Olympia Oyster Restoration: Habitat Suitability and Climate Considerations

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Abstract

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Oyster habitat suitability index (HSI) models can support conservation and restoration planning, siting aquaculture projects, and other purposes. In recent decades, partners have undertaken efforts to restore populations of Olympia oysters (*Ostrea lurida)* in the Salish Sea. Olympia oyster restoration projects are more likely to become self-sustaining and contribute to overall population growth when sited in locations with optimal conditions. This study describes the development and application of a preliminary HSI model for Olympia oyster restoration in the southern Salish Sea. Environmental data and tolerance thresholds for six habitat variables – tidal elevation, salinity, temperature, current velocities, low salinity events, and water residence time – are compiled to create a geospatial index of suitability. This study identifies potentially suitable habitat throughout the study region. HSI output is compared to oyster observations and abundance at restored sites to evaluate accuracy and consider potential applications. While predictions of suitable habitat and oyster presence and abundance align in some locations, there are limitations to using the index as a tool for restoration planning. In addition, this study provides an example of how the HSI may be used to explore climate change considerations for restoration projects. The results of this study, in combination with other methods and information, may provide a useful preliminary tool for identifying potentially suitable locations for Olympia oyster restoration projects in the region.

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“From a distance you might think they were glinting rocks, just another cobbly beach, rather than acres of living coastline. But if you stepped out of your boat and explored, old shells popping softly beneath your boots, you’d smell their salt-spray aroma and hear the crackling of receding water droplets and know that they were the living sea itself, holding on to the land to keep it from squirming away. And if you sat down among them and pried open some shells and tipped the briny flesh into your mouth, you might get some sense of how it had always been.”

—Rowan Jacobsen, *The Living Shore*

Chapter 1: Developing a Habitat Suitability Index for Olympia Oyster Restoration

1. Introduction

Coastal and estuarine ecosystems face negative impacts from anthropogenic stressors at local and global scales (Brophy et al., 2019; Halpern et al., 2008). Habitat loss, exploitation, pollution, and ecosystem disruption – compounded by climate change – contribute to declines in species abundance and diversity in estuaries and coastal oceans (Gattuso et al., 2015; Lotze et al., 2006; Worm et al., 2006). Oyster reefs are one example of a coastal and estuarine habitat type that has severely declined; an estimated 85 percent of native oyster reefs have been lost globally, and populations are functionally extinct in many bays (Beck et al., 2011).

The Olympia oyster (*Ostrea lurida)* is the only oyster species native to the west coast of North America. Olympia oysters were once abundant from Baja California to British Columbia, including in the estuaries of Washington's outer coast and within the Salish Sea (Baker, 1995; Blake & zu Ermgassen, 2015; Appendix A); the southern Salish Sea is the focus of this study (Figure 1; see detailed map in Appendix A for all locations). Native oysters played an important role in the traditional diets and cultures of indigenous tribes in the region (NWTT, 2003; Baker 1995). Large beds of Olympia oysters existed in coastal estuaries and the Salish Sea into the 1850s, at which point rapid increases in commercial harvest by European settlers drove declines throughout the species' range. In Washington, commercial overharvest in the early 20th century and environmental stressors including water pollution drove populations to near extinction (White et al., 2009b). Resource managers estimate that the current extent of Olympia oyster beds in Puget Sound is less than five percent of historic coverage (Blake & Bradbury, 2012).

Olympia oysters provide valuable ecosystem services in coastal and estuarine systems, such as water filtration (Gray et al., 2019), sequestering nutrients and toxins (Pritchard et al., 2015), increasing invertebrate abundance, and providing habitat structure (PSRF, 2009; Allen et al., 2015). As climate change and ocean acidification accelerate, restoring native species may support ecological communities more tolerant of changing ocean conditions (Washington State Blue Ribbon Panel on Ocean Acidification, 2012). For example, Olympia oysters possess traits that increase their tolerance to ocean acidification during the larval stage (Waldbusser et al., 2016). Rebuilding native oyster populations using conservation aquaculture and other approaches is considered a promising opportunity to restore ecosystem services on the west coast and in many other regions (Froehlich et al., 2017; Theuerkauf et al., 2019b).

Olympia oyster restoration efforts in Washington have been underway for over two decades; restoration is a priority for state, federal, tribal, and nonprofit partners working to improve the condition of the Salish Sea (Blake & Bradbury, 2012; WDFW, 2020a; NOAA, 2011; Barber, Greiner, & Grossman, 2015; Peter-Contesse & Peabody, 2005). The Olympia oyster is a candidate species for listing as endangered, threatened, or sensitive in Washington; it is also included on the priority habitat and species list for conservation and management, and a plan for rebuilding populations has been developed. The Washington Department of Fish and Wildlife (WDFW) co-manages Olympia oysters with

Puget Sound Treaty Tribes and the Washington Department of Natural Resources (DNR). Washington's first Olympia oyster rebuilding plan, developed in 1998, was not funded as a WDFW project, so restoration work was initiated by Puget Sound Restoration Fund (PSRF; Blake & Bradbury, 2012). PSRF is a local nonprofit organization that works in collaboration with partners to restore habitat-forming species, including Olympia oysters, throughout Puget Sound (PSRF, 2019).

Olympia oyster restoration work in the region is a coalition effort involving PSRF, several tribal natural resource divisions, WDFW, DNR, marine resource committees (MRCs), shellfish growers, universities, the public, and other partners (Appendix B). In some locations, such as Fidalgo Bay in northern Puget Sound, restoration efforts have engaged over 25 different organizations and served to build community between partners and volunteers (DeAngelis et al., 2018). At present, restoration efforts focus on 19 priority areas identified by the State for Olympia oyster restoration, based on assessment of historical populations and current opportunities (Blake & Bradbury, 2012). Partners have undertaken projects in numerous bays and inlets throughout the Salish Sea, and projects range widely in their objectives, methods, and scale (Appendix B). Restoration projects often consist of two primary activities: 1) planting seeded cultch, which is usually Pacific oyster shell seeded with hatchery-spawned juvenile Olympia oysters; and/or 2) spreading shell substrate in an area to support natural recruitment, often referred to as habitat enhancement. In addition to seeding juvenile oysters and substrate enhancements, single Olympia oysters are occasionally added to the substrate from hatchery and wild stocks. Restoration work may also entail a wide range of activities including site scoping, monitoring, measuring recruitment patterns, spawning oysters and raising larvae, among other undertakings (Peter-Contesse & Peabody, 2005; Dinnel, Peabody, & Peter-Contesse, 2009; Blake & Bradbury, 2012; Allen et al., 2015).

Rebuilding, enhancement, and restoration are all widely used terms that describe these activities; in this study, the term restoration is used to broadly describe efforts to re-establish Olympia oyster populations. Though the goals of specific projects may vary, the overarching goal of managers and restoration practitioners is to establish self-sustaining populations of native oysters and the habitat structure they provide (Dinnel, Peabody, & Peter-Contesse, 2009; Blake & Bradbury 2012). Due to habitat loss, competing management priorities, and other challenges, restoring native oyster beds to their historical extent in Puget Sound is not likely a realistic target (Blake & Bradbury, 2012).

The extent of an oyster bed, oyster density, and population structure are key metrics for setting restoration goals and assessing projects (Baggett et al., 2015). Densities of wild and restored Olympia oyster populations may range widely; definitions of "bed habitat" vary and beds may occur when densities exceed 30 oysters/m^2 to over 300 oysters/m^2 (Allen et al., 2015). In North Bay, Washington, the largest persistent Olympia oyster bed in the region, adult oyster densities exceeding 100/m^2 have been recorded in recent years, though densities fluctuate (Valdez et al., 2017; White et al., 2009a). Surveys in British Columbia found average densities in Nootka Sound of more than 300 oysters/m^2 and as high as 1,000/m^2 in some locations in 2008 (Beck et al., 2009), and densities at various sites in 2009 ranged between 7 and 385 oysters/m^2 (COSEWIC, 2011; Norgard, et al., 2010). Due in part to this variation, oyster restoration projects often do not specify a target densities for when a population is considered "restored." Restoration practitioners are working towards a near-term goal of restoring 100 acres of Olympia oyster habitat in Puget Sound by the end of 2020 (PSRF, 2019). Local restoration projects have received increasing attention as examples of efforts to improve the condition of the Salish Sea (DeWeerdt, 2019; Doughton, 2019; Dunagan, 2019; Haight, 2019), and momentum is building for coastwide Olympia oyster restoration work under the umbrella of the Native Olympia Oyster

Collaborative (NOOC). About 40 locations along the west coast have seen the implementation of restoration projects (NOOC, n.d.; Ridlon et al., 2020), though overall recovery of the species remains relatively low throughout its range (Pritchard et al., 2016).

The identification of optimal locations for restoration within a wider area of interest is a key initial step in the restoration planning and implementation process (Puckett et al., 2018; sources therein). Habitat suitability models quantify the relationships between species and communities and their environment. These models – also referred to as species distribution, bioclimatic, climate envelope, and ecological niche models – can be used to understand and predict species distributions. They are generally developed using species distribution data (e.g., presence/absence or abundance) and corresponding environmental data. Habitat suitability models and related modeling approaches have broad applications in conservation and resource management (Elith & Leathwick, 2009; Guisan, Thuiller, & Zimmerman, 2017). Habitat suitability index (HSI) models are a type of habitat-based suitability model that can be applied when distribution data are limited. They are widely used in resource management and conservation (Elith & Leathwick, 2009; Lewis, Fox, & DeWitt, 2019). HSI models were developed by the United States Fish and Wildlife Service (USFWS) in the 1980s to quantify the value of habitats when making management decisions (Theuerkauf & Lipcius, 2016; USFWS, 1981). Advances in geospatial data and analysis have enabled development and application of spatially-explicit HSIs as decision-support tools (Elith & Leathwick, 2009; Theuerkauf et al., 2019a). Researchers in the Pacific Northwest have recently developed HSIs to prioritize eelgrass restoration areas (Thom et al., 2018), and to estimate the distribution of bay clams in Oregon estuaries in a data-poor context (Lewis et al., 2019).

As oyster restoration efforts continue around the world, researchers are increasingly turning to suitability models to identify optimal oyster habitat and guide restoration decision-making. Suitability models and related decision-support tools have contributed to successful site selection for oyster restoration projects (Fitzsimons et al., 2019). Oyster HSI models may include only a few key environmental parameters, or represent more complex compilations of environmental thresholds, ecosystem services, and restoration planning considerations. Table 1, adapted from Theuerkauf and Lipcius (2016) to include additional oyster habitat suitability studies published in peer-reviewed journals the past five years, shows the range of environmental variables typically included in analyses. Recent oyster HSI studies include an analysis focused on identifying restoration locations for eastern oysters in the northern Gulf of Mexico (Linhoss, Camacho, & Ashby, 2016), and a multi-factor HSI that incorporated larval dispersal and logistical constraints to support identification of restoration sites for eastern oysters in Pamlico Sound (Puckett et al., 2018). Theuerkauf et al. (2019a) subsequently extended the Pamlico Sound HSI to consider ecosystem services. Snyder et al. (2017) used remote sensing to explore possible sites for oyster aquaculture in Maine, and Chowdhury et al. (2019) used an HSI to identify important environmental factors for intertidal rock oysters in Bangladesh. In addition to the published oyster HSI analyses described below that focus on other oyster species, recent masters theses have applied habitat suitability methods to understand Olympia oyster presence and suitable habitat in Yaquina Bay, Oregon, and for the west coast at a broad scale (Bohlen, 2019; Popel, 2016).

Across the 11 studies reviewed by Theuerkauf and Lipcius (2016) and the five studies reviewed here (numbers 12-16, Table 1), average salinity, bottom type/substrate, and water depth are the most common input variables to oyster HSIs. The five recent studies more frequently included dissolved oxygen and average salinity in their HSI models (Table 1). Recent studies have also sought to go beyond the basic requirements for oyster survival, by including practical considerations such as distance from the nearest boat launch, and ecosystem services considerations such as water filtration capacity (Puckett et al., 2018; Theuerkauf et al., 2019a). HSIs combine variables using a variety of approaches to identify optimal conditions for oyster conservation, restoration, or aquaculture, depending on the focus of the study. Most studies explore habitat patterns geospatially, identifying specific locations within coastal systems where factors combine to create optimal conditions for oyster survival, growth, and population persistence.

Table 1. Review of oyster HSI models from Theuerkauf and Lipcius (2016), numbers 1-11. Updated to included recent published oyster HSI studies, numbers 12-16; header numbers reference publications listed below the table.

Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Salinity, average	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
Bottom type/substrate	✓	✓		✓			✓	✓	✓	✓	✓		✓	✓		
Water depth	✓	✓			✓	✓			✓		✓		✓	✓		✓
Water temperature	✓	✓	✓	✓	✓							✓			✓	✓
Dissolved oxygen		✓	✓		✓	✓						✓	✓	✓		✓
Turbidity		✓	✓		✓	✓									✓	✓
Disease		✓	✓	✓			✓									
Predator intensity			✓	✓			✓									
Food availability		✓	✓		✓							✓	✓		✓	
Freshet frequency	✓			✓			✓									
Fouling organisms				✓			✓									
pH			✓									✓				
Water flow			✓									✓	✓			
Sedimentary environment									✓							
Salinity, spawning season										✓						
Salinity, annual minimum										✓						
Other												✓	✓	✓		

1. Barnes et al., 2007; 2. Battista, 1999; 3. Brown & Hartwick, 1988; 4. Cake, 1983; 5. Cho et al., 2012; 6. Pollack et al., 2012; 7. Soniat & Brody, 1988; 8. Soniat et al., 2013; 9. Starke, Levinton, & Doall, 2011; 10. Swannack, Reif, & Soniat, 2014; 11. Theuerkauf & Lipcius 2016; 12. Chowdhury et al., 2019; 13. Theuerkauf et al., 2019a; 14. Puckett et al., 2018; 15. Snyder et al., 2017; 16. Linhoss et al., 2016.

Location within bays and estuaries is a likely a key factor in Olympia oyster restoration project outcomes (Pritchard et al., 2015). To support restoration efforts in the Salish Sea and to advance the effectiveness and scale of restoration work, managers and practitioners need more research identifying what specific site characteristics are likely to contribute to successful restoration of Olympia oysters, and where these conditions are found. Researchers suggest that the use of suitability models and geospatial decision-support tools to guide development of restoration projects will contribute to more robust outcomes (Ridlon et al., 2020). This study describes the development of an HSI model for Olympia oyster restoration in the Salish Sea, applies the model to three bays in the region, and explores the utility of the index as a restoration planning tool using a preliminary evaluation. Though much research has been conducted on the relationship between Olympia oysters and their environment, and restoration practitioners have for decades been actively assessing seascapes for restoration projects, this is the first attempt to construct a geospatial HSI model for Olympia oysters in the Salish Sea. As rates of change accelerate in coastal and estuarine ecosystems due to climate change, ocean acidification, and other anthropogenic stressors, a robust understanding of the locations and dynamics of suitable habitat is essential for meeting restoration goals and understanding vulnerabilities. The approach and results described below are intended as an initial assessment that may inform future studies.

2. Methods

2.1. Study Species and Habitat Requirements

Typically found in protected bays, inlets, and estuaries, Olympia oysters inhabit low intertidal and shallow subtidal waters in the Salish Sea and throughout their range (Baker, 1995). Olympia oysters are found from the Bahía de San Quintín, Mexico, to Gale Passage, British Columbia, though some sources describe historical presence as far north as Alaska (COSEWIC, 2011; Polson & Zacherl, 2009). Olympia oysters are sequential hermaphrodites that alternate between male and female during their life cycle. Gametogenesis and spawning begin in the spring and summer when water temperatures reach a threshold. In years and at locations with high recruitment, two spawning peaks are sometimes observed with a large peak early to mid-summer followed by a smaller peak later in the season. Depending on location, Olympia oysters may spawn as early as April, but spawning is often later further north (Baker, 1995; Couch & Hassler, 1989; Hopkins, 1937). In Puget Sound, the reproductive season is generally May through September (Allen et al., 2015). After spawning and fertilization, females brood larvae for 10 to 12 days before releasing larvae into the water column; larvae remain in the plankton for an estimated 11 to 16 days, though studies describe a range from 5 days to eight weeks (Baker, 1995; Pritchard et al., 2015; Wasson et al., 2015). Larvae settle on hard substrates, including rocks and oyster shells. In Fidalgo Bay, peak settlement has been observed during neap tides in July, and larvae typically settle throughout the summer and early fall (Allen et al., 2015; Baker, 1995). In 2018, the highest counts of newly settled oysters were observed in August in Fidalgo Bay, and in June in Port Gamble Bay (DNR, 2019). Localized factors appear to drive recruitment, which can be highly variable year-to-year and among populations (Wasson et al., 2016). Olympia oysters feed on plankton and detritus (Dethier, 2006); they are relatively slow-growing and reach their maximum size after four years (Baker, 1995). Larval dispersal may be somewhat limited, potentially due to swimming behavior that allows larvae to be retained in estuaries (Peteiro & Shanks, 2015). It is believed that larvae remain somewhat close to the site where they were spawned (COSEWIC, 2011; Baker, 1995; Coe, 1932).

Though they inhabit a wide latitudinal range, Olympia oysters are vulnerable to environmental conditions that limit spawning, recruitment, and adult survival. Individual survival and population persistence are negatively affected by a wide range of abiotic and biotic factors (see Appendix C for detail and additional sources). Low salinity conditions inhibit growth and cause mortality (Cheng et al., 2016; Wasson et al., 2015); low water temperatures limit spawning and temperature extremes are fatal (Baker, 1995; Cheng, Komoroske, & Grosholz, 2017). Olympia oysters are most likely to survive at the appropriate tidal elevation, which is often near 0m MLLW; at high tidal elevations, oysters may desiccate or freeze, and they may be vulnerable to predation at low elevations (Pritchard et al., 2015; Wasson et al., 2015; Valdez et al., 2017). Olympia oysters require hard substrate for settlement, and silt and fine sediments can bury or smother oysters (Couch & Hassler, 1989; Tronske et al., 2018). Water currents and residence times affect settlement and recruitment (Kimbro, Largier, & Grosholz, 2009; Pritchard et al., 2016), and oysters are sensitive to water pollution (Couch & Hassler, 1989). Low pH, low dissolved oxygen levels, and low phytoplankton abundance reduce fitness and survival (Cheng et al., 2017; Hettinger et al., 2012; Hollarsmith et al., 2019). Predation by non-native oyster drills and other predators can have significant negative impacts at some sites, and large numbers of Pacific oysters can result in decreased survival of Olympia oysters (COSEWIC, 2011; Grason & Buhle, 2016; Trimble, Ruesink, & Dumbauld, 2009). Researchers ranked sedimentation, low salinity, predation, water and air temperatures, food limitation, and dissolved oxygen as stressors for which Olympia oysters have medium to high sensitivity; in Puget Sound sedimentation, predation, and competition are commonly identified threats (Wasson et al., 2015). The location of restoration sites must be carefully selected to minimize stressors and increase the chances that populations become self-sustaining (Pritchard 2016).

While many of the stressors described above constrain Olympia oyster survival throughout their range, studies have found evidence of evidence of genetic population structure that may be driven by local adaptation. For example, Olympia oysters may not begin spawning until water temperatures reach 16°C in California; threshold temperatures are lower in Oregon (~15°C) and in Washington (10.5-12.5°C) (Baker, 1995; Barber et al., 2016; Pritchard et al., 2016). In addition, there is evidence of population structure within Puget Sound despite the relatively close proximity of populations; studies have found evidence of significant phenotypic differences in fitness-related traits (Heare et al., 2017; Silliman et al., 2018). These differences are important to consider when drawing from literature describing life history throughout the species' range and applying this information to identify suitable habitat in a specific region.

2.2. Study Site

The Salish Sea is a large inland sea located in the northwest of the United States and extending into the Canadian province of British Columbia (Figure 1). Puget Sound makes up the southern portion of the Salish Sea within the state of Washington. A large estuarine system, Puget Sound encompasses the marine basins, channels, and bays from the border with Canada to the southern extent of the waterbody near Olympia, Washington. The system is often divided into smaller basins and geographic regions, including the San Juan Archipelago, the Strait of Georgia, the Strait of Juan de Fuca, Admiralty Inlet, Central Puget Sound, Whidbey Basin, Hood Canal, and South Puget Sound. Sills and narrow passages constrict water exchange between several of these basins. Deep passages, river deltas, mudflats, and islands characterize the Central and Whidbey Basins. South Puget Sound has the most shoreline and includes numerous islands and narrow inlets. Hood Canal has steeper, narrower shorelines compared to the other basins. Environmental conditions, including salinity and temperature, can vary widely by location and season (Bos et al., 2015; Burns, 1985). The study area included in this analysis stretches from the San Juan Islands in the north to South Puget Sound, and from the East Strait of Juan de Fuca to the eastern shore of the Central Basin. The HSI analysis is applied to three bays: Liberty Bay, Fidalgo Bay, and Case Inlet, which are shown on the map below (Figure 1; see Appendix A for a detailed map showing other locations discussed in chapters and appendices).

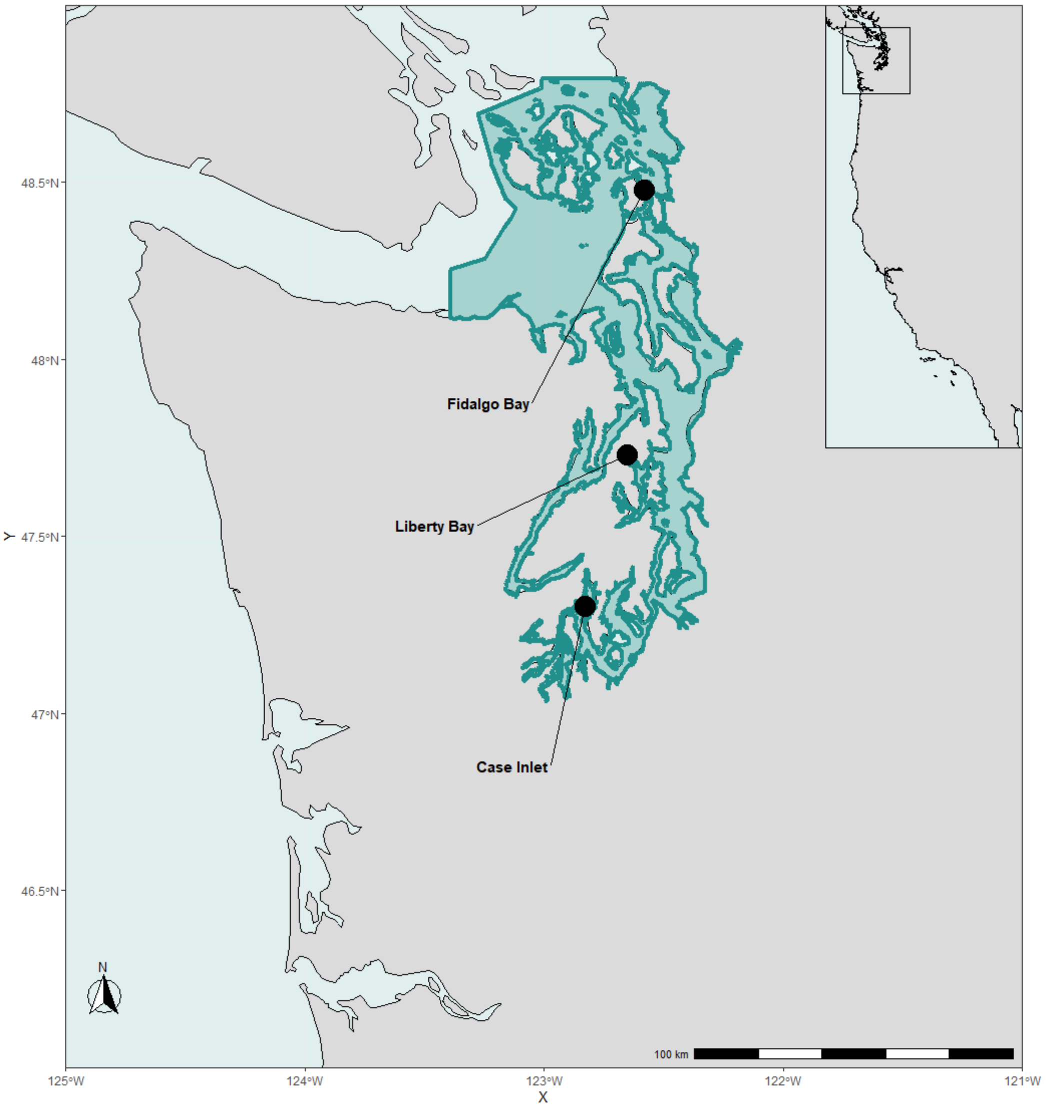

Figure 1. Study site. The green highlight shows the area included in this analysis and the three case study bays described in Section 3 are indicated. Map data from: Natual Earth; Washington State Department of Natural Resources, 2019.

2.3. HSI Development and Evaluation

Habitat suitability analyses typically involve developing an index and undertaking various analyses evaluate its accuracy. Theuerkauf & Lipcius (2016) describe model development, calibration, verification, and validation as the four stages of building an HSI model. Under their framework, development refers to defining the variables, suitability relationships, and compiling data. Calibration refers to ensuring that the HSI scores span from zero to one with excellent sites receiving high values and poor sites receiving low scores. Verification includes assessing the performance of the HSI model against independent data such as presence/absence, and validation requires statistically testing the model against independent quantitative data (Theuerkauf & Lipcius, 2016 and sources therein). Figure 2 outlines the methodology used in this study; full verification and/or validation of the model results were not conducted, rather this study provides a preliminary evaluation of model performance drawing from several available data sources describing Olympia oysters.

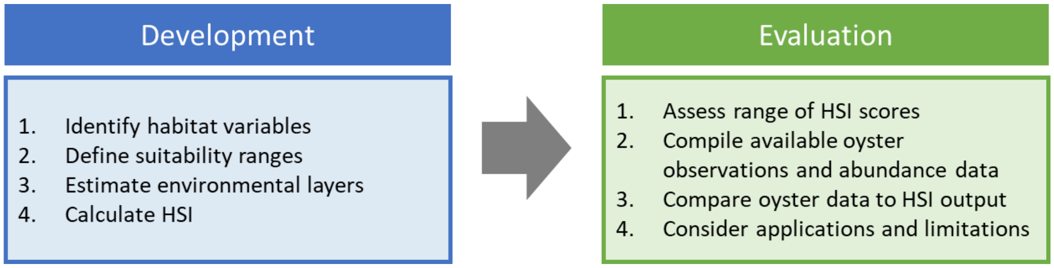

Figure 2. Methods overview. This process diagram illustrates the two overarching steps completed to develop and evaluate the HSI in this study and provides an overview of the process for each step.

2.3.1. HSI Development

To develop the model, I identified habitat variables, defined suitability ranges, estimated environmental layers, and then calculated the HSI (Figure 2).

Step 1. Habitat variables may be included in HSI models depending on both their relevance in determining habitat suitability in a given system and the availability of spatially explicit data describing the variable (Theuerkauf et al., 2019a). Candidate habitat variables relevant to oyster habitat suitability are described in Table 1, and in literature describing environmental requirements of Olympia oysters (e.g., Couch & Hassler, 1989; Baker, 1995; COSEWIC, 2011; Pritchard et al., 2015; Wasson et al., 2015). Based on literature review, data availability, and discussions with restoration experts, I selected tidal elevation, winter salinity, summer water temperature, current velocity, water residence time, and risk of low salinity events as the habitat variables to include in the HSI model. At high tidal elevations, Olympia oysters are vulnerable to air temperature extremes (Baker, 1995; Cheng et al., 2016); at low tidal elevations, oysters may experience greater predation and/or siltation (Valdez et al. 2017; Allen et al., 2015). Low salinities are correlated with low growth and recruitment rates, and exposure to low salinity events can cause widespread mortality (Wasson et al., 2015; Cheng et al., 2016). Olympia oysters begin reproduction when water temperatures reach 12.5 °C in Puget Sound, though this threshold may be lower further north (Baker, 1995; Barber et al., 2016). High current velocities may overcome larval swimming capabilities and prevent larvae from being retained in an estuary or bay (Peteiro & Shanks, 2015), and studies have found that moderate water residence times are correlated with high growth and recruitment (Kimbro, White, & Grosholz, 2019; Pritchard et al., 2016).

Step 2. To define suitability ranges, I applied a framework-based approach developed by Lewis et al. (2019) to estimate the distribution of bivalves in northeast Pacific estuaries. The framework to identify suitable bivalve habitat in estuaries (FISBHE) approach provides a useful and cost-effective tool for identifying suitable habitat, allowing for transparent compilation of natural history information to define thresholds that can be applied to existing environmental datasets. I adapted the FISBHE framework and applied it to define the suitability ranges used in this study. I compiled information regarding the tolerance of Olympia oysters to the range of possible conditions for each environmental variable in the HSI using natural history information available in published literature and gray literature, as appropriate. Sufficient literature describing Olympia oyster habitat requirements was identified for each habitat variable included the model, enabling development of the index (though see limitations described in the Discussion section and appendices). I then populated the suitability framework for each variable, including the tolerance ranges and thresholds described by each source. The framework tables include additional information: how suitability was measured, if the range described is partial or full, if the studies are qualitative or quantitative, and the geography of the study (Appendix D). Bohlen (2019) recently applied the FISBHE framework to identify suitable habitat for Olympia oysters in Yaquina Bay, Oregon. The application of FISBHE in this study was completed independently of the 2019 study, though cross-referencing the two could be beneficial. I then reviewed the suitability ranges described by all sources and assigned scores between zero and one for each habitat variable (Theuerkauf & Lipcius, 2016). Optimal ranges are assigned a value of one, and survivable levels assigned values of less than one, based on an assessment of the sources, including if they are local or regional, qualitative or quantitative, and other factors. Exclusion layers, which include risk of low salinity events and water residence times, are classified as zero or one only. Figure 3 and Table 2 below provides the classifications used in this model.

Step 3. Next, I compiled environmental data and created continuous raster data layers for each habitat variable (methods described in greater detail in Appendix E). Table 2 includes each data layer in the HSI, a brief rationale for inclusion, description of the data layer, suitability relationship, and the data source (table modified from Puckett et al., 2018). In general, data were compiled and prepared using R Studio (R: Development Core Team, 2016), and layers were generated from the data sets using ArcMap 10.7.1 (Environmental Systems Research). All data except for the digital elevation model were imported into ArcGIS as points and continuous surfaces were estimated using the kernel smoothing with barriers interpolation method, which allows for the inclusion of the shoreline as a barrier and can be applied in estuaries with complex shorelines (Krause, n.d.). A different interpolation technique was used to generate the low salinity risk layer.

Coastal topo-bathymetry digital elevation models (DEMs) were sourced from NOAA's National Geophysical Data Center, and converted to the mean lower low water (MLLW) tidal datum using NOAA's VDatum conversion program (NOAA, 2011b; 2014; 2019). Data describing temperature and salinity were sourced from the Washington Department of Health's (DOH) Shellfish Growing Area (SGA) Monitoring Program database (DOH, 2019). Current velocity and daily salinity data were sourced from the Salish Sea Model (SSM), a regional hydrodynamic model that simulates water quality parameters, run for the year 2014 (Khangaonkar et al., 2018). Residence time data were provided by the Department of Ecology (Ahmed et al., 2019). Additional discussion of the use of maximum current velocity and water residence time in this model is included in Appendix F. All layers were resampled to a 10 by 10-meter grid, which is the approximate resolution of the DEMs. This resolution was used because Olympia oysters inhabit a narrow depth band; however, the other data sources all had coarser resolution and thus the raster surfaces represent estimations that have varying uncertainties and error (Discussion section; Appendix E; Appendix I). The hypothesized suitability relationships for the four threshold habitat variable layers and the two exclusion layers included in the index are illustrated in Figure 3 below, with shading showing the optimal ranges identified using the FISBHE framework. These values were used to reclassify each habitat variable layer on a zero to one scale.

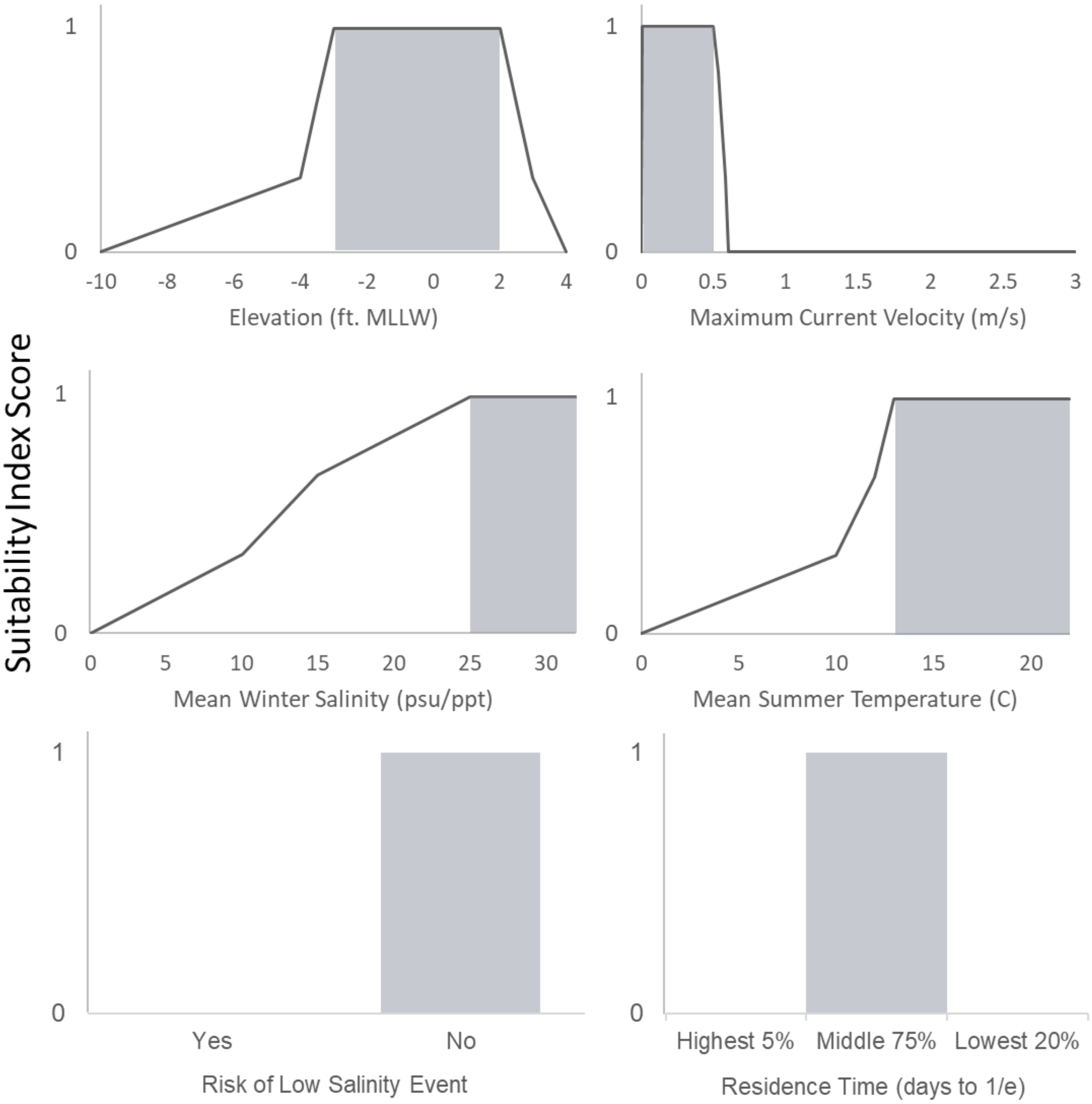

Figure 3. Visualization of suitability index values assigned for the habitat variables included in the HSI model.

Table 2. List of habitat variable layers included in the HSI model, data description, suitability classification, rationale, and source.

Habitat Variable	**Description**	**Suitability Ranges**	**Rationale**	**Data Source**
Threshold				
Tidal Elevation (MLLW, ft.)	Elevation above/below MLLW, raster grid, 10x10m resolution	Optimal (1): > -3 to ≤2 Suitable (0.66): > -4 to ≤ -3 and >2 to ≤3 Viable (0.33): > -10 to ≤ -4 and >3 to ≤4 Unsuitable (0): ≤-10, >4	Drives a range of conditions that affect oyster survival	NOAA's National Geophysical Data Center (NOAA 2011b, 2014)
Maximum Current Velocity (m/s)	Maximum possible surface velocity, point data at 6,383 nodes	Optimal (1): >0.01 to ≤0.50 Suitable (0.66): >0.50 to ≤0.55 Viable (0.33): >0.55 to ≤0.60 Unsuitable (0): >0.60	Important for larval retention (recruitment)	Department of Ecology/PNNL Salish Sea Model 2014 (Khangaonkar et al., 2018)
Mean Winter Salinity (PSU/PPT)	Mean salinity at shellfish growing areas during November-April, point data at 1,647 stations	Optimal (1): >25 Suitable (0.66): >20 to ≤25 Viable (0.33): >15 to ≤20 Unsuitable (0): ≤15	Important to oyster biological processes (survival)	DOH Shellfish Growing Area Monitoring Program (DOH, 2019)
Mean Summer Temperature (°C)	Mean temperature at shellfish growing areas from May-September, point data at 1,647 stations	Optimal (1): >13 Suitable (0.66): >12 to ≤13 Viable (0.33): >10 to ≤12 Unsuitable (0): ≤10	Important to oyster biological processes (reproduction, growth, survival)	DOH Shellfish Growing Area Monitoring Program (DOH, 2019)
Exclusion				
Residence Time (days to 1/e)	Measured as days until virtual dye reaches a concentration of 1/e, point data at 6,383 nodes	Suitable (1): Locations in the middle 75% of the values in the study area Unsuitable (0): Locations in the bottom 20% or top 5% of values in the study area	Short residence times contribute to low recruitment, sites with high residences may have lower growth/survival	Department of Ecology/PNNL Salish Sea Model 2014 (Ahmed et al., 2014)
Risk of Low Salinity Event	Daily mean bottom salinity, point data at 6,383 nodes	Suitable (1): Locations where mean bottom salinity does not drop below 10 for eight consecutive days Unsuitable (0): Locations where mean bottom salinity drops below 10 for eight consecutive days	Important to oyster biological processes (survival)	Department of Ecology/PNNL Salish Sea Model 2014 (Khangaonkar et al., 2018)

Step 4. An overall HSI score between zero and one for each raster cell was calculated from the reclassified layers using the following equation (Appendix H):

$$Threshold\ Mean = \sqrt[4]{(elevation * currents * salinity * temperature)}$$
$$HSI\ Score = Threshold\ Mean * low\ salinity * residence\ time$$

2.3.2. HSI Evaluation

The HSI model developed in this study serves as a hypothesis, based on best available natural history information and research, about what constitutes suitable habitat for Olympia oysters. Though scattered individuals are present throughout much of Puget Sound, Olympia oyster beds are limited to a few remaining locations (e.g., North Bay) and areas where habitat restoration projects have been implemented (Appendix B). Limited availability of species distribution data precluded developing a statistical species distribution model in this analysis. Many species distribution modeling approaches require assuming that a species is in equilibrium with its environment; underprediction of suitable habitat may result when using incomplete population estimates or when species are not present in locations that meet habitat requirements (Guisan et al., 2017). This would create challenges for modeling Olympia oyster habitat based on the current population distribution, given that populations were nearly eradicated by harvest and pollution and have not recovered since. Given these limitations, I have attempted to evaluate the HSI model using data currently available.

Step 1. As a first evaluation step, I examined the HSI output to determine if scores ranged from zero to one over the study area and confirm that zero values corresponded with areas classified as unsuitable (e.g., deep water). This initial assessment served as a “calibration” step.

Step 2. I then compiled both observations of Olympia oyster presence and data describing restoration outcomes. Olympia oyster observations in Liberty Bay and Dyes Inlet include data compiled from observations made during tideland surveys in 2018 and 2019 (Suquamish Tribe Fisheries Department, 2019), oyster presence in 2019 (Dohrn, 2019), restoration site surveys in 2014 and observations over several years (PSRF, 2019; see Figure 8a and 8b). For Hood Canal, Olympia oyster observations come from WDFW’s Pacific oyster population surveys in Hood Canal from 2014 to 2019 (WDFW, 2020b; see Figure 8c). The goal of the HSI model is to identify habitat where restoration projects are likely to succeed, and consequently, comparisons to restoration outcomes are more informative than comparisons to oyster observations. The Native Olympia Oyster Collaborative (NOOC) recently conducted a west-coast wide survey of Olympia oyster practitioners (NOOC, n.d.; Ridlon et al., 2020). Survey results include project descriptions; estimated oyster abundances at one, five, and 10 years after restoration; area of the project site; and other information. I selected projects in the study area that reported oyster abundance data five years after restoration (n=9; Figure 9).

Step 3. To further evaluate the model, I extracted the HSI scores and estimated habitat variables where Olympia oysters are observed to examine the relationship between oyster observations and HSI output**.** For the restoration outcomes survey data, I compared the reported abundance at year five to the total amount of suitable habitat (HSI>0) within the bay for each site. This approach assumes that there will be more oysters after year five if there is more available suitable habitat but does not adjust for the initial size of the restoration project or different methods used. Bays were defined using the geometry specified in the national hydrography dataset (U.S. Geological Survey, 2019), though Discovery, Sequim, and Fisherman Bays were not included in these data and were digitized separately. More information, such as density measurements at multiple locations within several restoration sites, would be required for a more robust assessment; however, this rough comparison may provide some information about how the HSI predictions compare to known restoration outcomes.

Step 4. Finally, I considered the HSI output and evaluation results to understand potential limitations and applications of this approach.

3. Results

3.1. Suitable Habitat in the Southern Salish Sea

Application of the HSI model identified habitat potentially suitable for Olympia oyster restoration (i.e., HSI>0) in varying proportions throughout the study area (Figure 4). South Puget Sound and the San Juan Archipelago had the highest and lowest amount of suitable habitat compared to area analyzed, respectively. South Puget Sound consists of many branching inlets, creating more potential habitat over gently sloping tidal flats. Conversely, the San Juan region is characterized by rocky shorelines and steeper topography, as well as low residence times and high maximum current velocities compared to other basins. These characteristics limit potentially suitable habitat. South Puget Sound also had the greatest percentage of highly suitable habitat (i.e., HSI>0.75). Overall, this study identified about 150 km^2 of habitat that could be considered for Olympia oyster restoration (HSI>0). The actual amount of habitat with restoration potential is much lower than this; the viability of areas is further constrained by practical, property, and management-related considerations not represented in this index. In addition, additional environmental factors not represented here may reduce a site's suitability, and population recovery may be prevented by factors other than environmental conditions.

The model identifies habitat potentially suitable for restoration in areas with tidal flats at low intertidal to high subtidal elevation, where winter salinities are high and low salinity events unlikely, where temperatures reach spawning thresholds, where current velocities are low, and residence times are moderate. Broadly, these conditions are met in the inlets of the South Sound; the bays and inlets on the west side of the Central Basin; large bays including Fidalgo, Padilla, Dabob, Quilcene, Discovery, and others; and sporadically in other locations. Tidal elevation was the primary habitat variable constraining restoration suitability. Suitable depths were restricted to a narrow band of low intertidal to high subtidal habitat based on the natural history of the species (Appendix C). Large areas at the appropriate elevation tend to be located at the heads of bays and in shallow inlets. Current velocities exceed threshold values throughout much of the northern extent of the study area, in the main stem of the Central Basin and in narrow passages throughout the study area. Locations immediately adjacent to major rivers (e.g., Skagit, Stillaguamish, Snohomish) are not considered suitable because of the risk of low salinity events; mean salinities are considered too low in these areas and in some additional locations (e.g., near the mouth of the Skokomish River). Portions of the Strait may not reach threshold temperatures for spawning, though generally temperatures are suitable throughout the region based on the temperature estimation included in this analysis. However, minimum spawning temperatures may vary among subpopulations (Barber et al., 2016). Areas of very high and very low water residence have been classified as unsuitable in this model; these are found in the Strait, the San Juan Islands, and the "hook" region of Hood Canal.

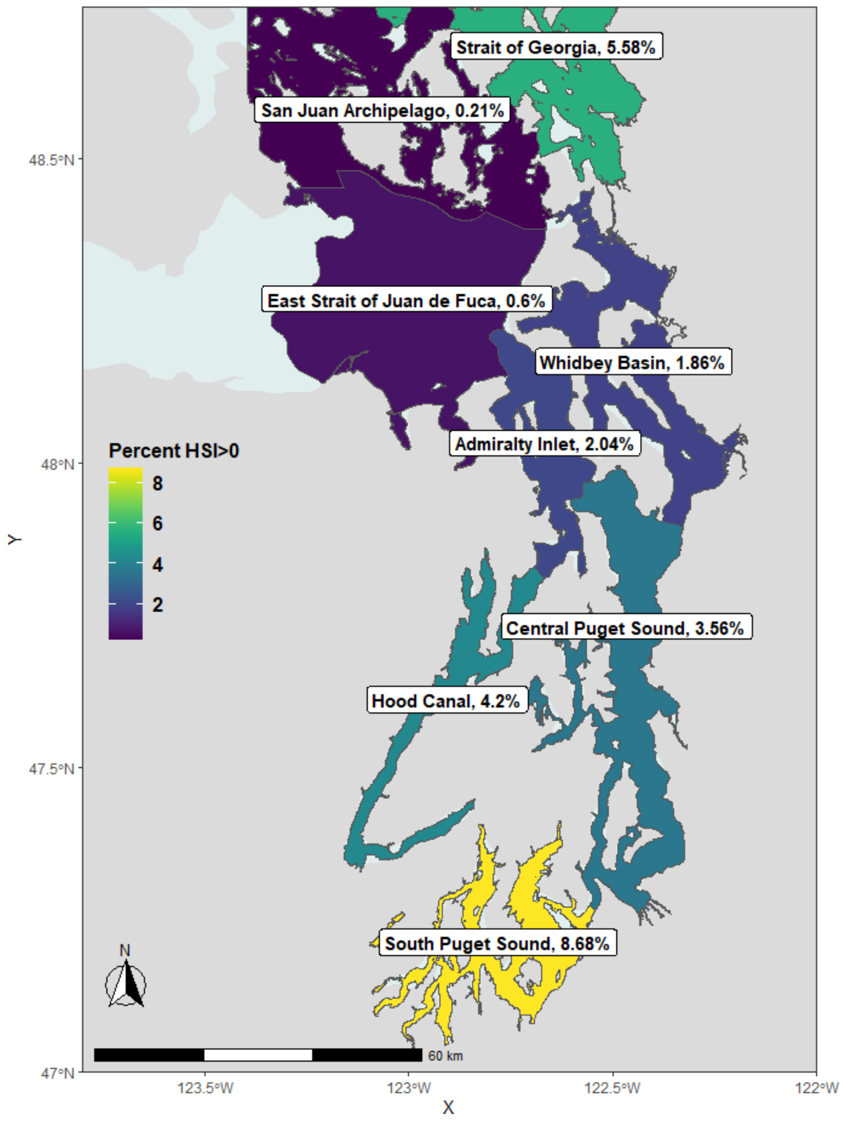

Figure 4. Proportion of suitable habitat by basin. The model identifies suitable habitat (HSI>0) in all basins in the study area, in different proportions relative to the area of each basin.

3.2. Habitat Suitability at the Bay Scale

Decision-making regarding siting restoration projects often occurs at the scale of a single bay. Liberty Bay located near Poulsbo, Washington in Central Puget Sound (Figure 1), provides an example of a location where there is an abundance of potentially suitable habitat for restoration (Figure 5). The nearshore environment is gently sloped, creating larger swathes of area at suitable tidal elevations. The maximum potential currents, summer temperatures, and residence times are optimal throughout the bay. At the head of the bay, salinities can be slightly lower than optimal, though the freshwater source here is a small stream, so there is low risk of low salinity events. Optimal habitat (HSI=1) is found along the eastern and western shores, and in Dogfish Bay, the small inlet at the southwest corner. Notably, this is the site of a well-established restored population. Some artifacts of the interpolation technique used are visible in the HSI map below. While Liberty Bay had good coverage from both the SGA monitoring data (n=16) and the SSM nodes (n=11), habitat variables assessed here are considered a rough estimation at this scale (Appendix I).

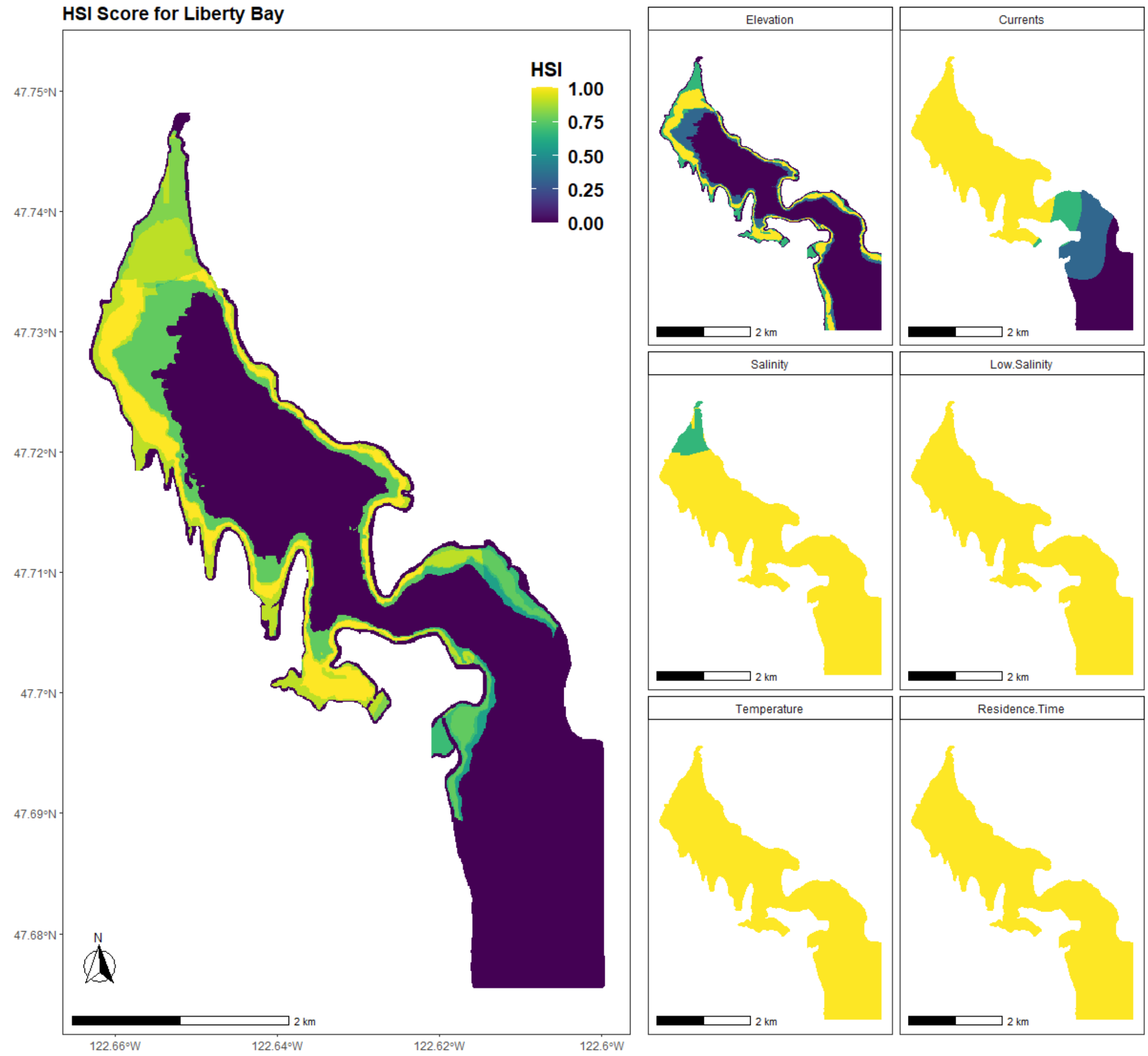

Figure 5. Habitat suitability in Liberty Bay, legend applies to all panels. Left: HSI output, calculated as described in the Methods section. Right: Suitability scores for elevation and maximum potential current velocity (top), suitability scores for mean winter salinity and risk of low salinity events (middle), suitability score for summer temperature and residence time (bottom).

Fidalgo Bay, Washington, is located near the city of Anacortes in the Strait of Georgia and is the site of a long-term Olympia oyster restoration effort (Figure 1). Figure 6 shows the results of the HSI model applied to Fidalgo Bay. The results of the HSI model indicate that a large area of Fidalgo Bay is potentially suitable, though scores are generally lower than found in Liberty Bay. The gentle slope of the bay creates significant area between -3 and +2 feet MLLW. Currents are low within the bay, salinities are on average high and there is no major freshwater inflow, and residence times are moderate. The estimated temperature indicates that average summer temperatures are at the lower range of spawning thresholds, which lowers the overall suitability within the bay, according to the model prediction. However, studies report that spawning threshold temperatures are typically reached in Fidalgo Bay by mid-May (Dinnel, 2009). There are only two SGA monitoring stations, located near the mouth of the bay, that inform the temperature prediction layer, which is a potential source of inaccuracy.

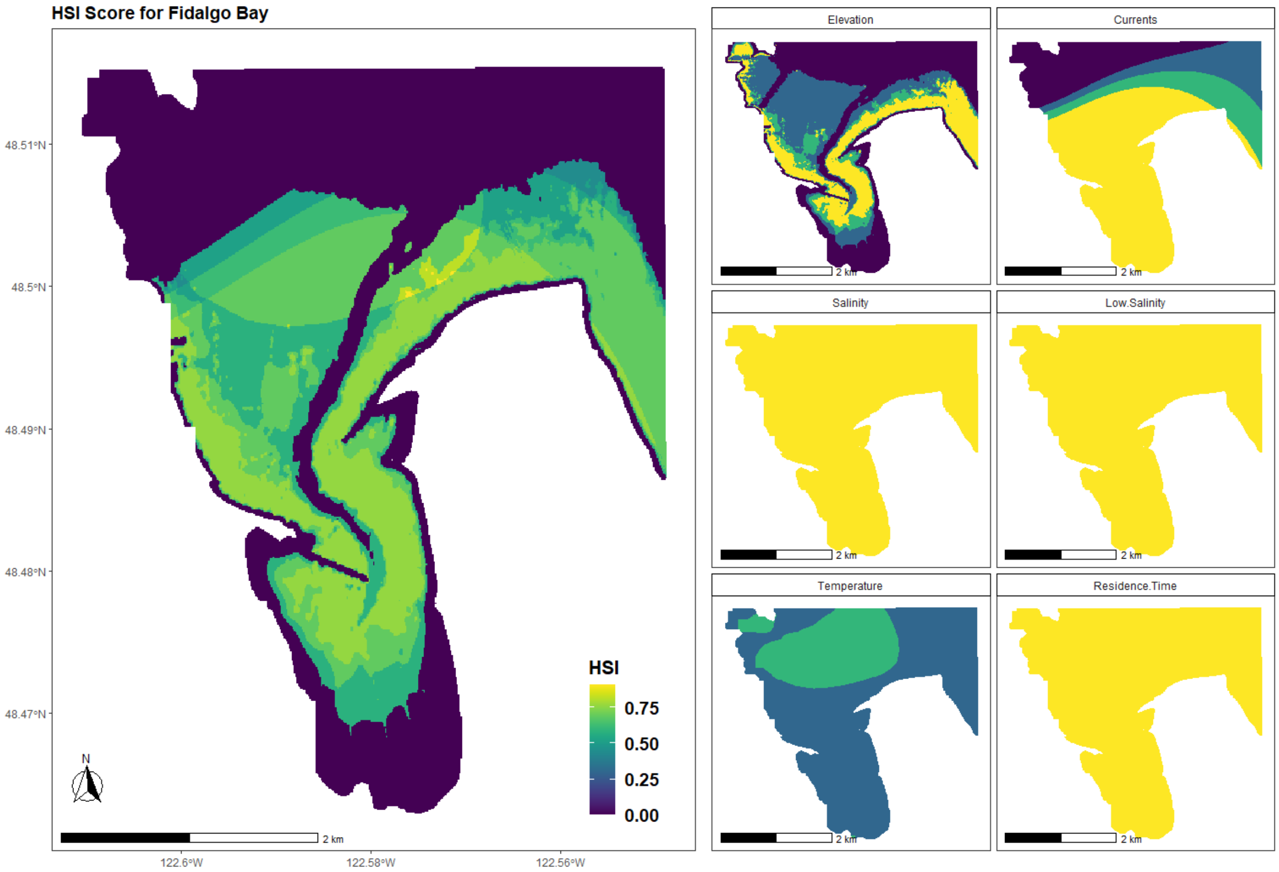

Figure 6. Habitat suitability in Fidalgo Bay, legend applies to all panels. Left: HSI output, calculated as described in the Methods section. Right: Suitability scores for elevation maximum potential current velocity (top), suitability scores for mean winter salinity risk of low salinity events (middle), suitability scores for summer temperature and residence time (bottom).

Case Inlet (Figure 7), is located in South Puget Sound, between Harstine Island and an arm of the Kitsap Peninsula in south Puget Sound (Figure 1). Suitable habitat (HSI>0) is found in North Bay, at the northern tip of the bay, along the eastern shore and in Rocky Bay and Vaughn Bay (i.e., the inlets on the eastern shore), as well as on the western shore surrounding Reach and Stretch Islands. The largest areas of suitable elevation are found in North Bay, Rocky Bay, and Vaughn Bay. Maximum current velocities may exceed suitable conditions through the narrow channel of North Bay. Salinities may be below optimal throughout the head of the bay, with a risk of low salinity events near where several small creeks flow into the bay. Temperatures and residence times are predicted to be within the optimal range. The North Bay oyster bed, the largest bed of native oysters in the Washington (White et al., 2009a), is located near the area of suitable habitat (HSI = 0.5-0.75) identified at the northern tip of Figure 7.

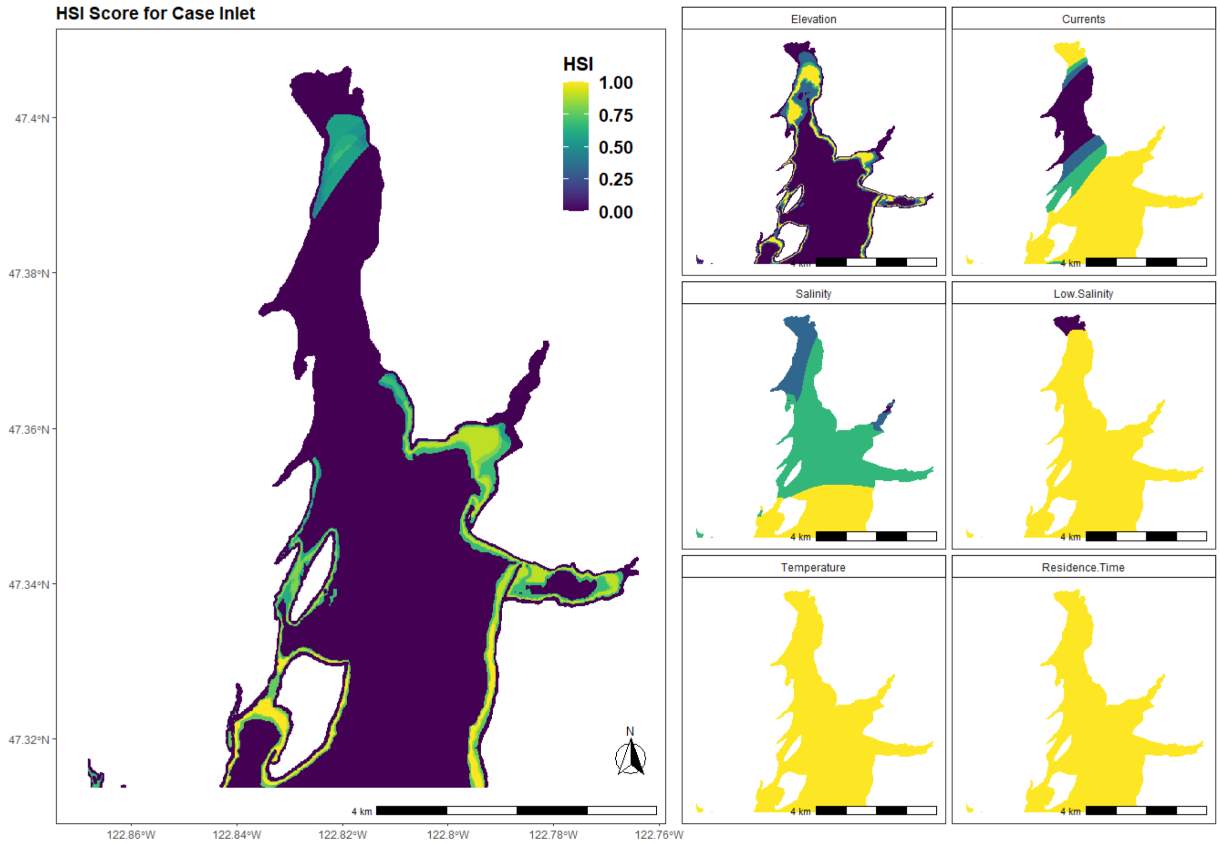

Figure 7. Habitat suitability in Case Inlet, legend applies to all panels. Left: HSI output, calculated as described in the Methods section. Right: Suitability scores for elevation and maximum potential current velocity (top), suitability scores for mean winter salinity and risk of low salinity events (middle), suitability scores for summer temperature and residence time (bottom).

3.3. HSI Evaluation

A critical step in implementing and interpreting HSI models is verification or validation using independent species occurrence data. Many HSIs for marine and estuarine species including oysters, particularly early examples, are not verified or validated despite the importance of this analysis (Theuerkauf & Lipcius 2016). The model developed in this study has not been statistically validated, due in part to data limitations. However, several steps were conducted as a preliminary evaluation to learn about how well the model performs and better understand limitations for potential applications (see Figure 2); the results of which are described here. Evaluation included an initial examination of the range of HSI scores, compilation of data describing oyster observations and abundance at restoration sites, and comparisons between oyster data and HSI scores. Applications and limitations are considered in the Discussion section below.

Figure 8 shows locations where Olympia oyster are present in Liberty Bay (Figure 8a) and Dyes Inlet (Figure 8b) in west Puget Sound (n=125). Oyster densities are not included; some observations may represent a single oyster, while others may represent an area where numerous oysters were counted. HSI scores for the location of each occurrence are reported in Figure 8d. At these West Sound sites, oyster observations coincide with HSI scores above 0.65. While alignment of high HSI scores with oyster observations may serve as a first-order verification that the model identifies habitat that supports oysters, this finding does not provide information regarding HSI scores where oysters are absent, or regarding the potential for high-scoring sites to support restoration goals.

In addition to West Sound, I also compared HSI scores with observations of Olympia oysters made during WDFW shellfish surveys in Hood Canal (n=235, Figure 8c). Observations in Figure 8c are locations where Olympia oysters have been observed during shellfish surveys from 2014-2019. Unlike for the West Sound locations, the model shows relatively poor alignment with oyster observations, with most observations occurring where HSI=0, and fewer observations where HIS>0.5 (Figure 8e). This finding raises questions about the validity of the model for identifying sites that support populations of Olympia oysters in Hood Canal and potentially in other locations.

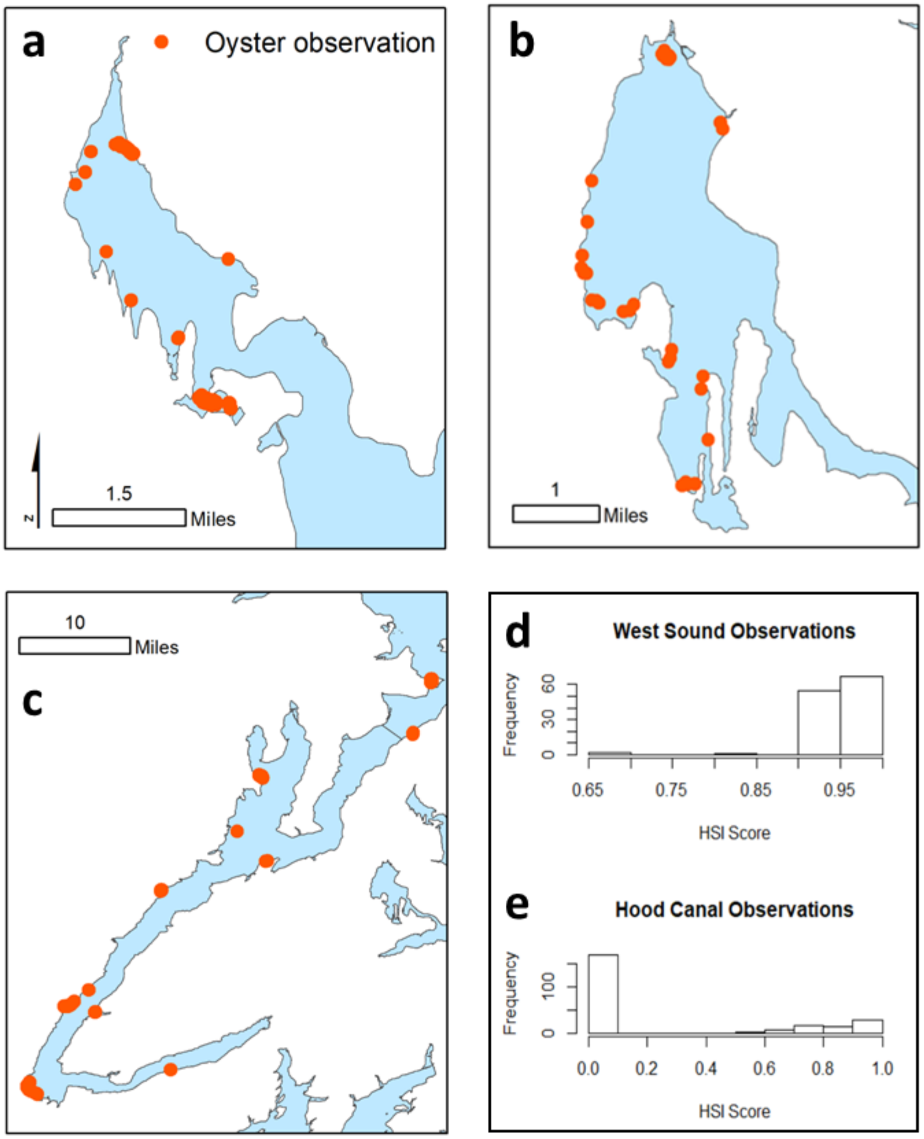

Figure 8. HSI verification based on oyster presence. HSI Values at oyster presence sites in Liberty Bay, Dyes Inlet (grouped together as "West Sound"), and Hood Canal.

Table 3 describes the estimated environmental conditions where oysters occur for each habitat variable included in the HSI. The mean, range, and standard deviation (SD) of values extracted from habitat layers at locations where oysters are observed are included. In general, Olympia oysters in Hood Canal experience a wider range of conditions than in West Sound. Oysters were observed in Hood Canal where conditions are within suitable ranges for most habitat variables, however current velocities at over two-thirds of locations where oysters were observed exceeded the limits defined as suitable in the model (Table 4). This was the main driver contributing to high counts of oyster observations where HSI = 0 in Hood Canal (Figure 8e; Table 4). Given the limited number of sources describing current velocity thresholds for Olympia oysters, it will be important to better understand the relationship between this habitat variable and oyster populations.

Table 3. Environmental conditions at locations where oysters are observed in West Sound and Hood Canal; SD = standard deviation.

Habitat Variable	**West Sound**			**Hood Canal**		
	Mean	*Range*	*SD*	*Mean*	*Range*	*SD*
Elevation (m; MLLW)	-0.08	-2.02-0.77	0.48	0.03	-3.20-1.07	0.59
Maximum current velocity (m/s)	0.28	0.09-0.48	0.14	0.59	0.24-0.91	0.14
Mean winter salinity (psu/ppt)	25.4	22.7-27.6	1.34	21.4	13.5-28.0	3.7
Low salinity events (no = 1, yes =0)	1	1-1	0	1	1-1	0
Mean summer temperature (°C)	16.4	15.4-17.3	0.40	16.1	13.3-17.8	1.2
Water residence time (days)	166	162-171	3.6	191	112-267	36

To test the HSI model output against restoration outcomes throughout the study area, I compared year five oyster abundance at restoration sites (n=9) to the total area of suitable habitat (HSI>0) available within each bay (Figure 9). Restoration project sites include: Fisherman Bay in the San Juan Islands, Discovery and Sequim Bays in the Eastern Strait of Juan de Fuca, Fidalgo Bay in the Strait of Georgia, Kiket Bay in the Whidbey Basin, Liberty Bay and Dyes Inlet in the western Central Basin, Lynch Cove in Hood Canal, and Palela Bay near Squaxin Island in South Puget Sound. Abundances were not adjusted by the area of the restoration site or area of the bay. This comparison assumes that more suitable habitat overall near a restoration site will result in higher oyster abundance after several years. Year five oyster abundances were reported in the survey conducted by NOOC as categorical ranges (1=>0-1,000; 2=1,000-10,000; 3=10,000-100,000; 4=100,000-1,000,000; and 5=>1,000,000). Area of potentially suitable habitat is reported as the number of square kilometers where HSI>0, ranging from 0 km^2 in Fisherman Bay and Lynch Cove, to over 5 km^2 in Fidalgo Bay (Figure 9).

The HSI model shows some alignment with restoration outcomes. Bays with at least two km^2 of suitable habitat had medium to high oyster abundances (>10,000 oysters) after year five. However, bays with the highest reported abundances (i.e., Liberty Bay and Dyes Inlet) had moderate amounts of suitable area compared to the other sites. Fidalgo Bay, which has the greatest amount of predicted suitable area (>5 km^2), had only moderate oyster abundance at year five. However, abundances after 10 years are reported to be above two million oysters (Dinnel, 2018), which aligns better with model predictions. Notably, two sites where there is no predicted suitable habitat, Belfair/Lynch Cove and Fisherman Bay, had no oysters present at year five. Palela Bay/Squaxin Island also had no oysters reported at the restoration site after year one and presumably after year five, though there is a small amount of suitable habitat at this location. One important outlier is in Kiket and Lone Tree Lagoons on the Swinomish Tribe tidelands. Though many oysters are reported there after five years, there is no predicted suitable habitat found in Kiket Bay. Elevation and current velocities are the limiting habitat variables in this location (Table 4). However, there is suitable habitat present nearby in Similk Bay, and exact locations of all oysters reported under this project were not available from the survey data and could potentially overlap with nearby suitable habitat (NOOC, n.d.; Ridlon et al., 2020). Looking across all nine sites, the HSI correctly predicts unsuitable habitat at two sites where oysters are not present after restoration (i.e. Lynch Cove and Fisherman Bay). Suitability predictions at two sites appear incorrect (i.e. Kiket Bay and Palela Bay), where predicted area of suitable habitat and oyster abundances do not align. The HSI identifies suitable habitat at five restoration sites where oyster abundance is moderate to high, though there is no relationship between quantity of habitat and oyster population abundance across these five sites. A simple linear regression shows a relatively weak positive influence of area HSI>0 on year five abundance (Figure 9; p=0.076).

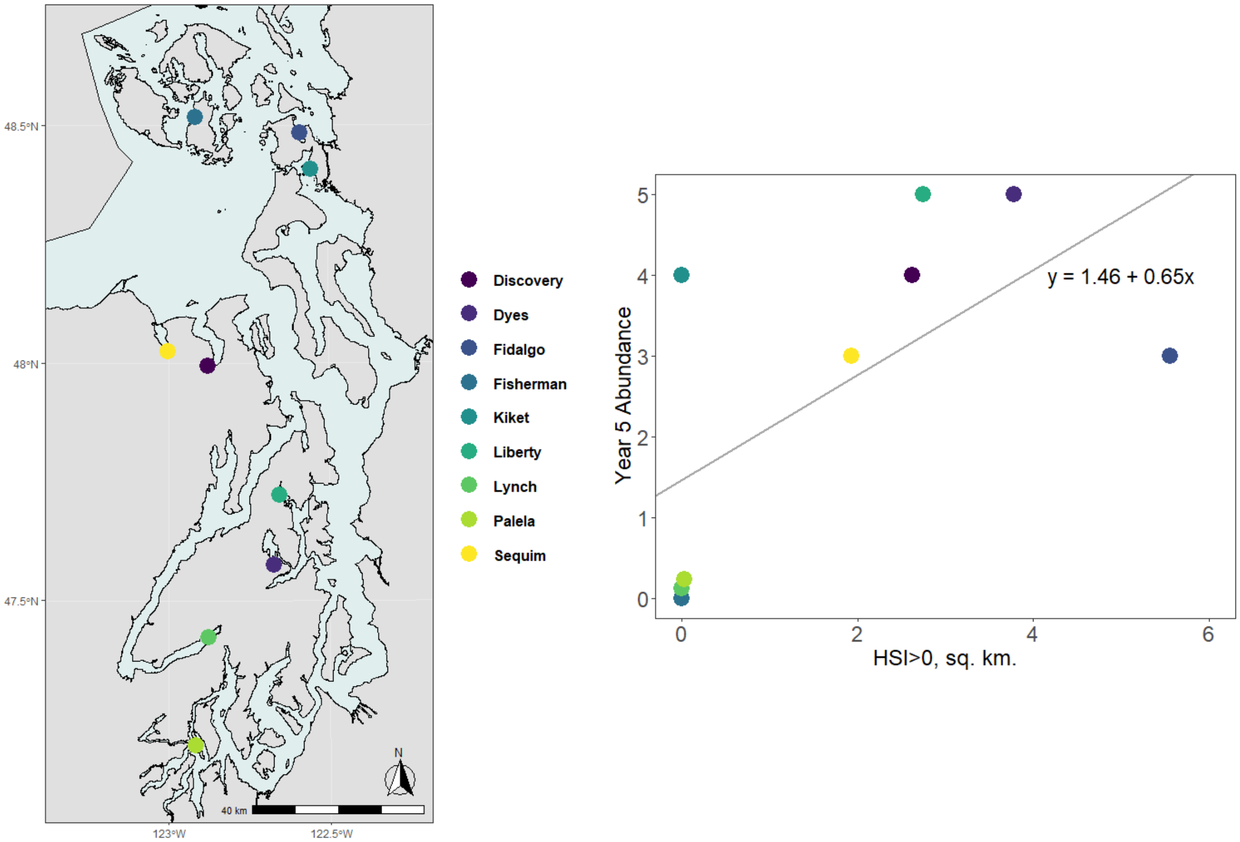

Figure 9. Relationship between restoration outcomes and area of suitable habitat at sites throughout Puget Sound. Points at Fisherman, Lynch, and Palela are all zero abundance and are vertically offset for visibility.

As described above, there are instances where both oyster observations and abundance at restoration sites do not align with HSI scores. Table 4 describes instances where the model appears to underpredict suitable habitat; these are locations where HSI=0 but oysters are present (Hood Canal) or abundant following restoration (Kiket Bay). In both locations, unsuitable current velocities are the main contributor to HSI equaling zero. In Hood Canal, current velocities exceed the defined suitable limit at 71% of locations where oysters are observed. Additionally, 5% of oyster observations coincide with mean winter salinities that are below the suitable threshold. For Kiket Bay, precise locations of oysters are not included in this analysis, but current velocities for the entire bay are considered unsuitable.

About 74% of the bay is at unsuitable elevations. Revising the model by excluding the current velocity habitat variable or expanding the range defined as suitable would result in greater agreement between the model and oyster data. However, much of the study area at the appropriate elevation would then be classified as suitable habitat. Despite the limited information regarding the relationship between current velocity and Olympia oysters, patterns of water movement are known to be important to restoration outcomes, so current velocity was retained in this analysis to represent these dynamics (Appendix F). A conservative estimate of suitability is preferable for this tool, given that it is intended to support restoration decision-making and projects require considerable investment.

Table 4. Habitat variables contributing to instances where oysters are present or abundant and HSI = 0. For Hood Canal, percentages are out of the total number of sites where oysters are observed. For Kiket Bay, percentages are out of the total area of the bay. Note that locations may be unsuitable due to more than one habitat variable; percentages do not add to 100.

Habitat Variable	**Hood Canal (n=235 observations)**	**Kiket Bay (n=1.8 km^2)**
	% of locations where suitability = 0, attributed by habitat variable	*% of bay where suitability = 0, attributed by habitat variable*
Elevation (m; MLLW)	0.4%	74%
Maximum current velocity (m/s)	71%	100%
Mean winter salinity (psu/ppt)	5.1%	0%
Low salinity events (no = 1, yes =0)	0.0%	0%
Mean summer temperature (°C)	0.0%	0%
Water residence time (days)	0.4%	0%

Without survey data and accompanying spatial information covering areas of shoreline inside and outside restoration project areas and where oysters are present and absent, it is difficult to assess instances where the model is overpredicting suitable habitat. One possible case is in Palela Bay, where the model predicts a small amount of suitable habitat, but no oysters were found on restoration substrates after year one. However, it may also be possible that it is difficult for oysters to re-establish in areas with only a small amount of suitable habitat. Survey data within the footprint of the restoration area for Dogfish Bay includes points where adult oysters are absent as well as where they are present. Mean HSI scores are lower where oysters are absent ($p=0.006$), however HSI scores in the surveyed area range from 0.9 to 1.0, indicating that the habitat quality according to this index is relatively homogenous. Patterns of oyster presence/absence patterns may be more likely attributed to patchiness than to fine-scale environmental differences. Survey data spanning wider areas that captures presence/absence and/or additional information describing where restoration projects have been unsuccessful could help better assess where this model may overpredict suitability.

4. Discussion

4.1. Identification of Suitable Habitat for Restoration

This study presents an initial effort to develop and apply an HSI model to identify suitable habitat for Olympia oyster restoration in the southern Salish Sea. HSI models can be a useful tool for understanding the relationship between a species and its environment. These models draw from available information and data collection efforts to identify locations for restoration, conservation, or other purposes (Table 1). HSIs and other forms of habitat suitability models have been widely applied to study native oyster populations and restoration opportunities (e.g., Chowdhurry et al., 2019, Puckett et al., 2018, and others). The suitability relationships in this model were defined using available natural history information from published and gray literature, and the model was constructed using readily available environmental data sets that spanned the entire study area. Suitability predictions for bays and locations other than the three described in this study can be generated with no new analysis. The straightforward methodology applied here allows for examination of the inputs, assumptions, and outputs, and may inform further analysis. For example, if more research on larval retention and current velocities is conducted, the model could readily be updated with refined suitability ranges. In addition, if restoration partners deemed some habitat variables more important than others, the simple averaging equation could be weighted to emphasize those variables.

I compiled available population information and restoration outcomes to perform a high-level evaluation of model predictions. Verification and/or validation of habitat suitability models is an essential step (Theuerkauf & Lipcius, 2016), without which the outcome of the model cannot be relied upon as a decision-making tool. This study presents a preliminary evaluation of the Olympia oyster restoration HSI. The model correctly identifies habitat that supports oyster presence and successful restoration sites (i.e., Dogfish Bay) in Liberty Bay and Dyes Inlet (Figure 8). This result provides verification that the model is identifying areas where oysters are known to be present in this region. However, it does not shed light on whether the model is overpredicting suitable habitat (i.e., generating high HSI scores in areas where oysters are absent), which limits its utility. Survey data including presence/absence and counts would benefit the bay-scale analysis in this study by allowing for examination of potential environmental differences between locations where oysters are present/numerous and where they are absent. Olympia oysters are present in small numbers throughout much of the study area, so while alignment of high HSI scores and oyster presence may serve as a first-order verification in some areas, it may not provide insight into the suitability of a site for restoring self-sustaining populations.

The overall amount of suitable habitat identified in the study area (150 km^2) and in some bays is very high and suggests that the model is likely over-predicting suitability. For perspective, anecdotal sources describe historical area of Olympia oyster beds as covering about 80 square kilometers, though the spatial extent for this estimate is not clear (Doughton, 2019), and could be a smaller or larger area than assessed in this study. However, if the scales are comparable and the historical estimate is accurate, this suggests that important limiting factors may be missing from this model, such as additional habitat variables, or constraints unrelated to the suitability of the physical environment. Low per capita reproduction due to low population size, predation, and/or alternative community states may contribute to the limited recovery of species after harvest pressure ceases. Researchers in Willapa Bay examined both recruitment and post-recruitment growth and survival to gain insight into factors limiting population recovery. They found that depensation is not likely the limiting factor in Willapa Bay, as recruitment has been high for the past five decades. They concluded that Olympia oyster recovery in Willapa Bay is limited by the removal of oyster shell habitat by the fishery, competition from exotic species, and introduced Pacific oyster shell substrate at high tidal elevations that acts as a recruitment sink (Trimble et al., 2009). In addition, studies have found variable but considerable effects of predation from non-native oyster drills on Olympia oyster survival (Buhle & Ruesink, 2009; Grason & Buhle, 2016). Recruitment dynamics in the Salish Sea are known to be variable; recruitment could be a limiting factor in some bays. Likewise, predation and competition may strongly influence the suitability of sites for restoration. While none of these constraints are directly included in this model, physical characteristics such as salinity and tidal elevation may mediate effects of predation and competition. Temperature thresholds are a proxy for potential reproduction, and recruitment dynamics could be more directly incorporated by scoring sites with consistent or high recruitment events more highly than others. The results of this HSI suggest that environmental conditions may be conducive to recovery in many areas throughout Puget Sound, though realizing this recovery may depend on adding durable substrate at the appropriate tidal elevations where competition and predation are low and in bays where conditions allow for recruitment. Given that the model appears to over-predict suitability at a broad scale, it may be preferable to focus only on areas identified as optimal (e.g., HSI>0.75), particularly given the cost and effort required to implement restoration projects.

While the model may overpredict suitability throughout much of the study area, there are also areas where the model appears to fail to identify potentially suitable habitat (Figure 8). Much of Hood Canal is classified as unsuitable by the HSI due to high maximum potential current velocities, which is the least well understood habitat variable included in the model (Table 4). This suggests the need for more examination of the relationship between current velocity and larval retention (Peteiro & Shanks, 2015), and consideration of other variables that describe water movement patterns. Comparing the model output to restoration outcomes (Figure 9), while limited without more detailed and verified data, yields some insights that may be further explored. For example, Lynch Cove is classified as unsuitable habitat due to extremely high water residence times. While a small restoration experiment in Lynch Cove did not succeed and no surviving oysters were found by year five (Figure 9), mortality was at least in part attributed to predation (Valdez et al., 2017), and Lynch Cove historically supported a large oyster bed (Blake & Bradbury, 2012). The classification of sites with extremely high water residence time as unsuitable is based on research in Tomales Bay, which may not apply to Hood Canal (Kimbro et al., 2009).

Considering another example, year five abundance in Fidalgo Bay was somewhat low compared to available suitable habitat. However, this site has increased in oyster abundance since year five and as of 2018 had an estimated population of 2.9 million oysters (Dinnel, 2018). Measured temperatures within Fidalgo Bay are warmer than the estimated mean temperature for the bay included in the index (Dinnel, 2018), suggesting that cold temperatures may not be limiting, as this model suggests (Figure 6). Other habitat factors or population dynamics may be contributing to the slower growth of this population. Density surveys are available for some of the restoration sites described in Figure 9 (e.g., Clallam Marine Resources Committee, 2017); analysis of any patterns in density at a restoration site compared to HSI predictions could provide more detail on the utility of this HSI model for siting restoration projects. Without more detailed spatial data describing restoration outcomes, the evaluation of the model described here is exploratory.

4.2. Limitations of HSI Development and Results

Uncertainty and error can enter HSI models in several ways, including through the variables selected, the accuracy of the environmental data, assumptions made about species relationships with environmental conditions, and other factors (Guisan et al., 2017; Theuerkauf & Lipcius 2016; Appendix I). HSIs are only as accurate as the environmental data layers from which they are constructed (Guisan et al., 2017), and the estimated environmental variables in this model range widely in their accuracy at different locations and some estimations have not been validated (i.e., interpolations of point data collected at SGA monitoring stations). The scale at which the HSI score is calculated in this study merits more consideration, given that only the elevation data are as finely resolved as the analysis presented here. There may be opportunities to further refine this analysis using more accurate environmental data. Nearshore and intertidal dynamics are challenging to resolve in models, and empirical data are often patchy and/or discontinuous. Sources of more robust empirical data (e.g., the Acidification Nearshore Monitoring Network) could be drawn from to assess environmental conditions more accurately at specific sites. In addition, the Salish Sea Model is currently being upgraded to have a higher resolution possible in nearshore areas; using these data could improve the accuracy and reduce error in the study presented here.

HSIs and other habitat suitability models should include all important predictors that define a species' environmental niche (Guisan et al., 2017). Adding more variables that can better describe optimal habitat for Olympia oysters in the study area could address some of the concerns about the model overpredicting suitable habitat. While salinity, water temperature, tidal elevation, and water movement patterns are known to contribute to population persistence, many more variables are relevant to Olympia oysters and potential restoration outcomes (Appendix C). Additional habitat variables could include substrate type or sediment conditions (discussed in Appendix G), better/more accurate representation of water residence time (discussed in Appendix F) at the appropriate scale for analysis, more information about currents, and/or data describing dissolved oxygen, phytoplankton abundance, and other factors. When constructing HSIs, it is best practice to include proximal predictors that fall into the categories of regulators (i.e., factors controlling metabolism), disturbances (i.e., natural and human perturbations, and resources (i.e., food). Variables such as elevation are indirect predictors. Inclusion of distal variables must be carefully considered (Guisan et al., 2017). Temperature and salinity are regulating variables for oysters, and low salinity events are a disturbance. In the current model, elevation and water residence time are indirect predictors, and more research is needed regarding current velocity. Some habitat variables, such as the presence of predators, may be difficult to include in a model while at the same time highly limiting to successful restoration.

Notably, the index approach used here (i.e., developing a model based on assumed relationships reported by the literature) differs from a potentially preferable methodology where relationships are measured from species distribution data, extrapolated over space, and then verified using an independent data set. While the latter approach may produce a more robust estimation, it was not deemed feasible for this study at this time, because the required data were not available. Furthermore, Olympia oyster populations never recovered from harvest and pollution impacts, so building a model from species distribution data may underestimate the potential range within the study area. Data used to verify the model in this study could be improved. Spatial data sets describing presence/absence and densities spanning more locations could provide useful information. Statistical validation could be conducted in the future should these data become available or other methods identified. In British Columbia, Olympia oyster index sites have been selected and are surveyed to assess population status (Norgard et al., 2018), and Bohlen (2019) recommended the establishment of index sites to monitor populations in Yaquina Bay. Establishment and regular monitoring of more index sites in the southern Salish Sea, such as in Fidalgo Bay, could provide valuable population data. In addition, data describing restoration outcomes from the coastwide survey has limitations, as oyster abundances are generalized to the bay/project scale and specific locations of oysters were not available and were thus approximated. This introduces some uncertainty; for example, Kiket and Lone Tree Lagoons are indicated as project sites, but elsewhere described as a project that spans Skagit, Similk Bays as well (NOOC, n.d.), and this analysis uses Kiket Bay to estimate area of suitable habitat compared to restoration outcomes. Regardless of improvements made to the model described here, there is no substitute for expert evaluation of individual sites through fieldwork, particularly considering that oyster survival can depend on factors difficult to model like the presence of standing water and seeps at low tide (Allen et al., 2015).

4.3. Value and Opportunities for Co-Production

A core aspect of this study is that it represents co-production of a model based on in-depth collaboration between PSRF and the author. As the lead implementing organization for oyster recovery in Puget Sound, PSRF works in partnership with tribal resource managers and WDFW to manage the recovery effort for Olympia oysters. Co-production requires collaboratively developing project goals and regular communication throughout the project's lifespan to increases the likelihood that the end product will be useful to resource managers and practitioners (Norström et al., 2020). In this study, the project concept was co-developed, and regular communication among project members maintained. I checked-in with the PSRF team at key intervals as the project developed and tried to raise limitations encountered so that partners were aware of areas where the project was not meeting initial goals and identify opportunities for improvement.

While many aspects of this study were co-produced among the immediate project team, there remains an opportunity to broaden engagement and input. There is a network of tribal governments, nonprofit organizations, community members, aquaculture companies, and other types of entities involved in Olympia oyster restoration (Appendix B). Broader engagement could improve both the quality of the information included in this analysis, as well as the likelihood of the tool being widely used.

4.4. Next Steps and Areas for Future Study

Despite the uncertainties and limitations described above, the approach outlined here and the HSI product is a useful preliminary tool for scouting potentially suitable habitat for implementing Olympia oyster restoration projects in the study area. To describe one such possible application, PSRF is in the process of identifying sites for restoration that will help meet their 2020 goal of restoring 100 acres. PSRF may use this model to assess areas within, for example, Liberty Bay, to conduct shell enhancement. In this example, PSRF may draw from model output – particularly if updates are made – as well as knowledge and field assessments, to identify an optimal area for a new project.

Undertaking this project has illuminated many potential areas for future study that span both the basic ecology of Olympia oysters and the socio-ecological dimensions of Olympia oyster restoration. Data describing existing populations of Olympia oysters in the study area, restoration outcomes at project sites, and reasons for mortality or suboptimal restoration performance could improve model development options and validation approaches. Identifying these outcomes in a systematic way can help guide future iterations of a suitability model. For example, when identifying potentially suitable sites it would be important to understand if oysters are dying because of sedimentation or predation by oyster drills, as neither of these are represented in the current version of the model. In addition, many sites within Puget Sound and along the west coast experience regular recruitment failures and high recruitment variability (Wasson et al., 2016). More detailed analysis of the relationships between larval abundance, settlement, residence times, and currents may yield helpful information for restoration planning. Analysis of eDNA data could provide information regarding relative abundances during spawning seasons and during seasons when DNA likely represents adult oysters only.

In addition to ecological factors, there are practical and regulatory barriers to restoration that could be incorporated into a suitability prioritization exercise. Other oyster HSI development projects have held workshops to determine important suitability variables, identify environmental data, establish appropriate weighting, and build buy-in among managers (e.g., Theuerkauf et al., 2019a). Partners could convene a workshop to identify top suitability constraints, broadening the discussion to include topics such as tideland ownership, availability, and/or access status, proximity to eelgrass or other types of protected habitats, and priority for providing ecosystem services like water filtration or habitat creation. The expertise of partners could be drawn upon to weight factors that are most important to their specific contexts, creating a customizable tool that may be relevant at finer scales. Indigenous science could be centered more in this research, as Coast Salish peoples have inhabited this region since time immemorial and maintain deep knowledge and relationships with the nearshore ecosystems and species throughout that time.

As availability of fine-scale spatial data for the Salish Sea and other regions increases, HSI models for species and communities may play an increasingly important role in planning restoration and enhancement projects. The southern Salish Sea is highly affected by development and other anthropogenic stressors, and a diverse coalition of actors are working to both undo legacies of environmental degradation and find balance between emerging threats in a growing region and the needs of human populations. Restoration and recovery are underway for many species and habitat types. Increasing populations of native Olympia oysters is just one in a suite of restoration and conservation strategies that are being undertaken with the goal of improving ecosystem condition. Olympia oysters, as a member of diverse benthic assemblages, can provide water filtration and foundation habitat where it may have been previously lost (Pritchard et al., 2015; Wasson et al., 2015). As climate change accelerates vulnerability of species and ecosystems at local, regional, and global scales, suitability models may be more widely applied to target restoration activities where they are most likely to achieve goals and build resilience.

Chapter 2: Climate Considerations for Olympia Oyster Restoration

1. Introduction

Anthropogenic climate change is significantly impacting coastal marine ecosystems around the world (Feely et al., 2008; Harley et al., 2006; and others), including nearshore habitat in the Salish Sea. It is critical that restoration efforts consider vulnerability to climate impacts when planning, implementing, and monitoring projects. This chapter provides a brief accompaniment to *Chapter 1: Developing a Habitat Suitability Index for Olympia Oyster Restoration*, in order to take a closer look at the climate considerations relevant to Olympia oyster restoration.

Olympia oysters are the only oyster species native to the west coast of North America. Once abundant in coastal bays and estuaries, Olympia oyster beds currently occupy less than five percent of their historic extent in Puget Sound (Blake & Bradbury, 2012). Olympia oyster beds provide valuable ecosystem services, including water filtration (Gray et al., 2019), increased abundance of epibenthic invertebrates (PSRF, 2009), and biogenic habitat creation in the nearshore environment (Dinnel, 2018). Restoration practitioners and resource managers are currently collaborating to re-establish self-sustaining populations of Olympia oysters throughout their range. *Chapter 1* focused on identifying suitable habitat for restoration using data describing past conditions. However, coastal ecosystems are changing rapidly, which will likely cause shifts in the location and amount of habitat suitable for Olympia oyster restoration.

The vulnerability of a species or ecosystem to climate change is a combination of its exposure to climate change stressors and its intrinsic sensitivity and adaptive capacity. Vulnerability is assessed using a range of possible approaches, including trait-based assessments, which may be applicable for species with ranges that have contracted due to other anthropogenic pressures (Foden et al., 2019; IPCC, 2007). Best practices for considering climate impacts in restoration include defining and identifying attributes of resilience, understanding climate impacts and projections, considering timeframe and risk, assessing interaction between climate change effects and restoration priorities, and identifying potential management measures (Beechie et al., 2013; Raymond et al., 2018; Timpane-Padgham, Beechie, & Klinger, 2017). This chapter combines key principles to develop and apply a restoration-focused climate change vulnerability assessment for Olympia oysters in the Salish Sea. The rapid assessment framework applied here includes 1) restoration objectives and resilience; 2) exposure to climate change stressors; 3) species sensitivity, adaptive capacity, and vulnerability; and 4) management considerations.

2. Olympia Oyster Restoration and Climate Change Vulnerability

2.1. Restoration Objectives and Resilience

Restoration actions are determined by assessing what is necessary for the recovery of local populations (Beechie et al., 2013); these priorities are typically defined in recovery and management plans (e.g., Blake & Bradbury, 2012). For Olympia oyster restoration, the goal is to re-establish self-sustaining oyster bed habitat at priority sites throughout Puget Sound, with some emphasis on restoring the biogenic habitat created by Olympia oysters. Restoration plans may evaluate potential impacts of climate change by determining if climate projections alter the types of actions necessary for recovery, asking if proposed restoration actions ameliorate predicted climate stressors, and assessing if restoration actions increase population resilience (Beechie et al., 2013). Resilience is defined as both the resistance of a system to change and its capacity to recover from a disturbance. Projects that incorporate process-based principles and include resilience as a specific planning objective may be more likely to achieve objectives, particularly in the context of climate change (Beechie et al., 2010; Timpane-Padgham, Beechie, & Klinger, 2017; Raymond et al., 2018). Identifying attributes that confer resilience may help guide both design of projects for resistance to negative climate impacts and monitoring the resilience of populations.

A range of attributes may confer resilience to restoration projects, depending on the focus and scale of restoration objectives. Population attributes, including size, density, and others, individual attributes including larval production and settlement, and process-based attributes including habitat structure (Timpane-Padgham, Beechie, & Klinger, 2017) are important to consider for Olympia oyster restoration. Designing for and monitoring attributes of populations that confer resilience may increase the success of restoration projects under climate change. Table 5 summarizes climate change and resilience considerations for restoration and provides examples of how these considerations may be applied to Olympia oyster restoration. Specific climate stressors and vulnerabilities for Olympia oyster restoration are discussed in greater detail in the following sections.

Table 5. Summary of key climate change and resilience considerations for restoration projects from the literature and how these considerations may apply to Olympia oyster restoration projects.

Climate change and resilience considerations for restoration	**Olympia oyster restoration examples**
Priority actions for recovering populations	Olympia oyster restoration is focused on re-establishing populations and habitat, actions include adding substrate and juvenile oysters at priority sites
Restoration actions altered by climate projections	Optimal locations for restoration projects may shift due to climate-related changes, including landward shifts of suitable elevation due to sea level rise, shifts away from freshwater sources where flood events may increase in frequency, and depth or latitudinal shifts due to air temperature extremes. Restoration methods (e.g., adding shell substrate) may need to be modified to adapt to sedimentation and erosion.
Restoration actions ameliorate climate stressors	Researchers are studying interactions between eelgrass and Olympia oysters, including the possibility that eelgrass may ameliorate stress caused by low pH. Findings suggest that eelgrass restoration efforts at estuarine sites with greater oceanic influence benefit Olympia oysters by improving shell strength, though these benefits may be counteracted by increased predation (Lowe et al., 2018).
Restoration actions increase population resilience	Restoration efforts focused on increasing population size and density, facilitating larval production and settlement, and improving habitat structure by building substrate may confer resilience.

2.2. Climate Change Exposure

Understanding restoration projects' exposure to climate change stressors is an essential element of incorporating climate change into restoration planning. Temperature, sea level, and acidification are three primary indicators of climate change for Washington's coastal ecosystems (Reeder et al., 2013). Rapid changes across these indicators have already been observed in Puget Sound, and projected changes are predicted to further stress organisms and ecosystems and affect restoration projects. Table 6 provides a brief overview of observed and projected changes.

Table 6. Observed and projected climate change pressures for marine environments in Puget Sound

Pressure	Observed Changes	Projected Changes
Increasing water temperature	Water temperatures have risen in Puget Sound from 1950 to 2009 by between 0.8°F to 1.6°F (Bassin et al., 2011; Mauger et al., 2015).	Northeast Pacific Ocean temperatures are projected to rise by about 2.2°F by the 2040s relative to 1970-1999, based on a moderate emissions scenario (RCP 6.0/SRES A1B; (Mauger et al., 2015; Mote & Salathé, 2010). 2.82°F of sea surface temperature warming in Puget Sound is projected by the 2090s compared to historical conditions under RCP 8.5 (Khangaonkar et al., 2019).
Rising sea level	Sea level is rising at most locations in Puget Sound. The Seattle tide gauge shows a record of sea level rising by about 8.6 inches from 1900 to 2008, or about 0.8 inches per decade (Mauger et al., 2015; National Research Council, 2012).	The central estimate (i.e., 50% probability of exceedance) for relative sea level change in Tacoma is 2.1-2.5 feet (RCP 4.5/8.5) in the year 2100, relative to contemporary sea level. Differences in local land motion account for the spread of projections throughout Puget Sound (Miller et al., 2018).
Increasing acidification	North Pacific Ocean has pH decreased by about 0.1 units due to anthropogenic CO_2 emissions (Sabine et al., 2004). It is estimated that ocean acidification has lowered natural pH levels in Puget Sound by 0.05-0.15 units since the pre-industrial period (Feely et al., 2010).	Changes in the pH of Puget Sound are expected to vary between -0.3 and -0.12 pH units in 2095, with an annual mean reduction of 0.18 units compared to historic conditions. River inputs and growth and nutrient cycles will cause localized variability (Khangaonkar et al. 2019)

In addition to the primary stressors in Table 6, additional changes specific to nearshore ecosystem processes and relevant to Olympia oyster restoration are expected (Table 7, summarized from Clancy et al., 2009; Raymond et al., 2018; Snover et al., 2019; Khangaoankar et al., 2019).

Table 7. Additional predicted climate change impacts to intertidal and nearshore environments in the Salish Sea

Pressure	Description
Altered erosion and sediment processes	Increased sediment supply from bluff erosion and streams, increased littoral drift rates, and loss of sediment sources caused by shore protection. Worsening beach erosion and shifts in areas of sediment accretion, landward shift of shore features and habitats.
Variable freshwater inputs	Altered freshwater input and changes in distributary channels, freshwater input predicted to become more variable due to reduced snowpack, higher winter stream flows, and lower summer streamflow.
Tidal dynamics	Shifting tidal channels and greater inundation and tidal flows into semi-enclosed areas.
Increased waves and detritus	Increased wave action from storms and surges. More detritus due to increased wave energy and higher river flows.
Increased air temperature	Predicted increase of very hot (>90F) days.
Dissolved oxygen	Predicted decreases in average dissolved oxygen.

2.3. Olympia Oyster Sensitivity, Adaptive Capacity, and Vulnerability

Sensitivity is defined as the degree to which a species is adversely or beneficially impacted by climate change. Adaptive capacity, the ability of a species to adjust to accommodate a change, can mitigate impacts of climate change on species (IPCC 2007; IPCC 2014; Foden et al., 2019). Table 8 summarizes known sensitivity and adaptive attributes of Olympia oysters that may determine how individuals and populations are affected by changing conditions. Attributes of sensitivity and adaptive capacity identified by Foden et al. (2019) are listed. The summary column indicates if the species does or does not possesses the attribute (checkmark or “x”), or if the information is not known (question mark). The description column provides detail on aspects of Olympia oyster ecology and biology relevant to each attribute. Climate change likely contributes to sensitivity across all attributes, with some unknowns. With regards to adaptive capacity, phenotypic plasticity identified in some studies may enable adaptation, but dispersal ability is relatively low and evolvability is not known.

Table 8. Rapid assessment of Olympia oyster climate change sensitivity and adaptive capacity. Attributes described by Fodern et. al (2019) and Fodern & Young (2016).

Attributes	**Summary**	**Description**
Sensitivity		
Specialized habitat and/or microhabitat requirements	✓	Historical and contemporary populations limited to specific habitat types and locations within the Salish Sea (Blake & Bradbury, 2012; Appendix A).
Environmental tolerances or thresholds that are likely to be exceeded due to climate change	✓	Threshold tolerance levels to air temperature, water temperature, salinity levels, pH, dissolved oxygen, phytoplankton abundance, and sediment characteristics (Wasson et al., 2015; Cheng et al., 2017; Gray & Langdon, 2018; Hollarsmith et al., 2019; Appendix C).
Dependent on environmental triggers that may be disrupted due to climate change	**?**	Unknown; however, reproductive behavior aligns with warm water temperatures.
Rarity	✓	Populations are reduced throughout most of the species’ range.
Sensitive life history	✓	Larval and adult stages sensitive to environmental conditions (Baker, 1995).
High exposure to other pressures	**?**	Unknown; populations may be vulnerable to other anthropogenic stressors such as pollution and/or harvest.
Adaptive Capacity		
Phenotypic plasticity	✓	Evidence suggests that populations adapt to localized conditions (Heare et al., 2018; Silliman, Bowyer, & Roberts, 2018).
Dispersal ability	**X**	Absence of larvae in coastal plankton suggests limited dispersal ability (Baker, 1995); British Columbia and Oregon populations distinct from Washington, and genetic differences likely within Puget Sound (Silliman, 2019).
Evolvability	**?**	Unknown, though genetic diversity may be low.

Olympia oysters have been assessed as having a high vulnerability to climate change, due to their sensitivity to salinity, dissolved oxygen, and pH levels (WDFW, 2015). As described in Tables 6 and 7, intertidal and subtidal areas typically inhabited by Olympia oysters may experience dramatic changes under future climate scenarios; Table 8 shows how Olympia oysters may be sensitive to climate stressors and their capacity to adapt. Table 9 combines the climate stressors and known sensitivities of Olympia oysters to describe species’ vulnerability. Based on this rapid assessment, future climate conditions in nearshore habitats in Puget Sound are likely to have mixed or negative effects on the amount of suitable habitat available to Olympia oysters (Table 9). Predicted impacts to populations and restoration sites are exacerbated by the sensitivities described above and mitigated by adaptive capacity (Table 8).

This rapid assessment framework does not account for combined and synergistic effects of stressors on Olympia oysters. Many studies that discuss potential combined effects of salinity and temperature are focused on California, where low salinity is seasonally offset from high temperatures (e.g., Cheng et al., 2017). Synergistic effects between high freshwater flows and high spring air temperatures may create more adverse conditions in Washington. In addition, there may be interactive effects among climate stressors. For example, while increasing water temperatures may increase Olympia oyster growth rates, temperature increases will likely favor proliferation of feral Pacific oysters (Valdez et al., 2017), which are known to compete with native oysters (Trimble et al., 2009). Predation rates by drills, green crabs, and other species may also be affected by climate change. While rising sea levels may expand potential habitat into higher elevations in some areas, the lower tidal elevation limits, which are often set by species interactions, will likely shift as well resulting in no net effect or potential losses of suitable habitat depending. Understanding competition and predation under climate change, particularly in the context of invasive species is an active research priority (Kimbro et al., 2019). Furthermore, higher elevations are more likely to be constrained by shoreline development, which could result in losses of potentially suitable habitat in many locations.

Table 9. Vulnerability summary table describing likely climate change pressures, and information regarding predicted impacts

Climate Change Pressure	Predicted Effect	Description
Increased water temperature	Mixed	Warmer water temperatures may increase growth rates (Gray & Langdon, 2018). Warming tolerance (i.e., difference between critical thermal maxima and habitat temperatures) is significant (Cheng et al., 2017), but warming may also favor predators and competitors.
Increased air temperature	Mixed	Reduced exposure to freezing temperatures could expand habitat, could be negated by thermal stress (Pritchard et al., 2015).
Rising sea level	Mixed	Suitable habitat may expand higher in the intertidal and into estuaries if lower limit does not shift (Hutto et al., 2015), otherwise available habitat will remain the same or contract if upland areas are armored or developed.
Increased acidification	Negative	Reduced fitness of larvae and carryover affects to adults (Hettinger et al., 2012).
Increased streamflow variability	Negative	Flooding events can cause mass die-offs of oysters due to low salinity (Cheng et al., 2016).
Shifts in tidal flat habitat	Mixed	Depending on expansion or loss of area at specific sites (Glick, 2007).
Decreased dissolved oxygen	Negative	Lower dissolved oxygen linked with low oyster growth (Jeppesen et al., 2018)
Increased erosion and sedimentation	Negative	Sedimentation described as a primary challenge to restoration success in Puget Sound (Wasson et al., 2015).

2.4. Management Considerations

Resource managers and restoration practitioners identify and prioritize sites for Olympia oyster restoration projects based on available information regarding the suitability of habitat present, historical populations, site access and availability, and other factors. The rapid assessment presented here may be drawn from to incorporate climate change into restoration decision-making. The following guiding questions, which are linked to restoration objectives, species sensitivity, adaptive capacity, and exposure, could be assessed during the restoration planning process:

1) What restoration actions are needed and how can resilience be included in project objectives, and measured?
2) Is there a risk that environmental tolerance thresholds will be exceeded if conditions change compared to long-term averages?
    a. Is there a snow-dominated freshwater source that may increase risk of low salinity events?
    b. Is there ample area at optimal tidal elevations, which may modulate oyster sensitivity to increasing air temperatures?
    c. Are pH/aragonite saturation and/or oxygen levels already near biological thresholds at this site?
    d. Is there potential for increased sedimentation?
3) Is there information available regarding how this site may contribute to overall metapopulation dynamics?
4) Are other non-climate stressors at this site likely to increase (e.g., development, water pollution)?
5) What is the potential for competition with Pacific oysters or interactions with other species (e.g., Japanese oyster drills) as conditions change?

To provide an example of incorporating climate considerations into one aspect of the restoration planning process, the output of the HSI model for Liberty Bay is revisited here (Figure 10). With a 1.1 foot increase in relative sea level (1% probability of exceedance, 2040, RCP 8.5; Miller et al., 2018), the window of suitable elevation shifts higher on the shoreline. While represented as a shift in the figure below, sea level rise could instead result in a habitat loss, particularly on the eastern shore of Liberty Bay near the town of Poulsbo where there is a seawall and other development. A temperature increase of 2.2°F (see Table 6) would increase the highest mean temperature areas in the Bay from 17°C to over 18°C, which could initiate changes in competition dynamics with Pacific oysters and other species; Valdez & Ruesink (2017) suggest that warmer temperatures may favor Pacific oysters over Olympias. Liberty Bay does not have a large freshwater source, but several small streams flowing into the bay could decrease mean winter salinities with more rainfall – in a scenario where mean salinities dropped by 2 psu, the overall suitability of the bay would be affected (note that this likely illustrates an extreme case and effects would likely be restricted to portions of the bay rather than uniform). Currents, residence times, and risk of low salinity events are unchanged. In this hypothetical future climate scenario, the overall suitability of areas within the bay decrease, with more habitat falling into marginally suitable categories. This brief analysis provides an example of how the framework and guiding questions described here can be combined with the HSI model described in *Chapter 1* to examine potential climate vulnerabilities, expansions, and shifts at restoration sites. This example is one aspect of incorporating climate change into restoration planning; restoration objectives and priority actions should also be considered through a lens of potential climate change impacts and attributes of resilience (Table 5).

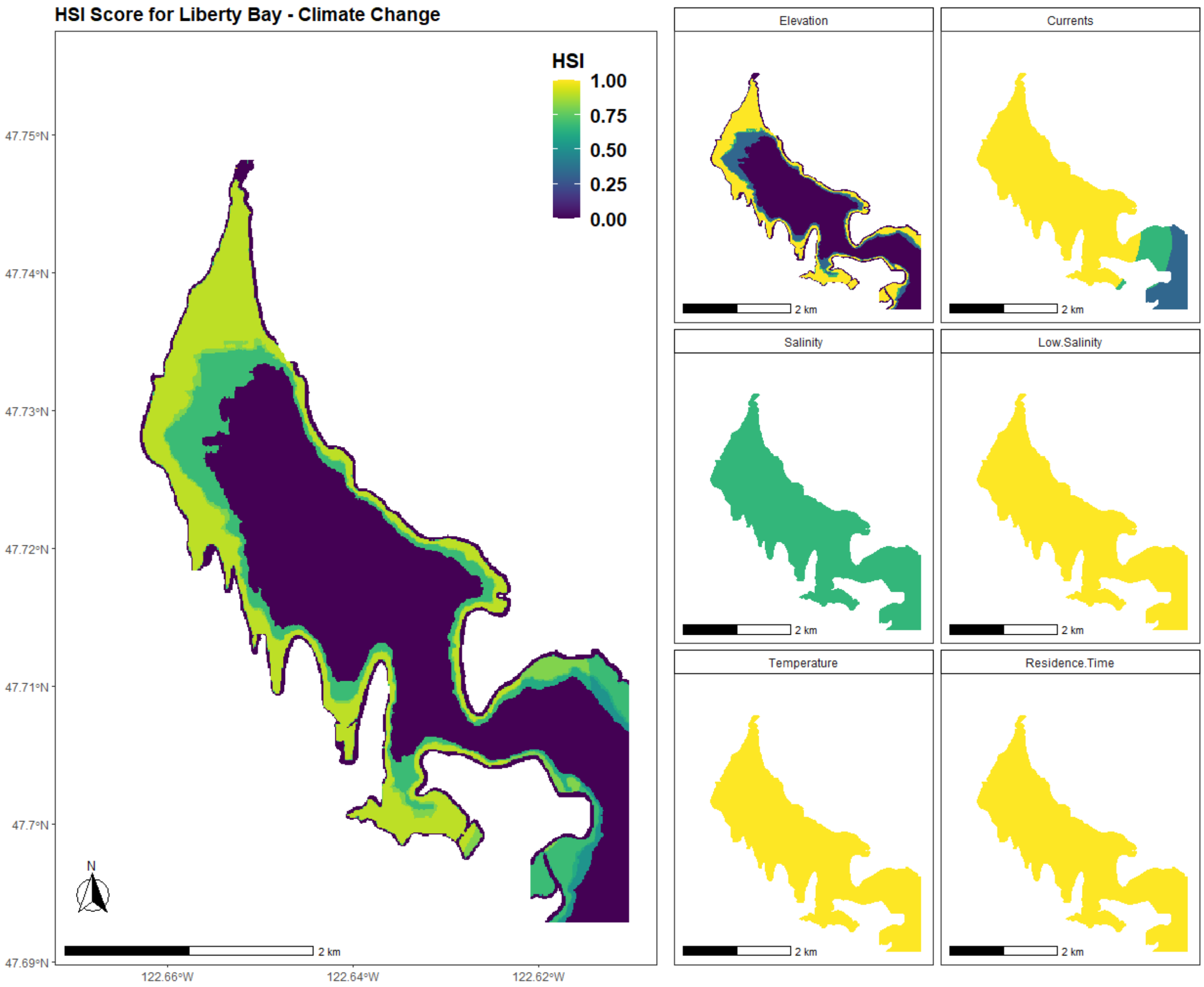

Figure 10. Habitat suitability in Liberty Bay under a hypothetical climate change scenario. Left: HSI output. Right: Suitability score for elevation and suitability score for maximum potential current velocity (top). Suitability score for mean winter salinity and suitability score for risk of low salinity events (middle). Suitability score for summer temperature and suitability score for residence time (bottom).

Appendices

A. Olympia Oyster Population Status

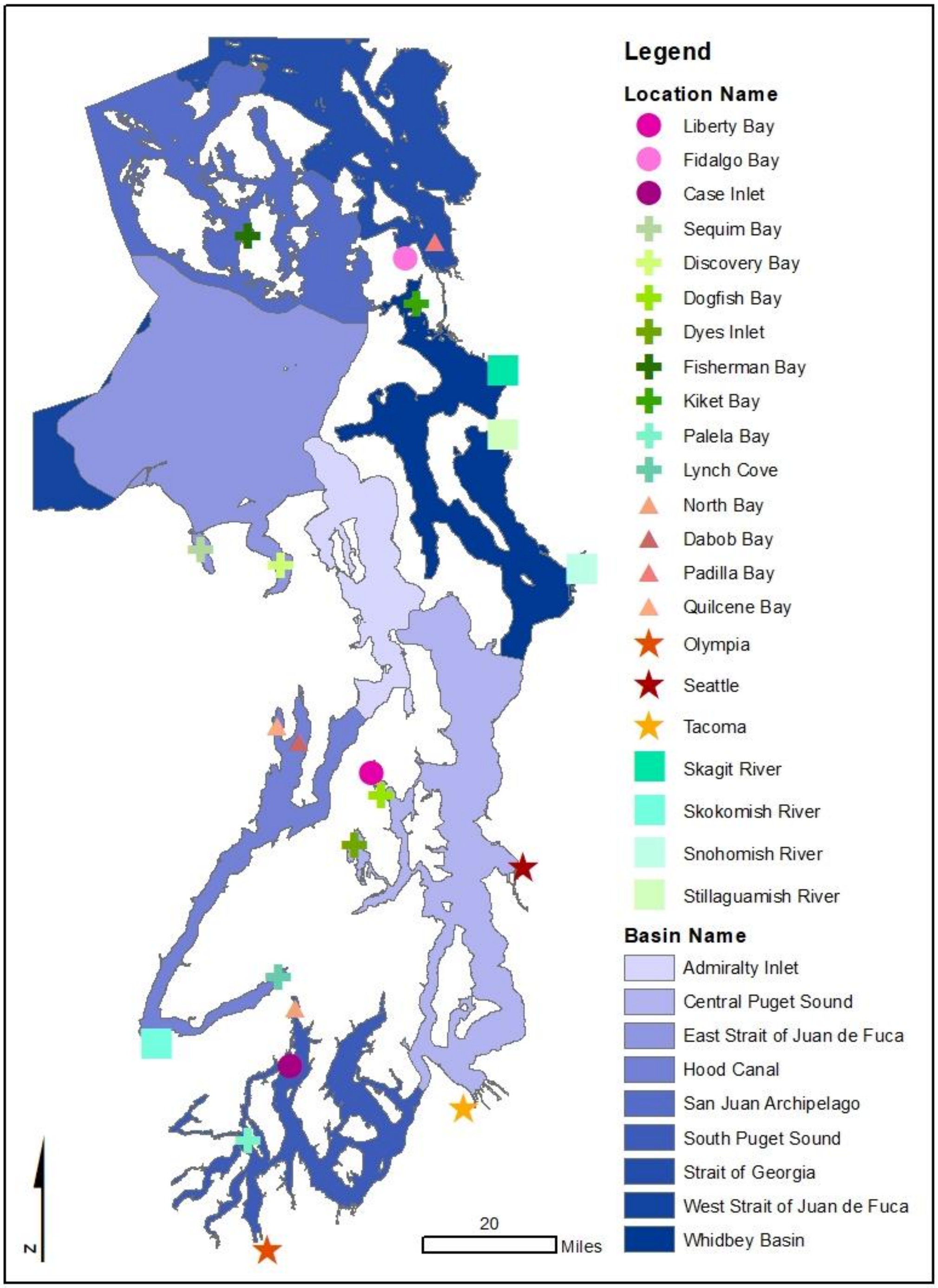

Figure 11. Map showing the extent of the study area and locations described in the chapters and appendices. The pink circles show the locations of case study sites where the HSI is applied and described, the plus signs indicate Olympia oyster restoration sites discussed, the triangles show additional locations mentioned in text, the stars show major cities for reference, and the squares show major river mouths for reference.

Olympia oysters were once economically important in the Salish Sea and along Washington's outer coast (White et al., 2009b). Olympia oysters were harvested and traded by many Coast Salish peoples since time immemorial (COSEWIC 2011 and sources therein); middens have been found dating back at least 4,000 years (White et al., 2009b). Tribal winter villages appeared to have been associated with dense oyster beds, and tribes may have cultivated oysters (Blake & Bradbury, 2012 and sources therein). Large beds of Olympia oysters existed in Puget Sound in the 1850s (White et al., 2009b and sources therein). However, the onset of large-scale commercial harvest around this time initiated a period of rapid overexploitation of native oyster beds. Figure 12, reproduced from White et al. (2009b), shows the precipitous declines in oyster production from Willapa Bay and Puget Sound. Production was sustained for slightly longer in Puget Sound due to aquaculture in diked systems, however this method relied on natural recruitment of seed oysters and clean water and was eventually discontinued as recruitment failure became more common (White et al., 2009b).

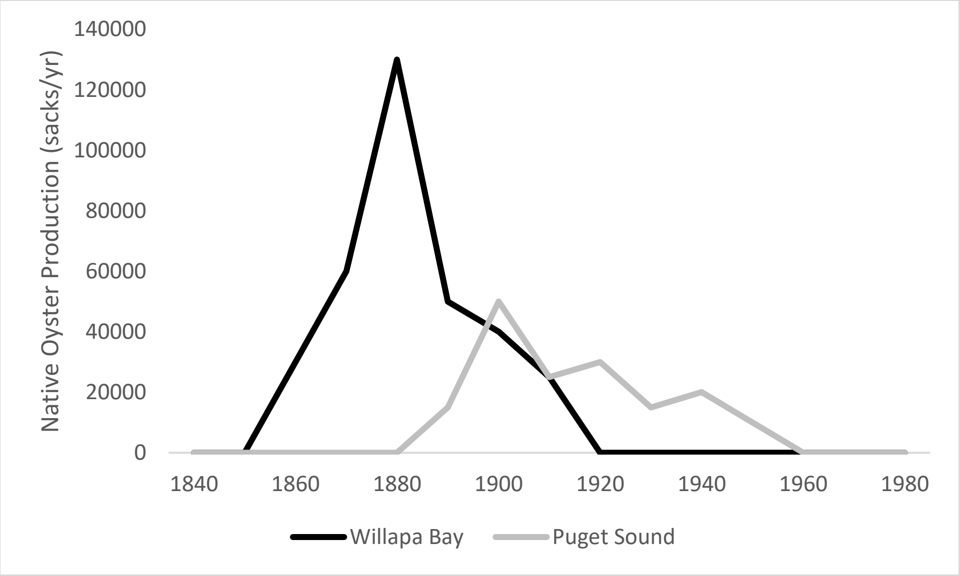

Figure 12. Historical Olympia oyster harvest production from Washington, reproduced from White et al. 2009b

Information about the specific historical locations of oyster beds within the Salish Sea is patchy, though estimates have been reconstructed from examination of historical records. Historical population locations should not necessarily be used to guide restoration strategy in contemporary conditions, as conditions have changed, and these sites may be constrained by a range of factors. However, knowledge of historical population locations is important context for this project. Information on pre-commercial harvest populations of Olympia oysters tends to be qualitative rather than quantitative; early records note that Olympia oysters were present in commercial quantities in Bellingham Bay, Samish Bay, Discovery Bay, Hood Canal, and in the inlets of Southwest Puget Sound (Baker, 1995 and references therein).

Table 10 describes historical Olympia oyster populations in the southern Salish Sea (i.e., circa 1850), from the WDFW Management and Stock Rebuilding Plan (Management Plan; Blake & Bradbury, 2012). While native oysters occurred throughout much of Puget Sound, reviews of historical data reveal that prior to intensive harvest, Olympia oysters did not occur in dense, large-scale natural beds throughout the region. Large beds were found in a limited number of locations where conditions were optimal, including at the heads of inlets, within constricted embayments, and in broad, shallow un-constricted bays; these sites are listed in the table below.

Current population status is also included in Table 10, based on the qualitative descriptions provided in the Management Plan (Blake & Bradbury, 2012). In addition to these descriptions, quantitative surveys have been conducted in specific locations for monitoring or research endeavors, such as at Fidalgo Bay (e.g., Allen et al., 2015; Dinnel, 2018; Clallam MRC, 2017) and in Hood Canal (WDFW, 2020b). Information from targeted surveys provides greater detail on population status than described in the table below. For example, Valdez et al. (2017) found Olympia oysters at low densities (6-8/m^2) at Twanoh, and the population of oysters in North Bay was estimated at 26.8 million in 2008 (White et al., 2009a). In unpublished observations, WDFW found mean densities of Olympia oysters between 1 and 7 oysters per square foot at sites in Hood Canal between 2014 and 2019 (WDFW, 2020b). More detailed population information is available for British Columbia, where presence/absence and abundance surveys have been conducted, though data, particularly time series, are still rare (COSEWIC, 2011). NAs in Table 10 below indicate where information is not provided in the Management Plan; populations may be described by other sources or nonexistent.

Table 10. Historical and contemporary information on native oyster populations (Blake & Bradbury, 2012)

Sub-Basin	**Site Name**	**Historical Population**	**Current Population**
North and San Juan Islands	Drayton Harbor	Large oyster beds	Known presence
	Bellingham Bay	Large oyster beds	NA
	Portage Island	Large oyster beds	NA
	Chuckanut Bay	Large oyster beds	NA
	Samish Bay	Large oyster beds; ~2,000 acres	Known presence
	Padilla Bay	Large oyster beds	NA
	Fidalgo Bay	Large oyster beds	Known presence, recent resurgence of natural larval sets
	Similk Bay	Large oyster beds	NA
	Dugalla Bay	Smaller beds/occurrences	NA
	Penn Cove	Smaller beds/occurrences	NA
	Shoal Bay Lagoon	NA	Known oyster presence
Strait/ Admiralty Inlet	Sequim Bay	Moderate-small oyster beds	NA
	Discovery Bay	Moderate-small oyster beds	Naturally occurring oysters present, appear self-sustaining with low density
	Kilisut Harbor	Moderate-small oyster beds	Naturally occurring oysters present, appear self-sustaining with low density
	Port Gamble Bay	Moderate-small oyster beds	Naturally occurring oysters present, appear self-sustaining with low density
Hood Canal	Quilcene Bay	Very large oyster beds	Naturally occurring oysters present throughout Hood Canal, small and large beds absent.
	Union River/Big and Little Mission Creek	Very large oyster beds	
	North Dosewallips Tidelands	Very large oyster beds	
	Lynch Cove	Large oyster beds; ~500 acres	
Central	Liberty Bay	Large oyster beds	Naturally occurring oysters present

	Dyes Inlet	Large oyster beds	Naturally occurring oysters present
	Sinclair Inlet	Large oyster beds	NA
	Port Madison	NA	Naturally occurring oysters present
	Manchester	NA	Naturally occurring oysters present
	Brownsville	NA	Naturally occurring oysters present
South	Budd Inlet	Large oyster beds	Naturally occurring oysters present
	Henderson Inlet	Large oyster beds	Naturally occurring oysters present
	Carr Inlet	Large oyster beds	Naturally occurring oysters present
	Totten Inlet	Large oyster beds	Naturally occurring oysters present, bed structure not present but supports commercial collection of wild origin spat
	Big Skookum Inlet	Large oyster beds	Naturally occurring oysters present
	Eld Inlet	Large oyster beds	Naturally occurring oysters present
	Oakland Bay	Large oyster beds	Naturally occurring oysters present
	North Bay	Large oyster beds	Naturally occurring oysters present, single example of a naturally self-sustaining native oyster bed in region

B. Olympia Oyster Restoration in the Southern Salish Sea

Olympia oyster restoration has been underway for over two decades in the Southern Salish Sea. PSRF has served as a leader in initiating and coordinating restoration efforts, and many partners have been involved in restoration endeavors (Table 11). Groups in addition to those listed in Table 11 have likely provided direct and indirect support to projects and the broader effort. Roles include implementing restoration work, providing in-kind and financial support for restoration actions, and managing and overseeing recovery efforts.

Table 11. Landscape of partners involved in Olympia oyster restoration

Entity Type	Names
Pacific Northwest Tribes and Tribal Organizations	Jamestown S'Klallam Tribe, the Lummi Nation, the Swinomish Indian Tribal Community, the Skokomish Tribe, the Squaxin Tribe, the Suquamish Tribe, the Samish Tribe, Northwest Indian Fisheries Commission
Shellfish Industry	Drayton Harbor Oyster Company, Taylor Shellfish Farms, Seattle Shellfish Company, Olympia Oyster Company, Blau Oyster Company
State Agencies and Federal Agencies	Washington Department of Fish and Wildlife, Washington Department of Natural Resources, National Oceanic and Atmospheric Administration, US Navy Manchester, USDA
Marine Resource Committees and Regional Marine Management Entities	Northwest Straits Commission, Northwest Straits Foundation, Whatcom County MRC, Clallam County MRC, Jefferson County MRC, Skagit County MRC
Nonprofits and Foundations	Puget Sound Restoration Fund, The Nature Conservancy, Slow Food Puget Sound, Washington Sea Grant, Nooksack WCC, Shannon Point Marine Center, Rose Foundation for Communities and the Environment, Coastal Volunteer Program at Padilla Bay, Salish Sea Stewards
Education	University of Washington, Western Washington University, Bellingham Technical College
Other	Port of Seattle, Port of Brownsville, City of Anacortes, Shell Puget Sound Refinery, Skagit County Public Works, Port of Anacortes

Olympia oyster restoration projects have been implemented from near the Canadian border to southern Puget Sound in Washington's waters of the Salish Sea, and involved many of the partners listed above. The term "restoration" is used broadly to describe a wide range of activities related to recovering the population of Olympia oysters. Activities include enhancing habitat by adding clean Pacific oyster shell to the substrate, spreading Pacific oyster shell seeded with Olympia oysters (sometimes called spat-on-shell or seeded cultch), out planting single Olympia oysters, or adding bags of oyster seed. Activities also include capturing natural oyster "set" and monitoring recruitment.

To the author's knowledge, there is limited data describing restoration projects that have been implemented in the Salish Sea that includes quantitative population assessments following restoration. Few projects have had support for long-term monitoring to understand restoration outcomes at these sites and use findings to inform additional restoration planning. The Management Plan describes early restoration efforts, which distributed hatchery-produced Olympia oyster seed throughout Puget Sound. Outcomes of these efforts are unknown and have not, in many locations, been shown to contribute to re-establishing sustainable oyster populations (Blake and Bradbury, 2012). Restoration outcomes from later and ongoing projects are known at some sites. For example, projects in Liberty Bay/Dogfish Bay and Fidalgo Bay have contributed to increased extent, abundance, and reproduction of oyster populations. In 2019, the Native Olympia Oyster Collaborative (NOOC) undertook an effort to survey restoration practitioners and compile information on restoration sites and outcomes from Canada to Southern California (NOOC, n.d.). The survey identified 39 restoration sites coastwide, including 16 in the Salish Sea (15 in Washington; 1 in Canada). Several sites may be the location of more than one project, either at unique sites within a bay or during different years. Researchers have previously identified over 40 restoration projects in Washington (White et al., 2009b), and early seed distribution projects included about 80 locations throughout the region (Blake & Bradbury, 2012).

Table 12 below provides an inventory of many of the Olympia oyster restoration projects within the study region. This table was developed based on the data compiled by the NOOC team, as well as supplementary review of monitoring reports and other project documentation where available. Future research could engage practitioners to ensure that the list of sites and projects are complete, the descriptions of the projects is accurate, and outcomes are up to date. Importantly, PSRF and partners are conducing restoration actions each year as they work towards their goal of 100 acres by the end of 2020. The table is organized by the general location of the restoration site. The years listed describe the dates that restoration actions were implemented; there may be additional years of monitoring or later restoration actions not described in the documentation as many of these projects are ongoing. Primary project partners are listed, though projects may include additional partners. Project goals are paraphrased from the data collected by NOOC or other project documents. The description provides a high-level overview of the types of restoration activities conducted at each site, including if the project was a substrate enhancement or if it involved outplanting oysters seeded onto Pacific oyster shells or as individuals, and, if available, information about the chronology these actions were taken. Status/outcomes provide a snapshot of the population data available for each site following restoration. For sites included in the NOOC survey, overall abundances in years one, five, or 10 are listed; for sites where more detailed monitoring has taken place, mean densities are included. No information on population or outcomes is available for some sites. The sources listed describe the restoration projects, including any project or monitoring reports, published papers identified, and databases; bolded entries are the primary sources for the information included in the table.

Table 12. Olympia oyster restoration projects.

Site	Years	Partners	Goal	Description	Status/Outcomes	Sources
Belfair/ Lynch Cove	2013, 2015	PSRF, UW	Restore Olympia oysters, involve citizen scientists, explore impacts of oyster outplants on eelgrass	Study tested several restoration methods: seeded shell spread on test plots, seeded shell on stakes, and spreading single Olympia oysters. Oyster and eelgrass survival and growth was monitored.	Widespread mortality of out planted oysters due to sedimentation and potential effects of predation or competition. Zero oysters on restoration substrates after year 5.	NOOC, n.d.; **Valdez et al., 2017**; Valdez & Ruesink, 2017
Budd Inlet	2006, 2012	PSRF, Pacific Shellfish Institute, Squaxin Island Tribe	Reestablish Olympia oyster populations	250,000 Juvenile oysters scattered on the beaches of Tykle Cove in 2006. Olympia oyster seed out planted along a beach in East Bay in 2012.	NA	**Pacific Shellfish Institute (PSI), 2013**
Chuckanut Bay	2018	Whatcom MRC	Explore restoration potential for native oysters and involve community members	Potentially suitable sites identified in 2016 and 100,000 oysters spread at seven subplots in 2018; monitoring is ongoing.	NA	**NOOC, n.d.; Rose, 2018**
Discovery Bay	2014, 2016	Jamestown S'Klallam Tribe, WDFW, Jefferson MRC	Expand small extant population of Olympia oysters in Discovery Bay	Half acre of oyster shell added in 2014 and more added to the tidelands in 2016 near the main population in the Bay.	Monitoring indicates natural recruitment and presence of multiple age classes. Average densities of about 38 oysters/m^2 in the oyster bed. Number of oysters on the restoration substrate increased from 1-1,000 after year 1 to 100,000-1,000,000 by year 5.	Jefferson County Marine Resources Committee, 2016, 2017, **2019**; Lull, 2006, 2010; **NOOC, n.d**.
Drayton Harbor	2014-2017	PSRF	Restore dense, persistent native oyster populations creating biogenic habitat	Bags of seeded cultch shell and single oysters were deployed as oyster restoration substrate.	Estimated 10,000-100,000 oysters on restoration substrates after year 1.	**NOOC, n.d.**
Dyes Inlet	2011-2018	Suquamish Tribe, PSRF	Recover oyster bed habitat at ecologically significant scales	Bags of seeded shell spread in Ostrich Bay, Mud Bay, and other locations in Dyes Inlet.	Estimated increase in number of oysters on restoration substrates from 100,000 - 1,000,000 after year 1 to >1,000,000 after year 5.	**NOOC, n.d.**
Eld Inlet	2003-2007	PSRF	Seed native oysters on tideland properties, enhance available substrate, monitor recruitment	Seeded cultch spread on tidelands.	Estimated 10,000-100,000 oysters on restoration substrates after year 1.	**NOOC, n.d.**
Elliot Bay	2018	PSRF, Port of Seattle	Restore and improve critical aquatic habitat in urban bays, create and monitor blue carbon storage.	In 2018, project partners added 3 tons of seeded oyster shell in Smith Cove. The project is also testing bull kelp and eelgrass plantings.	NA	**Cain, n.d.**

Site	Years	Partners	Goal	Description	Status/Outcomes	Sources
Fidalgo Bay	2002	Skagit MRC	Re-establish the first viable and naturally sustaining bed of Olympia oysters in Fidalgo Bay.	Restoration work began in 2002, with planting of seed oysters and in subsequent years. Survival, growth, and recruitment indicated favorable conditions. Out planting in sites around the bay have had mixed success. Additional shell substrate added in 2018, including seeding with juvenile oysters.	Survey results estimate a population of Olympia oysters that has steadily increased from about 50,000 oysters in 2002 to about 2.9 million oysters in 2018. Estimated number of oysters on restoration substrates has increased from 10,000-100,000 after year 1 to an estimated 100,000-1,000,000 after year 10.	Allen et al., 2015; Barsh et al., 2004; Dinnel, 2016, **2018**; Dinnel et al., 2009a; Dinnel et al., 2009b, 2006; Dinnel, et al., 2011; Gabrian-Voorhees, Dinnel, & Siu, 2013; **NOOC, n.d.**
Fishermen's Bay	2013	Kwiaht: Center for the Historical Ecology of the Salish Sea	Bring native oysters back into Fishermen's Bay, and create a nursery	Olympia oysters and Pacific oyster shell added to the bay.	Estimated number of oysters on restoration substrates declined from 0-1,000 after year 1 to zero after year 5.	**NOOC, n.d.**
Henderson Inlet	2007, 2018	PSRF, DNR	Enhance native Olympia oyster stock	Monitoring of native oyster population in 2006 and shell enhancement in 2007 at Woodard Bay NRCA. Olympia oyster seed outplanted into bags on the shoreline and distributed loose onto the substrate.	NA	**NOOC, n.d.**; PSRF, 2008
Liberty Bay	2001-2011	PSRF	Restore native biogenic oyster bed habitat at scales to achieve population connectivity and ecosystem services within the bay	Olympia oyster juveniles on shell added to the site.	Restoration work has been conducted at several locations. Dogfish Bay has had particularly positive outcomes. Densities within Dogfish Bay estimated at 165/m^2. Estimated number of oysters on restoration substrates increased from 0-1,000 after year 1 to greater than 1,000,000 after year 10.	**Doughton, 2019; NOOC, n.d.**
Port Gamble Bay	2014-2017	PSRF	Facilitate ecosystem recovery by rebuilding biogenic habitat structure in the intertidal environment, and enhancing food and habitat resources for tribes and the surrounding community into the future	Seeded Pacific oyster shells and individual Olympia oyster juveniles spread on the tideland.	NA	**NOOC, n.d.**

Site	Years	Partners	Goal	Description	Status/Outcomes	Sources
Quilcene Bay	2016-2018	Jefferson MRC, PSRF, WDFW, Tribal Co-managers	Test feasibility of re-establishing beds in Quilcene Bay under current conditions	Hatchery and wild-seeded Olympia oyster cultch placed in test plots in 2016, 2017, and 2018.	Number of spat per shell decreased from 2017 to 2018, prompting a decision to consider a new location at a lower tidal elevation.	Jefferson County Marine Resources Committee, 2016; **NOOC, n.d.; Puget Sound Partnership, 2019**
Sequim Bay	2012-2013, 2018	Jamestown S'klallam tribe, Clallam MRC, PSRF	Restore the ecosystem services that dense beds of native oysters once provided	Restoration work began on the tidelands of the Jamestown S'Klallam Tribe in 2012. Seeded cultch (~500,000 oysters) were spread onto the tidelands in 2013, and again in 2014 (~250,000) oysters. The total restoration site area is about 1.5 acres. Seeded cultch added at an additional site in 2016/2017. Sites monitored annually.	Mean oyster density in sampled plots has decreased from 2014 to 2018, oyster population area has increased. 2018 population estimated to be about 20,000 oysters. Number of oysters on restoration substrates estimated at 10,000-100,000 after year 1 and after year 5.	Clallam County Marine Resources Committee, 2016, 2017; **NOOC, n.d.**; Riccio, 2016; **Tobin, 2018**
Sinclair Inlet	2019	PSRF, Suquamish Tribe	Restore a healthy population of native oysters	1500 cubic yards of oyster shell added to the tidelands in 2019.	NA	**Dunagan, 2019**
Skokomish Estuary	2018, 2019	Skokomish Tribe, PSRF, USDA	Restore native oysters	A small amount of shell substrate spread in 2018 to assess site dynamics, with the plan for seeded cultch to be spread on the tidelands in 2019.	NA	**Northwest Treaty Tribes (NWTT), 2018**
Squaxin Island	2010, 2011	Squaxin Island Tribe, PSRF	Implement a shell enhancement and monitor recruitment	Natural set collection attempted with bags of Pacific oyster shell bag and other methods; set captured in low magnitudes.	Zero Olympia oysters on restoration substrates after year 1.	**NOOC, n.d.**
Swinomish Tidelands	2012, 2016	Swinomish Indian Tribal Community	Restore, enhance, and protect native oysters on Swinomish tidelands; research the ecological effects of Olympia oyster restoration in northern Puget Sound	Seeded Pacific oyster shell were distributed in Lone Tree and Kiket Lagoons in 2012 and 2013 and monitored for survival, growth, and recruitment. Additional oysters added to the lagoon sites in 2015.	Initial results indicated that the lagoons provided favorable habitat for Olympia oyster restoration, though larvae may be swept out during tidal exchange. Olympia oysters on restoration substrates increased from zero to an estimated 100,000-1,000,000 after year 5.	Barber et al., 2016, **2015**; **NOOC, n.d.**

C. Olympia Oyster Habitat Requirements

As interest and involvement in restoring Olympia oysters has grown in recent years, researchers have increasingly focused on understanding what environmental conditions create suitable habitat for Olympia oysters to survive and reproduce. There have been several reviews published that describe the relationship between Olympia oysters and their environment, requirements for survival, and stressors (Baker, 1995; COSEWIC, 2011; Couch & Hassler, 1989; Pritchard et al., 2015; Wasson et al., 2015). Starting with these five sources, I reviewed and compiled information on the habitat requirements of Olympia oysters, described in Table 13 below. Each of these five reviews describes additional primary literature. I then conducted a keyword search in Web of Science[1] to identify additional sources describing habitat requirements published since 2015. Table 13 provides a summary of factors that may influence the suitability of a site for restoring Olympia oysters, organized alphabetically.

Table 13. Habitat Requirements and Descriptions.

Habitat Factor	Detail and References
Acidification	• **Effects:** Studies have found sublethal effects of acidification on Olympia oysters including shell growth (Wasson et al., 2015, Pritchard et al., 2015), and there may be carryover effects for larvae exposed to low pH (Pritchard et al., 2015). In California, sublethal effects observed when levels were below 7.9 for 52 days (Hettinger et al., 2012). In Puget Sound oysters, elevated pCO2 was found to negate the positive effects of elevated temperature, and offspring of parents exposed to elevated pCO2 showed higher survival in some bays, demonstrating a carryover effect from parental exposure (Spencer et al., 2019). Olympia oysters, which build shells slowly and brood their larvae, are thought to experience less negative impacts from ocean acidification during the shell building stage than Pacific oysters (Waldbusser et al., 2016). • **Future concern:** Ocean acidification is of great concern for native oysters (Blake & Bradbury, 2012; WDFW, 2015).
Competition	• **Sessile invertebrates:** Slipper shells, jingle shells, barnacles, mussels, sponges, bryozoans, polychaetes, and other invertebrates may compete with Olympia oysters for food and space, and in some cases cause smothering (Couch & Hassler, 1989; Baker, 1995; Wasson et al., 2015; Pritchard et al., 2015). High cover of other sessile invertebrates has been found to contribute to reduced juvenile/recruit abundance, growth, and survival; competition/fouling is more severe at lower tidal heights (Deck, 2011; Wasson et al., 2015). Non-native fouling organisms, including ascidians, present a threat to juvenile survival; studies have documented reduced oyster survival by 50% in the presence of fouling organisms (Trimble et al. 2009; COSEWIC 2011). • **Pacific oysters:** Competitive effects from Pacific oysters (*Crassostrea gigas*) vary. Some sources indicate it can be a competitor, while others describe Pacific oysters as an important settlement substrate (Baker, 1995). Pacific oysters may create a larval sink by providing substrate at high tidal elevations (Trimble et al. 2009; Pritchard et al., 2015; COSEWIC 2011). Competitive effects from Pacific oysters may increase as waters warm (Valdez & Ruesink, 2017). In Willapa Bay, Olympia oyster growth rate and survival declined with increasing Pacific oyster density (Buhle & Ruesink, 2009). • **Burrowing shrimp:** Burrowing shrimp can destabilize sediments and contribute to smothering (Couch & Hassler, 1989; Baker, 1995; COSEWIC, 2011; Pritchard et al., 2015).

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[1] Web of Science keywords search: ("olympia oyster" OR "ostrea lurida") AND (habitat OR environment* OR ecology); Dates: 2015-2019; Results: 35, 22 relevant

Habitat Factor	Detail and References
Hypoxia	• **Hypoxic conditions:** Oyster die offs can occur in areas where tidal exchange is restricted and anoxic conditions are present. Diel cycling hypoxia can have sublethal effects, including reduced growth (Cheng et al., 2015; Wasson et al., 2015). Sub-lethal effects have been observed when dissolved oxygen is below 0.6 mg/L for 8 hours. Oysters are likely sensitive to hypoxia in Washington (WDFW, 2015) • **Dissolved oxygen levels:** Lower dissolved oxygen was linked with low oyster growth in Elkhorn Slough, California, and negative effects of hypoxia may outweigh positive effects of temperature and chlorophyll-a levels (Jeppesen et al., 2018). Olympia oysters in Washington require relatively high levels of dissolved oxygen (Dethier, 2006).
Elevation	• **Common ranges and observed populations:** Olympia oysters are most common at shallow subtidal and low intertidal elevations (COSEWIC, 2011). Though Olympia oysters have been found at depths over 10 meters (Baker, 1995) and as deep as 50-70m (Couch & Hassler, 1989; COSEWIC, 2011), they are rarely found in waters more than a few meters deep (Baker, 1995; Dethier, 2006). Olympia oysters are known to be present at low intertidal and subtidal depths in Grays Harbor, Willapa Bay, and Netarts Bay, which complicates survey efforts (Polson & Zacherl, 2009). In Puget Sound, oysters are primarily found in the mid-low intertidal range, with occasional observations of subtidal beds associated with intertidal beds and tidal channels (Blake & Bradbury, 2012; Allen et al., 2015) • **Site specific upper and lower limits:** Oyster abundance at different tidal elevations varies by site. In general, oysters are abundant around 0m MLLW (Wasson et al., 2015) and within the range of +0.5 to -1.0/-1.5m MLLW (Deck, 2011; Kimbro et al., 2009). In Puget Sound, oysters are primarily found between -3.0 and +1.0 ft. MLLW (Blake & Bradbury, 2012; Allen et al., 2015). Successful restoration sites in Fidalgo Bay are located at about -2 to -4 ft MLLW (Dinnel et al., 2009). Oysters may be found as high as 2m/5 ft. above MLLW, though abundance generally decreases rapidly above +1ft (Allen et al., 2015). Other studies have documented low survival at +0.3m MLLW compared to lower elevations (Pritchard et al., 2015) and low densities above +0.2m MLLW (Tronske et al., 2018). Maximum densities may vary in elevation within the same bay as well as between sites; Olympia oysters were found to be most dense in Twanoh on the east side at 0m MLLW, and at -0.6m MLLW on the west. In Nahcotta, oysters were most dense at +0.3 within a Pacific oyster reef. In North Bay, the population is between -1 and 0.3m MLLW (White et al., 2009a). In Newport Bay, maximum densities were observed at -0.15m MLLW (Zacherl, Moreno, & Crossen, 2015). • **Elevation and recruitment:** Studies have found that more than twice as many oysters recruited below than above MLLW (Trimble et al., 2009; Zabin et al., 2016). Recruitment was consistently higher at 0 than +0.6 MLLW in North Bay, Washington (White et al., 2009a). • **Other interactions:** Elevation interacts with many environmental factors, including feeding time, duration of air exposure, and competition with other sessile invertebrates (Wasson et al., 2015). For example, oysters may show higher growth rates subtidally than intertidally due in part to feeding time (Pritchard et al., 2015). In Hood Canal, the lower elevation limit may be set between -3.0 and 0.0 ft. MLLW due to suspected sea star predation (Allen et al., 2015; Blake, 2014).
Exposure and air temperatures	• **Low temperatures:** Olympia oysters cannot withstand freezing temperatures, which may set the upper limit of their range at higher latitudes (Baker, 1995; Contesse & Peabody, 2005; Trimble et al., 2009; COSEWIC, 2011; Wasson et al., 2015, Pritchard et al., 2015). Significant mortalities in Washington and Canada have been attributed to unusually cold weather (COSEWIC, 2011; Blake & Bradbury, 2012). Early culture techniques in Washington involved constructing dikes to hold water during low tides to mitigate low temperatures (Trimble et al., 2009). • **High temperatures:** Mortality begins to occur at air temperatures at or above 40°C for eight hours (Wasson et al., 2015; Wasson, Zabin, Bible, Ceballos, et al., 2014); high summer temperatures can cause mortality in young-of-the-year oysters and recruitment failure in the intertidal zone (COSEWIC, 2011). Desiccation during low tide may contribute to juvenile mortality (Kimbro et al., 2018).

Habitat Factor	Detail and References
	• **Juvenile mortality:** Trimble et al. (2009) found high juvenile mortality with longer durations of air exposure (Pritchard et al., 2015); survival dropped by 50% with air exposure times of 2-10%. • **Reducing exposure:** Vulnerability to air temperature extremes likely explains the limitation of large beds to low tidal elevations, lagoons, or habitats with standing water (COSEWIC, 2011). Standing or flowing water during low tides, including from seeps and moist substrates, provides thermal refuge for oysters and is a key consideration for restoration (Dinnel et al., 2008; White et al., 2009a, Blake, 2014; Allen et al., 2015; Valdez & Ruesink, 2017).
Phytoplankton abundance	• **Chlorophyll a levels:** In California, chlorophyll a concentrations are correlated with oyster performance, including juvenile growth rates and recruitment (Hollarsmith et al., 2019; Wasson et al., 2015). Studies have found oyster growth rates correlated with phytoplankton productivity in Tomales Bay (Kimbro et al., 2009). In Puget Sound, oyster spawning timing may correlate with chlorophyll a levels, but needs further investigation (Heare et al., 2017).
Location	• **Shoreline types:** Throughout its range, the Olympia oyster is considered an estuarine species and generally restricted to bays, estuaries, tidal channels, sounds, lagoons, coves, and protected locations (Couch & Hassler, 1989; Baker, 1995; Pritchard et al., 2015; COSEWIC, 2011). In Puget Sound, Olympia oysters are associated with shore types including estuarine deltas, estuaries, and low-energy bays that provide protection from wind, waves, and currents (Contesse & Peabody, 2005; Dethier, 2006), and shorelines with low to moderate drift cell function (Blake, 2014; Allen et al., 2015). Shorelines with a gentle slope (e.g., 1-5%) may provide conditions suitable for oysters (Blake, 2014). • **Estuary characteristics:** Estuary size showed a slight negative correlation with recruitment failure, and estuaries with a greater network of population sites are also less likely to experience recruitment failure (Wasson et al., 2016).
Parasites and disease	• **Parasites:** Species of parasitic copepod (oyster redworm), flagellated protozoans, and protistans can affect the health of Olympia oysters (Couch & Hassler, 1989; Baker, 1995; Pritchard et al., 2015; COSEWIC, 2011), but Olympia oysters are not considered highly sensitive to parasites (Baker, 1995; Wasson et al., 2015). • **Disease:** Some believe that Denman Island disease contributed to population declines and low population levels (COSEWIC, 2011)
Predation	• **Oyster drills:** Introduced predators including the Japanese oyster drill (Couch & Hassler, 1989; Baker, 1995; Blake & Bradbury, 2012; Wasson et al., 2015; Pritchard et al., 2015) can negatively impact Olympia oyster populations. At restoration sites in Liberty Bay, Japanese oyster drills demonstrated a strong negative impact on juvenile oyster survival (Grason & Buhle, 2016). Drills caused near zero survival of experimentally outplanted oysters at some sites in Padilla Bay (Lowe et al., 2019), and are known to contribute to mortality in Hood Canal and Willapa Bay (Valdez et al., 2017; Buhle & Ruesink, 2009). Atlantic oyster drills also caused mortality at some sites in British Columbia, though their numbers have diminished (COSEWIC, 2011). Atlantic oyster drills remain a threat in California (Grosholz & Zabin, 2009; Kimbro et al., 2019), where higher temperatures and more variable salinity along the estuarine gradient favor invasive drills (Cheng & Grosholz, 2016). Olympia oysters may rapidly evolve adaptive defenses to invasive predators, such as the Atlantic oyster drill (Bible, Griffith, & Sanford, 2017). Non-native drills may be a limiting factor at some sites but appear to co-occur in abundance at others (Blake & Bradbury, 2012). • **Native and invasive crabs:** Several species of crab are known predators of Olympia oysters, particularly at higher salinity sites (Couch & Hassler, 1989; Baker, 1995; Wasson et al., 2015; Pritchard et al., 2015). The invasive European Green Crab has shown a preference for Olympia oysters in laboratory experiments, though the effect on wild populations in Canada or Puget Sound has not been quantified (COSEWIC, 2011).

Habitat Factor	Detail and References
	• **Other predators:** Native sea ducks (e.g., Scaups and Scoters) are known to predate on oysters (Couch & Hassler, 1989; Baker, 1995; COSEWIC, 2011). The Japanese flatworm has also been known to negatively affect populations (Couch & Hassler, 1989; Baker, 1995; Blake & Bradbury, 2012; COSEWIC, 2011). Seastars are also known predators (Wasson et., al 2015; Allen et al., 2015). It is recommended that restoration sites are fairly free of oyster drills, sea stars, moon snails, and other natural enemies of oysters (Contesse & Peabody, 2005).
Salinity	• **Optimal levels:** Optimal salinity levels are above 25 ppt/psu (Couch & Hassler, 1989; Dethier, 2006; Pritchard et al., 2015). Studies found a strong negative correlation between exposure to salinities below 25 and average size, recruitment rate, and growth (Wasson et al., 2015). In southwest Puget Sound, the lower salinity limit for large populations was found to be 23-24 ppt on average during winter months (Baggett et al., 2014; Baker, 1995; Contesse & Peabody, 2005). However, brooding activity has been documented at lower mean salinities (~20-23) in north Puget Sound (Barber et al., 2016). In California, peak recruitment occurs when salinity is 25-30 (Chang et al., 2018), and larvae were found to be most abundant in Oregon at salinities above 25 (Peteiro & Shanks, 2015). • **Survivable levels:** Oyster can tolerate exposure to lower salinities, including several weeks of exposure to salinity levels at 15 ppt (Baker, 1995; Pritchard et al., 2015). Historically, their range was constrained between polyhaline and mesohaline zones (Gray et al., 2019). • **Impacts of low salinity:** Oyster performance in inner bays near freshwater sources may be negatively impacted (Hollarsmith et al., 2019; Pritchard et al., 2016). Researchers observed mass mortality across several sites in San Francisco Bay when salinity dropped below 6.3 for 8 continuous days (Cheng et al., 2015, 2016). Olympia oysters experienced significant mortality when exposed to salinity below 10 for five days in the lab (Wasson et al., 2015) and at salinity levels of 5 for 7 days (Bible, Cheng, et al., 2017), though lethal effects may not be observed over shorter durations (e.g., 5 days) (Maynard et al., 2018). Oysters did not experience significant mortality in a lab setting with exposure to low salinity for 4 days (Cheng et al., 2017). In a study conducted in Oregon, oyster clearance rates declined precipitously between salinities of 18 and 10, and oysters ceased feeding until salinities were greater than 10 (Gray & Langdon, 2018; Gray et al., 2019). However, others report that oysters can survive low salinity for two to three weeks (Pritchard et al., 2015). • **Interactions:** Low salinity and temperature effects may have interactive effects; oysters experienced high mortality after 7 days at 5 psu and 10 psu with thermal stress (Bible, Cheng et al., 2017). Frequent low salinity events may reduce predators as well as contribute to oyster mortality (Couch & Hassler, 1989; Cheng & Grosholz, 2016; Kimbro et al., 2018). Researchers assessing recruitment dynamics coastwide found a positive correlation between higher winter salinities and more frequent recruitment failure and a negative correlation between recruitment failure and estuaries with stronger freshwater inputs, potentially indicating that more heterogeneity and weaker marine influence may lessen risk of recruitment failure (Wasson et al., 2016).
Substrate and sediment	• **Settlement substrate:** Oysters require hard substrate for settlement. Settlement substrate may include small pieces of hard substrate in softer mud areas, as well rocky reefs, smaller rocks, piles, and other surfaces (Baker, 1995; COSEWIC, 2011; Wasson et al., 2015; Pritchard et al., 2015). Examples of suitable substrate include: a base of firm sand/mud with a presence of emergent shell and gravel (Allen et al., 2015; Blake, 2014); firm substrate, composite areas of sand, mud, shell material, and rock (Contesse & Peabody, 2005); rocks cobble or other hard substrate (Deck, 2011); shallow subtidal muddy habitats with harder substrate like shells or pebbles (Dethier, 2006); firm substrate composed of gravel and accumulations of clam and oyster shells (Dinnel, 2009); and rocks and cobbles (Kimbro et al., 2009). A survey of bays in Southern California found that Olympia oyster density varied among substrate types and

Habitat Factor	Detail and References
	between bays; though generally densities where higher on both natural and human-introduced hard substrates (Tronske et al., 2018). Studies comparing recruitment found that Olympia oyster shell received significantly more recruits than gravel or bare areas (White et al., 2009a); others found more recruitment on shell substrates located in cobble environments compared to mud, but lower survival (Zabin et al., 2016). Degradation of restoration substrates can be a reason for declines in restored populations (Dinnel, 2018). • **Sedimentation:** Silt and fine sediments can smother oysters, limiting water circulation and creating challenges for feeding and respiration (Couch & Hassler, 1989; Blake & Bradbury, 2012; Wasson et al., 2015). Hard substrates in deep mud may sink and result in smothering (Pritchard et al., 2015); thus, vertical relief from sedimentation is important (Zacherl et al., 2015). Sedimentation from floods and landslides may pose risks to population persistence (COSEWIC, 2011). Newly settled, juvenile oysters may be particularly sensitive to smothering by fine sediments (Dinnel et al., 2009; Valdez et al., 2017). In Puget Sound, ideal habitat is characterized by low suspended sediments (Dethier, 2006). Softer conditions may be amenable to shell-based enhancement if tidal prism function is sufficient to prevent accumulations of silt (Blake, 2014).
Water temperature	• **Spawning threshold temperatures:** Oysters begin spawning when summer water temperatures reach a minimum threshold (COSEWIC, 2011), which may vary by latitude. Spawning generally occurs when water temperatures reach 13-16°C (COSEWIC, 2011; Couch & Hassler, 1989; Moore et al., 2016; Peter-Contesse & Peabody, 2005; Polson & Zacherl, 2009). The lower limit for spawning has been reported at a daily minimum of 12/12.5°C (Baker, 1995; Peter-Contesse & Peabody, 2005; Dethier, 2006; COSEWIC, 2011) or 13°C (Pritchard et al., 2015). However, recent research in northern Puget Sound found evidence of brooding when water temperatures reached 10.5°C, two weeks before temperatures of 12.5°C were recorded (Barber et al., 2016). In Fidalgo Bay, brooding was observed about 3 weeks after water temperatures passed 13°C (Allen et al., 2015); spawning temperature thresholds were reached by mid-May (Dinnel, 2009). In California, peak recruitment occurs when temperatures exceed 16°C (Chang et al., 2018). In Coos Bay, Oregon, larvae were found to be most abundant when water is warm >16°C (Peteiro & Shanks, 2015); the critical threshold for gametogenesis in Coos Bay is 15°C daily minimum; below which adults may not be capable of spawning (Pritchard et al., 2016). In a coastwide study of recruitment failure, temperature during the breeding period was negatively correlated with recruitment failure (Wasson et al., 2016). Larval development and duration and timing of reproductive phases are thought to be temperature dependent (COSEWIC, 2011). • **Temperature and oyster performance:** Research in California found positive correlations between the percent of days with water temperatures above 12°C and growth rate, average size, recruitment rate, and adult density (Wasson et al., 2015). In addition, juvenile oysters showed increased growth at 24°C compared to 20°C (Cheng et al., 2015). In Tomales Bay, cold water temperatures were found to correspond with low oyster growth and warmer temperatures corresponded with higher oyster growth, though inner bay temperatures may reach levels that stress juvenile oysters (Hollarsmith et al., 2019). Other studies in Tomales Bay have found that phytoplankton concentration and dissolved oxygen patterns may better explain patterns of oyster size and growth (Kimbro et al., 2009; Jeppeson et al., 2018). In a lab study, optimal temperatures for oyster growth with abundant food increased linearly from 16 to 30°C; under low rations, highest growth rates were recorded at a threshold of 19.3°C (Cheng et al., 2017). A recent study in Oregon observed maximum clearance rates for Olympia oysters at 25°C (Gray & Langdon, 2018). In Puget Sound, oysters exposed to the warmest temperatures grew to the largest size (Heare et al., 2017). Oysters in this region experience wide temperature ranges; Olympia oysters in Dabob Bay may be exposed to temperatures as high as 29°C during the summer or as low as 3°C during the winter (Heare et al., 2017). Temperature may affect competition with Pacific oysters, which require warmer temperatures for recruitment (Valdez & Ruesink, 2017).

Habitat Factor	Detail and References
	• **Temperature extremes and mortality:** Olympia oysters are sensitive to temperature extremes and cannot survive freezing temperatures (Couch & Hassler, 1989). Lab studies found >50% probability of mortality (LT50) in sea water above about 37.6-39°C for one to five hours (Bible, Cheng, et al., 2017; Brown et al., 2004; Cheng & Grosholz, 2016; Cheng et al., 2017; Heare et al., 2017; Wasson et al., 2015).
Water residence time and currents	• **Larval dispersal:** Olympia oyster larvae are rarely found in the nearshore coastal plankton; they are thought to stay in or near their place of origin, though dispersal has been documented over longer distances (Baker, 1995). Pelagic larval periods are suspected to be relatively short, limiting dispersal opportunities (COSEWIC, 2011). Sources indicate larval durations of 11-16 or 30 days (Couch & Hassler, 1989; Dethier, 2006; Dinnel, 2009). Recruitment densities have been found to be highest near restored oyster beds in Fidalgo Bay (Pritchard et al., 2015; Allen et al., 2015), suggesting retention behaviors for larvae. Bay currents are thought to be an important determinant of recruitment patterns (Dinnel, 2018). • **Water residence times:** Water residence times need to be sufficiently long for local retention in the bay or estuary. Restoration is recommended mid-bay where water residence times are long enough and current speeds slow enough to allow larvae to settle without being swept out of the bay, but tidal flushing is sufficient to deliver food and oxygen (Pritchard et al., 2015). In Tomales Bay, Olympia oyster larval duration is 28-42 days, and mean water residence time is 60 days. Recruitment density increases towards the inner bay, likely due to long residence times , allowing more larvae to complete development and settle rather than being flushed out (Kimbro et al., 2018); intermediate residence times allow for settlement and are associated with the greatest phytoplankton blooms (Kimbro et al., 2009). In Coos Bay, larvae are most abundant when residence times are higher (Peteiro & Shanks, 2015). Pritchard et al. (2016) found more abundant larvae riverward, suggesting that longer residence times in the inner bay facilitate larval retention. In a multivariate analysis, residence time was identified as an important contributor to the separation of estuaries with and without recruitment failure; 3 of 4 estuaries with recruitment failure have residence times shorter than two weeks, and at all eight estuaries in the study, there was generally near-zero recruitment in marine influenced sites near the mouth (Wasson et al., 2016). • **Currents:** Studies in Coos Bay showed that larvae perform vertical migrations, allowing them to be retained in the bay. Current speeds that exceed 0.5 m/s may prohibit this behavior (Peteiro & Shanks, 2015). In Puget Sound, Olympia oyster habitat is typically found in areas with limited exposure to the effects of wind, waves, and currents (Dethier, 2006; Allen et al., 2015; Contesse & Peabody, 2005).
Water quality and contaminants	• **Pollution:** Oysters are sensitive to water pollution (Couch & Hassler, 1989). In Puget Sound, early declines in oyster populations were linked sulfite pollution from pulp mills and untreated sewage (Baker, 1995; COSEWIC, 2011). In Canada, oyster declines may be associated with domestic pollutants from urbanization, industrial pollutants, and antifouling paints (COSEWIC, 2011). Recent studies have found oysters to be somewhat resilient to contaminants; individuals are found near water treatment outfalls, marinas, and in areas with long lasting pollutants (Wasson et al., 2015). • **Other water quality impacts:** Cumulative impacts of human alteration of estuarine environments including urbanization, sedimentation, bark decay, log storage, dredging, diking, filling, and pollution likely contributed to declines in Coos Bay and are of concern for sites in British Columbia (COSEWIC, 2011). In Puget Sound, shoreline/tideland modifications are a stressor (Blake & Bradbury, 2012; Blake, 2014). Studies of oyster clearance rates in Oregon show declines with increasing turbidity (Gray & Langdon, 2018), and high turbidity was a likely factor contributing to poor oyster condition in Willapa Bay at up estuary sites (Lowe et al., 2019).

D. FISBHE Tables and Model Development

The "framework to identify suitable bivalve habitat in estuaries" (FISBHE) provides a useful and cost-effective tool for translating natural history information into a spatial estimation of suitable habitat, particularly when population information is limited (Lewis et al., 2019). Tables 14-17 below are adapted from Lewis et al., (2019) and contain information for each environmental variable in this study. The following steps describe the process for defining HSI scores using FISBHE for guidance.

1. **Conduct literature review:** I compiled information (see Appendix C) regarding the tolerance of Olympia oysters to salinity, temperature, tidal elevation, and residence time conditions from published literature as well as key technical reports and gray literature/white papers.
2. **Populate FISBHE tables:** I first added the suitability information for each of the five key review papers (see Appendix C). The sources cited by these reviews are footnoted. I then added suitability information for all additional sources captured by the literature review. Additional sources included new research published since 2015 and sources from prior to 2015 if not already cited, including information from monitoring reports and other documents. The initial tables contained sources describing salinity tolerance (n=14), elevation tolerance (n=13), residence time tolerance (n=5), and temperature tolerance (n=18). Sources were added row-wise to the tables.
3. **Interpret and add suitability ranges:** I then filled in the suitability ranges for each source (i.e., gray shading). The tales also include descriptive information, such as: the measure of suitability for each study (e.g., mortality, growth, recruitment), if the ranges are described as full (e.g., range describes the upper and lower limits) or partial (e.g., upper/lower limit, optimal), if the description is qualitative or quantitative, and the geography.
4. **Limit to most relevant sources:** To simplify determining the suitability ranges, I limited the number of sources for each variable to 10, first selecting the review papers and then including additional sources based on their relevance. I prioritized sources that measured the species response to the environmental variable directly, and/or were from the Pacific Northwest.
5. **Define HSI score:** Based on the suitability ranges from the literature, I then assigned the four levels of HSI scores. Lewis et al. (2019) used a binary classification scheme to assign suitability scores, combining layers additively and resulting in a cumulative score between one and four. Theuerkauf and Lipcius (2016) describe that HSIs are generally between zero and one, with zero values assigned to unsuitable conditions and higher values assigned to more suitable conditions. The approach used here is similar to Theuerkauf and Lipcius (2016), where intermediate values are possible rather than only zero or one. In summary, optimal ranges are assigned a one, and survivable levels receive less than one, based on an assessment of the sources. This method, and calculating the overall HSI value using the geometric mean, results in any area where conditions are unsuitable for a variable being classified as unsuitable overall. This represents a more conservative estimation of suitability for applications to restoration.

The translation from the FISBHE tables to the threshold values used in the index is made using the authors' best assessment of the most relevant information for the application of restoration decision-making in the Southern Salish Sea. While this method requires some judgement, the information informing these decisions and any decision-points are described below, which makes this analysis both replicable and revisable if new information or interpretation emerges.

Salinity

Table 14 provides the suitability framework for salinity. Salinity levels constrain the physiological processes of many marine and estuarine organisms, including Olympia oysters (Wasson et al., 2015; Appendix C). Extreme low salinity events can cause mass mortality (e.g., Cheng et al., 2016), and salinity levels are also correlated with recruitment, feeding behavior, and growth. Optimal salinity levels for Olympia oysters are often described as over 25 (HSI = 1, green). Gray & Langdon (2018) found that Olympia oyster clearance rates were unaffected by salinities between 20 and 30,and Barber et al. (2016) observed reproduction at salinity levels as low as 20; thus I set the minimum of the second break at 20 (HSI = 0.66, yellow). Baker (1995) and Pritchard (2015) report relatively high survival among oysters exposed to salinities of 15 for several weeks; I set the minimum of the third break at 15 (HSI = 0.33, orange). Several studies report mortality at salinity exposures between 5 and 10 for varying amounts of time. Salinities below 15 were set at the lowest score (HSI = 0, red).

Table 14. Suitability Framework for Salinity

Mean wet season salinity (psu or ppt)

	Fresh																																**Marine**	**Measure**	**Range**	**Data type**	**Geography**
Source:	0	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	>32				
Baker 1995[1]															▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Abundance	Full	Review	PNW
Barber et al. 2016																				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Reproduction	Partial	Quantitative	PNW
Bible et al. 2016						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Mortality	Full	Quantitative	Other
Cheng et al. 2015 & 2017								▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Mortality	Full	Quantitative	Other
Cheng et al. 2016							▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Mortality	Full	Quantitative	Other
Couch & Hassler 1989[2]																										▨	▨	▨	▨	▨	▨	▨	▨	Survival	Partial	Review	PNW
Gray & Langdon 2018																				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨				Feeding	Partial	Quantitative	PNW
Hollarsmith et al. 2019																	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Growth, survival	Full	Quantitative	Other
Pritchard 2015[3]															▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Survival	Full	Review	General
Wasson et al. 2015[4]																									▨	▨	▨	▨	▨	▨	▨	▨	▨	Recruitment, growth, survival	Partial	Review, Quantitative	General
HSI SCORE	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟧	🟧	🟧	🟧	🟧	🟨	🟨	🟨	🟨	🟨	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				

[1] Hopkins 1937; Gibson 1974

[2] Korringa 1976

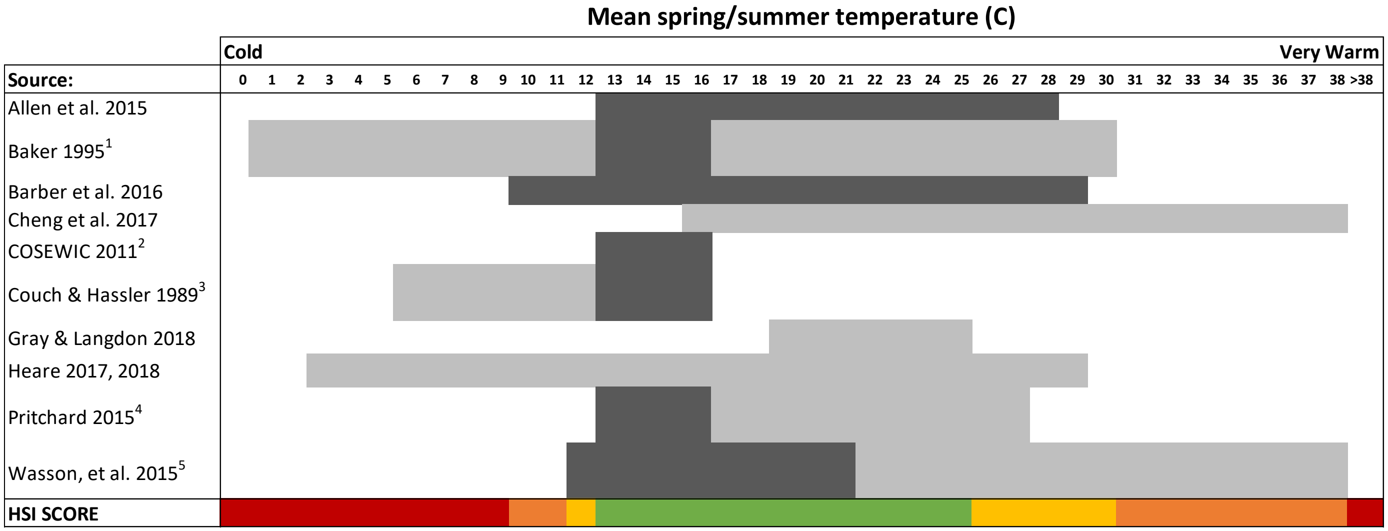
[3] Gibson 1974; Korringa 1976; Contesse & Peabody 2005

[4] Gibson 1974; Oates 2013; Cheng et al. 2015, Wasson et al. 2014

Temperature

Table 15 provides the suitability framework for temperature. Like salinity, temperature is associated with many physiological processes, including survival, growth, feeding behavior, and reproduction (e.g., Wasson et al., 2014). Spawning and brooding behavior are typically observed after temperatures reach 12.5 or 13°C (e.g., Baker, 1995; Allen et al., 2015), thus I set 13 as the lowest optimum average temperature (HSI=1). Oysters can survive at lower temperatures to freezing, but without enough days above the spawning threshold, restored populations in cold waters would not be expected to be self-sustaining. However, reproduction thresholds may be lower in different locations; Barber et al., 2016 observed brooding in north Puget Sound at 10.5°C, therefore lower thresholds are scored above 0 in this index. Mean temperatures below 10°C are ranked as a zero. Several studies have found that the upper limit for Olympia oyster survival is 38-39°C (Brown, 2004; Cheng et al., 2017), thus this is the upper temperature threshold (HSI = 0). One study (Gray & Langdon, 2018) found maximum clearance rates for Olympia oysters at 25°C. Others have found linear increases in oyster growth from 16°C to 30°C under high food availability, and an optimal temperature at about 19°C under low food availability. Thus, temperatures above 30°C and above 25°C are scored as HSI = 0.33 and 0.66, respectively. Mean temperatures in the Salish Sea are not typically this high, though temperature maximums in the intertidal may be quite warm. In Table 15 below, studies that describe reproductive behavior are marked as dark gray, while thresholds that describe survival and growth are light gray. While the lower limit is generally associated with reproduction and the upper ranges with overall performance and survival, research from central California found positive correlations with growth rate, average size, recruitment rate, adult density, and percent of days with water temperatures above 12°C (Wasson et al., 2014).

Table 15. Suitability Framework for Temperature



Measure	Range	Data type	Geography
Reproduction	Partial	Quantitative	PNW
Survival, reproduction	Full	Review	PNW
Reproduction	Partial	Quantitative	PNW
Growth	Partial	Quantitative	Other
Reproduction	Partial	Review	PNW
Reproduction, mortality	Partial	Review	PNW
Filtration	Partial	Quantitative	PNW
Presence	Full	Quantitative	PNW
Reproduction, presence	Partial	Review	General
Reproduction, survival	Full	Review	General

[1] Stafford 1915; Hopkins 1937; Davis 1955

[2] Hopkins 1937 and Strathman 1987

[3] Coe 1932; Hopkins 1937; and Davis 1955

[4] Stafford 1913; Hopkins 1937; Garcia & Peteiro-Shanks 2015; Carson 2010

[5] Santos et al. 1993; Brown 2004; Seale and Zacherl 2009; Oates 2013; Wasson et al. 2014; Cheng et al. 2015

Elevation

The suitability framework for tidal elevation is described in Table 16 below. Unlike salinity and temperature which directly affect physiological processes, tidal elevation is a proxy for several abiotic and biotic factors that determine the distribution of Olympia oyster populations, including predation, competition, and desiccation. Surveys have found that Olympia oysters are most common at about 0m MLLW, though optimal elevation may vary depending on the specific environmental factors (e.g., Wasson et al., 2015, Valdez et al., 2016). The amount of habitat at the appropriate tidal elevation is an important consideration for restoration planning. Where only a narrow band within the appropriate elevation exists (e.g., steep drop-off, armored shoreline, etc.) enhancement/restoration potential may be limited.

Table 16. Suitability Framework for Elevation

Bathymetric depth (ft. MLLW)

	Subtidal																					**High Intertidal**	**Measure**	**Range**	**Data type**	**Geography**
Source:	**<-10**	**-10**	**-9**	**-8**	**-7**	**-6**	**-5**	**-4**	**-3**	**-2**	**-1**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**>10**			
Allen et al. 2015 and Blake 2014									▨	▨	▨	▨	▨											Presence	Partial	Qualitative	PNW
Baker 1995[1]	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨						Presence	Full	Review	PNW
COSEWIC 2011[2]	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨						Presence	Full	Review	PNW
Couch & Hassler 1989[3]	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												Presence	Full	Review	PNW
Dinnel 2009								▨	▨	▨														Presence	Full	Quantitative	PNW
Pritchard 2015[4]									▨	▨	▨	▨	▨	▨										Survival, growth	Partial	Review	General
Tronske 2018												▨	▨											Density	Partial	Quantitative	Other
Valdez et al. 2106										▨	▨	▨	▨											Density	Partial	Quantitative	PNW
Wasson et al. 2015											▨	▨												Abundance	Partial	Quantitative	Other
White et al. 2009									▨	▨	▨	▨	▨											Presence	Full	Quantitative	PNW
HSI SCORE	🟥	🟧	🟧	🟧	🟧	🟧	🟧	🟨	🟩	🟩	🟩	🟩	🟩	🟨	🟧	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥				

[1] Hopkins 1937 and others

[2] Bernard 1983

[3] Hertlein 1959

[4] Deck 2011, Trimble et al. 2009

Water Residence Time and Currents

Table 17 shows a generalized suitability framework for water residence time. Studies in Coos Bay, Oregon, Tomales Bay, California, and across west coast estuaries have found that water residence time is correlated with Olympia oyster recruitment, larval abundance, and growth (Kimbro et al., 2009; Deck, 2011; Pritchard et al., 2016; Wasson et al., 2016). At sites near the mouths of bays and estuaries, low water residence times may cause larvae to be transported out of the bay before settlement. Larval abundance is high at the head of bays, but recruitment and adult populations were found to be lower in Coos Bay, potentially due to exposure to freshwater or other factors (Pritchard et al., 2016). In Tomales Bay, recruitment is high at the head of the bay, but growth and survival are highest mid-bay (Kimbro et al., 2008; Deck, 2011; Kimbro et al., 2019); phytoplankton are abundant were residence times are moderate. The number of days associated with optimal conditions vary between sites, so in this model, the lowest 20% of residence times and highest 5% are unsuitable (HSI = 0), and all other values are suitable (HSI = 1). A suitability framework is not included for current velocity because there is only one primary source available. Peteiro & Shanks (2015) describe that retentive behaviors of larvae were no longer effective at current velocities greater than 0.5 m/s.

Table 17. Suitability Framework for Water Residence Time

Water residence time (generalized)

	Low	**Moderate**		**High**	**Measure**	**Data type**	**Geography**
Source:							
Kimbro et al. 2019			▨	▨	Recruitment	Quantitative	Other
Pritchard 2015[1]		▨	▨		Growth, survival, recruitment	Review	General
Pritchard et al. 2016		▨	▨		Larval abundance, recruitment, adult presence	Quantitative	PNW
Wasson et al. 2016		▨	▨	▨	Recruitment failure	Quantitative	Other
HSI Model	🟥	🟩	🟩	🟥			

[1] Peteiro & Shanks 2015; Pritchard 2013; Kimbro 2008; Deck 2011; Rimler 2014

E. Estimation of Environmental Data Layers

Salinity and Temperature

The Washington State Department of Health (DOH) conducts marine water quality monitoring for shellfish growing areas throughout the state. Data is collected to measure fecal coliform, salinity, and temperature. The marine water quality monitoring program includes over 1800 stations, the majority of which are monitored six to 12 times per year, depending on status. DOH uses a systematic random sampling method, meaning they sample randomly with respect to tides, conditions, and time of year. However, samples are usually collected at tides high enough to ensure that the sites are covered by water (ebb or flood). Samples are typically collected in three to 12 feet of water. Temperatures may be biased high in the summer and low during the winter relative to deeper areas because tidal water temperatures are affected by the temperature of the shore during low tide. Stations are located near creeks, ditches, and other pollution sources, which may also bias temperature and salinity at times. Samples are collected from six inches below the surface of the water (DOH, pers. comm). While bottom water samples may be a more accurate representation of the conditions experienced by benthic organisms like oysters, DOH conducts this monitoring for shellfish growing, so it is assumed that these nearshore stations are representative of conditions relevant to oysters. Monitoring stations were established as early as 1934, though most stations were established after 1988. Data are collected as point measurements associated with a specific station. Data were downloaded from the DOH website for stations within the study area in December 2019, compiled into a single dataset, and then joined to the geometry of the stations using R Studio (DOH, 2020; 2019). This data set includes over 300,000 observations of salinity and temperature from over 1800 stations, including stations outside the study area (i.e., west of the boundary of the East Strait of Juan de Fuca basin). Observations from stations outside the study area were eliminated from the dataset.

I then created a dataset of mean winter salinities for each station within the study area. I first removed "NA" measurements from the data, then removed outliers over 40 psu that were assumed to be measurement error. I then selected the winter months (i.e., November-April), to capture the likely lowest salinity period. Note that this could later be refined; nearshore areas may experience the lowest salinities during different months depending on localized precipitation and snowmelt patterns. However, this month range is meant to capture likely low salinity periods for west coast watersheds (Lewis et al., 2019). I then calculated the mean winter salinity for each monitoring station, using all available years of data; the number of years included may vary greatly by station. For some stations in the study area, it was not possible to determine the sampling month. I chose to include these stations to improve the coverage of the point data set, using the overall mean. I followed a similar process to create a dataset of mean summer temperatures, including removing "NA" measurements, removing outliers over 40C, and selecting summer months (May-September) to capture the temperature during the reproductive season. I then calculated mean summer temperature, including an annual mean for stations where it was not possible to determine the month.

Mean salinities and temperatures at 1647 stations were included in the analysis (Figures 13 and 14). Points estimates were interpolated across the extent of the study area to create a continuous estimated surface for each environmental variable. I used the kernel interpolation method for this interpolation as it is one of the only geostatistical methods that allow for the inclusion of barriers, which is very important in complex estuaries like Puget Sound (Krause, n.d.). The "Geostatistical Wizard" tool in

ArcMap 10 was used for these interpolations. A bandwidth of 4000m was used to balance data coverage and accuracy, and the root-mean-square of the prediction model was reviewed. I then exported the prediction surface at a resolution of 300x300m, which is approximately the distance between some of the closer stations included as point measurements. I filled “nodata” areas within the with the local mean of the nearest 50 cells (ESRI, n.d.), and repeated this with a mean of the nearest 200 cells to cover the sparsest areas and ensure a continuous raster surface across the study area. Layers were resampled to the 10x10 meter grid matching the resolution of the elevation data using bilinear interpolation and means used to fill in gaps over this extent. With regards to the accuracy of these prediction layers: the goal of this study was not to generate fine-scale estimations of environmental variables, but rather to spatially represent areas that are likely optimal, suitable, and unsuitable for Olympia oysters. Environmental layers were reclassified into these categories as described in Appendix D. Mean salinity and temperature layers are likely highly inaccurate in areas where there are no or few sampling locations. Furthermore, these measures are snapshot rather than detailed continuous data from which a more accurate mean could be calculated. These layers may be replaced with better estimates for more detailed studies of specific areas and/or with model output, which provides coverage and increasingly accurate predictions for nearshore areas.

In addition to the mean salinity and temperature layers, an additional exclusion layer for areas where there is a risk of low salinity events was also generated and included in the HSI. Monitoring data for shellfish growing areas is collected monthly or bimonthly; and does not include daily or continuous data. Therefore, daily mean bottom salinities were extracted from the 2014 model run of the Salish Sea Model (SSM; Khangaonkar et al., 2018). The SSM is a regional model that simulates hydrodynamic and water quality properties throughout the Salish Sea. The model has been run and validated for several years; 2014 is the most recent year described by the model. Including the salinity data from the Salish Sea Model allowed for an approximation of continuous salinity data available over the study area. It is expected that the model output from the current configuration bay be slightly biased towards saltier and colder conditions in the intertidal. This layer was created by calculating a daily mean from the hourly model output over the year at the lowest depth layer. I then identified locations where bottom salinity is less than 10 for 8 consecutive days using a function in R Studio. I generated a point file of 0 (low salinity events occur) or 1 (low salinity events do not occur) at 6,383 nodes in the study area. I interpolated these data across the study area using inverse distance weighting and filled in empty cells with a local mean. I reclassified values as 0 or 1 after the interpolation where the interpolation created intermediate values.

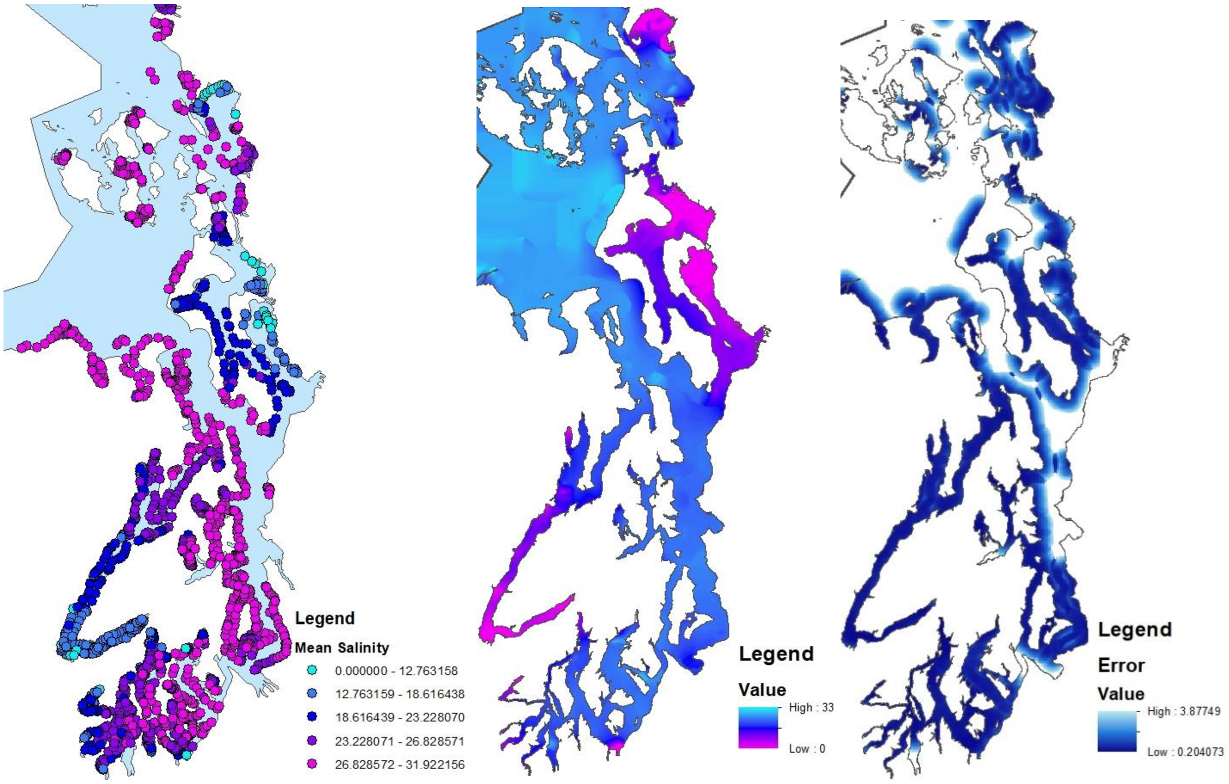


Figure 13. Left to right: salinity point observations, interpolated estimation layer, and error estimate.

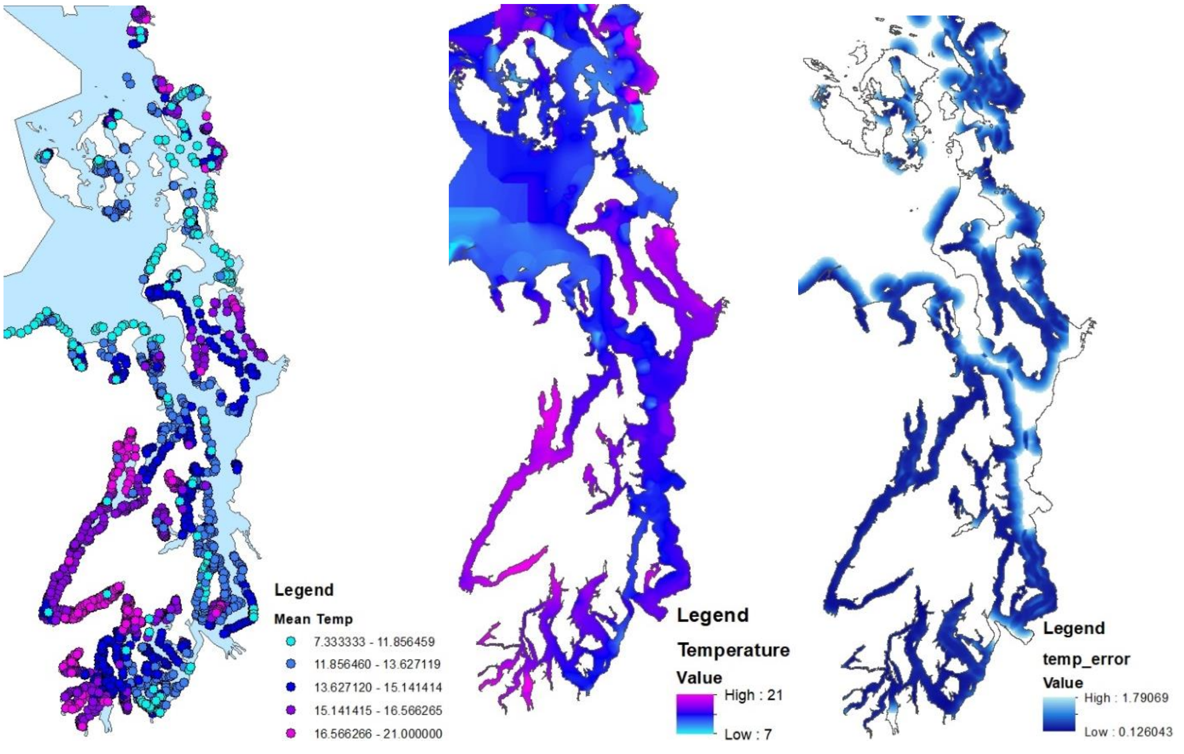


Figure 14. Left to right: temperature point observations, interpolated estimation layer, and error estimate.

Elevation

Elevation data were sourced from high resolution coastal digital elevation models (DEMs) created by NOAA's National Geophysical Data Center (NOAA 2014; NOAA 2011b). These data, titled "Puget Sound" and "Port Townsend," are integrated bathymetric-topographic DEMs developed to support tsunami modeling efforts. The elevation data in the DEMs were compiled from bathymetric, topographic, and shoreline data from various sources, included NOAA, the United States Geological Survey, the Puget Sound Lidar Consortium, and other federal, state, and local sources. The original resolution (i.e., grid spacing) of these DEMs is ⅓ arc-second, or about 10 meters. The DEMs were downloaded as netCDF files, referenced to the vertical datum NAVD88 and horizontal datum of WGS84. NAVD88 is the vertical control datum for North America. The elevation information was extracted from the netCDF files and converted to the ESRI ASCII raster grid format.

The DEMs were then converted to the mean lower low water (MLLW) tidal datum using NOAA's VDatum conversion tool (NOAA, 2019). Each DEM was loaded into the tool, with the vertical datum specified as NAVD88 and the horizontal datum specified as NAD83 (2011). NAD83 was used as the horizontal datum because it is the current official datum of the United States, and VDatum will not accept WGS 84 as an input datum. The difference between NAD83 and WGS84 is minimal (see VDatum frequently asked questions), and inaccuracies due to this difference are much smaller when compared to inaccuracies of the DEMs themselves. The DEMs were converted using the "file conversion" tab of the VDatum tool and output in the MLLW tidal datum and the horizontal datum of NAD83 (2011). The DEMs were then mosaiced into a single DEM using ArcGIS, and assigned the projection associated with NAD83 (EPSG: 4269). I assessed the conversion by calculating the difference between the MLLW DEM and a mean high water (MHW) DEM for Puget Sound provided by NOAA. The tidal gradient was then visually compared to the Puget Sound tide model for accuracy (Figure 13; Mofjeld, et al., 2002); the values in the tide model panel (center) are roughly equivalent to the absolute values of the right panel (i.e., 0 MHW - 2MLLW = -2, difference of 2 in the Puget Sound Tide Model). The combined elevation raster was then converted to the projected coordinate system used in this study at a resolution of 10x10 meters (WGS 84, UTM Zone 10 N, EPSG 32610). Layer construction was conducted in ArcMap 10.

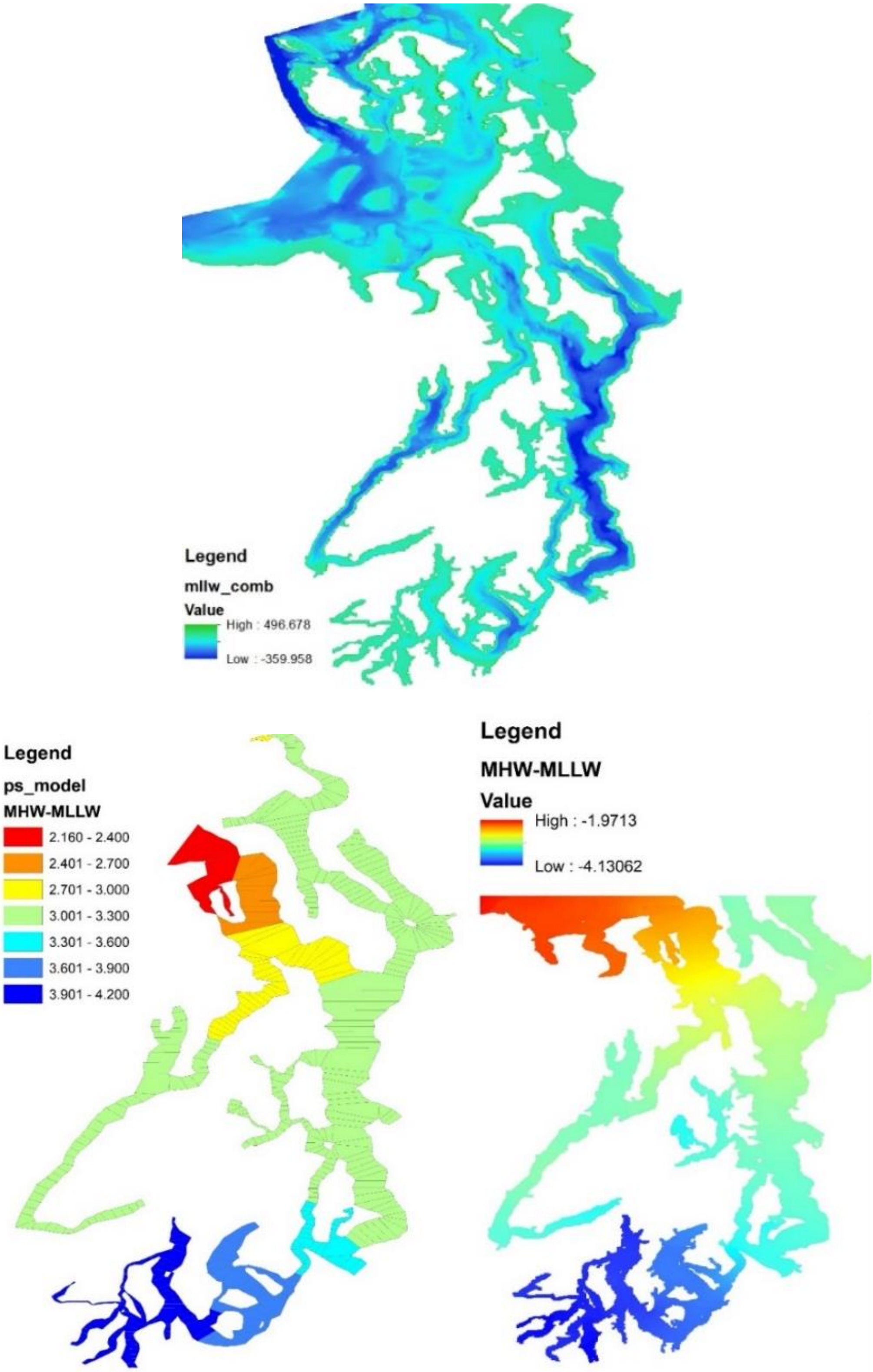


Figure 15. Top: converted MLLW DEM; Left, Puget Sound Tide Model; Right: Difference between MHW and MLLW DEMs. Comparison between the tidal gradients in the Puget Sound Tide Model and the difference calculation show the same pattern.

Water Residence Time and Currents

Data describing patterns of water residence time were provided by the Department of Ecology (Ahmed et al., 2019). Researchers at Ecology used the 2014 SSM run to estimate water residence times for one year throughout the Salish Sea. Water residence describes the amount of time a parcel of water stays within a reservoir until it moves beyond a boundary. In these data, residence time was calculated as the number of days for a concentration of virtual dye at each node in the model to decline to a concentration of 1/*e*, or about 37%. The open boundary was set at the mouth of Strait of Juan de Fuca; so, the days in the figure below are relative to a zero value at this boundary. These data are used to represent general patterns of how water moves in Puget Sound. 2014 is at the residence time index baseline, indicating that it was a representative year in Puget Sound (Ahmed et al. 2019).

E-folding times for 2014 from the model were loaded into R Studio and configured as a shape file of point values, with an e-folding time associated with the xy coordinates of each node in the model; 9,013 nodes in total. The nodes within the study area were then selected for a total of 6383 nodes. The methods used to create a continuous prediction surface were the similar to the methods described for temperature and salinity. The model nodes were interpolated across the study area using kernel interpolation with barriers, using the base presets for the function (polynomial 5) and the ridge (50). The results of this method can be seen in Figure 16. After the prediction surface was generated, the data were exported as a raster with 100mx100m grid cells. No gaps were visually observed, but "nodata" values were replaced with a mean of the 100 nearest cells to ensure full coverage. Data were down sampled to the 10x10 meter grid of the elevation data.

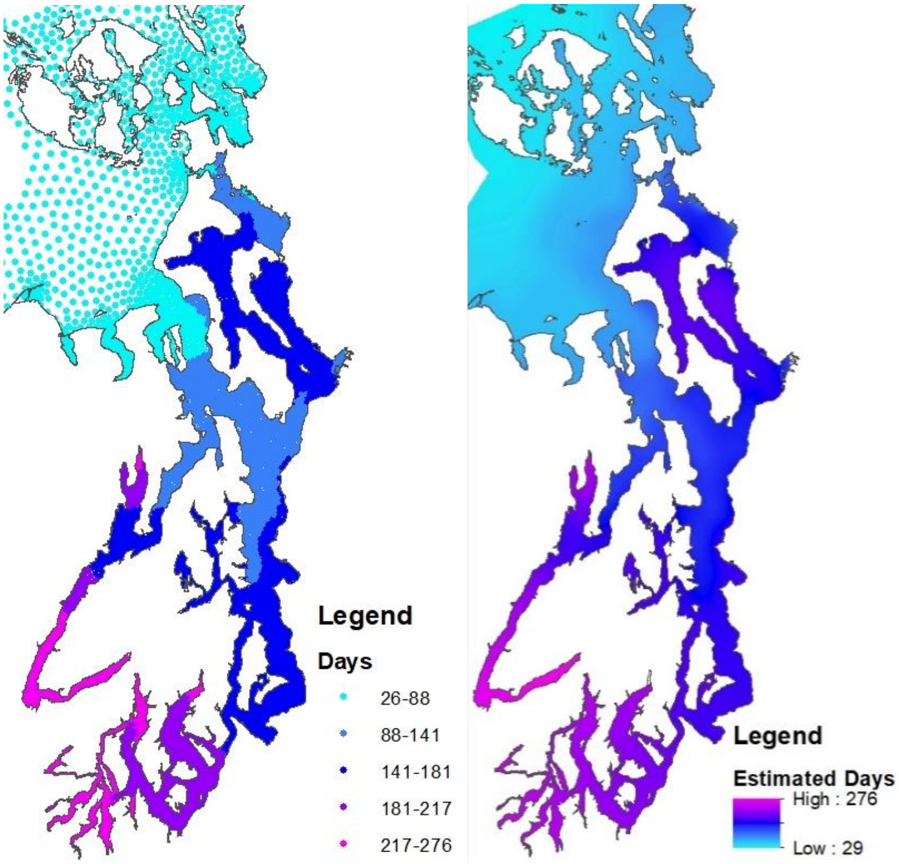


Figure 16. Residence time model output points (L) and estimated residence time layer (R).

A very similar approach was used to develop an estimation surface for maximum current velocities. Using R Studio, I extracted the maximum daily velocity in the u direction and in the v direction at the surface for all nodes in the SSM 2014 output. I combined the velocity vectors using the equation $(u^2 + v^2)\text{^}^{1/2}$ to obtain an overall maximum possible daily current velocity. A point file of maximum velocity was generated, interpolated, and down sampled using the steps described above (Figure 17).

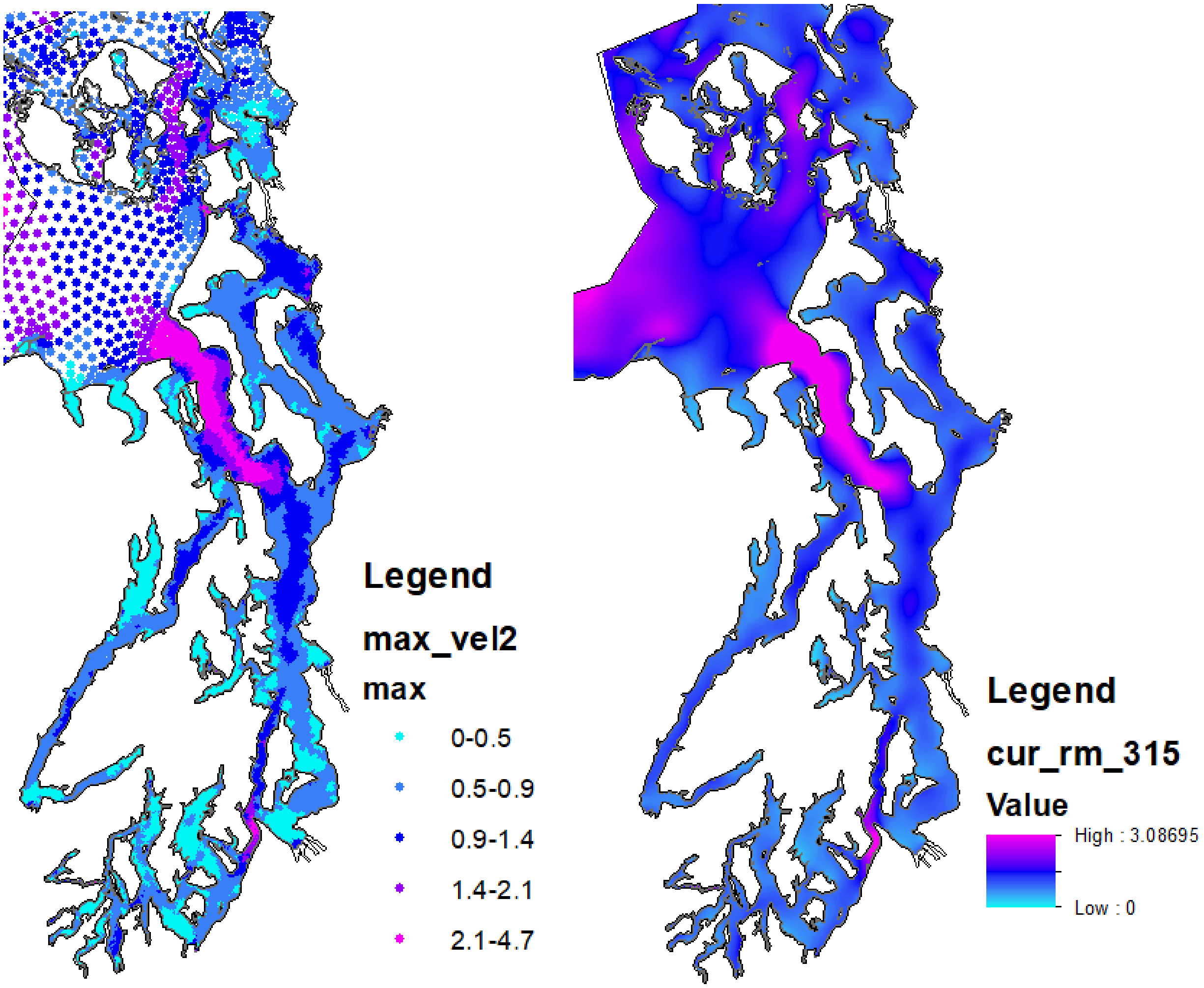


Figure 17. Maximum potential current speeds at model nodes (L) and estimated maximum velocity layer (R).

F. Discussion of Residence Time and Current Velocity

Water residence time gradients in estuaries and coastal bays effect biological and chemical conditions experienced by oysters and other benthic organisms. Residence times effect nutrient availability, sediment dynamics, larval dispersal, and chlorophyll levels, as well as physical properties of water including salinity and temperature (Wheat, Banas, & Ruesink, 2019; sources therein). Residence time patterns in estuarine environments have been linked to the condition of commercially harvested Pacific oysters (Wheat et al., 2019); the larval abundance and growth of Olympia oysters in Tomales Bay (Deck, 2011; Kimbro et al., 2009, 2019); larval abundance, settlement patterns, and presence of Olympia oysters in Coos Bay (Peteiro & Shanks, 2015; Pritchard et al., 2016; Pritchard et al., 2015); and patterns of recruitment across west coast estuaries (Wasson et al., 2016). There has been limited assessment of the relationship between water residence time and Olympia oyster abundance in Puget Sound.

Conceptually, “water residence time” describes how long a “parcel” of water, starting from a specific location within a body of water, will remain in the body of water before exiting (Monsen, et al., 2002). How this measure is operationalized in models and empirical studies varies greatly. For example, Kimbro et al. (2009) define residence time as the age of water in Tomales Bay since it was upwelled, measured using a salt balance equation. In Coos Bay, studies describe the residence time as the flushing time, or the time necessary to replace the fresh water within the estuary at a rate that is equal to the discharge of the river, calculated using the modified tidal prism method which estimates exchange flows between segments of the estuary (Arneson, 1976; Peteiro & Shanks, 2015). In models, residence time is often measured by tracking the fate of virtual particles released at a location. For example, in a study of intertidal residence times, Wheat et al. (2019) define residence time as the length of time that more than half of 16 virtual particles released in each 200m square at high tide continue to be found in the intertidal zone at successive high tides.

The literature linking Olympia oyster populations and residence time focuses primarily on two important mechanisms: settlement and growth. The planktonic larval duration for Olympia oysters is commonly cited to be 11-16 days (e.g., Couch & Hassler, 1989; Dethier, 2006), though estimates range from 7 days to 8 weeks (reviewed by Baker, 1995 and Pritchard et al., 2015) and 5 days to 4 weeks (reviewed by Wasson et al., 2015). Studies in Coos Bay and Tomales Bay have found that larvae are most abundant towards the head of the bay where residence times are longer, and larvae are absent or in low abundance at seaward sites (Kimbro et al., 2009, Deck, 2011, Pritchard et al., 2016). Wasson et al., (2016) found that three of four estuaries that experience estuary-wide recruitment failure had average water residence times that were less than two weeks, and that recruitment is minimal at the mouth of all estuaries studied. Water residence times are also linked to the growth and survival of settled oysters. In Tomales Bay, oysters at mid-bay sites perform the best, because residence times and abundance of marine nutrients support phytoplankton, and predation is lower (Kimbro et al., 2009;2018). The mean saltwater residence time in Tomales Bay is about 60 days, ranging from about 15 at sites near the mouth to about 80 at the head (Deck, 2011). In Coos Bay, riverward sites at the head of the bay had high larval abundance but low recruitment, potentially caused by environmental extremes. The mid-region of the bay had relatively high larval abundance, recruitment, and adult populations; seaward sites at the mouth of the bay had low abundance of all life stages. In Coos Bay, residence times range from under 10 days at seaward sites, to 23 days mid-bay, to over 40 days at the head of the bay (Peteiro & Shanks, 2015). Some researchers have drawn from these studies to recommend restoration at mid-bay sites, where water residence times are long enough to retain larvae and conditions support recruitment and survival (Pritchard et al., 2015).

Given the importance of water residence time to successful restoration, how should this environmental variable be incorporated into an assessment of habitat suitability? Compared to Coos Bay and Tomales Bay, Puget Sound is large and complex. Patterns of water residence time and flushing time have been described by several studies, including: Sutherland & MacCready (2011), where authors modeled estuarine circulation of the Salish Sea including overall and basin-scale estimates of saltwater residence time; Banas et al. (2015), which assessed freshwater age and circulation using particle tracking simulations; as part of a nutrient reduction study conducted by the Department of Ecology (Ahmed et al., 2019); and in some finer scale analyses in south Puget Sound and the western Central Basin (Ahmed, Pelletier, & Roberts, 2017; Wang, Yang, & Brandenberger, 2014). While information describing circulation patterns in Puget Sound as a whole and in some cases for specific bays and inlets is available, the challenge lies in obtaining data that is relevant to the scale of Olympia oyster population dynamics and restoration decision-making.

There is evidence of population structure within Puget Sound despite the relatively close proximity between populations; studies have found evidence of significant phenotypic differences in fitness related traits (Heare et al., 2017; Silliman, Bowyer, & Roberts, 2018). A genetic study of all west coast populations found strong evidence of population structure coastwide, with populations falling into six distinct geographic groups. Among Puget Sound sites (i.e., Discovery Bay, Liberty Bay, Triton Cove, North Bay) genetic variation was relatively low, with the exception of Discovery Bay; results suggest that adaptive divergence occurs even with relatively high gene flow (Silliman, 2019). Larval connectivity is currently being studied using trace elemental fingerprinting, which may provide information on population connectivity at spatial and temporal scales that are more relevant to restoration decision-making (Becker Lab, n.d.). Given these findings, water residence times may create conditions where larvae are maintained and settle within bays and inlets, with more limited dispersal to sites throughout Puget Sound.

Restoration projects are implemented at the bay/inlet scale. While the overall goal is to restore populations throughout Puget Sound and coastwide, sites are not currently being selected for their value as a potential source for the repopulation of other areas. The more immediate and measurable goal is to re-establish self-sustaining populations at restoration project locations. Ideally, water residence times within a bay/inlet of interest could be calculated relative to the boundary of that body of water or at a slightly larger scale (i.e., a complex of inlets). Information at this scale would allow for within-bay comparisons of where water residence times are optimal – sufficiently long to retain larvae, with enough turnover to both supply marine nutrients[2] that support phytoplankton and maintain dissolved oxygen. However, this type of detailed residence time data is not available across the study site in a form that allows for comparison. Descriptions of water residence times for some bays of interest can be found, though these numbers may not be comparable to each other or necessarily representative of processes affecting larval dispersal. The reported mean water residence times of 25 and 28 days[3] for Dogfish Bay and Fidalgo Bay (Doughton, 2019, Wasson et al., 2016), respectively,

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[2] Noting that in the low inflow season when studies in Tomales Bay were typically conducted, nutrients were primarily marine-derived. While the majority of nutrients in Puget Sound are marine derived, the pattern of a phytoplankton peak mid-bay observed in Tomales Bay may not hold sub-estuaries and inlets depending on local dynamics.

[3] Noting that these may be defined and calculated differently.

anecdotally appear suitable based on pelagic larval duration of the species. Notably, Fidalgo and Dogfish Bays are the locations of some of the most successful local Olympia oyster restoration efforts (PSRF pers. comm), though more information about how these residence time estimates were calculated is needed to make meaningful comparisons.

In this study, I incorporated residence time into the suitability index using a data set that describes annual mean water residence time for the Salish Sea in 2014 (Figure 16 above, displaying values at model nodes, data from Ahmed et al., 2019). The year 2014 is at the residence time index baseline, indicating that it was a representative year for residence times in Puget Sound (Ahmed et al., 2019). In these data, residence time was calculated as the number of days for a concentration of virtual dye at each node in the model to decline to a concentration of 1/*e*, or 37%. The open boundary was set at the mouth of Strait of Juan de Fuca; meaning that values in the Figure can be thought of as relative to the Strait, where e-folding time is zero. This information is not at the ideal scale for assessing restoration suitability. The number of days to a concentration of 1/*e* with an open boundary at the Strait cannot directly be mapped on to the estimates for the larval duration of Olympia oysters. However, these data can be used to observe and account for the larger scale patterns that are relevant. Therefore, areas with the lowest 20% of residence times and the highest 5% of residence times are considered unsuitable (HSI=0) in this model. This represents an assumption that very low residence times would not allow for recruitment. Very high residence times are indicative of potential hotspots for biogeochemical stressors (Ahmed et al., 2019), which are likely not optimal for Olympia oysters. It should be noted that this relative classification is not as robust as using actual values from the literature, as for the other environmental variables included in the model. The suitability scoring for residence time cannot be considered completely independent of information known about Olympia oyster populations in Puget Sound.

In addition to the e-folding time data included in the model, Wang, Yang, and Brandenberg (2014) modeled water residence time for West Sound, behind Agate and Rich Passages. These data also show the results of releasing a virtual dye into the study area, measuring how many days it takes for the concentration to reach zero. Locations such as Liberty Bay have a higher residence time relative to the open boundary at Agate and Rich Passages. In general, the data show a pattern of increasing water residence times towards the heads of bays and into inlets. While this analysis provides information about water circulation in this system, it may not provide information that is necessarily meaningful in terms of numbers than can be compared to larval duration or recruitment patterns; transport patterns between adjacent bays may be more informative. This analysis can be compared to the data from Ahmed et al., (2019) to determine that the general patterns from different modeling exercises are similar.

Water current velocities are also associated with patterns of Olympia oyster settlement and are an important environmental variable to consider with regards to site suitability. Research conducted by Peteiro & Shanks (2015) in Coos Bay suggests that Olympia oyster larvae are retained in the bay throughout their development, and that both current velocities and residence times may play a role in larval retention. Olympia oysters perform vertical migrations at low current speeds, behavior which may allow them to be retained in an estuary during tidal exchanges. Larvae are found deeper in the water column during falling tides compared to rising tides. However, retentive behaviors of larvae were no longer effective at current velocities greater than 0.5 m/s, and larvae were equally distributed throughout the water column (Peteiro & Shanks, 2015). Timing of larval release during the summer, when residence times are at their annual maximum, may be an additional strategy for retaining larvae, as currents at the mouth of Coos Bay exceed this threshold. Given these findings, maximum possible daily surface current velocities were included in this HSI study, to more precisely capture the potential influence of water movement patterns on site suitability and provide more information than can be drawn from the residence time data. Suitability scores were assigned corresponding to the 0.5 m/s threshold identified in Peteiro & Shanks (2015) and described in Appendix D and E. However, more analysis would be required to understand potential relationships between current dynamics and settlement and appropriate threshold values in Puget Sound.

G. Including Sediment in the HSI

Sedimentary conditions are important for Olympia oyster restoration. As described in Appendix C, Olympia oysters require both hard substrate and appropriate sedimentary conditions to support recruitment and survival. Populations of Olympia oysters built “reefs” over time, settling on the shells of conspecifics and shell material that accumulate at sites. The fact that oysters that were harvested live and shipped in their shells depleted shell substrate available for settlement of new recruits and has contributed to limited recovery (Blake & zu Ermgassen, 2015; Peter-Contesse & Peabody, 2005). This information and the presence of Olympia oyster larvae in the plankton support the hypothesis that a lack of hard substrate in the nearshore environment is limiting the recovery of the species. Thus, restoration practitioners often add substrate – usually either Pacific oyster shell or shell seeded with Olympia oysters – as a habitat enhancement technique. However, sedimentation is among the leading barriers to success for restoration projects. Oysters can easily smother or have their filtration capacity reduced when conditions are silty, or the substrate is deep mud. Wasson et al. (2015) recommend that substrate be added that corresponds to the depth of the mud to prevent the restoration surfaces from sinking and smothering new oysters. Sedimentation from other sources including agriculture, logging, construction projects, altered sedimentary regimes of rivers, and resuspension of sediments, can all contribute to smothering and be detrimental to oyster recovery.

Sediment is not included in the current iteration of the HSI model because I have not identified a dataset that could accurately describe these constraints. It is possible that sediment monitoring data from the Department of Ecology could be utilized. It would be difficult to include hard substrate as a criteria of habitat suitability, because oysters can recruit to any hard substrate – it could be small pebbles, sea walls or bulkheads, etc., and this detail is likely not captured by sediment grain size data. Furthermore, restricting the restoration model to areas that already have hard substrate would not necessarily be useful, as adding substrate is the primary means of restoring otherwise unsuitable habitat. The sedimentary environment could also be considered for inclusion in the HSI. Data describing risk of sedimentation would improve the HSI’s ability to identify sites where restoration projects have a higher chance of success. It is possible that sediment grain size data describing % silt-clay could be used, as in other studies (e.g., Bohlen, 2019; Lewis et al., 2019). However, it is not clear how these measures correlate with suitability for Olympia oysters. Some basic information on suitable substrates are included in the suitability framework below. These could be refined to map on to an available grain size dataset (see Bohlen, 2019), but it is not immediately clear how this would be implemented.

Table 18. Sediment Suitability Framework

	Sediment Composition								
	Hard Substrate (general)	**Mud/Sand**	**Rocks/Gravel/ Cobble**	**Shell**	**Deep mud/silty conditions**	**Measure**	**Range**	**Data type**	**Geography**
Source:									
Allen et al. 2015 and Blake 2014		▨	▨	▨		Presence	Full	Qualitative	PNW
Baker 1995[1]	▨	▨	▨	▨		Abundance, settlement	Full	Review	PNW
COSEWIC 2011[2]	▨	▨	▨	▨		Settlement	Full	Review	PNW
Couch & Hassler 1989[3]			▨	▨		Presence	Full	Review	PNW
Dethier 2006		▨	▨	▨		Presence	Partial	Qualitative	PNW
Dinnel 2009	▨		▨	▨		Presence	Partial	Quantitative	PNW
Pritchard 2015[4]	▨	▨	▨	▨		Settlement	Full	Review	General
Tronske 2018	▨					Density	Partial	Quantitative	Other
Wasson et al. 2015	▨					Settlement, mortality	Full	Review	General
White et al. 2009				▨		Settlement	Partial	Quantitative	PNW
HSI Score	🟩	🟩	🟩	🟩					

[1] Fasten 1931, Townsend 1893, and others

[2] Baker 1995

[3] Steele 1957; Kozloff 1973

[4] Groth & Rumrill 2009, Wasson 2010

H: HSI Calculation Code and R Packages

Code to Reclassify Habitat Layers and Calculate HSI

```
#Purpose: Final model code
#updated: 3/16/20

library(sf)
library(dplyr)
library(raster)
library(rgdal)

##### Load Environmental Layers and reclassify
#Elevation
elev <- raster("Elevation/comb_prj.tif")

elev.m <- matrix(c(-Inf,-10,0,-10,-4,0.33,-4,-3,0.66,
            -3,2,1.00,2,3,0.66,3,4,0.33,4,Inf,0), ncol =3, byrow = T)

elev.m[1:7,1] <- 0.3048*elev.m[1:7,1]
elev.m[1:7,2] <- 0.3048*elev.m[1:7,2]

elev.r <- reclassify(x=elev, rcl=elev.m, right = T)
#writeRaster(elev.r,"CombinedModel/Output_316/elev_r.tiff")

#Low salinity
lowsal <- raster("interp/lowsal_m2r315/w001001.adf")
#writeRaster(lowsal,"CombinedModel/Output_316/lowsal.tiff")

#Currents
cur <- raster("interp/cur_rm_315/w001001.adf")
cellStats(cur, max)
cur.m <- matrix(as.numeric(c(-1,0.01,0,0.01,0.5,1,0.5,0.55,0.66,
           0.55,0.6,0.33,0.6,5,0)), ncol = 3, byrow = T)

cur.r <- reclassify(x=cur, rcl=cur.m, right = T)
#writeRaster(cur.r, "CombinedModel/Output_316/cur_r.tiff")

#Water Residence
res <- raster("interp/ef_mrm_315/w001001.adf")

lower <- cellStats(res,max)-cellStats(res,max)*0.8
upper <- cellStats(res,max)-cellStats(res,max)*0.05
res.m <- matrix(c(-Inf,lower,0,lower,upper,1,upper, Inf,0),
          ncol = 3, byrow = T)

res.r <- reclassify(x=res, rcl=res.m)
#writeRaster(res.r, "CombinedModel/Output_316/res_r.tiff")
```

```
#Mean Salinity
sal <- raster("interp/sal_315nmm2rm/w001001.adf")

sal.m <- matrix(c(-Inf,15,0,15,20,0.33,20,25,0.66,25,Inf,1),
            ncol = 3, byrow = T)

sal.r <- reclassify(x=sal, rcl=sal.m, right = T)
#writeRaster(sal.r, "CombinedModel/Output_316/sal_r.tiff")

#temperature
temp <- raster("interp/tem315ff/w001001.adf")

temp.m <- matrix(c(-Inf,10,0,10,12,0.33,12,13,0.66,13,25,1,
               25,Inf,0.66), ncol = 3, byrow = T)
temp.r <- reclassify(x=temp, rcl=temp.m, right = T)
#writeRaster(temp.r, "CombinedModel/Output_316/temp_r.tiff")

#####
#Combined HSI
HSI <- (elev.r*cur.r*sal.r*temp.r)^(1/4)
HSI <- HSI*(lowsal*res.r)
#writeRaster(HSI, "CombinedModel/Output_316/HSIfinal.tiff")

#####
#Stack of the base file, the reclass file, and the final
HSI_stack <- stack(elev, elev.r, lowsal, cur, cur.r, res, res.r, sal, sal.r,
            temp, temp.r, HSI)

names(HSI_stack) <- c("elev","elev_r","lowsal","cur","cur_r","res","res_r",
                "sal", "sal_r", "temp","temp_r","HSI")
#writeRaster(HSI_stack,"CombinedModel/Output_316/HSIstack.tiff", bylayer = T)
```

Citations of Primary Packages Used

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I. Assumptions of Habitat Suitability Models

In their book *Habitat Suitability and Distribution Models,* Guisan et al. (2017) describe the theoretical and methodological assumptions that underpin habitat suitability models. Table 19 below includes each of these assumptions, a description of the relevance to this study, and how each assumption has or has not been addressed. The assumptions below are more applicable to habitat suitability and species distribution models built from population datasets. Nevertheless, they are also relevant to the index approach used in this study and may inform future analyses.

Table 19. Assumptions Behind Habitat Suitability Models

Assumption	Description	In this Study
Theoretical Assumptions		
Species-environment equilibrium assumption	Underlying assumption of models built from species data is that species are at equilibrium with their environment, i.e., the species is present most of the suitable habitat in the study area.	This limitation is somewhat avoided by applying an index-based approach. Verification and validation approaches and future modeling attempts must consider this.
Availability of all important predictors for the niche being captured	Absence of important predictor layers may limit the utility of the model.	Important predictors may be absent from this study. Predictors identified based on literature and expert input. Other potentially important predictors are described throughout and could be added to the model or assessed in the field to improve accuracy.
Appropriateness of species observations	Building a model from species presence-absence data may include sink populations, which has implications for the applicability of the model to conservation decision-making.	Further consideration of this limitation would be beneficial. Species presence data may not be an appropriate verification, and more information is needed regarding restoration outcomes.
Methodological Assumptions		
Appropriateness of statistical methods	Statistical methods applied must be appropriate to the type of species data used.	NA
Predictors measured without error	Guaranteeing zero error in GIS environmental predictor layers is impossible, but spatial uncertainty should be assessed.	Habitat prediction layers, particularly mean salinity and temperature, likely have many inaccuracies due to patchy data and interpolation artifacts. Layers based on model output represent only one year of modeled conditions.
Unbiased species data	Species data need to include all possible environments that represent suitable habitat for the species modeled, so species data need to be unbiased. Bias can arise through nonrandom sampling.	Not likely available. Species data included here is the result of nonrandom sampling.
Independence of species observations	Spatial autocorrelation can limit accuracy of statistical methods.	NA

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