are enhanced to levels observed in reference habitats following restoration (but see Beheshti et al., 2022; Orth et al., 2020). We encourage practitioners to explore avenues for evaluating habitat use in restored and reference habitats that may be amenable to limited project funding or capacity. For example, water samples can be collected and stored for later eDNA analysis, should a project acquire funding to process samples post-restoration, offering a low effort but high yielding potential dataset capable of addressing data gaps on the recovery of or compensation for lost biological functions. Furthermore, with carbon services becoming of increasing regional (e.g., Prentice et al., 2020; Ricart et al., 2021; Ward et al., 2021) and global (Friess et al., 2022; Macreadie et al., 2021) interest, assumptions of functional recovery can become even more tenuous. For example, eelgrass can store high quantities of organic carbon in sediment, serving to mitigate climate change—a well-studied ecosystem function (Fourqurean et al., 2012). However, this carbon is sequestered over millennia, with the top meter of seagrass at times representing over 500 years of carbon sequestration (Ward et al., 2021). Dredging, trawling, or degrading a meadow can lead to loss of these long-standing carbon stores, emitting a significant amount of carbon back to the atmosphere (Lovelock et al., 2017; Pendleton et al., 2012). In an example where the top 2 m of seagrass meadow is dredged, a resulting mitigation meadow might begin to sequester carbon, but it is inconceivable that it will recover a comparable climate mitigation function if the impacted meadow represented 1000 years of carbon storage. This line of reasoning could be similarly applicable to other, slow-to-recover functions, offering more questions than answers. For example, how should policies define and monitor ecosystem functions? When might functional recovery not accompany structural recovery? How can we improve our management of eelgrass to preserve biogeochemical functions? Each of these is essential to consider given so much of the West Coast's restoration occurs via mitigation and with new policy considerations on the table.

Mitigation projects are typically required to restore a predetermined area of eelgrass relative to the impacted area (e.g., at a ratio of 1.2:1) and monitor the meadow's area and shoot densities over time (for 5 years in California). The median applied mitigation ratio (2.8:1) was considerably higher than that generally required. This ratio can be inflated if the total required mitigation area decreased following transplanting based on a lower-than-expected impact, thereby increasing the ratio. Some projects also transplanted over a greater area than required to "bank" mitigation credits for future anticipated impacts. Most typically though, practitioners used a higher-than-required ratio to allow for eelgrass losses during the project while still meeting the minimum required ratio by the time of project completion. On one hand, this practice may benefit eelgrass populations more broadly, given larger areas are restored than are required. On the other hand, this practice allows for the possibility that eelgrass area could decline throughout the duration of the project, while still qualifying as a "success" at the time of project completion by meeting the minimum required ratio despite a downward trajectory. In this way, we see that while the prescriptive guidelines for mitigation play a vital role in regional eelgrass protection, their focus on checking the "compliance" box has its drawbacks. Mitigation projects often do little in the way of critically evaluating and disseminating information on restoration methods, site suitability, environmental drivers of success, or associated ecosystem functions—all data that would contribute to the scientific body of knowledge on eelgrass restoration to improve future restoration outcomes. We acknowledge that ensuring adequate research does not necessarily fall under the purview of state and federal compliance policies; yet given the fact that majority of eelgrass restoration occurs via mitigation, these are considerable barriers within the region.

Data accessibility challenges

The lack of data access is arguably one of the greatest barriers to improving eelgrass management—a problem that is true regionally and globally, and reflected across marine habitat restoration more broadly. For example, Eger et al. (2022) note that "there is no coherent data recording format or framework for marine restoration projects. As a result, data are inconsistently recorded and it is difficult to universally track progress, assess restoration's global effectiveness, reduce reporting bias, collect a holistic suite of metrics, and share information." Similarly, specific to seagrass, Strachan et al. (2022) report the "need for open data if effective knowledge sharing is to take place, and to ensure that ocean science can fully support countries to achieve the 2030 Agenda for Sustainable Development." Of the 82 projects included in this study, only 6 were extracted from peer-reviewed literature. The effort required to track down, extract, and coalesce data from individual practitioners, websites, and consulting repositories should not be the standard for knowledge building. Moreover, once found, data were often poorly reported (e.g., no units), requiring QA/QC through communication with original data collectors or that data be thrown out when QA/QC was not possible. For example, many reports were missing essential data such as initial transplant density, transplant area, or final restoration area. These challenges highlight the value of standard operating protocols (SOPs) such as those used in both mitigation (e.g., shoot density and areal coverage) and nonmitigation projects (Kincade et al., 2022; McCune et al., 2020), given they enable cross-project comparisons. Nonetheless, having adequate SOPs is not a standalone solution—data must also be made available to drive progress and inform best practices. At present, there are few incentives for consultants conducting mitigation projects to broadly disseminate results, unlike academic, NGO, or other practitioners who have more time and incentive to invest in sharing, publishing, and releasing findings. These barriers merit careful attention and consideration regionally and globally.

CONCLUSIONS AND RECOMMENDATIONS

The long restoration history along the West Coast represents a tremendous knowledge base that can be used to improve upon the practices, policies, and outcomes of restoration both along the West Coast and globally. Through this synthesis process, we glean essential information about the history of eelgrass restoration approaches, regional success rates, and likely drivers of failure. We also take stock of eelgrass mitigation projects, exploring the strengths and weaknesses of these practices—a surprisingly absent component of the literature despite the high prevalence of mitigation and its importance to eelgrass populations, monitoring, and science.

Based upon these findings and from past work (Boyer & Wyllie-Echeverria, 2010; Campbell, 2002), we recommend eelgrass restoration practitioners along the West Coast and globally use the steps outlined in Figure 5 to guide restoration efforts. These steps include assessing the suitability of a proposed restoration and paired reference site(s). Site suitability should include evaluation of environmental factors (using models or more qualitative evaluations) (Hu et al., 2021; Newmaster et al., 2011; Stankovic et al., 2019; Tan et al., 2020; van der Heide, 2009; van Katwijk et al., 2009), logistical factors, and social and governance factors (Fischer et al., 2021). Once identified, multiple methods should be chosen and tested through pilot studies, which can then inform the design of the full-scale restoration project. Conducting a pilot study that extends beyond a single growing season is ideal to identify the factors that may contribute to the loss of restored eelgrass (see Figure 4) within a proposed restoration site allowing practitioners to be adaptive (i.e., move a restoration site, alter methods) and fully weigh the advantages and disadvantages of various methods (Appendix S1: Figure S1). However, we recognize that pilot studies can incur additional costs and will be contingent on a project's budget. After initial restoration, both restoration and reference

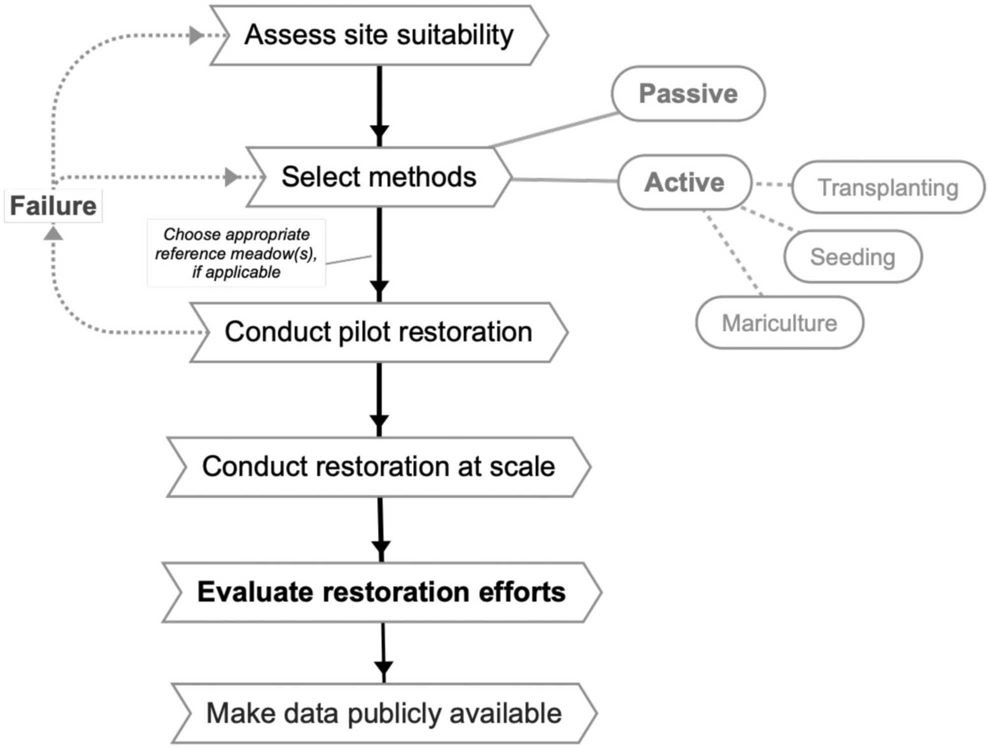

FIGURE 5 Proposed eelgrass restoration approach. We recommend practitioners use the above adaptive restoration approach for all eelgrass restoration projects as a framework for minimizing uncertainty and maximizing the likelihood of meeting stated project goals.

sites should be co-monitored for as long as funding allows, but will of course be based on project goals and logistical and budgetary constraints. Lastly, all eelgrass restoration project data should be made publicly available.

As marine habitat restoration becomes more prevalent in the face of burgeoning carbon markets and habitat and biodiversity targets and initiatives (Saunders et al., 2020; Waltham et al., 2020), we urge practitioners to consider these steps to improve restoration practices and outcomes. More broadly, data synthesis efforts such as the one herein are important reminders to take stock of decades worth of work that can be built upon for future restoration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ward & Beheshti, 2023) are available from Dryad: https://doi.org/10.5061/dryad.3j9kd51q6.

ORCID

Melissa Ward https://orcid.org/0000-0001-6651-4715
Kathryn Beheshti https://orcid.org/0000-0001-7991-4371

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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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