



Conservation of Marine Foundation Species: Learning from Native Oyster Restoration from California to British Columbia

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Abstract

Marine foundation species are critical to the structure and resilience of coastal ecosystems and provide key ecosystem services. Since many have suffered severe population declines, restoration of foundation species has been undertaken worldwide. The Olympia oyster (*Ostrea lurida*) is a foundation species, and the restoration of depleted populations is a priority for maintaining ecosystem function of estuaries along the west coast of North America. Here, we synthesize all native oyster restoration projects conducted from California, USA, to British Columbia, Canada, and analyze project goals, methods, and outcomes. Currently, restoration projects are spread unevenly across the species' range, driven by locally varying goals and implemented with contrasting approaches. We highlight the value of regional strategic planning and decision support tools to evaluate project design and methods for restoration, including the selection of substrates and the targeted use of aquaculture. We recommend future investment in larger projects, which our analysis found were more cost-effective, but which have been relatively rare for this species. We also recommend that funders support monitoring over broader temporal and spatial scales than in the past to better characterize long-term effects of restoration on oyster populations and the services they provide beyond the project footprint. We found that most projects successfully supported native oysters and engaged local communities, and recommend similar efforts to continue to enhance understanding of Olympia oysters, which remain unfamiliar to many coastal residents. We believe that the results of this synthesis are broadly applicable to marine foundation species generally, and can inform restoration and conservation efforts worldwide.

Keywords Foundation species · Olympia oyster · Restoration

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Introduction

Marine foundation species such as kelps, mangroves, sea grasses, corals, and oysters are critical to the structure and resilience of coastal ecosystems and provide key ecosystem services to human communities around the world (Angelini et al. 2011; Zu Ermgassen et al. 2013). Many marine foundation species have suffered severe population declines due to human activities including overfishing, habitat loss, and climate change (Kirby 2004; Hoegh-Guldberg et al. 2007). In response to these losses, restoration of foundation species has been undertaken worldwide (e.g., Orth et al. 2006; Barbier et al. 2008; Chung et al. 2013; van Oppen et al. 2015), most extensively with oysters. Large-scale restoration efforts with *Crassostrea virginica* in Chesapeake Bay and the Gulf of Mexico exemplify how restoration of foundation species can re-establish populations (Hernández et al. 2018), restore associated habitat (Grabowski and Peterson 2007), and increase or maintain ecosystem services provided by the oysters (Coen et al. 2007; Scyphers et al. 2011). Coastal restoration ecology has been employed at large scales only in recent decades; thus, its approaches and methods are still being developed and tested.

The Olympia oyster (*Ostrea lurida*) is the only oyster species native to the west coast of North America north of Baja California Sur, Mexico (Polson et al. 2009; Polson and Zacherl 2009), where it creates habitat for numerous estuarine and coastal species (Ramsay 2012; Kimbro and Grosholz 2006), and supported a once vital fishery dating back to pre-colonial history (Baker 1995). Populations have declined precipitously due to human-induced impacts including overharvest (White et al. 2009), the alteration of estuarine habitats (Dimick et al. 1941), poor water quality (Hopkins et al. 1931), sedimentation (Gilbert 1917), introduced predators (Kimbro et al. 2009), and a changing climate (Hollarsmith et al. 2019; Bible et al. 2020). As a result, Olympia oyster populations are estimated to be at 1% of historic levels and face local extinction in some regions (Kirby 2004; Zu Ermgassen et al. 2012). Consequently, restoration of Olympia oyster populations and the habitat they provide has become a priority for maintaining ecosystem function of estuaries along the West Coast (Brumbaugh et al. 2006; Baggett et al. 2014; Wasson et al. 2015).

Restoration of Olympia oysters has been underway on the West Coast for the past two decades. Scientific knowledge gained from pilot studies has been used to develop effective methods that often serve as a critical proof-of-concept for scientists, restoration practitioners, and funders (Murcia and Aronson 2014). However, very few studies of Olympia oyster restoration have been published. Published investigations have explored the optimal tidal elevation for achieving restoration goals with Olympia oysters, including minimizing non-native cover (Zabin et al. 2016; Fuentes et al. 2019) and

comparisons of shell application methods and thicknesses (Zacherl et al. 2015). Yet until now, there has been no broader synthesis of approaches or comparison among regions.

Restoration of other oyster species has provided guidance in recent years for oyster restoration and monitoring (e.g., Brumbaugh et al. 2006; Baggett et al. 2014; Hernández et al. 2018; Fitzsimons et al. 2020), most resulting from restoration and enhancement of *Crassostrea virginica* on the Atlantic and Gulf coasts of North America. While some of this guidance provides a valuable model for restoration of Olympia oysters (Brumbaugh and Coen 2009), the approaches, methods, and outcomes of restoration of *Crassostrea* species are largely not transferable, due to fundamental differences between the biology and ecology of these oysters. Much less is known about the biology and restoration of *Ostrea* species than *Crassostrea* with two orders of magnitude fewer scientific papers published on *O. lurida* (Trimble et al. 2009). This leaves gaps not only in our understanding of best methods for restoration but also in its desired outcomes. For example, Olympia oysters have a smaller body size, larger gill ostea, and less developed gill filaments than *Crassostrea* (Elsey 1935; Cranford et al. 2011), which diminishes their capacity for water filtration, a key ecosystem service provided by oysters, relative to *Crassostrea* species (Zu Ermgassen et al. 2013; Gray and Langdon 2018, 2019). Furthermore, Olympia oysters form low-profile beds of clusters of individuals, often surrounded by a matrix of other species and substrates, in contrast to the high-profile reefs built by *Crassostrea* species (Beck et al. 2009). While both species are ecosystem engineers that create beds providing critical structure and habitat for other species (Jones et al. 1994; Ruesink et al. 2005), *Crassostrea*'s more substantive beds provide comparatively extensive shoreline protection (Morris et al. 2019), while the shoreline-protecting functions of *O. lurida* beds may be more modest, though still apparent (Boyer et al. 2017). Finally, the challenges that face these oyster species differ and can impact the methods and success of restoration. For example, two factors that hinder restoration of *C. virginica*—disease and commercial harvest—are not currently important for *O. lurida*, which is comparatively disease-free (Moore et al. 2011) and does not support a widespread commercial fishery. These fundamental differences require that Olympia oyster restoration and enhancement be designed and evaluated based upon the unique biology and ecology of the species.

Here, for the first time, we have synthesized data on historical and current Olympia oyster restoration projects in order to inform future efforts. We collected data for all known restoration projects along the entire range of the species and characterized geographic patterns in project numbers and budget, in order to detect potential uneven investment that could be remedied by future investments in underrepresented areas. We tallied total monetary investment and restoration, to compare with other species, and examined project budgets to determine

the proportion allocated to monitoring. We assessed whether cost-per-area decreases with project size. We characterized goals of the restoration and queried respondents on success at achieving them. We quantified the proportion of projects that used different restoration approaches, including substrate types, elevation profiles of constructed beds, and use of aquaculture. To quantify restoration success across projects, we assessed what parameters were monitored, so we could make recommendations on improved monitoring. We evaluated restoration success and identified the most common challenges, so these can be addressed or avoided in new restoration projects. Our goal is to highlight lessons which can be applied to future projects with this species, as well as more broadly to restoration of marine foundation species worldwide.

Methods

We obtained information about past and present Olympia oyster restoration or enhancement projects. We developed an initial list of projects by contacting experts in each region, examining a NOAA Restoration Center database of funded projects, and sending emails out broadly to over 100 people on a listserv of Olympia oyster stakeholders. We only included projects that deployed permanent settlement substrate or live oysters with the purpose of benefiting Olympia oyster populations; projects that were only scientific in purpose, such as tiles deployed to study recruitment rates, were not included. Both completed and ongoing projects were included up to the spring of 2019. Thus, we were able to obtain information from all known projects on the Pacific coast ($n = 39$, locations indicated in Fig. 1), except for one project in San Francisco Bay for which we could not locate the original practitioners or the resulting data.

We obtained information about the projects through an internet survey, which was filled out between November 2018 and June 2019 by 26 separate practitioners for the 39 projects (some people lead multiple projects). The survey included questions on project timing (start date), duration, and funding (cash and in-kind), including an estimate of total cost, an estimate of monitoring cost, and a listing of funding sources. Respondents were asked whether they considered the project to be restoration—an attempt to increase oyster distribution or numbers because there is evidence that historic levels were higher than currently in this region or enhancement—an effort to boost this species for other reasons such as the ecosystem services it provides or because it has clearly decreased throughout its range, but not necessarily in the project area. The survey requested a statement of overarching qualitative goals in the respondents' own words as well as providing prompts about different categories of specific objectives.

The survey included numerous questions about project methods, including substrate types deployed and their longevity, tidal elevations, and use of aquaculture. The survey queried respondents about the parameters they had monitored and about project outcomes with regard to various metrics (measures evaluating outcomes) at different temporal scales and spatial scales. Respondents were also asked to quantify the importance of various challenges to restoration success, as well as describing overarching issues in their own words. The original survey and complete database of all survey responses can be downloaded from <https://olympiaoysternet.ucdavis.edu/west%20coast%20projects>). We also used the survey data to prepare a visual summary of all projects (<https://projects.tnerr.org/oystermmap/>).

We summarized answers for each of the major components of the survey using a variety of descriptive statistics presented in summary tables and figures, as well as statistical analyses using R version 3.5.2 (R Core Team 2018) for specific comparisons and to examine relationships with regression. We always used all available data, but due to missing information (some respondents did not complete all fields in survey), sample sizes varied for different analyses. Each section of the extensive survey involved specific definitions and multiple choice categories and was analyzed with different approaches; these detailed Methods as well as additional Results are presented in the Supplementary Information 1, under headings corresponding to those used in the Results subsections.

Results

Number, Timing, and Location of Projects

A total of 39 Olympia oyster projects meeting our definition criteria for restoration or enhancement have been implemented on the west coast of North America (Table 1), beginning with a project in 2001 in Liberty Bay, Washington, USA, by Puget Sound Restoration Fund (PSRF). The majority of projects were implemented within the last decade (70%, see Table S1). Though efforts span nearly the entire 2500-km stretch of the coast comprising the known range of this native oyster, Washington and California each accounted for 38% of the projects. Only one project has been implemented in British Columbia, Canada, and none has been undertaken in Baja California, Mexico.

Funding

Survey respondents provided funding information for 32 of the 39 (82%) Olympia oyster restoration projects. The combined funding for these 32 projects was approximately 8.2 million US dollars (\$). Funding per project varied by time period and

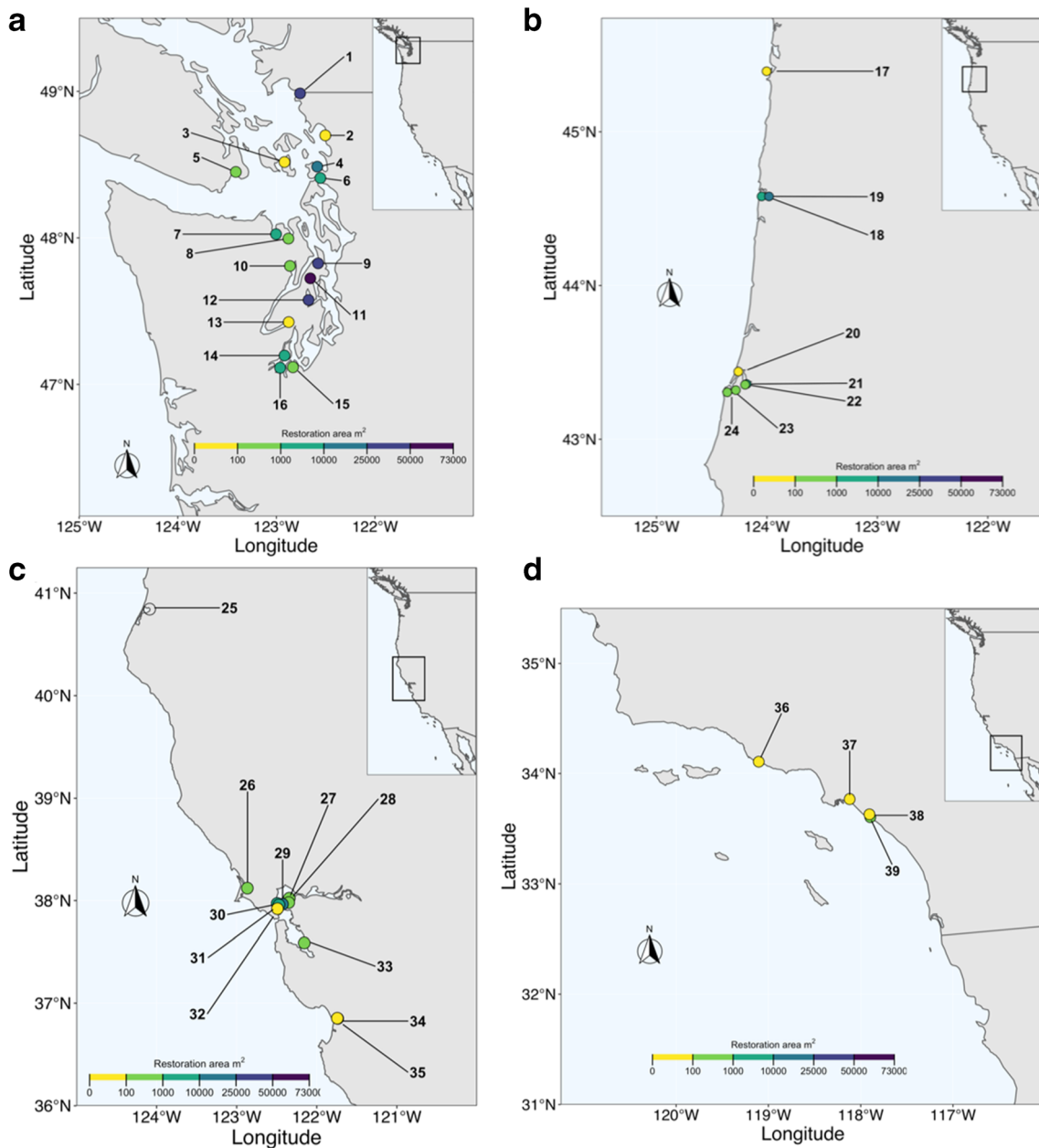


Fig. 1 Map of Olympia oyster restoration projects. Projects are broken into four regional panels: (a) Salish Sea, (b) Oregon and far Northern California (Humboldt Bay), (c) Northern California, and (d) Southern

California. The area of each project is depicted by the color scale; empty circles represent restoration projects where these data were not available (project 25) (see Table 1 for more information on each project)

region (Fig. 2a). Project cost ranged from \$1500 (for a small pilot in Oregon) to \$2,050,000 (for a large living shoreline project in San Francisco Bay, which included eelgrass restoration and other components in addition to oyster restoration). Per project funding was highest on average in California and lowest in Oregon, but there was high variation within states: mean and standard deviation for Washington was \$229K ± \$388K, for Oregon \$75K ± \$72K, for California \$371K ± \$555K (the sole project in British Columbia cost \$50 K).

About a third (37%) of the project cost was spent on monitoring across all projects combined, but the amount varied

from 0 to 100% of the project cost. In Washington, the mean and standard deviation percentage of total funding spent on monitoring were 19% ± 20%, in Oregon 60% ± 26%, and in California 44% ± 18%.

Cost per restoration area (area of mudflat over which substrates or oysters were deployed) varied tremendously, from \$1 to \$3763/m². Cost generally increased with decreasing latitude: the mean and standard deviation were \$176 ± 408/m² for Washington, \$686 ± 1406/m² for Oregon, and \$1296 ± 1030/m² for California. Similar patterns were obtained for the cost of new Olympia oysters present on restoration

Table 1 Summary information about Olympia oyster restoration projects. Project numbers in the first column are the same as in Fig. 1 and run from north to south, and are used throughout the text in abbreviated form (e.g., P1, P2). Location is in the second column (SS, Salish Sea; SFB, San Francisco Bay). The ID code of the project in the Story Map (<https://projects.trnerr.org/oystermapp/>) is in the third column; state or province in the fourth. The year the restoration started is in the fifth column. Estimated cost of the project is in the sixth column, and

estimated percent of that spent on monitoring in the seventh. The restoration area is estimated in the eighth column. The ninth column identifies those projects that used aquaculture, deploying hatchery-raised oysters. The tenth column identifies those projects that only added low-profile substrates that were elevated less than 20 cm above the mud-flat; other projects either were entirely or partly higher than this. Columns 6–8 are shaded, with darker tones indicating higher numbers.

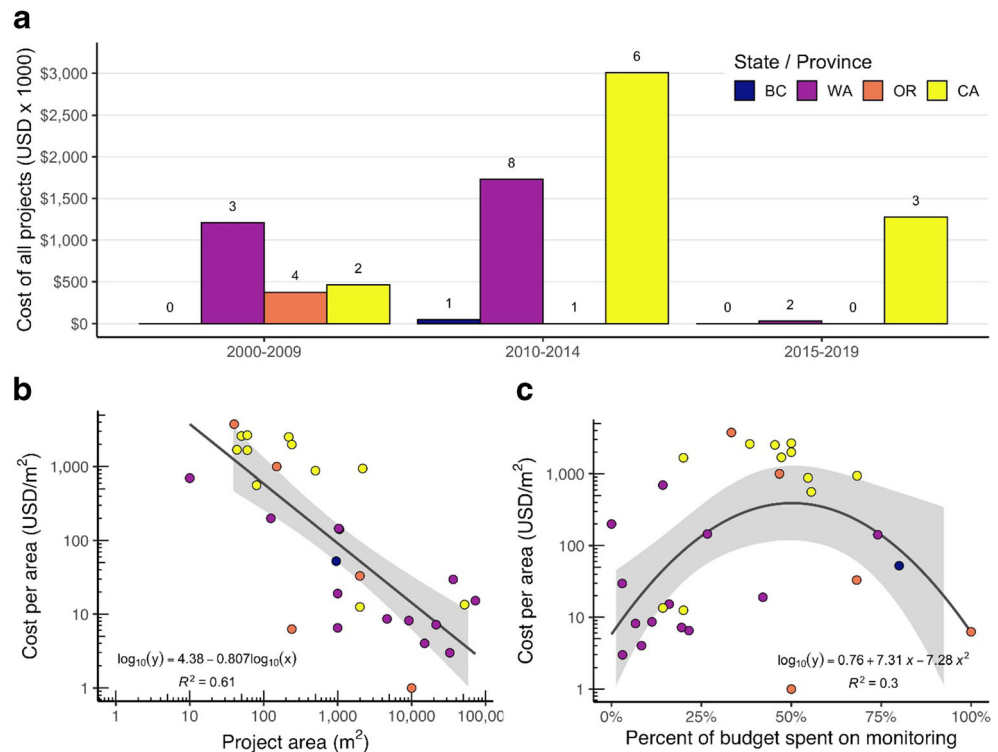
ID	Location	Story Map ID	State or Province	Year (start)	Cost estimate (USD)	% Budget monitor	Project area (m ²)	Hatchery used	Low profile (<20 cm)
1	Drayton Harbor, SS	WA01	WA	2014	\$97,796	3%	32,847	X	X
2	North Chuckanut Bay, SS	WA02	WA	2018			24	X	X
3	Fisherman Bay, SS	WA03	WA	2013	\$7,000	14%	10		X
4	Fidalgo Bay, SS	WA04	WA	2002	\$60,000	8%	15,000	X	X
5	Gorge Waterway, Portage Inlet, SS	BC01	BC	2011	\$50,000	80%	955		
6	Swinomish, Skagit & Similk Bays, SS	WA05	WA	2012	\$149,900	74%	1,057	X	X
7	Sequim Bay, SS	WA06	WA	2012			8,094	X	X
8	Discovery Bay, SS	WA07	WA	2014	\$19,000	42%	1,000		X
9	Port Gamble Bay, SS	WA08	WA	2014	\$1,078,788	3%	36,475	X	X
10	Quilcene Bay, SS	WA09	WA	2016	\$6,500	22%	1,000	X	X
11	Liberty Bay, SS	WA10	WA	2001	\$1,109,404	16%	72,900	X	X
12	Dyes Inlet, SS	WA11	WA	2011	\$154,000	19%	21,460	X	X
13	Mission Creek, Hood Canal, SS	WA12	WA	2013	\$150,000	27%	1,032	X	X
14	Squaxin Island, SS	WA13	WA	2010	\$75,000	7%	9,186		X
15	Henderson Inlet, SS	WA14	WA	2018	\$25,000	0%	125	X	X
16	Eld Inlet, SS	WA15	WA	2003	\$40,000	11%	4,653	X	X
17	Netarts Bay	OR1	OR	2005	\$150,000	33%	40	X	X
18	Yaquina Bay	OR2	OR	2009	\$66,000	68%	2,000		X
19	Yaquina Bay	OR3	OR	2011			10,800		X
20	Isthmus Slough & Haynes Inlet, Coos Bay	OR4	OR	2011			3		X
21	Isthmus Slough, Coos Bay	OR5	OR	2008	\$10,000	50%	10,000		X
22	Isthmus Slough Bridge, Coos Bay	OR6	OR	2010			150		X
23	South Slough, Coos Bay	OR7	OR	2008	\$149,844	47%	150	X	
24	South Slough, Coos Bay	OR8	OR	2012	\$1,500	100%	240		X
25	Humboldt Bay	CA01	CA	2007	\$10,000	70%	3		
26	Tomaes Bay	CA02	CA	2002	\$439,237	55%	500	X	
27	Point Pinole Regional Shoreline, SFB	CA03	CA	2013			1,000		
28	Giant Marsh, SFB	CA04	CA	2019			485		
29	San Pablo Bay, SFB	CA05	CA	2018	\$700,000	14%	52,043		
30	San Rafael, SFB	CA06	CA	2012	\$2,050,000	68%	2,180		
31	San Rafael, SFB	CA07	CA	2004	\$25,000	20%	2,000		
32	Tiburon Audubon Center, SFB	CA08	CA	2004	\$60,050		12		
33	Hayward, SFB	CA09	CA	2012	\$550,000	45%	218		
34	Elkhorn Slough	CA10	CA	2018	\$100,000	20%	60	X	X
35	Elkhorn Slough	CA11	CA	2012	\$130,000	38%	50		
36	Magu Lagoon	CA12	CA	2008	\$73,380	47%	43		
37	Alamitos Bay	CA13	CA	2013	\$160,000	50%	60		X
38	Newport Bay	CA14	CA	2016	\$478,398	50%	240		X
39	Newport Bay	CA15	CA	2010	\$45,000	56%	80		X

substrates (averaged for 1 and 5 years after the project was started): \$68 ± 121 per oyster in Washington, \$80 ± 147 in Oregon, and \$339 ± 757 in California.

Cost per square meter restored declined as a function of total project area ($F_{1,28} = 44.46$, $R^2 = 0.61$, $p < 0.0001$) (Fig. 2b), and initially increased and then declined once the percent budget allocated to monitoring increased past 50% ($F_{2,27} = 5.676$, $R^2 = 0.3$, $p = 0.0088$) (Fig. 2c). A multiple regression exploring the effects of both total project area and percent

budget allocated to monitoring on cost per square meter returned a significant regression equation ($F_{3,29} = 20.13$, $R^2 = 0.70$, $p = p < 0.0001$). Both total project area ($p < 0.0001$) and percent budget allocated to monitoring ($p = 0.0270$ and $p = 0.0170$ for X and X^2 of the polynomial equation, respectively) were significant predictors of cost per square meter. Total project area ($R^2 = 0.61$) explained more of the variation in cost per square meter than did percent budget allocated to monitoring ($R^2 = 0.3$).

Fig. 2 Cost of Olympia oyster restoration. **a** Sums of documented project costs totaled by period and state/province. The number of projects included in each group is shown above each bar. Categorization of projects into periods was based on start date; in some cases these continued into the next period. Not all projects reported costs, so these numbers represent underestimates. **b** Log₁₀ cost per area (\$USD per m²) as a function of log₁₀ project area (m²). **c** Log₁₀ cost-per-area (\$USD per m²) as a function of percent budget spent on monitoring. Gray shaded areas are 95% confidence intervals of the fitted line



Many different sources provided funding for these Olympia oyster projects, including federal, state, and local governmental agencies, tribal organizations, businesses, charitable foundations, and non-profit conservation organizations (which also ranged from small local ones to national organizations). Most projects had multiple funding sources typically 4–5 per project. The most frequently listed funding sources in declining order were the US National Oceanic and Atmospheric Administration (including NOAA Restoration Center, National Marine Fisheries Service and Office for Coastal Management) (19 projects), state agencies (natural resources departments, California State Coastal Conservancy, etc.) (13 projects), The Nature Conservancy (8 projects), and the United States National Fish and Wildlife Foundation (8 projects).

Project Goals

Objectives

Questions in the survey about objectives revealed that relatively few of the projects had involved concrete targets for oyster numbers, densities, or recruitment (Table 2). Less than a third of respondents to these questions ($n = 37$) had specific objectives for oyster populations on the restoration substrates that were deployed. Even fewer (5–14%) had objectives for oyster populations in the immediate vicinity (1 km of shoreline encompassing project area), and no projects had objectives for the larger surrounding area (20 km of shoreline).

In contrast to the limited number of projects with explicit oyster objectives, about two-thirds of projects listed specific objectives related to community engagement, and nearly half mentioned objectives related to conducting scientific research, testing methods, and informing and strengthening future restoration efforts. Comparatively fewer projects had concrete objectives related to ecosystem services and functions. About a quarter of projects had objectives related to animal diversity or abundance, primarily desired increases in fish abundance, and epifaunal invertebrate richness in the restoration area. Only a few projects had objectives related to shoreline protection (11%) and improved water quality (5%).

When asked to describe project goals in their own words (rather in the categories we provided above for specific objectives), respondents mentioned additional components. One goal listed by four projects was to re-establish oysters in bays where they had been historically or prehistorically present, but were now absent. This applied to two embayments in the Salish Sea in Washington (P3, P4, P10), as well as Netarts Bay (P17) and South Slough (P23) in Oregon. At one site in California (Elkhorn Slough, P34-35), a related goal was to prevent local extinction of oysters from an estuary where this seemed imminent. All of these projects thus shared the goal of significantly increasing oyster numbers and recruitment in the local embayment (from zero or near-zero pre-project). All other projects were conducted in areas with existing oyster populations and thus were not conducted in order to significantly increase oyster numbers across the entire estuary or bay.

Table 2 Restoration objectives and success at achieving them. The first column lists the number of projects that included each objective; the second column provides this as a percent of the total 37 projects in the database that provided data on objectives. The third column lists the number of projects that indicated they had evidence of success at

achieving this objective; the fourth column provides this as a percent of the subset of projects that used this as an objective (third column divided by first column). Darker shading in the percent columns represents higher numbers

	Projects (out of 37)		Projects reporting success	
	Number	Percent	Number	Percent
NUMERIC OYSTER OBJECTIVES	23	62%		
<i>On deployed restoration substrates</i>				
Numbers	5	14%	3	60%
Densities	11	30%	8	73%
Recruitment	10	27%	4	40%
<i>In immediate vicinity (1 km of shoreline)</i>				
Numbers	3	8%	2	67%
Densities	2	5%	1	50%
Recruitment	5	14%	1	20%
<i>In larger area (20 km of shoreline)</i>				
Numbers, Densities, Recruitment	0	0%	na	na
PEOPLE OBJECTIVES	30	81%		
Community engagement	24	65%	22	92%
Science / Learning / Testing methods	16	43%	14	88%
ECOSYSTEM SERVICES/FUNCTIONS	12	32%		
Increase in desired animal species	9	24%	3	33%
Shoreline protection	4	11%	0	0%
Improved water quality	2	5%	1	50%

In Washington, almost every project included the goal of increasing natural, biogenic oyster bed habitat. This was not listed as a goal in Oregon or California, though some of these mentioned increasing representation of structured habitat (through shell bags or reef balls) in mudflat environments.

Many projects in all regions included a learning component in their overarching goals: the project was designed in part to inform and strengthen future restoration efforts by testing approaches, building capacity, etc. Many projects also mentioned engagement of the community as a part of overarching motivation for the work. Only two projects (P9, P19) mentioned human harvest as one of the goals; both were conducted in collaboration with Native American tribes seeking to restore a historic fishery.

The proportion of projects that reported success at achieving specific objectives varied greatly by category of objective (Table 2). The highest rate of success was reported for objectives related to engaging the community (92%) or science and learning (88%). The next highest were success rates for achieving objectives regarding oyster numbers or densities directly on the restoration substrates or in the immediate vicinity (50–73%). Less success was documented for objectives related to oyster

recruitment (20–40%) and ecosystem services (32% overall, 0–50% by service).

Restoration vs. Enhancement

We found that the majority of respondents considered their projects to represent restoration, which we defined in the survey as an attempt to return an ecosystem to a historical trajectory or towards past conditions rather than enhancement, which we defined as an effort to boost the species for other reasons, such as decreases throughout the range but not necessarily in the project location, or to enhance ecosystem services regardless of history. Of the 37 projects for which we received responses, 31 (84%) projects were considered restoration and 6 (16%) were considered enhancement. None of the projects in Washington was considered enhancement; the single project in British Columbia, one project in Oregon, and four in California were.

In terms of evidence for considering the project restoration (vs. enhancement), most of the 31 restoration projects cited evidence of higher past abundance in the embayment, though not typically at the exact site where the project occurred, due to limited data availability or land use changes. Historical evidence of higher past

abundance from post-European colonization was listed for 16/31 projects, mostly consisting of commercial harvest of formerly more extensive beds. Pre-historical evidence of higher past abundance, including Native American middens or fossil beds, was listed for 8/31 projects. Both types of evidence were provided by 5/31 projects, and none by 2/31. The Salish Sea region appears to have the most detailed historical information documenting extensive beds in numerous areas early in the European colonization period, which have now declined (Blake and Bradbury 2012). Historical records of

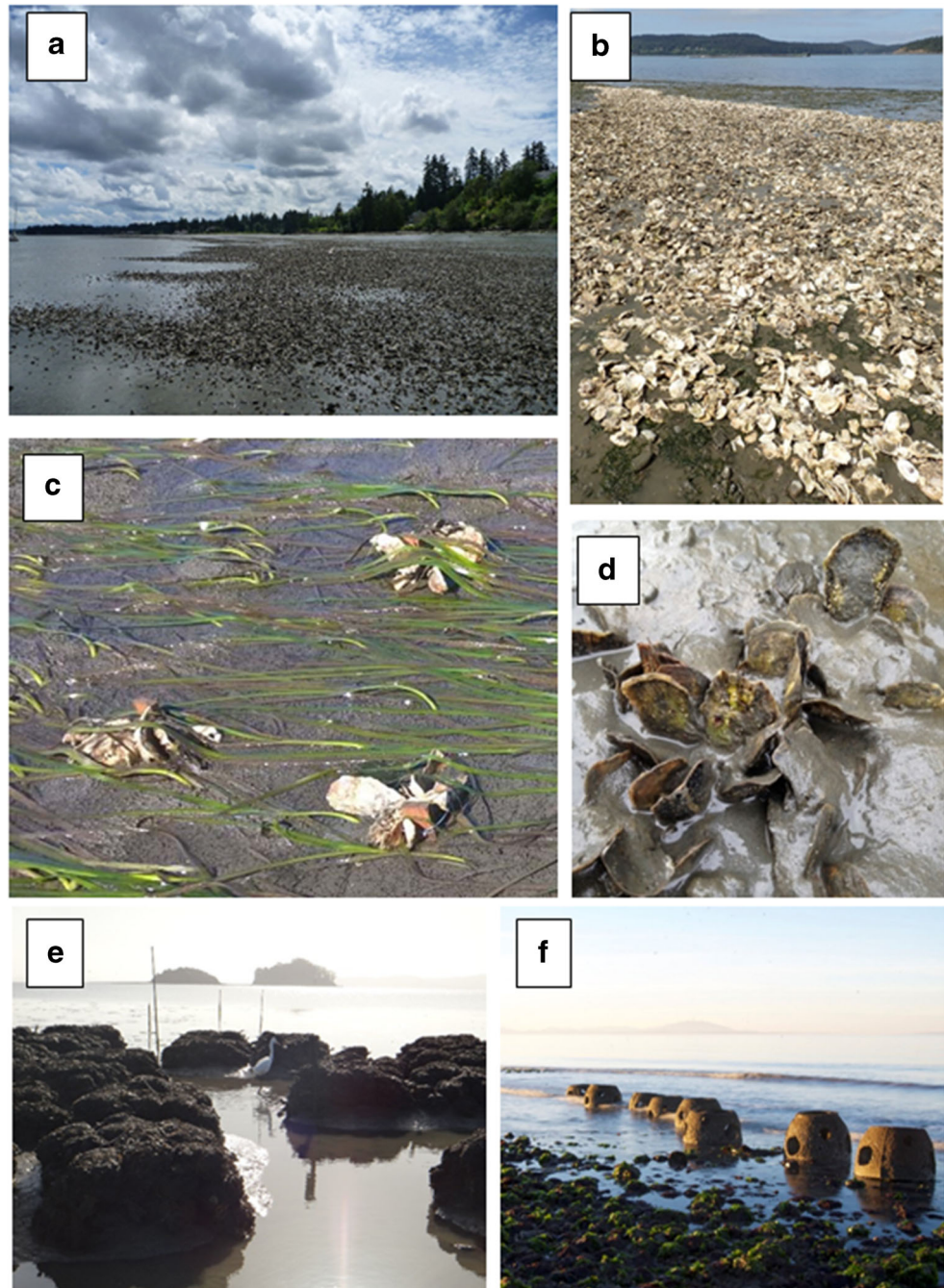
extensive beds in past centuries declined with latitude, with very few cited for southern Oregon and California.

Methods, Size and Duration of Projects

Deployment of Hard Substrate

Almost all (36/39) projects involved deployment of hard substrate as at least one component of restoration activities (Fig. 3, Fig. 4a). The remaining three projects involved deployment of individual live *Olympia* oysters, either hatchery-

Fig. 3 Visual portfolio of *Olympia* oyster restoration approaches. Restoration of historical low-profile, biogenic habitat using loose *Crassostrea gigas* shells in (a) Liberty Bay (Project 11) and (b) Skagit Bay (P6), WA. (c) Restoration effort mimicking natural *Olympia* oyster clusters with *C. gigas* shells attached to buried stakes among seagrass, in Hood Canal (P13), WA. (d) Cluster of *Olympia* oysters settled on loose *C. gigas* shells partly buried in mud in Alamitos Bay (P37), CA. (e) Stacked bags of *C. gigas* shells in San Rafael (P30) and (f) reef balls at Point Pinole (27), both in San Francisco Bay, CA



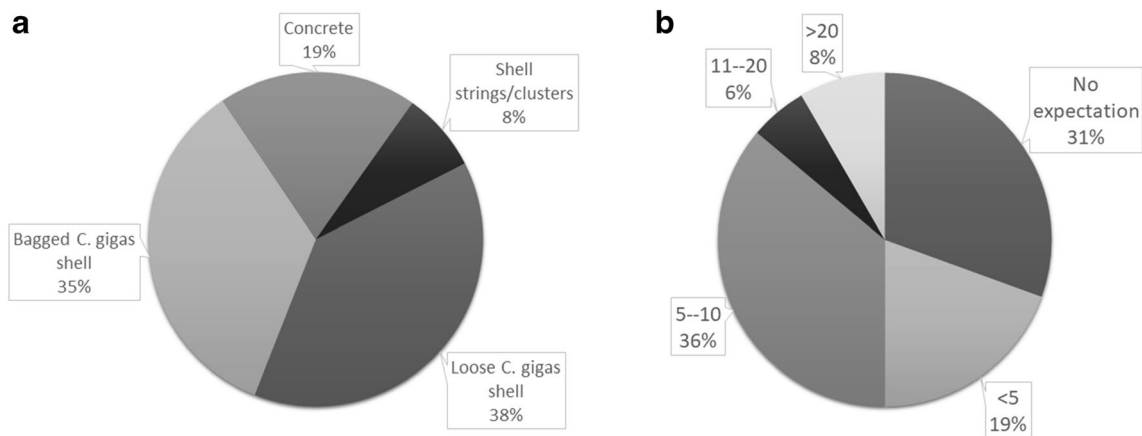


Fig. 4 Comparisons of type and duration of substrate. **a** Numbers of projects deploying different substrate types for settlement of Olympia oysters are shown; many of the projects deployed multiple types (e.g.,

raised or transferred from another site. The live oysters themselves comprise substrate for future oyster settlement, so in a sense even these projects involve deployment of hard substrate.

Of the projects deploying hard substrate, almost all (32/36) used shells of *Crassostrea gigas* (the non-native Pacific oyster that is farmed extensively on this coast), at least as one component of substrate addition. Thirteen deployed loose shells only (Fig. 3a, b, d), 11 deployed shell bags (Fig. 3e), and 7 both. The four projects that used no *C. gigas* were a project in South Slough, Oregon, and San Francisco Bay, California using concrete and Olympia oyster shell (Fig. 3f), and two projects in Elkhorn Slough, California that primarily used large native clam shells (as well as stakes and reef balls).

Two-thirds of projects (26/39) deployed shells or live oysters with a low profile (<20 cm above mudflat surface). Typically, this occurred by spreading loose shell on the mudflat, or by placing a single layer of shell bags on the mudflat (and sometimes opening these later). All projects in Washington State were low-profile, as were most in Oregon. In contrast, only four of 15 projects in California were low-profile, with all nine projects in northern California (Humboldt Bay, Tomales Bay, San Francisco Bay) and two south of San Francisco employing higher profile structures.

Ten projects included concrete elements. One of these was in British Columbia, one in southern Oregon, and the rest in California. Since Washington State objectives involved restoration of natural biogenic habitat, it is not surprising that no concrete was used in projects there. The most frequent use of concrete was in “reef balls” that included local sediment and oyster shells (developed in partnership with the Reef Ball Foundation), but other types of modular structures were also used. Eight of the shell/concrete projects were high-profile (>20 cm above mudflat). A low-profile project (P20) using concrete was conducted in Coos Bay, Oregon: “OlyRocs” (Olympia oyster Restoration On Cement Substrata) was built

concrete reef balls and shell bags, or loose and bagged shell). **b** Expected duration of substrate as estimated by survey respondents

from Olympia oyster shells embedded in cement paving stones, measuring only 10 cm high.

Four projects deployed aggregations of shells, which mimic naturally occurring clusters of Olympia oysters (Fig. 3c). A project (P13) in Hood Canal, Washington, and Elkhorn Slough, California (P34) attached clusters of shells (*C. gigas* and *Tresus nutallii* - gaper clams, respectively) to wooden stakes. A project in Elkhorn Slough (P35) and one in Alamitos Bay, California (P37) used strings of shells (gaper clam and *C. gigas*, respectively).

A minority of projects incorporated other restoration substrates. A project in Tomales Bay, California tested rip rap, PVC, and ceramic tiles. A project in Elkhorn Slough and in Mugu Lagoon, California used wooden or PVC stakes, some covered with mortar. A project in Newport Bay incorporated mussel shells mixed with *C. gigas* shell.

Substrate Longevity

About a third of projects (for $n = 36$ that answered this question) had no stated objectives or expectations regarding the duration of the deployed substrates. A fifth expected them to last less than 5 years, and just over a third expected them to last 5–10 years. Only 14% of substrates were expected to last more than 10 years (Fig. 4b). The survey also attempted to determine how long substrates actually did last relative to these expectations. However, the results were inconclusive: 24/25 of the projects that provided numeric expectations for longevity also had fewer years of monitoring data than the expected longevity (either because monitoring ceased or because the project is still relatively new). For those 30 that provided an estimate of actual observed duration of restoration substrates, the average was 5 years, but again, this represents an underestimate of actual longevity for the many recent projects where only a few years of monitoring data are available. The longest duration of deployed substrates was 15 years. The

shortest were two reports of deployed loose shells being buried or swept away within a single year. In many cases, projects reported mixed results for substrate duration which were not included in these estimates, for instance, indicating that some loose shell was still present at the site, but that some had been lost, or that some bags of shell were buried but others still present.

Size

The size of restoration projects varied tremendously. The volume of hard substrate added varied from zero (for sites only adding live oysters, no other substrates) to 3134 m³, with a median of 11 m³, and average and standard deviation of 204 ± 546 m³. The average amount of hard substrates added was highest in Washington (372 m³), with Oregon averaging less than half this area (135 m³) and much smaller amounts of substrate added in California (76 m³) and British Columbia (32 m³). The footprint of the restoration area (which typically included areas of mudflat interspersed with added hard substrate) ranged from 3 to 72,900 m², with a median of 500 m², average and standard deviation 7471 ± 16,109 m². The average size of the restoration area was much larger in Washington (13,595 m²) than elsewhere (British Columbia: 955 m²; Oregon 1798 m²; California 4212 m²).

Tidal Elevation

All projects were intertidal, centered at somewhat below local mean lower low water (average tidal elevation for project substrates was -0.18 ± 0.44 m mean lower low water (MLLW)). The lowest deployed substrates of any project were at -1.8 m MLLW, the highest at $+1.1$ m (Supplementary

Information 1, Table S2). The only projects with average elevations 0.1 m or more above MLLW occurred in California.

Restoration Aquaculture

Sixteen of the 39 projects (41%) incorporated hatchery-raised oysters (Table 1). Of these, the majority of projects (12/16, 75%) were in the Salish Sea, Washington, using local broodstock. Numbers of hatchery-raised oysters outplanted ranged from 13,000 to 1.5 million across projects, with a median of about 250,000 per project. Most were outplanted as spat on *C. gigas* shell, spread loose on the mudflat or bagged.

Only two projects used hatchery-raised oysters in Oregon: one in Netarts Bay (P17) using local broodstock, and one in South Slough (P23) using Netarts Bay and Willapa Bay broodstock. Millions of juveniles were outplanted in both projects, mostly as spat on *C. gigas* shell.

In California, two projects used hatchery-raised oysters: a small restoration experiment (P26) and a proof-of-concept restoration aquaculture project (P34). No restoration aquaculture has been conducted in British Columbia, Canada, or Baja California, Mexico.

Monitoring of Restoration Projects

Of the 39 projects, 35 monitored the restoration substrates and made at least some measurements of the areas surrounding the project (“immediate vicinity” and “larger surrounding area,” see Methods, Supplementary Information 1). Three projects had monitored the restoration project only, and one (P15) indicated that there had been no monitoring of the project itself (only of the surrounding area). In all cases, more

Table 3 Monitoring metrics. The metrics most commonly measured by restoration projects in our survey, by state or province. Includes new projects that supplied details of their planned monitoring. Oyster size frequency and/or recruitment were combined into a single metric, to align

with Baggett et al. 2014, who suggested measurements of oyster size frequency as a way to measure recruitment. *It was not clear in all cases that these measurements were being made to evaluate oyster-restoration benefits (goal-based metrics) or for other purposes

Metric	Scale	Baggett et al. 2014 definition	BC	WA	OR	CA	Total	Percent of total
Size frequency or recruitment	Restoration substrates	Universal metric	1	12	8	12	33	87
Oyster density	Restoration substrates	Universal metric	1	12	6	12	31	82
Areal extent of project	Restoration substrates	Universal metric	1	10	4	7	22	58
Oyster density	General restoration area	Goal-based?*	1	8	4	9	22	58
Water temperature	General restoration area	Universal environmental parameter	1	6	2	12	21	55
Tidal elevation/height bed	Restoration substrates	Goal-based	0	7	2	12	21	55
Oyster recruitment	General restoration area	Goal-based?*	1	8	2	9	20	53
Cover of sessile species	Restoration substrates	Goal-based?*	1	5	1	10	17	45
Salinity	General restoration area	Universal environmental parameter	1	4	2	10	17	45
Oyster size frequency	General restoration area	Goal-based?*	1	4	4	6	15	39
Dissolved oxygen	General restoration area	Universal environmental parameter	0	2	2	8	12	32

parameters were measured directly within the project footprint than in the larger areas.

The most commonly measured parameters were the universal metrics recommended by Baggett et al. 2014 (Table 3). The combination category of oyster size frequency/recruitment was measured most frequently (87% of projects). Oyster density on restoration substrates was measured in 82% of projects. The third universal metric, areal extent of project, was measured in 58% of projects. Many projects also measured the universal environmental parameters (Baggett et al. 2014). Water temperature was measured by more than half of all projects (55%), salinity in 45% of projects, and DO in 32%. Tidal elevation or height of substrates/oyster reefs/oyster beds was measured in 55% of projects.

More than half (58%) of the projects made oyster measurements within the general restoration area (as opposed to just on restoration substrates), with 58% measuring oyster density and 53% measuring oyster recruitment to the larger area. Cover of other sessile species and oyster size frequency in the general restoration area were monitored by about a third of all projects.

The number of parameters monitored varied by state/province. Across all projects within California, 33 parameters were monitored, 30 in Washington, 15 in Oregon, and 11 in the one project in British Columbia. California projects typically monitored a greater number of parameters; 13 parameters were measured by 7 or more of the 15 projects in California, while 8 parameters were monitored by 7 or more of the 14 projects in Washington and 6 parameters by 4 or more of 8 projects in Oregon.

There were also some differences among states in what was monitored. In general, Washington and Oregon projects tended to focus more on oyster metrics in the restoration project and the general area around the project and on some environmental parameters, although some projects also investigated ecological interactions/effects of restored oyster beds. In addition to oyster metrics, California projects tended to also measure parameters having to do with ecological communities and physical metrics of the restoration projects, such as sediment accretion/erosion. This trend may have been driven in part by a handful of projects that had multiple objectives (including restoration/enhancement of multiple species), and which included testing potential effects of oyster projects on shoreline protection, eelgrass restoration, and a broad suite of species including invertebrates, fish, and birds. California projects also monitored non-native invertebrate species recruiting to oyster substrates.

Monitoring duration varied from 1 to 16 years to post-construction. Monitoring had just begun on two new projects and was slated to begin in 2019 for a third. Including the planned length of monitoring for these new projects, on average, projects had been monitored for 4.5 years at the time of the survey. However, half of all projects were still being monitored at the time of the survey.

Achieving Restoration Success

We examined four different oyster metrics for restoration success, reported on separately below. Scores for all four metrics of restoration success for individual projects are shown in Table S4. A summary of averages by state and by whether the project deployed hatchery-raised oysters is shown in Table S5. A summary of regressions we conducted examining the same potential correlates of restoration success for each of the four metrics is shown in Table 4; the significant relationships are shown in Figs. S1–4. Below, we discuss each metric in turn, first providing a summary of how projects scored overall, then describing patterns by state and by whether the project deployed hatchery-raised oysters, and then reporting on various regression analyses conducted with potential correlates of restoration success.

Recruitment into Restoration Area—Oyster Metric 1

As the first oyster metric of restoration success, we examined recruitment onto the deployed substrates in the restoration area in year one (Y1, which had many more projects reporting than Y5 or Y10). Overall, for 25 projects reporting, 36% had index of 0 (no recruitment), 32% had index 1 (<10 recruits/m²), 16% had index 2 (<100/m²), 12% had index 3 (<1000/m²), and 4% had index 4 (>1000/m²). The average recruitment index was higher in CA than that in OR and WA (Table S5), and there was a significant negative relationship with latitude (Table 4, Fig. S1A). Projects that deployed hatchery-raised oysters (16/39) had somewhat lower recruitment in Y1 than those that did not (*t*-test, *p* = 0.085; Table S5). The recruitment rate on restoration substrates was positively related to recruitment rate in the immediate vicinity (Table 4, Fig. S1B). However, the recruitment rate on restoration substrates was not correlated with number of oysters in the immediate vicinity (Table 4) or larger area (*R* = 0.12, *p* = 0.63).

Restored Oyster Numbers—Oyster Metric 2

As a second oyster metric of restoration success, we looked at numbers of oysters the project initially generated (Fig. 5)—numbers of oysters on the restoration substrate at Y1 (it would have been preferable to look at Y5 or Y10, but too few projects had data for these longer time periods). Overall, for 28 projects reporting, 86% documented oysters on the deployed substrate after 1 year: 14% had index 0 (no oysters on deployed substrates at Y1), 32% had index 1 (<1000), 21% had index 2 (<10,000), 25% had index 3 (<100,000), and 7% had index 5 (>1 million). There were no differences in the average index for this metric across states (Table S5) and no effect of latitude (Table 4). There was no difference in projects that deployed hatchery-raised oysters vs. bare substrates (*t*-test, *p* = 0.47, Table S5). At sites that deployed

Table 4 Summary of relationships between oyster metrics of restoration success and potential correlates. The Pearson correlation coefficient (*R*) and *p* value are shown for each; if significant, the direction of relationship is shown (these significant relationships are graphed in Figs. S1–4).

	<i>Potential correlates of restoration success</i>				
	Latitude	Volume of substrates deployed (log)	Recruitment on restoration substrate Y1	Recruitment in vicinity	Number of oysters in vicinity
Restoration success metric					
1 - Recruitment into restoration area	– R = -0.42 P = 0.036	NS R = 0.29 P = 0.17	n.a.	+ R = 0.7 P = 0.001	NS R = 0.12 P = 0.96
2 - Restored oyster numbers	NS R = -0.049 P = 0.81	+ R = 0.45 P = 0.019	+ R = 0.67 P = 0.00025	NS R = 0.37 P = 0.12	NS R = -0.035 P = 0.87
3 - Change in restored oyster numbers	+ R = .54 P = 0.018	NS R = -0.37 P = 0.13	NS R = -0.43 P = 0.085	NS R = -0.28 P = 0.34	+ R = 0.54 P = 0.026
4 - Effect on immediate vicinity	NS R = -0.15 P = 0.47	+ R = 0.43 P = 0.029	+ R = 0.49 P = 0.015	NS R = 0.24 P = 0.33	– R = -0.66 P = 0.00027

hatchery-raised oysters, the restored oyster numbers at year 1 represent a combination of the hatchery-raised oysters initially deployed and new recruits. For the 9 projects that reported numbers outplanted and numbers at year 1, 67% had fewer

than initially deployed (due to mortality of deployed animals and lack of recruitment), 22% had about the same (either low mortality or mortality balanced by recruitment), and 11% had more (which had to be due to recruitment). Across all projects

Fig. 5 Restored oyster numbers as a metric of success. Numbers of adult oysters on restoration substrates at 1 year post deployment, scored by order of magnitude categories (0, 1 ≤ 1000, 2 ≤ 10,000, 3 ≤ 100,000, 4 ≤ 1 million, 5 ≥ 1 million). Projects are listed from North to South, and color coded by state/province: BC (dark blue), WA (purple), OR (orange), CA (yellow). Striped columns are the average for each state. Projects with missing data are omitted (those listed here with no bars had zero oysters)

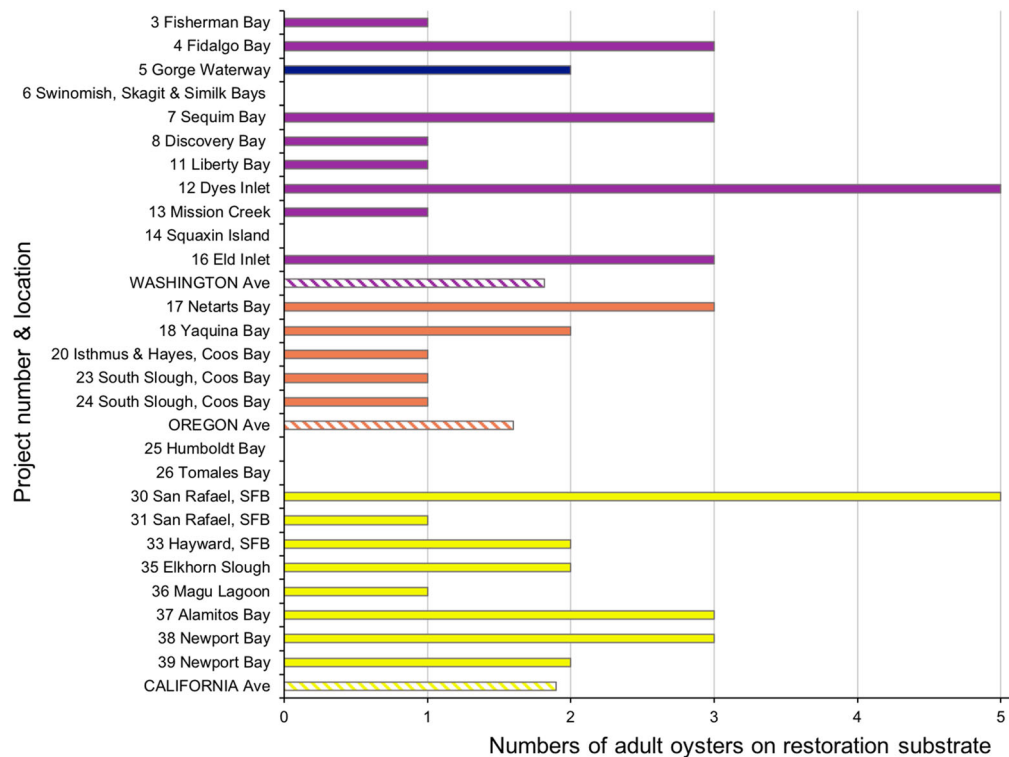
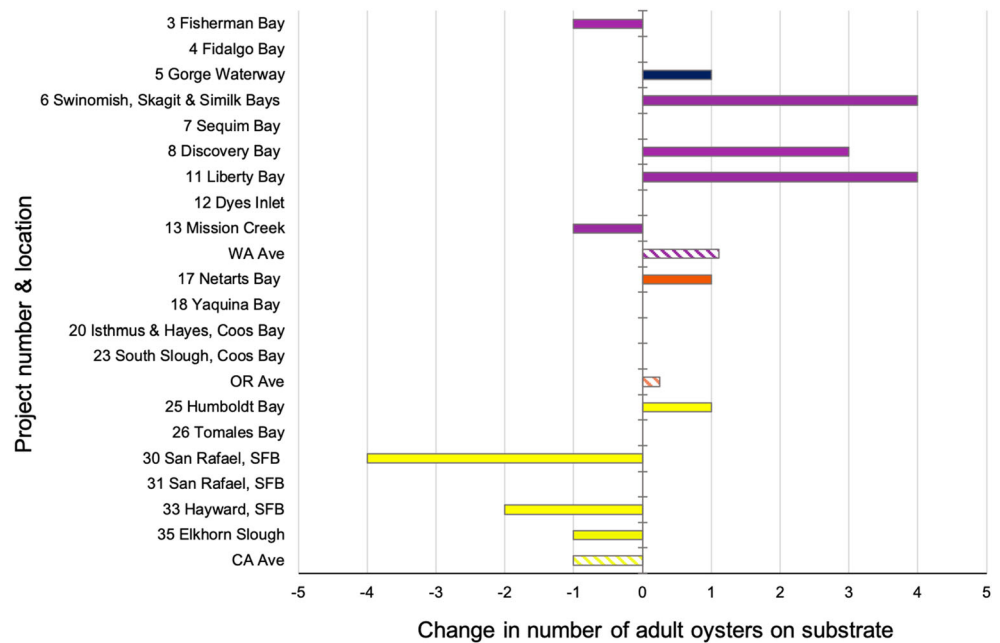


Fig. 6 Changes in number of restored oysters as a metric of restoration success. Change in the number of adult oysters on the restoration substrate between 1 and 5 years post deployment (0, $1 \leq 1000$, $2 \leq 10,000$, $3 \leq 100,000$, $4 \leq 1$ million, $5 \leq 1$ million). No visible bar (0) indicates no change in total number; each unit of + or - indicates an order of magnitude change from the starting number of oysters. Projects are listed from North to South, and color coded by state/province: BC (dark blue), WA (purple), OR (orange), CA (yellow). Striped columns are the state average.



combined, there was a significant positive relationship between restored oyster numbers and recruitment on restoration substrates in Y1 (Table 4); this relationship was stronger for projects that did not deploy hatchery-raised oysters (Fig. S2A). There was no relationship of restored oyster numbers and recruitment in vicinity (Table 4). Restored oyster numbers correlated positively with the volume of hard substrates deployed (Table 4, Fig. S2B).

Change in Restored Oyster Numbers—Oyster Metric 3

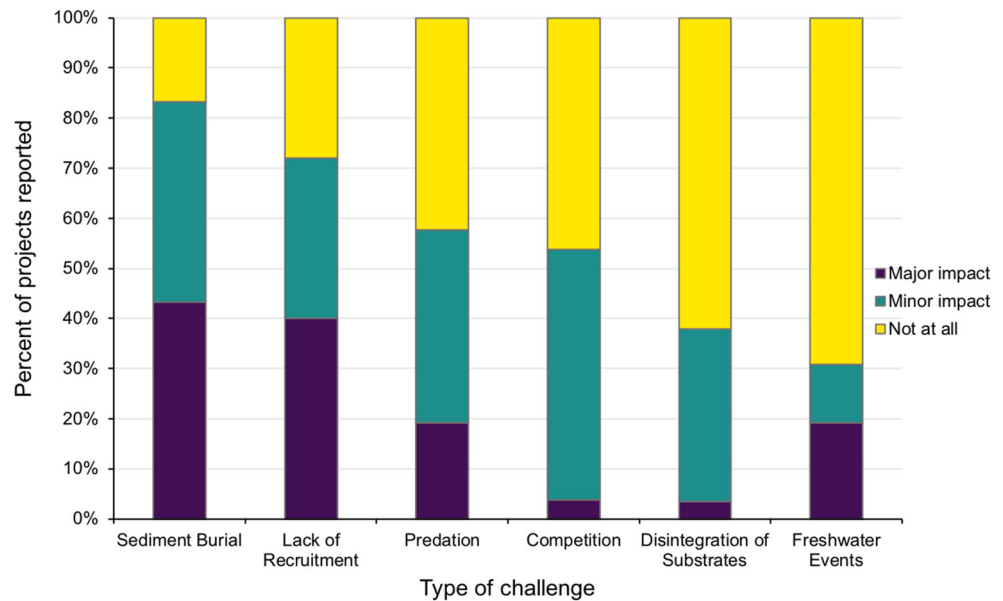
As a third oyster metric, we looked at change in restored oyster numbers over time (Fig. 6), which can be affected both by recruitment and mortality. Overall, for 19 projects reporting estimates of numbers at Y1 and Y5, the majority of restoration projects reported either stable or increasing restored oyster populations within the first 5 years of the project: 42% had no change (by order of magnitude estimate), and increases were reported by 32% of projects, 16% with one order of magnitude increase and 16% with greater. Decreases were reported by 26% of projects, 16% with one order of magnitude loss and 10% with two or more orders. On average, restored oyster numbers declined in California but increased in Washington (Table S5), and there was a significant increase in this metric with latitude (Table 4, Fig. S3A). We expected hatchery projects to have more of a decline than others because they were conducted in areas of low recruitment, where mortality might exceed recruitment, but no significant difference was found in this metric between projects that used hatchery and those that did not (t -test, $p = 0.18$; Table S5). Indeed, the reverse result as expected was obtained—1/9 hatchery projects documented a decline in this period,

vs. 4/10 projects without hatchery (Table S4). Surprisingly, there was no positive relationship between change in restored oysters and recruitment (Table 4)—the relationship, which was marginally significant, was negative. There was a significant positive relationship between change in restored oyster numbers and oyster numbers in the vicinity (Table 4, Fig. S3B).

Effect on Oysters in Immediate Vicinity—Oyster Metric 4

As a fourth metric of restoration success, we examined the magnitude of difference between restored oyster numbers and those in the immediate vicinity. We calculated the difference between the number of oysters on restoration substrates at Y1 and the number of oysters in immediate vicinity before restoration, using the order of magnitude indices provided in the survey. If the restoration project added about equal number of oysters, the value of this difference index is 0; if the project added an order of magnitude of oysters than were already there, the value is 1, and so on. Overall, the average number across projects ($n = 30$ respondents) was 0.28—so between an equal number and an order of magnitude, more oysters were generated on the restoration substrates than had been in the vicinity of the project initially. There were more oysters on substrates than in the vicinity in California, versus a similar number on substrates and vicinity in Washington (Table S5), but there was no significant effect of latitude (Table 4). This metric correlated positively with volume of substrate deployed and with recruitment rate onto the deployed substrates (Table 4, Fig. S4A–B). There was a strong negative relationship for this metric with number of oysters in vicinity, as expected—projects that had the greatest success by this metric

Fig. 7 Challenges to oyster restoration success. Respondents ranked challenges for each project from “Not at all” (purple) to “Minor impact” (teal) to “Major impact” (yellow). Number of total projects reporting varied by category: Sediment burial ($n = 30$), lack of recruitment ($n = 34$), predation ($n = 26$), competition ($n = 26$), disintegration of substrates ($n = 29$), freshwater events ($n = 26$)



were ones conducted where oyster numbers were low in the immediate vicinity, such that the project had a proportionately large effect (Table 4, Fig. S4C). Overall, the numbers of restored oysters, oysters in the immediate vicinity, and the larger area showed variable patterns across projects (Fig. S5).

Challenges to Restoration Success

Overall, sediment burial, lack of recruitment, and predation were the top three challenges to restoration projects, ranked as either minor or major challenges at 83% (of 30 projects), 72% (of 34 projects), and 54% (of 26 projects) respectively (Fig. 7). Competition for space was a challenge for over half of the projects reporting (14/26) as well, but it only posed a major challenge to 4% of projects. A majority of projects (18/24) reported bare space on the restoration substrate a year after deployment (Fig. S5), indicating that space is not an immediate limiting factor for native oyster recruitment, and that competition with settling larvae of other species, including *C. gigas*, which only recruited to restoration substrata at five restoration sites (Fig. S6), is also not a major cause for the observed lack of settlement or growth on the substrates (more detail in Supplementary Information 1). Freshwater events and the disintegration of substrates were not a problem at most sites (18/26 and 18/29 respectively, Fig. 7). However, where freshwater events occurred, they were considered a major challenge, one equal to predation, and more of a concern than competition or disintegration of substrates combined.

Sedimentation was a challenge for all but five projects (in Washington). Respondents cited three major types of sediment issues at their sites: sedimentation on top of restoration substrates, sinking of the substrates themselves into the mudflat that they were originally placed on, and burial of

substrates due to tidal currents or storms. Higher-relief structures and reefs seemed to provide some respite from both burial and settling substrate. Yet, in some places, even a 50-cm emergent reef was insufficient to prevent burial, and heavier high-relief structures such as reef balls quickly sank into soft mud. Many cited sedimentation as the motivation for selecting sites with firmer sediment on which to place their restoration substrates, based on their observations from previous years of monitoring.

Recruitment posed the second most common challenge to restoration and was cited as important in estuaries throughout the oyster’s range. Indeed, half of all projects that experienced limited recruitment (9/18) cited no recruitment at all on the restoration substrates for at least one, and in some cases all of the years for which data were taken.

Predation was the third most common challenge to restoration, but most projects did not regularly or directly measure predation effects as part of their monitoring protocol, even if they estimated these effects for our survey. Even among sites where predation posed a major challenge, only a few could confirm the identity of the problematic predator(s): the Atlantic and Japanese oyster drills, *Urosalpinx cinerea* and *Ocenebra inoratus*; the North American raccoon, *Procyon lotor*; and various sea star species were observed preying on native oysters. Whether predation was important or not, we asked participants to indicate which potential predators were present. The introduced European green crab, *Carcinus maenas*, was the most frequently observed potential oyster predator across all projects (present at 29%). The Atlantic oyster drill, *Urosalpinx cinerea*, and the native lurid rock snail, *Ocenebra lurida*, were nearly as common: present at 22% and 21%. Other crab species, including the red rock crab, *Cancer productus*; the Dungeness

Table 5 Summary of key results of the synthesis and recommendations

	RESULTS OF SYNTHESIS	RECOMMENDATIONS
INVESTMENT	A total of 39 native oyster restoration projects were conducted between 2001-2019, for a total investment of about 8.2 million US dollars (\$)	<i>Invest more in native oyster restoration on this coast</i>
	Cost per area declined with the size of the restoration area, which was far greater in Washington State than in other areas	<i>When possible, design large projects which are more cost effective</i>
	The geographic distribution of these projects is uneven, with virtually no restoration in the southern and northern ends of the species range	<i>Conduct regional strategic planning leading to investment in underrepresented areas</i>
GOALS	Measurable objectives were rarely specified for projects	<i>Specify measurable objectives (for oysters, ecosystem functions and services)</i>
	Restoration of natural, biogenic oyster bed habitat was a primary goal for all Washington projects but rare elsewhere	<i>Consider whether restoring natural habitat structure might be appropriate more broadly</i>
APPROACH	Virtually all restoration projects included provision of hard substrates, most commonly <i>Crassostrea gigas</i> shells	<i>Thoroughly assess all possible restoration approaches to choose the most effective at achieving objectives, which will likely result in some changes to past geographic patterns</i>
	All projects in Washington had a low profile above the mudflat, while most in California had a high profile	
	Less than half of the projects incorporated aquaculture as a tool, and most of these were in Puget Sound	
MONITORING	The majority of projects included monitoring of oysters on the restoration substrates in the first years following restoration; few projects monitored effects of the restoration on oysters or ecosystem functions and services beyond the restoration footprint	<i>Funders should provide sufficient monitoring resources to allow effects of restoration project to be evaluated broadly in space (beyond the restoration substrates themselves) and time (for 5-10 years, not just the first year)</i>
	Monitoring was typically limited in duration, so longevity of project substrates and long-term outcomes for oysters on them could not be assessed	
SUCCESS	Most deployed restoration substrates hosted native oysters in the first years following restoration	<i>Select sites with adequate recruitment or use hatchery-raised spat, and choose sites or methods that avoid sediment burial; if these issues are addressed, probability of short-term success at growing oysters on restoration substrates is high</i>
	Burial by sediment and lack of recruitment were by far the most common challenges to restoration success for these projects; predation, competition, and other factors less frequently caused problems	
PEOPLE	Almost all projects successfully engaged the community in restoration projects and/or involved students and scientists to learn from the projects	<i>Continue to engage people in restoration, because coastal communities in this region remain largely unaware of native oysters, and there is still much to be learned by students and scientists</i>

crab, *Metacarcinus magister*; and *Hemigrapsus* spp., were potential predators present at 14% of sites. Finally, sea star predators, including the six-rayed star, *Leptasterias*

hexactis; the mottled star, *Evasterias troschelii*; and Pisaster stars, *Pisaster* spp., were present at 14% of restoration projects.

Discussion

Our synthesis of historical and current Olympia oyster restoration projects revealed that the majority succeeded in growing oysters on deployed substrates, and succeeded in engaging community members in coastal habitats and learning. Our synthesis also highlights how little investment has been made in native oysters on this coast. While cost per unit area significantly declined with the overall areal footprint of the project, as with Blomberg et al. (2018), which evaluated the same relationship among projects primarily from the US East and Gulf Coasts, the combined funding documented for all Olympia oyster restoration projects spanning two decades was about \$8.2 million US dollars. This contrasts with an average of \$2.5 million US dollars per project for recent *Crassostrea* projects (Edwards et al. 2013). Thus, our overarching recommendation is greater future investment in Olympia oyster restoration, particularly in larger, more cost-effective projects.

Below, we explore various themes that emerged from our synthesis, starting with broad context before discussing Olympia oyster issues. Since the results of our synthesis and our thematic discussion of them are extensive, we have summarized the most important findings and recommendations (Table 5).

Matching Approach to Goals

Restoration can encompass diverse goals and methods, but is typically defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed” (Society for Ecological Restoration International, 2004). More recently, and especially in complex coastal and estuarine ecosystems, a broader definition of restoration activities has been required to achieve project goals (Gann et al. 2019; Fitzsimons et al. 2020). The Olympia oyster projects synthesized here used a diversity of approaches to achieve a range of goals. The majority of projects were considered restoration towards prior conditions, but particularly for Oregon and California, little historical data on oyster numbers or bed distributions are available. Nearly all projects in Washington had an explicit goal of restoring natural biogenic habitat comprising low-relief oyster beds, and as a result, project approach involved deploying shells in low-profile configurations to increase settlement structure. In contrast, various projects in California used high-relief concrete structures or stacks of shell bags to create a living shoreline to enhance ecosystem services such as shoreline protection and fish habitat.

The difference in approaches and goals between regions is likely partly due to historical accidents, in terms of the preferences of key regional organizations, e.g., favoring restoration

of low-profile biogenic reefs resembling historic beds in the Salish Sea vs. high-profile structures in San Francisco Bay. The regional difference in approaches may also be partly due to logistics—many California estuaries are eutrophic and have deep, organic-rich fine sediments on the tidflats where low-profile oyster beds could easily be buried. Nevertheless, it is worth at least considering all approaches in all regions. It seems plausible that high-profile living shorelines, strategically used to replace concrete bank armoring, might be valuable in some Washington estuaries, while restoration of natural, low-profile biogenic beds could expand to more California estuaries, in carefully selected locations with gentle slopes and low sedimentation. Based on our findings, we recommend an explicit mechanism for goal-setting for Olympia oyster projects, and for selecting best methods for achieving specific goals. We have developed a decision support tool (see Supplementary Information 2) to stimulate thoughtful consideration of desired goals and best approaches to achieving them.

Measuring and Understanding Restoration Success

Long-term ecological monitoring of marine foundation species is rare, but has great value for advancing conservation outcomes (Menge et al. 2019; Bell et al. 2014; Forrester et al. 2015; Hughes et al. 2017). Evaluating restoration success requires monitoring relevant parameters at spatial and temporal scales that match project goals. Detailed guidance has been generated in recent years for shellfish restoration monitoring (e.g., Brumbaugh et al. 2006; Baggett et al. 2014; Walles et al. 2016; Fitzsimons et al. 2019).

We found that less than a third of Olympia oyster projects set numeric objectives for numbers of new oysters resulting from the effort. It is difficult to predict exact oyster numbers given high interannual variability in recruitment and survival. Setting minimum targets for oyster numbers as a result of the restoration effort is necessary so that success can be more uniformly evaluated, reported, and compared among projects.

Despite the lack of numeric objectives for oysters, the majority of projects monitored the critical metrics identified by Baggett et al. 2014, including recruitment, density, and areal extent of the project, as well as two critical environmental parameters, water temperature and salinity. The average length of monitoring also met minimum recommendations (Baggett et al. 2014) of at least 2 recruitment seasons. However, variability among metrics used in different projects to capture oyster numbers, densities, and recruitment rates highlights the challenge of comparing data across sites without fully standardized methods. We also found that most monitoring for Olympia oyster projects was not very broad in space or time, presumably due to limitations of funding and project timelines. Most monitoring was focused narrowly on the restoration footprint, and lasted only a few years. This

severely limits an assessment of the effects of restoration at larger spatial and temporal scales. It also means that the longevity of added substrates is largely unknown, which is problematic considering that the main approach for many restoration projects is to deploy hard substrate (Mann and Powell 2007). To quantify longevity of restoration substrates and measure effects of restoration projects beyond project boundaries and over decadal time scales, funders should provide substantial long-term funding for monitoring oyster metrics and relevant ecosystem services.

Overall, restoration success was high for Olympia oyster projects—the majority of restoration projects resulted in oysters on the restoration substrate in the first year, and either stable or increasing oyster numbers over the first 5 years. The majority of restored oyster numbers exceeded the numbers originally in the vicinity, indicating a strong local effect on oyster populations. Ideally, monitoring of local populations could predict restoration success prior to initiation of a restoration. In terms of predicting the magnitude of local effect, this is certainly true—as expected, we found that projects conducted in areas with few oysters in the vicinity had a proportionately larger effect of increasing local native oyster population sizes. However, other metrics of restoration success—recruitment and restored oyster numbers in the first year were not correlated with monitored metrics of the surrounding population. These metrics were correlated with latitude, in opposite directions; recruitment decreased with latitude but restored oyster numbers increased with latitude. The disparity between these metrics suggests that post-settlement mortality outweighs recruitment in predicting restored oyster numbers. Change in restored oyster numbers over time did correlate with oyster numbers in the immediate vicinity, so monitoring of local populations can predict stability of the restored population.

Ecosystem-Based Management and Restoration

Ecosystem-based management is widely recognized as an essential approach for coastal ecosystems (e.g., Leslie and McLeod 2007; Barbier et al. 2008), and restoration of foundation species would benefit by incorporating the context of the larger system. These species uphold ecosystem processes and functions (Byers et al. 2006), including resilience to changing environmental conditions (Thomson et al. 2015; Angelini et al. 2011) which are compromised when populations decline, often well before the species is completely lost from the system (Ellison et al. 2005). The success of restoration efforts with marine foundation species is, in turn, likely to be affected by overall ecosystem conditions. For example, water quality can determine regional coral diversity (De'ath and Fabricius 2010), and increased temperatures can result in large-scale mortality events for corals (Baird and Marshall

2002), seagrasses (Marbà and Duarte 2010), and oysters (Gouletquer et al. 1998).

There is important synergy between Olympia oyster restoration and ecosystem-based management. On the one hand, oysters provide ecosystem services such as water filtration and community engagement in meaningful coastal activities. Conversely, broader ecosystem processes shape success of oyster restoration. Sedimentation was the biggest challenge to Olympia oyster restoration projects, and especially constrains the success of low-profile projects restoring natural bed structure, due to the threat of burial in sediment. Ecosystem-level management to reduce nutrient loads can decrease the organic mud common in polluted estuaries, providing firmer mudflat habitat for oyster beds. Reduction of sediment inputs from anthropogenic sources such as agriculture or mining can also decrease burial of oysters. Since vast portions of former estuarine habitat remain behind dikes and water control structures and these areas largely have stagnant conditions that do not support the oysters that formerly inhabited them (Wasson 2010), ecosystem management such as dike removal could result in more oysters than traditional approach of deploying substrate. These issues can be considered with the use of our new decision support tool (see Supplementary Information 2) that guides practitioners in considering the environmental conditions and other limitations to maintaining Olympia oyster populations that need to be addressed for restoration to be successful.

Motivations Beyond the Focal Species: Engaging the Community

Restoration efforts for marine foundation species are often necessarily focused on increasing or conserving populations of a focal species. However, increasingly, the motivations for restoration encompass goals that do not relate directly to a target species, but to other aspects of a project that ensure restoration success. Community engagement, in particular, is increasingly recognized as a vital component of restoration. High levels of community engagement can be vital to effective adaptive management more broadly, as participation of community members can result in public support for ecosystem-level conservation efforts (McKinley et al. 2017; Aceves-Bueno et al. 2015; DeAngelis et al. 2020). Finally, restoration projects are often reliant upon the increased workforce created by volunteers from the community to implement projects or maintain them over time (Silvertown 2009), and multiple benefits of this approach are well-documented for marine and coastal restoration (Cigliano et al. 2015).

Olympia oyster projects provide an excellent illustration of broader motivations for restoration. Most projects (65%) had objectives related to community engagement, and 43% had objectives tied to piloting methods or learning from the project to improve future projects—with high success reported for

both (Table 2). Despite the importance of, and reported success with, community engagement by many projects, Olympia oysters are still much less familiar to coastal residents than the introduced Pacific oyster, which is the most common commercially produced (and eaten) oyster species on the North American West Coast. There is an urgent need to increase public awareness of Olympia oysters, and plentiful opportunities to do so.

Regional Approach to Restoration Strategy

Regional approaches have been successful in simultaneously supporting the conservation of threatened marine species and the restoration and management of coastal ecosystems (e.g., Beger et al. 2015; Micheli et al. 2013). For any declining species, local restoration can be informed by regional planning to prioritize restoration where it is most needed and most likely to succeed, thus maximizing investments while expanding geographic scale of the restoration impact (*Ostrea edulis*: Pogoda et al. 2019; *Crassostrea virginica*: Hernandez et al. 2018; Salmonids: Roni et al. 2018). Regional strategies can also address environmental equity issues, by explicitly including human well-being considerations to guide site selection, and community engagement to ensure that the benefits of restoration are more equitably distributed among human communities (Stanford et al. 2018), particularly to those most connected to and reliant upon coastal resources (e.g., indigenous communities, Poe et al. 2016).

The West Coast estuaries that host Olympia oysters are widely spaced, posing challenges to connectivity among oyster populations and people involved in their restoration. The Native Olympia Oyster Collaborative (NOOC) is a newly formed network of collaborators (<https://olympiaoysternet.ucdavis.edu/>) and this synthesis, as well as an interactive story map highlighting the same projects (<https://projects.trnerr.org/oystermapp/>), was generated by its members. In the future, taking a broad regional approach to conserving this species could help prioritize locations with the greatest need for new restoration projects—places where oysters have declined the most and appear unlikely to expand without targeted projects. A regional approach could help match the right project type to local conditions. For instance, a geographic analysis could be conducted to identify places where naturally forming, low-relief beds would thrive, or places where high-relief “living shorelines” could be used to replace bank armoring along urban shores. A regional analysis is also needed to identify locations that would benefit most from the application of conservation aquaculture. Salish Sea projects often involve hatchery-raised juvenile oysters, which is appropriate given our finding here that recruitment rates decrease with increasing latitude. However, individual estuaries elsewhere are also recruitment limited (Wasson et al. 2016) and could benefit from use of aquaculture (Wasson et al. 2020).

Finally, a shared regional database of consistent monitoring data would allow for robust analyses comparing success of different restoration approaches, which we could not accomplish here due to differences among projects in data collection and lack of a shared quantitative database. Working together, restoration practitioners, scientists, funders, permittees, and coastal communities can restore the iconic native oyster to bays and estuaries from British Columbia to Baja California.

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