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Investigating Larval Spillover From Oyster Aquaculture Through Geospatial Habitat Suitability Index Modeling: A Damariscotta River Estuary Case Study

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Abstract:

The eastern oyster (*Crassostrea virginica*) supports the ecological function of estuarine ecosystems by creating biogenic reef habitat (Purchon, 2013), and positively influencing coastal biogeochemistry in intertidal, and subtidal environments (Humphries et al., 2016; Ray and Fulweiler, 2020). As anthropogenic impacts continue to influence the health of marine environments globally (Halpern et al., 2008), oyster reef restoration is gaining increased attention as a means of maintaining the function of estuarine systems (Beck et al, 2011).

Shellfish aquaculture has gained increased attention, contributing 21% of all aquaculture production globally (FAO 2020). Shellfish aquaculture provides a suite of social-ecological benefits while contributing to provisioning and supporting ecosystem services including nutrient removal, water clarification, coastal protection, and habitat creation (Gentry et al. 2020; Grizzle et al. 2008; Dame and Kenneth, 2011; Kellogg et al. 2014). In this way, shellfish aquaculture can exist in synergy with ecosystem processes, resulting in positive environmental outcomes while creating livelihoods through supply of seafood and commercial products (referred to as restorative aquaculture) (Blanchard et al., 2017). Despite the range of ecosystem services provided from bivalve aquaculture, the role of larval subsidy in population restoration has yet to be recognized (van der Schatte Olivier et al., 2020). However, evidence of green lipped mussel (*P. canaliculus*) restoration via larval subsidy has been documented (Norrie et al., 2020).

Habitat suitability index (HSI) models have proven effective in facilitating population restoration of the American oyster in estuaries of the eastern United States by providing spatially explicit information regarding the quality of habitat over broad areas of interest (Soniat and Brody, 1988; Barnes et al., 2007; Starke et al., 2011; Pollack et al., 2012; Linhoss et al., 2016; Theuerkauf and Lipcius, 2016; Puckett et al., 2018). This study employs a geospatial HSI model

for the eastern oyster to investigate a recent population resurgence in an estuary where oysters were once extirpated, the Damariscotta River estuary (DRE), Maine, USA. As a means of internal validation, we combine HSI model predictions with local ecological knowledge gained through participatory interviews and surveys of local shellfish harvesters targeting eastern oysters, oyster aquaculture producers operating within the estuary, and researchers familiar with the system.

By assessing the viability of incidental restoration resulting from larval subsidy from oyster aquaculture, this study explores the implications of low-cost restoration strategies which integrate fisheries, aquaculture, and conservation interests within a reciprocal conservation paradigm.

Introduction:

Ecosystem Services

Foundation species facilitate the existence of diverse communities through habitat creation (Dayton, 1975; Bertness and Callaway, 1994). These species significantly increase the scale and complexity of associated food webs through positive trophic, and non-trophic interactions (Borst et al., 2018; Kefi et al., 2015; Sanders et al., 2014; Coen and Luckenbach, 2007; Stachowicz, 2001).

Oyster reefs also regulate ecological function within estuaries by preventing the accumulation of dissolved organic matter, through the suspension feeding of phytoplankton (Ulanowicz and Tuttle, 1992) which prevents hypoxic conditions in areas exposed to high nutrient inputs with low tidal exchange rates (Jeppesen et al., 2018), and facilitates the growth of submerged aquatic vegetation and macro algae by improving water clarity, stabilizing benthic and intertidal habitat, and fertilization via deposition of biodeposits (Grabowski and Peterson, 2007). The cumulative nonmarket value of direct and indirect ecosystem services provided by restored oyster reefs is estimated between $5,500 and $99,000 per hectare per year (Lotze et al., 2006; Grabowski et al., 2012).

Despite the significant nonmarket value of reef forming invertebrate populations, habitat fragmentation, changes in freshwater inflows, nutrient loading, sedimentation, over-fishing, and pollution continue to negatively impact the diversity and abundance of these species in estuarine and coastal ecosystems (Gattuso, 2015; Hoegh-Guldberg and Bruno, 2010; Halpern et al., 2008; Worm, 2006; Anderson et al., 2004). As populations decline, their ability to remove dissolved organic matter is diminished, making hypoxic conditions, toxic algal blooms, and parasitic diseases more prevalent (Jackson et al., 2001).

When combined with the associated impacts of climate change such as ocean acidification, warming, storms of greater intensity, and increasing freshwater discharge volumes, these stressors pose a significant threat to bivalve species population distribution, recovery, and migration in the future (Gaylord et al., 2011; Salisbury et al., 2008; Schwartz et al., 2001). As a result, oyster reefs remain one of the most at-risk marine habitats globally, with many populations in the northeastern United States remaining functionally extinct (Beck et al., 2011).

Maine's Populations

The eastern oyster's historic range which stretched along the western Atlantic coast (Brazil to Atlantic Canada) has been dramatically reduced due to anthropogenic impacts (Carriker and Gaffney, 1996). Globally, oyster reefs have been degraded, now comprising only 15 percent of their historic area, and in the Cold Temperate Northwest Atlantic eco-region many populations remain functionally extinct (Beck et al., 2011; McAfee and Connell, 2021). High latitude populations, such as extant eastern oyster populations in the Gulf of Maine, can be traced to a hypsothermal period (eight thousand years ago) when lower sea levels, and minimal tides resulted in lagoon like conditions with warm summer temperatures (Campbell, 1986). This resulted in colonization by warm temperate species whose populations were contiguous from the Chesapeake to the Gulf of St. Lawrence (Bousfield and Thomas, 1975). As sea level and tidal ranges increased, the Gulf of Maine cooled (Greenberg et al., 2012). As a result, warm temperate species such as the eastern oyster were restricted to estuaries where summer temperatures still reached adequate temperatures for reproduction, such as the upper estuaries of the Piscataqua and Sheepscott River, where the only two extant oyster populations remain in the state (Larsen et al., 2013). The extant population in the upper estuaries of the Sheepscott River is the northernmost eastern oyster population in the United States and has led to the listing of the area as a critical area for Maine's natural resource management (Cowger, 1975).

Population Restoration

Fortunately, marine invertebrates with sedentary life strategies have high potential to develop self-replenishing populations (Bell, 2005; Rodney and Paynter, 2006). The effects which epibenthic bivalve species have on habitat enhancement, in combination with their sedentary life cycle contributes to their appeal to resource managers seeking to enhance, restock and restore declining populations (Bell et al., 2008). For the eastern oyster, meta-population persistence is vital for habitat niche restoration due to the high value of the species for commercial and recreational harvesters (Coen and Luckenbach, 2000).

Traditional eastern oyster restoration strategies have included four main components: (1) construction and placement of reef structures (2) Conservation of existing reefs and management as sanctuaries (3) rehabilitation of natural populations for fishery harvesting (4) and community participation in restoration initiatives (Brumbaugh et al., 2000). Unfortunately, the combination of artificial reef installation, hatchery rearing, and deployment of adult oysters tends to make the traditional effort-based stock enhancement, and restoration strategies cost prohibitive (Murray et al., 1999; Hunter et al., 2010). Low cost, collaborative strategies for population restoration of foundation species has become increasingly important for marine resource management.

Larval subsidy and restoration

As resource managers continue to explore low-cost strategies for population restoration, larval subsidy from sanctuary habitat plays an important role in species diversity and abundance proximal to sanctuary sites, such as marine protected areas (Christie et al., 2010; Harrison et al., 2012). With evidence proving larval spill over from sanctuary sites, it is important to understand aquaculture's role in larval production, dispersal, and recruitment. This is particularly important for endangered, and threatened species whose historic populations have been drastically reduced due to anthropogenic impacts, and over exploitation such as the eastern oyster (Soto et al., 2007). As ambient ocean temperatures increase due to climate change, rapid range shifts are likely to occur for many marine species (Burrows et al., 2011). Warm temperate invertebrate species such as the eastern oyster which exhibit high dispersal capacity and ecological generalism, will likely see an increase in reproductive activity, and latitudinal range shifts with rising ocean temperatures in higher latitudes (Fabioux et al., 2005; Pouvreau et al., 2006; Sunday et al., 2015).

Larval dispersal from green lipped mussel (*Perna canaliculus*) aquaculture sites has been proven as a means of supporting restoration efforts, and establishing sub-populations (Norrie et al., 2020). The results of this study indicate that broad scale, aquaculture of foundation species may play a significant role in supporting traditional stock enhancement strategies where biological, and physical factors are conducive to sub-population persistence. However, because larval connectivity amongst eastern oyster sub-populations with adequate demographic characteristics is required to ensure meta-population persistence (by ensuring the replacement of adults with larvae which survive to reproduce) (Hastings and Botsford, 2006; Lipcius, 2008), it remains unclear as to whether larval subsidy from bivalve aquaculture can assist in meta-population restoration.

Augmenting wild populations through larval spill over from aquaculture sites does pose significant risks. Genetic introgression in motile, higher trophic level species (Jensen et al., 2010; Hutchings and Fraser, 2008), and sessile bivalves, can negatively influence the fitness of wild populations within larval settlement ranges of aquaculture sites (Apte et al., 2003). Likewise, extrinsic outbreeding depression can significantly diminish local adaptations of isolated subpopulations (Waples et al., 2012). Understanding the influence of such processes on naturally occurring wild species in zones of highly developed mariculture production should be of significant value to resource managers and aquaculture producers alike.

Despite the far-reaching value of bivalve aquaculture from an ecosystem enhancement perspective, the contribution of larvae from aquaculture sites has not been identified as an ecosystem service (van der Schatte Olivier et al., 2020). Despite the risks mentioned, integrated strategies combining non-fed, foundation species aquaculture with restoration initiatives can provide ecological, and economic benefits on local and regional scales (Norrie et al., 2020).

Because the long-term success of many constructed reefs is dependent on the habitat quality of specific sites (Powers et al., 2009), a valuable first step in restoration initiatives is the identification of suitable habitat within broad areas of interest (Weinstein, 2007). Habitat suitability index (HSI) models have proven effective in locating specific areas of high-quality habitat by defining a given specie's physiological requirements and identifying habitat with the corresponding structure and composition requisites needed for population persistence (Roloff and Kernohan, 1999).

Larval Spillover’s Effects on Ecosystem Services

In attempts to understand the linkage of social and ecological systems affected by larval spillover of oyster aquaculture, the system was diagrammed (figure 2) within the context of ecosystem service categories and the Food and Agriculture Organization of the United Nation’s sustainable design goals (Herrero et al., 2020).

The wild oyster fishery in the DRE currently provides significant direct market value to local and regional markets. Wild oysters from the estuary are typically sold raw in the same markets as aquaculture product, and thus reach a per piece value comparable to oysters produced in aquaculture systems.

Figure 1: Wild harvested oysters in half shell markets

In terms of supporting services, the restoration of bivalve reefs in bare sediment habitats will positively influence the species richness, and abundance of infauna, epifauna, and necton (Zimmerman et al., 1989; Meyer et al., 2000; Hosack et al., 2006; Lejart and Hily, 2011; Gain et al., 2017). Increases in habitat complexity through growth of biogenic reef substrate likely enhances predator prey interactions by increasing shelter, foraging, and reproduction sites (Crooks, 2002; Kingsley-Smith et al., 2012). Furthermore, increased algal grazing enhances the nutrient transfer to benthic invertebrates, in turn increasing the nutrient flux of the system towards predatory fish and invertebrate species which are often commercially harvested (Grabowski and Peterson, 2007; Laugen et al., 2015). Conversely, it is unclear how the biofouling of aquaculture oysters, or the propagation of spat influences aquaculture production, and whether propagation of spat conflicts with genetic patents of eastern oysters actively breeding in the estuary.

Population restoration in bays, and river basins regionally will allow the local shellfish industry to attain greater diversity. This may potentially take pressure off other high value shellfish species such as the soft-shell clam (*Mya arenaria*) which has experienced population declines due to climate related changes in reproduction (Phillipart et al., 2003), and increases in invasive predator populations (Whitlow 2010, Tan et al., 2015). Keystone species restoration also presents potential opportunities for ecotourism and environmental education.

Genetic introgression resulting from larval spillover poses a significant risk to the fitness of conspecific bivalve populations as illustrated in the green lipped mussel (*Perna canaliculus*) (Apte et al., 2003). It remains unclear how oysters bred for disease resistance, aesthetics, and growth rates, will influence the long-term adaptability of nearby extant populations. Additionally, because the eastern oysters produced in aquaculture production systems in Maine are bred and purchased from hatcheries, it is unclear how genetic patents will interfere with the propagation of spat for use in aquaculture.

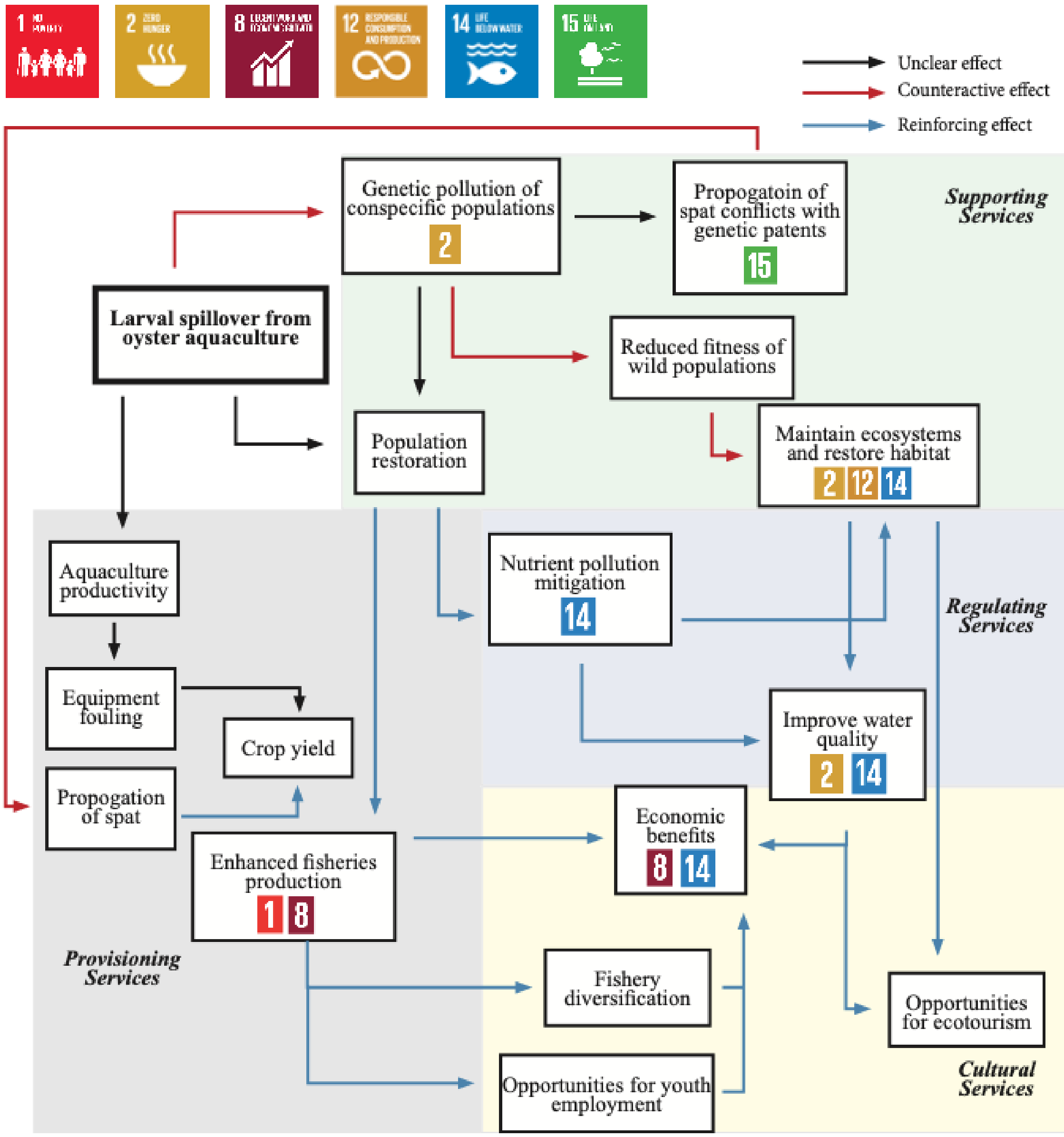

Figure 2: Potential effects of larval dispersal from oyster aquaculture as they pertain to the FAO's sustainable development goals, and the four ecosystem service categories

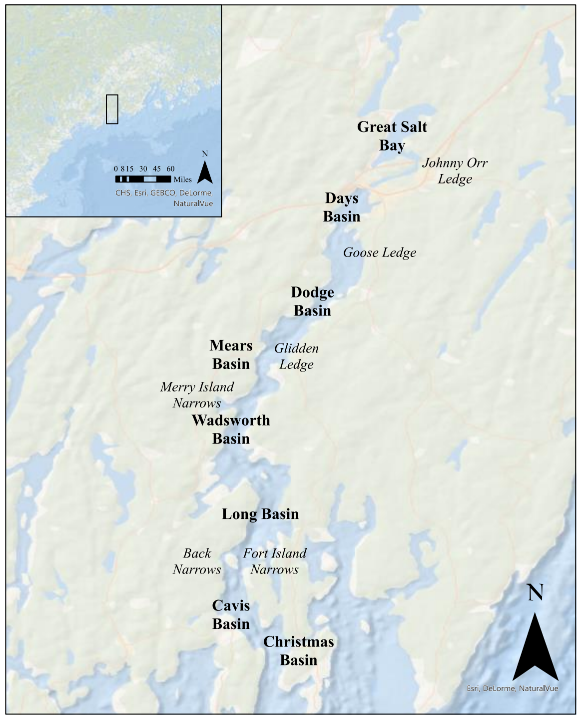

Figure 3: Subbasins of the Damariscotta River

0 0.531.05 2.1 3.15 4.2 Miles

Table 1: HSI Model Variables Assessed in Scientific Literature

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Salinity, average	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x
Dissolved Oxygen		x	x		x	x		x	x	x							x
Substrate Characteristics	x	x		x						x		x	x	x	x	x	x
Temperature	x	x	x	x	x		x	x	x		x						
Turbidity		x	x		x	x		x	x		x						
Water flow velocity			x			x	x										
Hydrologic residence times							x										
Freshet frequency	x			x			x					x					
Tidal elevations							x										
pH			x			x											
Reproductive activity on sites																	
Adult Concentration										x							x
Larval export										x							x
Phytoplankton availability		x	x		x	x					x						x
Predator intensity			x	x								x					
Disease prevalence			x	x					x			x					
Water depth	x	x			x			x	x	x				x		x	x
Shellfish leases										x							x
SAV										x							x
Public boat ramps										x							x
Military zones										x							x
Navigation channels										x							x

Oyster HSI literature references mentioned in the table above include:
1.Barnes et al., 2007 2. Battista, 1999 3. Brown and Hartwick 1988 4. Cake, 1983 5. Cho et al., 2012 6. Chowdhury et al., 2019 7. Dohrn 2020 8. Linhoss et al., 2016 9. Pollack et al., 2012 10. Puckett et al., 2018 11. Snyder et al., 2017 12. Soniat and Brody, 1988 13. Soniat et al., 2013 14. Starke et al., 2011 15. Swannack et al., 2014 16. Theuerkauf et al., 2019 17. Theuerkauf and Lipcius, 2016

Role of Habitat Suitability Index (HSI) Models in Restoration

Geospatial habitat suitability index (HSI) models applied to the eastern oyster have proven to be highly valuable tools for natural resource managers seeking spatially explicit representation of biophysical data (Theuerkauf and Lipcius, 2016), and have been applied effectively in identifying sites conducive to commercial oyster aquaculture (Silva et al., 2011; Snyder et al., 2017; Palmer et al., 2020), broad scale, population restoration (Soniat and Brody, 1988; Barnes et al., 2007; Starke et al., 2011; Pollack et al., 2012; Linhoss et al., 2016; Theuerkauf and Lipcius, 2016; Puckett et al., 2018), and the associated ecosystem services provided via restoration (Theuerkauf et al., 2019).

In the 17 articles reviewed (Table 1), the most assessed factors in oyster HSI models are salinity, substrate availability, temperature, and water depth, however site specificity is an overarching component in variable selection. Recent HSI models pertaining to oyster restoration also include practical components required for successful restoration (ie: distance from boat launches, shellfish lease locations, military zones, and navigable channels), as well as factors associated with larval connectivity amongst existing and restored sub-populations (Puckett et al., 2018; Theuerkauf and Lipcius, 2016).

The integration of biological and physical factors into HSI models contributes to the success of restoration initiatives (Fitzsimmons et al., 2017), and can inform restoration strategies focused on fisheries enhancement through ecosystem service provisioning (Theuerkauf et al., 2019). Ecosystem based HSI models will prove valuable for future restoration initiatives as only a small proportion of historic distributions overlap with present day model predictions of suitable habitat due to changes in estuarine systems resulting from changing land use, historically destructive fishing practices, and overfishing (Puckett et al., 2018; Jackson et al., 2001).

Larval spillover from commercial aquaculture of foundation species has significant implications for conservation and restoration (Norrie et al., 2020). Understanding commercial aquaculture's role in this process will be critical for initiatives in the Northeastern United States, where eastern oyster populations remain functionally extinct, and only small, extant populations remain (Beck et al., 2011). In effort to inform collaborative efforts between commercial aquaculture and restoration initiatives, this study seeks to identify sites where biophysical conditions are conducive to larval recruitment proximal to aquaculture sites in the DRE.

Methods

Maine's Populations

The eastern oyster's historic range which stretched along the western Atlantic coast (Brazil to Atlantic Canada) has been dramatically reduced due to anthropogenic impacts (Carriker and Gaffney, 1996). Globally, oyster reefs comprise only 15 percent of their historic area, and in the Cold Temperate Northwest Atlantic eco-region many populations remain functionally extinct (Beck et al., 2011). High latitude populations, such as extant eastern oyster populations in the Gulf of Maine, can be traced to a hypsothermal period (eight thousand years ago) when lower sea levels, and minimal tides resulted in lagoon like conditions with warm summer temperatures (Campbell, 1986). This resulted in colonization by warm temperate species whose populations were contiguous from the Chesapeake to the Gulf of St. Lawrence (Bousfield and Thomas, 1975). As sea level and tidal ranges increased, the Gulf of Maine cooled (Greenberg et al., 2012). As a result, warm temperate species such as the eastern oyster were restricted to 'Virginia refugia', areas in the head of estuaries where summer temperatures still reached adequate temperatures for reproduction, such as the upper estuaries of the Piscataqua and Sheepscott River, where the only two extant oyster populations remain in the state (Larsen et al., 2013). The extant population in the upper estuaries of the Sheepscott River is the northernmost eastern oyster population in the United States and has led to the listing of the area as a critical area for Maine's natural resource management (Cowger, 1975).

Study System – The Damariscotta River estuary (DRE)

The rugose coastline of Maine consists of large tidal river systems, and long, shallow embayments surrounded by steep cliffs (fjards). The DRE extends for 18 miles through estuarine habitat and exhibits both dramatic tides (3.35 m), and numerous bedrock constrictions which create eight discrete subbasins (image 1) resulting in long hydrological resonance times (3 weeks) for the estuary (McAlice, 1977; Shipp, 1991). The longer residence times for the estuary occur in the Dodge, Days, and Salt Bay subbasins north of Glidden Ledges (Thompson et al., 2006). Resuspension of sediment is typically greatest at low tides, and despite freshwater input from the Damariscotta lake at the river's northern reach, the estuary remains highly saline (~25-32.5 psu) (Snyder et al., 2016). The combination of conditions has allowed the DRE to historically be one of the largest oyster aquaculture production zones in Northern New England, with harvests in the river comprising 67.5% of all eastern oyster landings in the state of Maine representing millions of dollars in revenue (Maine DMR commercial landings 2019, maine.gov/dmr).

Large wild oyster populations once inhabited the DRE during the Holocene epoch, as can be witnessed by shell middens 30 feet high covering as much as sixty acres in several areas. The combination of changing biophysical conditions associated with sea level rise, and the deleterious environmental practices associated with European settlement led to the eventual extirpation of this subpopulation (Sanger and Sanger, 1986).

Habitat Suitability Index (HSI) models

The utility of HSI models in informing conservation and restoration strategies inherently depends upon their accuracy. To ensure model accuracy, a four-step process including development, calibration, verification, and validation is required to ensure the models can be applied with confidence (Reiley et al., 2014; Theuerkauf and Lipcius, 2016).

Prior to model development, the relevance of model factors (described in Table 1) were determined through literature review, and discussions with professionals familiar with the Damariscotta River system working in the fields of marine conservation, marine research, and aquaculture. Factors which have limited spatially explicit data describing the variable, or which have low relevance in influencing habitat suitability within the specific system were excluded from the model as per (Theuerkauf et al., 2019). In the end, only variables that were deemed most relevant based upon literature review, discussions with professionals, and for which spatially explicit data was available were included in the model.

Variables considered herein include temperature, feed availability (chlorophyll a concentration), turbidity, substrate availability, depth, and estimated larval density surrounding aquaculture production sites. Temperature is fundamental to numerous physiological processes including dictating rates of filtration (Loosanoff, 1958), the growth of juveniles and adults, the onset of gametogenesis, spawning, and the extent of larval duration (Ingle, 1951; Cake, 1983; Stanley and Sellers, 1986; Fabioux et al., 2005; Pouvreau et al., 2006). Food availability, which is best indicated by phytoplankton (chl a) concentration (Bourles et al., 2009), positively correlates with fecundity (Chavez-Villalba et al., 2002), and is there for a significant aspect in both recruitment and population persistence. Likewise, the proportion of phytoplankton in total dissolved organic matter is a key aspect of site suitability for the eastern oyster (Newell et al., 1989). Chlorophyll a concentration above 10μg/L are cleared through the digestive system as pseudofeces, therefor concentrations above 10μg/L are considered unsuitable herein (Epifanio and Ewart, 1997; Snyder et al., 2017). Because high levels of suspended particulate matter dilute phytoplankton concentrations with inorganic matter, levels of suspended particulate matter above 10 mg/L increase production of pseudofaeces, negatively influencing oyster feeding rates (Haven and Morales-Alamo, 1966; Hawkins et al., 2013). Benthic substrate conditions were deemed relevant because populations existing on hard substrate are less likely to subside into mud or silt bottoms (Schulte et al., 2009), and recruitment success positively correlates with availability of cultch or other hard substrate (Barnes et al., 2007). Bathymetry was also considered directly as a factor in limiting suitability below MLW mark, and as a surrogate variable for temperatures above MLW. Air temperatures well below the physiological tolerance range for the eastern oyster regularly occur in winter months in Maine, leading to mortality due to exposure, and physical impacts from ice scouring in intertidal habitats. For these reasons depths 1m above the MLW mark were considered unsuitable.

Coastal satellite imagery layers include high spatial resolution ($30m^2$) satellite images of multispectral visible data derived from the Thermal Infrared Sensor (TIRS), and Operational Land Imager (OLI) onboard the Landsat 8 satellite. Data images used for analysis were collected biweekly from 2013 to 2016 and were processed and made available by the University of Maine's Coastal Satellite Oceanography group (Snyder et al., 2017).

For sea surface temperature (SST), Thermal Infrared Sensor (TIRS) images were processed using the NASASeaDAS platform, and products were atmospherically corrected using regression analysis of TIRS SST images, and concurrent, atmospherically corrected NOAA AVHRR derived SST as mentioned in (Thomas et al., 2002; Snyder et al., 2017). Ocean color multispectral OLI sensor data was used to derive chlorophyll a and turbidity after atmospheric correction was applied via algorithms described in (O'reilly et al., 1998; Nechad et al., 2010; Snyder et al., 2017). Satellite data values were validated via correlation analysis with in situ data derived from the Land Ocean Biogeochemical Observatory (LOBO), and Northeastern Regional Association of Coastal Ocean Observing Systems (NERACOOS) buoys within the Gulf of Maine, with the exception of chlorophyll a which did not correlate with in situ fluorescence measurements (Snyder et al., 2017).

Biophysical variables were spatially overlayed using ESRI Arc GIS Pro 2.7. Habitat suitability index scores based upon physiological tolerance ranges were derived from literature review (Table 1), and HSI scores were calculated for independent variables based on the environmental data available (Table 2). However, chlorophyll a measurements did not correlate with in situ fluorescence measurements in (Snyder et al., 2017), likely a result of errors in the NASA Ocean Biology Processing Group's algorithm (O'Reilly et al., 1998) designed to retrieve chlorophyll a from total reflectance.

In seeking a simple strategy for estimating larval dispersal from farm sites, the density of adult diploid female oysters being grown on farms sites was estimated based upon acreage. Additional assumptions include the approximate sex ratio to length of adult oysters during production. Harding et al. 2013 noted a 1:1 sex ratio at 65mm left shell length for 5 eastern oyster reefs in Pamlico Sound, North Carolina. Because the legal limit for harvest of the eastern oyster is 63.5mm, and the highest return on investment for producers is over 75mm, we assume a 1:1 sex ratio as a modest estimate. When estimating the proportion of diploid to triploid production, we used personal correspondence with hatchery managers, and survey information from aquaculture producers regarding diploid to triploid production ratios in the region (25% diploid seed sold by hatchery) and within the estuary (>50% diploid grown by farms)

(Stevenson, 2020). We assumed 25% diploid production as a modest estimate. Likewise, we assumed a modest estimate of lease acreage used for adult grow out (25% of total lease acreage), and adult density estimates based upon the predominant surface culture method within the river system (234,000 adults/acre), as estimates for bottom planting are typically much greater (400,000-500,000 adults/acre), and more variable due to attrition through natural processes. Lastly, the number of spat produced per diploid female represents 1% of hatchery estimates for larval survival (Wallace et al., 2008).

Centroids to each farm represent estimated values of larvae incidentally produced as a result of adult oyster spawning on farms. Larval density estimates are based upon number of estimated parameters including: acreage in adult production, estimated proportions of diploid to triploid production, and adult density estimates based upon predominant surface culture methods as mentioned. Larval production by farm was estimated using Kernel Density analysis on a $30m^2$ spatial resolution vector grid (Silverman, 1986). Using the estimated density results, larval density suitability scores were ranked on a continuous scale (0-1) with the highest and lowest density estimates corresponding to the highest and lowest suitability scores respectively.

Table 2: Larval Density Estimation Parameters

Parameter	Estimated Value or Percentage
% Acreage in adult production	25%
% Females in population	50%
% Diploid production	25%
Spat released per female	10,000
Adult density	234,000

Table 3: HSI Variable Value Scores

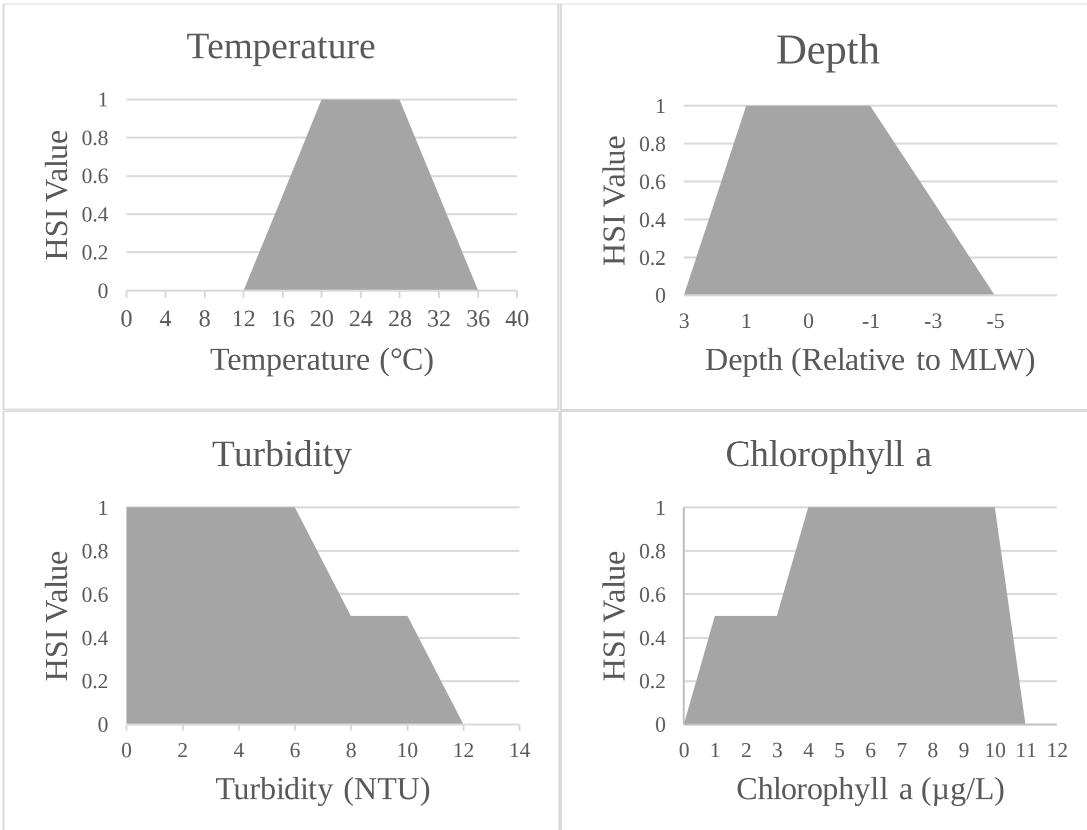

Table 4: HSI Model Variable Details

Layer	*Description*	*Type*	*Weight*	*Values*	*Source*
Chlorophyll a concentrations	Yearly average chlorophyll a concentration (µg/L)	Threshold	17.45%	Optimal (1): 3-10 µg/L Suitable (.5): 1-3 µg/L Unsuitable (0): <1µg/L; >10µg/L	UME coastal satellite imagery
Average summer temperature	Yearly average summer sea surface temperatures (°C)	Threshold	19.3675%	Optimal (1): > 20 °C Suitable (.5): 16-20 °C Unsuitable (0): < 16 °C	UME coastal satellite imagery
Turbidity	Yearly average turbidity (NTU)	Threshold	24.6375%	Optimal (1): < 8 mg/L Suitable (.5): 8-10 mg/L Unsuitable (0): >10 mg/L	UME coastal satellite imagery
Depth	Depth relative to MLW mark (M)	Threshold	18.0375%	Optimal (1): 1m above MLW to 3 m below MLW Suitable (.5): 3-5 m below MLW Unsuitable (0): < 5 m below MLW	UNH Center for Coastal and Ocean Mapping
Benthic Substrate	Potential substrate for recruitment	Exclusion	N/A	Optimal (1): Subtidal and intertidal ledges, boulder beaches, boulder ramps, gravel beaches, mixed sand and gravel beaches, man made structures, and coarse-grained flats Unsuitable (0): Other substrate	Maine DMR Marine Geologic Substrate
Larval Export from Aquaculture Sites	Estimate larval density per 30m² raster grid	Threshold	20.2375%	Continuous (0-1) scale based upon highest larval density estimates	Maine DMR Aquaculture Leases

Each layer was spatially represented over a $30m^2$ grid of the Damariscotta River estuary which matched the coarsest resolution of the coastal satellite imagery used to estimate sea surface temperature, turbidity, and chlorophyll a. Each $30m^2$ grid contained a variable HSI value based upon the suitability range value scores described. Values for each threshold layer were assigned on a scale of 0 to 1 representing unsuitable, and ideal habitat respectively based upon the physiological tolerance ranges derived from literature review (Table 2). Qualitative information from firsthand observation, and local expert interviews and surveys were also used to tailor suitability ranges to best match the system's conditions. Likewise, exclusion layers were assigned binary scores wherein unsuitable and suitable habitat were assigned scores of 0 and 1 respectively.

Through discussion with a 4-person stakeholder panel, individuals independently weighed each threshold variable relative to a given variable's perceived influence to physiological processes so that the weight of all variables combined equated to 100% with higher and lower weighting corresponding to greater and lesser importance respectively. All weighting values were averaged for application in the model.

<u>Model Calculation</u>

Weighted suitability scores for each cell (*Sj*) were calculated with the GIS field calculator using the formula:

$$Cj = \sum_{x=1}^{5} (Lxj * Wx)$$

$$Sj = Cj * Ej$$

Where Cj is the value of grid cell *j* calculated as the product of the threshold value *L* of cell *j* for threshold layer *x*, and the weight *W* of layer *x* summed across all 5 threshold layers. Ej is the score for cell *j* based on the value of the exclusion layer described in (Puckett et al., 2018). Unweighted suitability scores for cells (*Sj*) were calculated with the field calculator using the formula:

$$Cj = \sum_{x=1}^{5} Lxj$$

$$Sj = Cj * Ej$$

These habitat suitability scores were represented on a graduated color gradient geospatially representing a scale of 0 to 1 (least suitable to most suitable respectively). In the validation process, the habitat suitability assessment is simplified to only include layers assigned threshold values.

Aquaculture Practitioner Surveys

A brief survey was sent to all Limited Purpose Aquaculture Lease holders growing eastern oysters in the DRE. A LPA license permits the licensee up to 400 square feet of area for one calendar year for the culture of certain shellfish species and marine algae using certain types of gear. Numerous LPA's can be held by a single license holder, and are often used as a way to test the suitability of new areas for production. LPA license holders were asked the percentage of diploid vs triploid seed grown on their farms, and whether they have witnessed wild oyster populations within 1km of their farm site(s).

Stakeholder Interviews

As a means of internally verifying model predictions, a variety of stakeholders including shellfish harvesters targeting 'wild' eastern oysters in the DRE, aquaculture practitioners operating in the river, and researchers familiar with the system were asked questions regarding characteristics of sites in the DRE where wild oyster populations were observed. These characteristics include the type of substrate, depths, subbasin locations, and specific locations within subbasins where populations were observed. Wild oyster harvesters were also asked the approximate yields they harvest per tide in different subbasins, and the timeframe (decades) when wild oyster populations began to be noticed and harvested if applicable.

Results

The HSI model predicted a limited amount of area as suitable for restoration. The northernmost basins of the DRE possess the vast majority of suitable habitat within the estuary. Overall, benthic substrate for recruitment proves to be the primary variable limiting habitat suitability throughout. Larval density, and turbidity also limit suitability in the southern, and northern portions of the estuary respectively.

The three northern basins comprise the majority of highly suitable depths within the estuary. While bathymetry data for the Salt Bay basin was not included in this model, nautical charts indicate that much of the Great Salt Bay basin would be considered high suitability. While the Great Salt Bay possesses depths conducive to aquaculture production, two factors inhibit the production of adult oysters within the basin: contamination due to fecal coliform, and navigational hazards in the course north from Days basin. Therefore, larval production within the upper Salt Bay Basin is considered null herein. Turbidity is also a component which limits suitability proximal to shore in the entire estuary, and the abundance of silt within the Great Salt Bay's abundant mud flats result in a turbid microclimate.

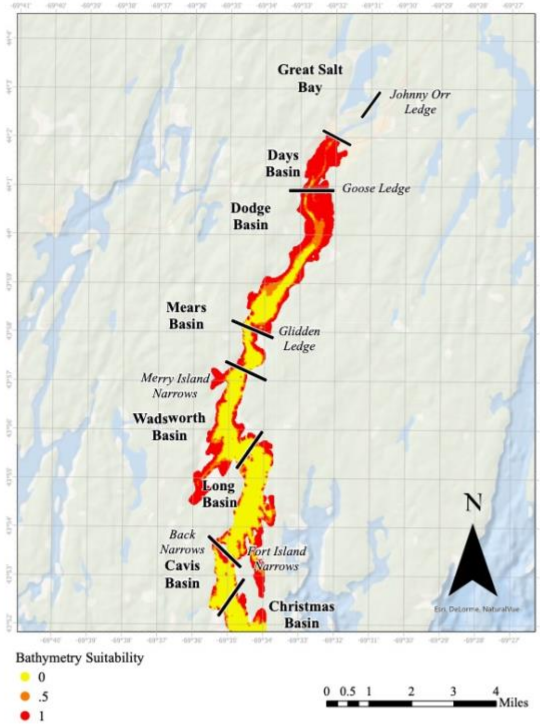

Figure 4a: Bathymetry Suitability scores

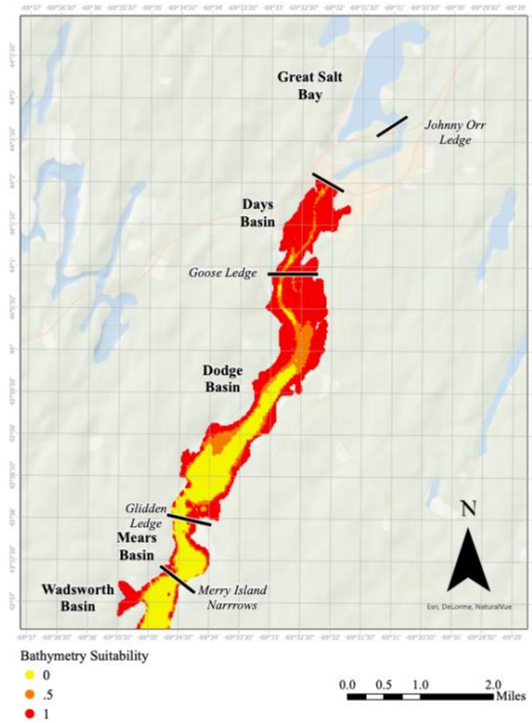

Figure 4b: Bathymetry Suitability scores

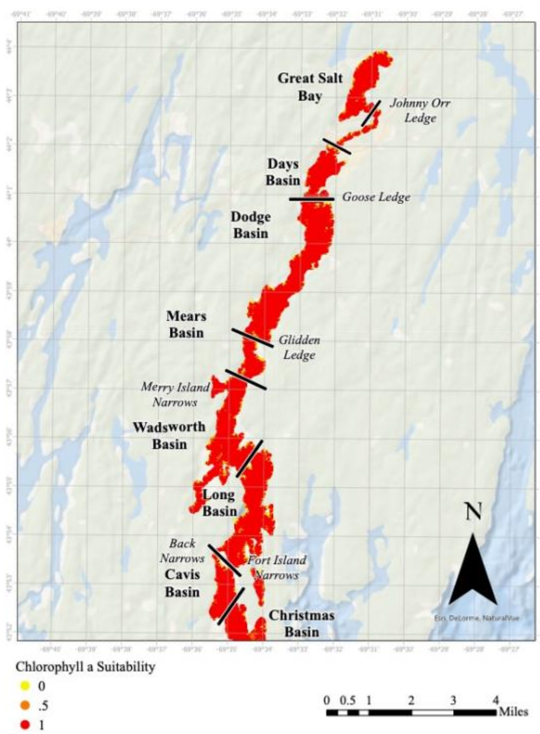

Figure 5a: Chlorophyll a Suitability scores

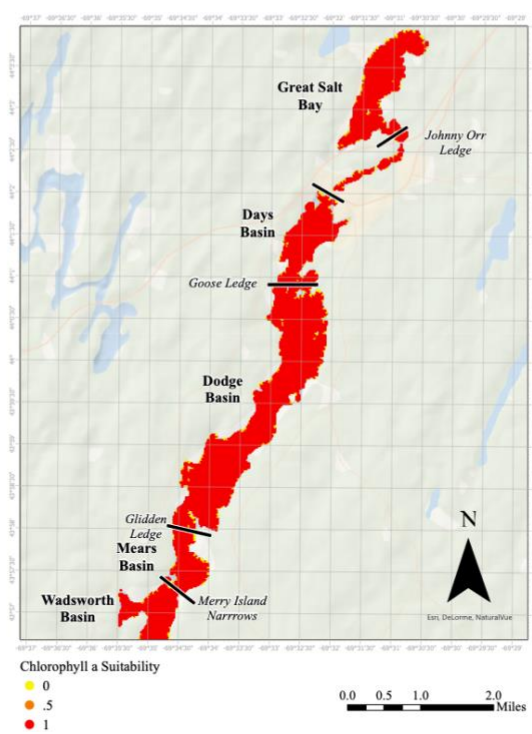

Figure 5b: Chlorophyll a Suitability scores

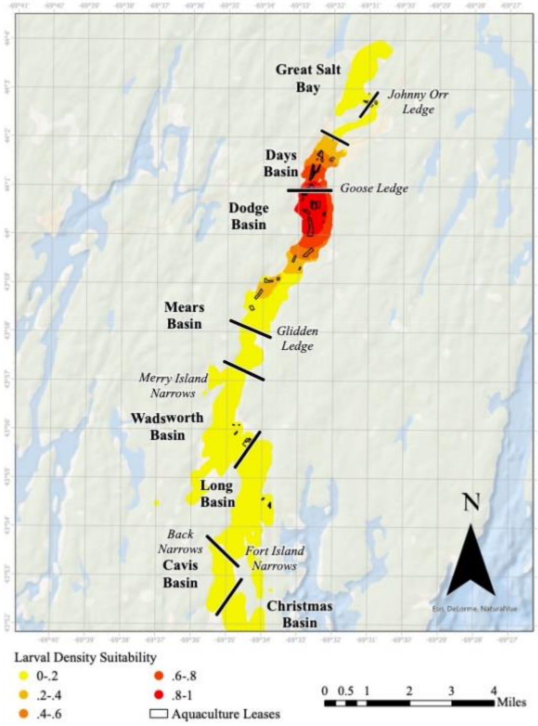

Figure 6a: Larval Density Suitability scores

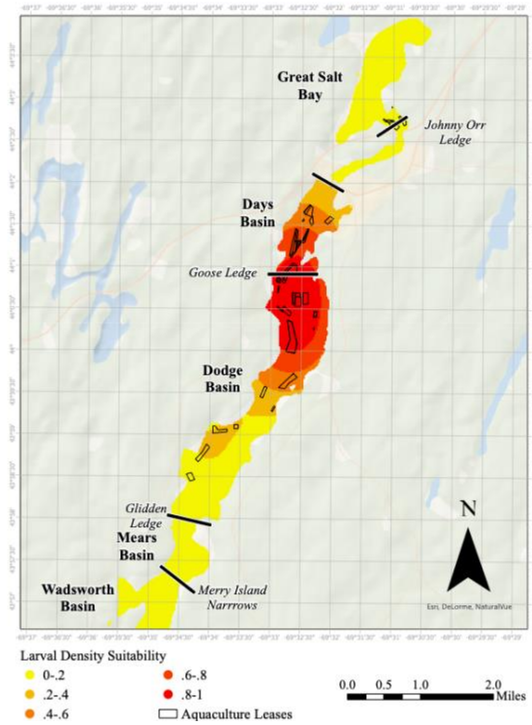

Figure 6b: Larval Density Suitability scores

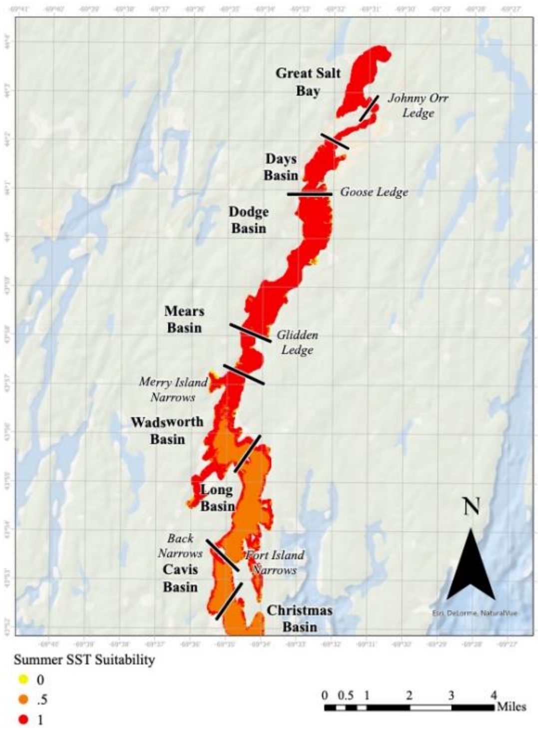

Figure 7a: Sumer Sea Surface Temperature Suitability scores

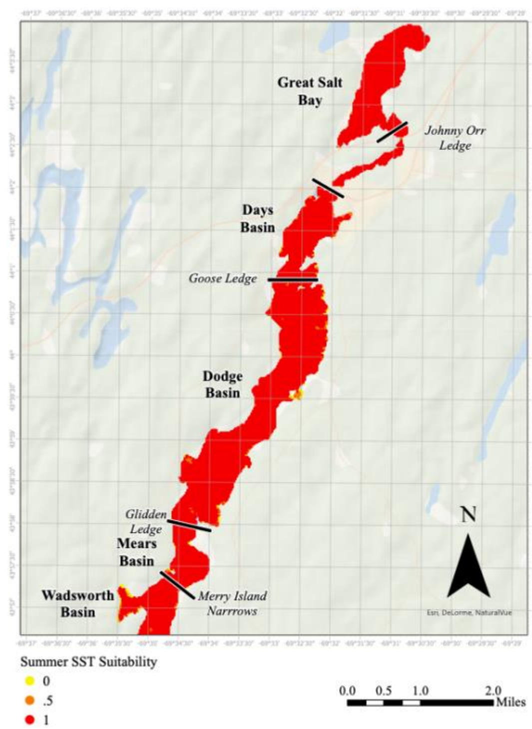

Figure 7b: Sumer Sea Surface Temperature Suitability scores

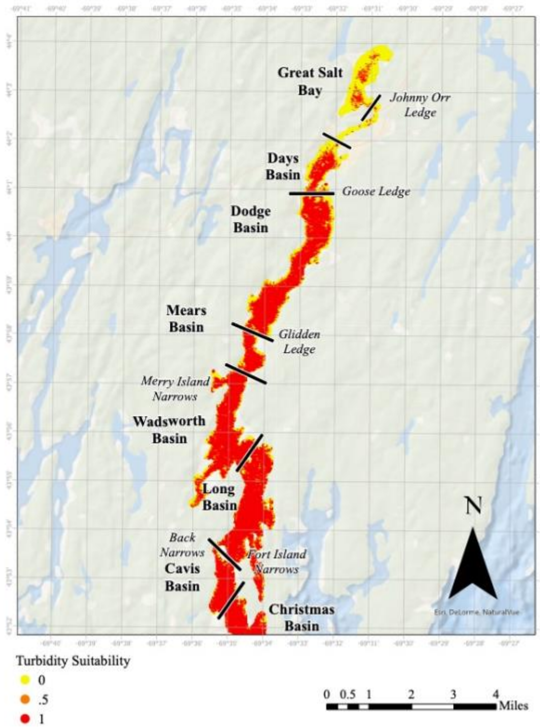

Figure 8a: Turbidity Suitability scores

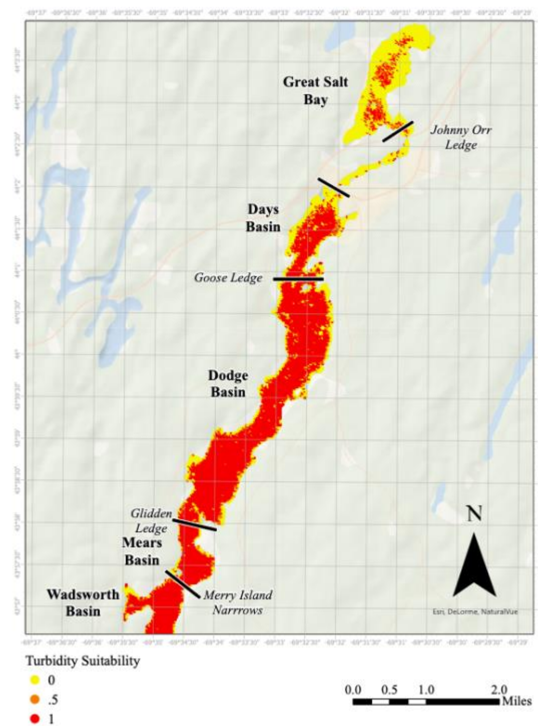

Figure 8b: Turbidity Suitability scores

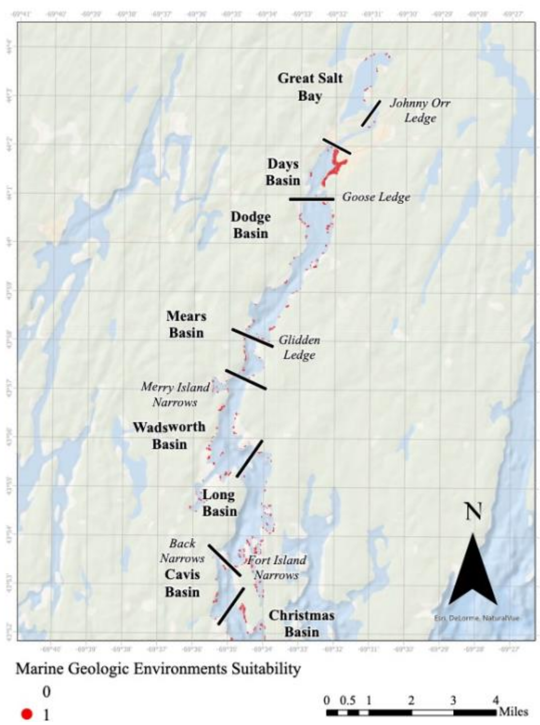

Figure 9a: Benthic Substrate Suitability scores

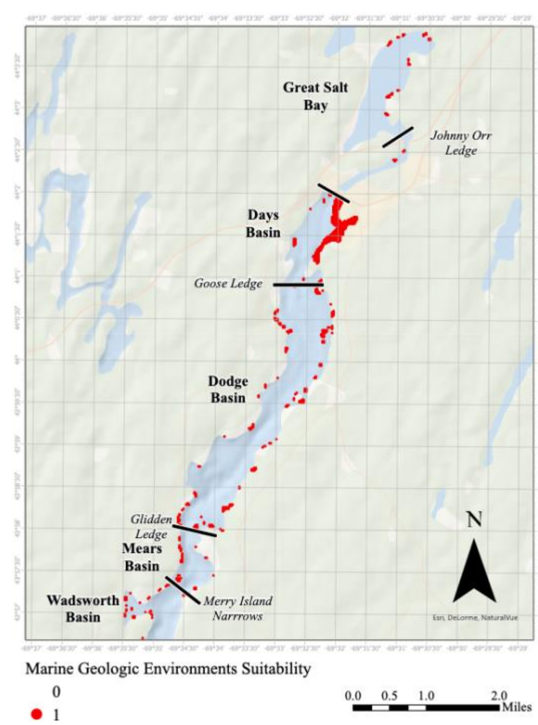

Figure 9b: Benthic Substrate Suitability scores

Preliminary Sensitivity Analysis Observations

Sensitivity analysis has proven valuable for quantifying the influence of individual model variables on habitat suitability predictions (Theuerkauf et al., 2019). The validity of future HSI models can be enhanced by prioritizing the acquisition of data for variables with (1) disproportionate influence on suitability predictions, (2) high spatial variability, and (3) minimal amounts of unsuitable area within broad areas of interest (Puckett et al., 2018).

Preliminary observations indicate turbidity as the primary variable limiting suitability in the northern basins. The area of marginal suitability in the northern portion of Day's basin is likely influenced by turbid water entering from the Great Salt Bay (Figure 10a). The middle portion of the estuary near Glidden ledges and Merry Island appears to be equally influenced by turbidity, larval concentration, and bathymetry. For example, the bathymetry surrounding Glidden ledges is conducive to restoration despite depths greater than 5m throughout the majority of Dodge and Wadsworth basins (Figure 10b). Similarly, bathymetry, estimated larval concentration, and sea surface temperatures limit the suitability of habitat in the mouth of the estuary. Temperature appears to be the factor influencing suitability most in the mouth of the estuary, with areas of highest suitability occurring in the coves proximal to the Fort Island Narrows (Figure 10c). Furthermore, sea surface temperatures prove to create discrete zones of suitability through the estuary. Shorter residence times in the mouth of the estuary appear to maintain a cooler microclimate, while long residence times north of Glidden ledges create an incubation zone for cool, nutrient rich water entering from the Gulf of Maine (Figure 11).

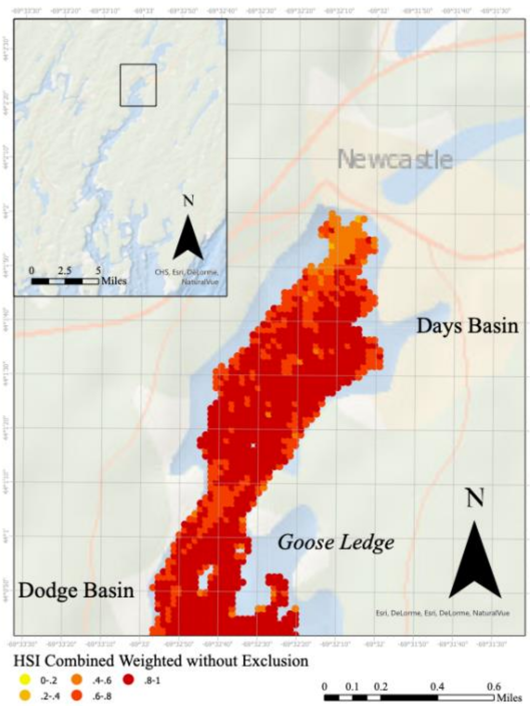

Figure 10a: HSI Combined Weighted Suitability Scores without Exclusion – Days Basin

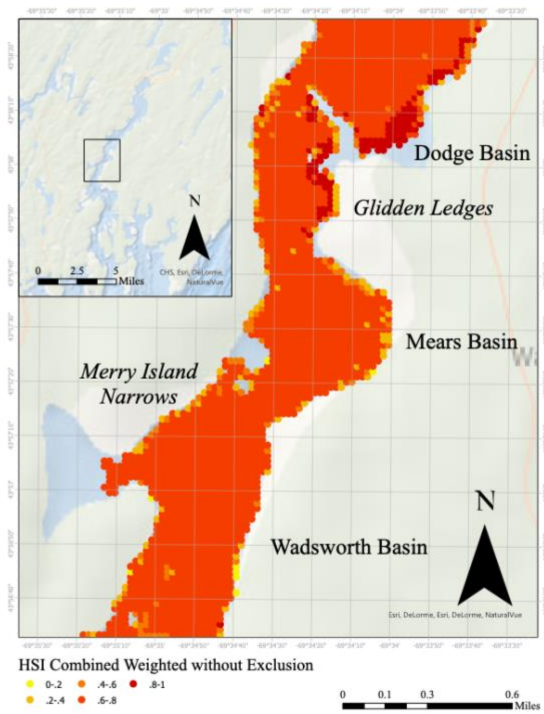

Figure 10b: HSI Combined Weighted Suitability Scores without Exclusion – Merry Island Narrows

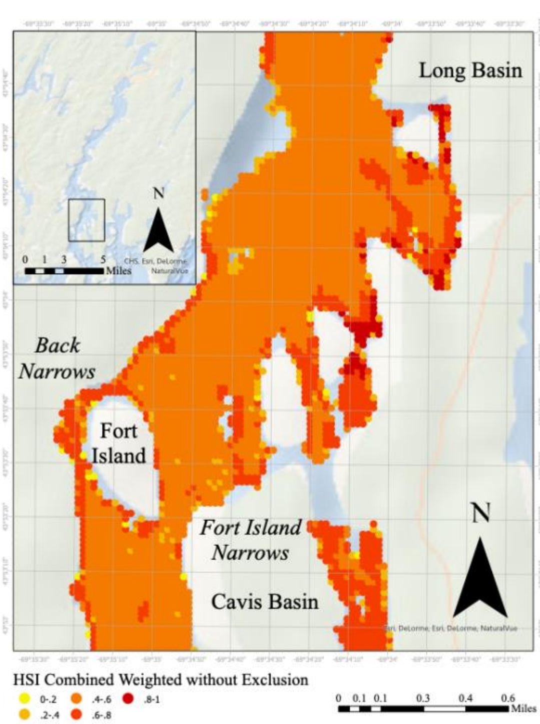

Figure 10c: HSI Combined Weighted Suitability scores without Exclusion – Fort Island Narrows

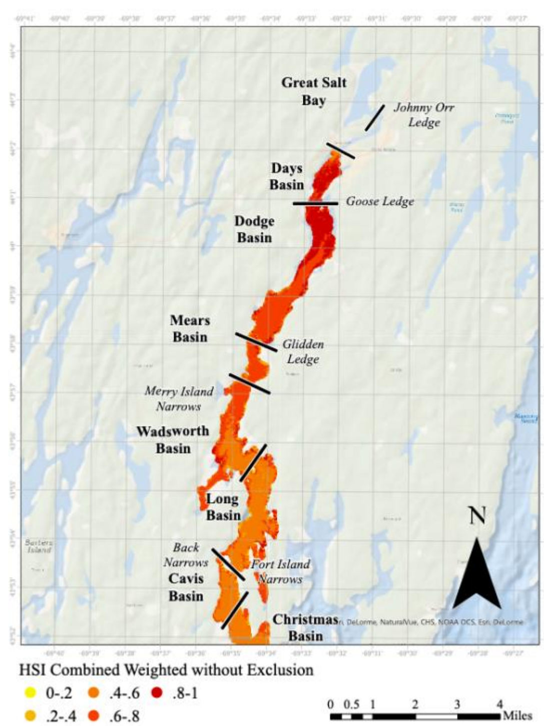

Figure 11: HSI Combined Weighted Suitability scores without Exclusion – Damariscotta River Estuary

HSI Distribution

Model results indicate a total of 29.7 ha of suitable habitat (cell values ranging 1- 0.5), and 2.2 ha of marginally suitable habitat (cell values ranging 0.3-0.5) within the estuary. Less than .5 hectares of suitable habitat are located within aquaculture lease boundaries. Of the 29.7 ha of suitable habitat identified, 5.1 ha occur within Day's Basin, an area of intensive aquaculture production. Due to a lack of bathymetric data for the northernmost basin, the Great Salt Bay, the suitable habitat therein is likely significantly underestimated. Likewise, because the bathymetryic data applied in the model was from the 1940's, the extension of the intertidal zone due to sea level rise likely results in an underestimation of suitable habitat.

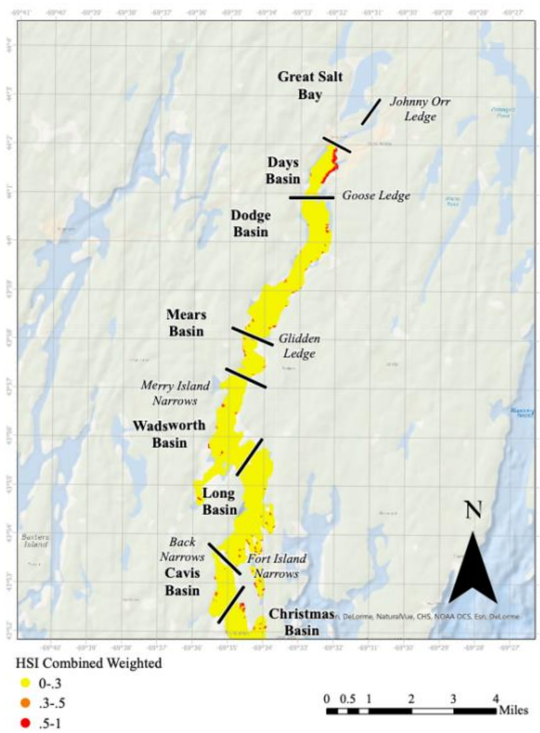

Figure 12a: HSI Combined Weighted

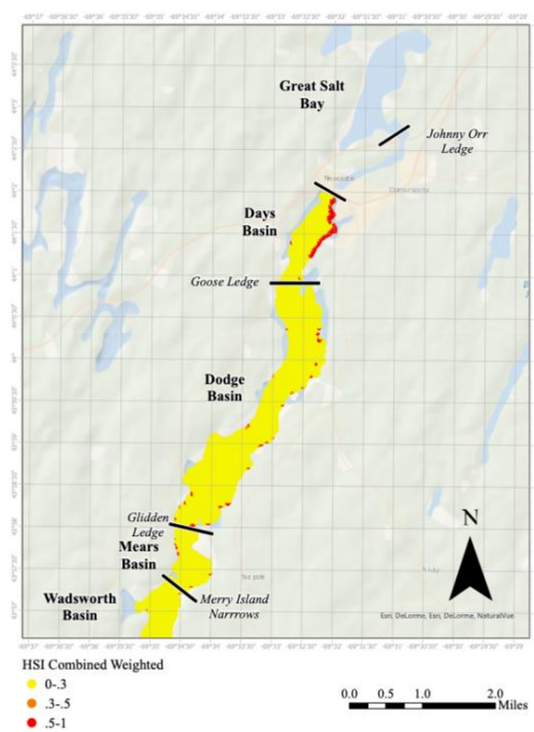

Figure 12b: HSI Combined Weighted

Overall, the primary limiting factor within the combined HSI model is suitable benthic substrate (Figures 10a,10b,12a and 12b). When comparing the combined weighted HSI model (Figure 12a and 12b) with the combined weighted HSI model not considering marine geologic environments (Figure 11), it is evident that all areas studied possess habitat suitable for restoration. Acquisition of marine geologic environments data with greater spatial resolution would likely significantly increase suitability values, and likewise increase the validity of future models for use in marine resource management decisions. Additionally, the availability of suitable substrate in the form of shell cultch, which remains abundant throughout the estuary in all geologic environments, would also increase the area of predicted habitat suitable for larval recruitment.

Despite a lack of quantitative results regarding the influence of specific threshold factors on combined suitability predictions, the combined weighted HSI model not including marine geologic environments (Figure 11) indicates a range of suitability zones indicative of discrete microclimates within the estuary. Not surprisingly, the warmest zones of the estuary support the largest ‘wild’ populations where substrate is available. Conversely, sporadic populations exist in the lower reaches of the estuary, matching qualitative reports from researchers, and shellfish harvesters.

Aquaculture Practitioner Surveys

A survey and communications with state hatcheries informed model estimations of diploid versus triploid production within the estuary. Of approximately 25 commercial leases within the estuary, 5 indicated production of >50% diploid. Conversely, one of two state hatcheries indicated regional sales of diploids were approximately 25%. As a modest estimate, 25% diploid production was used as the metric to which the adult ploidy ratio was measured by.

As a means of qualitatively verifying the HSI model predictions with ecological knowledge, farm lease holders were also asked whether they have observed wild populations within 1km of their lease boundaries. All 7 participants indicated that wild oysters can be found throughout Dodge Basin (head of estuary).

<u>Local Stakeholder Interviews</u>

In depth ecological knowledge pertaining to the system was provided by a range of stakeholders including wild shellfish harvesters targeting the eastern oyster, aquaculture practitioners, and researchers familiar with the system. Participants were asked the depths and substrate where oysters can be found, and locations ranging from the subbasin to specific areas within each subbasin. Shellfish harvesters were additionally asked the months they typically harvest, and average yield per trip in respective sub basins.

Stakeholders indicated that wild oyster populations can be found as in low intertidal depths, and as deep as 5 m. Harvesters indicated working within the intertidal zone only, and reported reductions in shell length sizes associated with shallow depths.

Participants reported population presence not being solely restricted to hard substrate as was assumed in the model. Additionally, areas reported as having suitable substrate by practitioners were not present in the spatial model particularly within the western shore of Days basin. Participants also reported that limited harvesting does occur in soft substrate proximal to farm leases where cultch is present.

Figure 14: Eastern oysters present on the western bank of the Damariscotta River in Newcastle, Maine

Figure 15: Eastern oysters present on the eastern bank of the Damariscotta River in Damariscotta, Maine

Figure 16: Wild oysters found on the banks of Oyster creek in Nobleboro, Maine

The uppermost basins north of Glidden ledges were reported as having the highest concentrations of wild oyster populations. Harvesters reported difficulty in reaching quotas south of the Wadsworth basin, however all stakeholders report sporadic populations throughout the length of the estuary. Interestingly, populations were reported in the aptly named Oyster creek, an upper estuary located in the Great Salt Bay. It is worth noting that the Great Salt Bay, and the eastern portion of Day's Basin are restricted shellfish harvesting zones due the presence of fecal coliform.

Discussion

This study represents the first time an HSI model has been applied to investigate the role of larval spillover from aquaculture assisting in the restoration of a population considered extirpated. Larval spillover from aquaculture raises many concerns pertaining to the long-term genetic viability of populations 'enhanced' with individuals bred for disease resistance (Hare et al., 2006), and the influence of genetic introgression for relict populations proximal to aquaculture production (Waples et al., 2012). However, the restoration of the eastern oyster in areas where they were once extirpated presents numerous positive effects for the social ecological system in question.

Implications of Larval Spillover

While the social acceptance of bivalve aquaculture has increased in the region, the high market value of oysters in the region (>US$5.20/kg in 2019), and the capital costs of aquaculture production, make the product a luxury protein. This has marginalized parts of the rural fishing community. The resurgence of a 'wild' fishery presents opportunities for equity within the shellfish industry for harvesters. Likewise, by increasing the diversity of shellfish species permitted for harvest, the local industry may attain greater resilience in a rapidly changing climate (Hughes et al., 2005).

Industrial pollution in rivers and streams heavily impacted estuarine systems, and led to the extirpation of oyster reefs, a valuable nursery ground for Gulf of Maine finfish stocks (Ames, 2004). Because oyster reefs provide biogenic habitat for benthic invertebrates, motile crustaceans and fish (Bahr & Lanier 1981; Coen et al., 1999; Lenihan et al., 2001; Peterson et al., 2003), the expansion of oyster populations in the region may potentially assist in restoration, and the long-term sustainability of fisheries species stocks in the region.

The American lobster (*Homarus americanus*) comprised 79% of the value (approximately $408,000,000) of all fisheries in the state of Maine in 2020 (Maine DMR commercial landings 2020, maine.gov). The social and economic condition of Maine's fishing industry is therefore highly dependent on the health of this single fishery (Steneck et al., 2011). The increase of nursery habitat associated with the expansion of oyster populations, may assist in the restoration of commercially valuable fish species which were historically Maine's most valuable marine resource monetarily (Collins and Rathburn, 1887).

Because the traditional user interest, marketplace framework insufficiently captures the value of ecosystem services (Ruffo and Kareiva, 2009), nonmarket values must be interpreted according to an incomplete understanding of ecosystem function, which consequently impedes long range decisions regarding sustainable management strategies (Nelson et al., 2009). This study begins to investigate an ecosystem service of aquaculture with direct market value in the form of fisheries landings.

Predicting Incidental Restoration through HSI Models

As a tool in restoration, habitat suitability indices identify locations with the requisite conditions for species population persistence over broad areas of interest (U. S. Fish Wildlife Service 1981; Roloff and Kernohan, 1999). Only a small proportion of historic distributions of eastern oyster populations overlap with present day model predictions due to changing land use, and historical overfishing (Jackson et al., 2001; Puckett et al., 2018). Unfortunately, populations within New England's coastal waters remain functionally extinct, with only isolated extant populations remaining (Beck et al., 2011).

Few HSI models have been applied to quantify the value of habitat for restoration of the eastern oyster in the Northeast US (Starke et al., 2011), however HSI models have proven effective components of restoration strategies in areas where meta populations remain (Battista, 1999; Barnes et al., 2007; Pollack et. al., 2012; Soniat et al., 2013; Swannack et al., 2014; Theuerkauf & Lipcius, 2016; Puckett et al., 2018).

This HSI model seeks to predict areas within the DRE where larval subsidy from aquaculture is most likely to assist in restoration of an extirpated population. This represents a component of conservation aquaculture not yet considered in the literature (Froehlich et al., 2017). Because meta-population persistence is highly dependent upon sub-population connectivity and local retention (Puckett et al., 2014), restoration of oyster reefs requires a deep understanding of meta population dynamics (Hastings and Botsford, 2006; Lipcius et al., 2008). Because populations were previously extirpated within the estuary, gaining independent data regarding species distribution, and survival of juveniles to sexual maturity in sites identified as high suitability would provide insight into the long term sustainability of the DRE population amidst harvesting pressure.

Limitations to Variable data

The eastern oyster's broad geographical extent spans tropical, subtropical, and temperate climates along the western Atlantic coast (Burroker, 1983; Kennedy et al., 1996). Due to the wide physiological tolerance range of the species, and diversity of habitat in which it persists, HSI models for the eastern oyster should focus on the variables which are the most influential to restoration success within a specific system (Theuerkauf and Lipcius, 2016). Of 4 eastern oyster HSI models ranging from the Gulf of Mexico to the Gulf of Maine, only 3 studies had variables in common (salinity, substrate, and depth), representing a small fraction of all variables considered (Cake, 1983, Starke et al., 2011; Snyder et al., 2017; Puckett et al., 2018). For the study system in question, several variables have data limitations worth noting.

The availability of modern multi-beam radar bathymetry data for estuarine systems is currently limited in Maine. The bathymetric layer therefor consists of 1940's single-beam radar data which does not include the northernmost Salt Bay Basin. Because global mean sea level rise for the 20th century is estimated to be 1.7mm per year (Church and White, 2006), corrected sea levels, and data availability for all basins would increase the validity of the model.

The vector grid developed for the model matches the coarsest spatial resolution of the coastal satellite data (30m^2). Therefor grid cells may not adequately represent small areas of suitable substrate within respective grid cells, because cell values consist of the average values for a given data layer. Likewise, the exclusion of shell cultch as a suitable substrate for recruitment misrepresents the true quantity of substrate available. Because substrate availability proved to be the primary limiting factor for identifying suitable habitat, developing approaches to refine and increase the spatial resolution of marine geologic environments data would likely enhance the quality of model predictions.

Additionally, the dynamic nature of the system with regards to oceanographic circulation has not been considered within this model. Understanding the influence of current speed and directions on larval dispersal patterns would significantly influence the spatial estimates of larval density assumed within the model.

Current temperature data is an additional component that would significantly enhance estimates of larval density within the river basin. Summer temperatures dictate the timing and frequency of sexual maturation, spawning, and recruitment for oysters (Diederich et al., 2005). Because the data included was gathered on a biweekly basis between 2013 and 2016, gaining access to updated data with higher temporal resolution would provide insight into the timing and frequency of spawning events, and extent of larval duration. Lastly, the disproportionate influence older, larger oysters have on larval production (Mann, et al 2014) is not represented by the adult density estimates developed herein.

Lastly, errors in chlorophyll a measurements are likely a result of Colored Dissolved Organic Matter (CDOM) concentrations which have high temporal, and spatial variability along Maine's forested coastline (Thompson, 2006; Roesler and Culbertson, 2016). Absorption of blue green wavelengths by CDOM likely alter the NASA Ocean Biology Processing Group's algorithm (O'Reilly et al., 1998) designed to retrieve chlorophyll a from total reflectance (Siegel et al., 2005). Additionally, in situ fluorescence yields are also subject to error due to algal taxa variability, and nutrient limitations (Cullen, 1982). For the reasons mentioned, chlorophyll a measurements did not significantly correlate with insitu measurements (Snyder et al., 2017).

Omitted Variables

In addition to the data limitations of the variables included, several variables were omitted due to limited spatial and temporal data resolution. Biological variables such as the effects of predators and pathogens, on larvae, and newly settled juveniles would inform the model significantly. The Damariscotta River estuary hosts protozoan parasites of significant concern including *Haplosporidium nelsoni* (MSX) and *Perkinsus spp.* (Dermo). MSX was associated with large die offs in waters in the 1990's (Barber et al., 1997), and 2000's (Bouchard, 2012). As a response, the aquaculture industry has selectively bred oysters with resistance to MSX (Giray, 2016). Dermo was low in prevalence in the 1990's and 2000's within Maine waters (Kleinschuster and Parent, 1995; Pecher et al. 2008). However, recent studies in the Damariscotta River indicate a 15-to-65-fold increase in *Perkinsus spp.* within a period of 12 years (Marquis et al., 2015). A common proteobacterium pathogen of juvenile oysters which has not yet been selectively bred for, *Alliiroseovirus crassostrea* (ROD), has also been recorded in Maine (Maloy et al., 2005; Maloy et al., 2007; Boardman et al., 2008; Degremont et al., 2015; Robledo et al., 2018).

Likewise, the recent increase in invasive green crab (*Carcinus maenas*) populations has negatively impacted important commercial shellfish populations such as the softshell clam (*Mya arenaria*) within the region (Whitlow, 2010). Further studies regarding the vulnerability of juvenile oysters to predation in comparison to other shellfish populations may inform management strategies in the future.

Competition for substrate with macroalgae is another biological consideration not included within the model. Rockweed (*Ascophyllum nodosum*) has been shown to inhibit invertebrate (barnacle) recruitment (Hawkins et al., 1983; Jenkins et al., 1999; Jenkins et al., 2004), however, it remains unclear whether macroalgae negatively influences the recruitment of eastern oyster larvae. Another biological component not considered in the model that may be potentially influencing recruitment is the availability of cultch. An abundance of cultch within the estuary resulting from 30+ years of oyster aquaculture, and historic populations makes this recruitment substrate available in all substrate types considered. However, this material likely lacks the vertical, three-dimensional structure required for recruitment and survival (Brumbaugh and Coen, 2009; Powers et al., 2009).

One abiotic factor that significantly influences larval development, recruitment, and growth of shellfish species are depressed carbonate ion saturation states associated with ocean acidification. These factors have been shown to increase larval energy expenditure during initial shell formation, reduce juvenile and adult fitness by influencing basal energy consumption, and shell strength and formation (Waldbusser et al., 2013, Waldbusser et al., 2011; Beniash et al., 2010; Kleypas et al., 2006). Depressed aragonite saturation states are of particular concern for early life stages of oyster development in estuarine sites in Maine as climate change continues to influence riverine discharge volumes (Salisbury, 2008).

Another physical component that may be limiting larval recruitment is current speed. The combination of high tidal exchange rates, and numerous constrictions within the estuary result in a unique hydrodynamic environment within the river basin. Benthic flow velocities have been shown to influence recruitment dynamics (Whitman and Reidenbach, 2012), and physiological processes (Grizzle et al., 1992). Because flow rates >4,000 cfs limit recruitment (Wilson et al., 2005; Barnes et al., 2007), understanding the influence of current speed on larval recruitment would likely enhance the model's validity.

Salinity is the most common variable included in the oyster HSI models reviewed due to the eastern oyster's evolution in mesohaline, and polyhaline conditions, and the resultant inability to tolerate long periods of extreme salinities (< 5ppt or >35 ppt) (MacKenzie, 1981; Cake, 1983; Barnes et al., 2007). The DRE is unique in that it is a high salinity environment ranging from 25-32.5 ppt (Snyder et al., 2017). Additionally, qualitative reports from local expert interviews indicate eastern oyster populations proximal to the primary source of freshwater inflow in the upper estuary, Damariscotta lake. In the end, salinity was omitted in this model due to limited availability of spatial data for the parameter, information derived from literature review, and qualitative information indicating the nonlimiting role of the factor in dictating recruitment and survival within the system.

Because microbial decomposition often depletes dissolved oxygen levels for benthic invertebrate species (Powers et al., 2005; Seitz et al., 2009) dissolved oxygen was explored as a potential variable limiting suitability. However, benthic hypoxia is not of concern for autotrophic systems with high net ecosystem metabolism where gross primary productivity is proportionally higher than total respiration, such as in the DRE (Caffrey, 2003; Miller, 2017). This fact, in combination with a lack of spatial data, limited the model's ability to characterize dissolved oxygen.

Lastly, the entirety of the upper Great Salt Bay basin, and the eastern half of Days basin are prohibited for adult shellfish grow out and harvesting due to water quality concerns. Qualitative reports indicate that the areas in Days basin and select areas in the Great Salt Bay basin have notable populations where substrate is not limiting. Investigating the role prohibited harvesting areas have on oyster density and abundance would be valuable for predicting the larval output of various locations within the estuary. Additionally, because oysters bio assimilate land derived nitrogen on variable temporal and spatial scales (Carmichael et al., 2012; Kellogg et al., 2014), the role population restoration within the northernmost basins has on harvesting, and bioremediation goals may provide innovative conservation opportunities for local municipalities.

Next Steps

Incorporating local stakeholder knowledge can greatly enhance the efficacy of HSI models through variable selection and weighting (Theuerkauf and Lipcius, 2016; Puckett et al., 2018; Theuerkauf et al., 2019). As a means of verification, local stakeholder interviews informed model assumptions regarding the relevance of variables to recruitment and survival, and species distribution predictions for the river basin. Interviews indicated areas with large, harvested populations that were not recognized in the model likely due to a low degree of spatial resolution, or additional variables that might play a role when analyzing benthic substrate availability.

Independent quantitative data characterizing species distribution within the river basin is required to adequately test and ensure the efficacy of the model's predictions (Brooks, 1997; Araujo and Guisan, 2006; Tirpak et al., 2009). When validated with independent species distribution data, geospatial models can serve as robust predictors of suitable habitat for restoration (Theuerkauf & Lipcius, 2016; Puckett et al., 2018). While species distribution information would inform the extent of restoration within the river basin, additional information is required to confirm the role of larval spillover from aquaculture in population restoration.

Particle tracking models incorporating oceanographic circulation, planktonic larval duration, and larval behavior have been applied to investigate oyster larvae dispersal patterns of native (Narvaez et al., 2012; North et al., 2008), and invasive populations (Laugen et al., 2016). Hydrodynamic modeling would inform predictions of the movement of larvae during the 15-25 days of planktonic development (Kennedy, 1996). While shallow well mixed systems maintain mollusc populations through larval invasion (Roegner, 2000), river basins with restricted entrances, and retentive local circulation, have been found to retain larvae in the Chesapeake Bay (Southworth and Mann, 1998).

An additional strategy beyond larval circulation modeling for understanding population dynamics includes genetic analysis. Numerous studies have employed genetic sequencing to investigate population connectivity amongst Atlantic oyster populations (Hoover and Gaffney, 2005; Xiao et al., 2010; Lazoski et al., 2011; Gomez-Chiarri et al., 2015). In addition to population dynamics, genetic analysis can provide insights regarding the efficacy of population supplementation with disease tolerant strains (Hare et al., 2006). While supplementation of wild populations with inbred, disease tolerant stocks can result in genetic bottlenecks (Wang and Ryman, 2001), it is unclear how larvae from hatchery reared stocks can influence the long-term genetic health of reintroduced populations in river basins where populations were recently extirpated.

In addition to larval spillover from oyster aquaculture, it is important to consider the role aquaculture production of all habitat forming species may have on conspecific populations, and ecosystem function. Despite being overlooked as an ecosystem service (van der Schatte Olivier et al., 2020), the value of larval spillover in the restoration of extirpated bivalve populations has been noted in northern New Zealand (Norrie et al., 2020). Likewise, the decline of native kelp populations in shallow coastal zones of the south western Gulf of Maine (Harris and Tyrrell, 2001; Dijkstra et al., 2017) raises questions regarding the ethics of macroalgae aquaculture as increasing attention is being given to industrial scale production of kelp species as a renewable source of biofuels and chemicals (Kraan, 2013; Wei et al., 2013).

Oyster Populations and a Warming Climate

Average global sea surface temperatures were the highest on record in 2016 due to elevated greenhouse gas levels, and an El Nino event (Dunn et al., 2017). In the Gulf of Maine, 2012 and 2016 were the two warmest years in the OISST record (Pershing et al., 2018). Future climate projections have grown increasingly valuable as a means of informing fisheries management strategies (Pershing et al., 2018). Incorporating climate projections within habitat suitability assessments for invasive Pacific oysters in Scandinavia provides valuable insight for resource managers seeking to limit a rapidly expanding population (Laugen et al., 2016). Future investigations should extrapolate the model to investigate the role a rapidly changing climate may have on habitat suitability for regional estuaries with similar hydrogeologic conditions as the DRE in coastal Maine, and eastern Canada.

Within the last decade the Gulf of Maine has experienced marine 'heat waves' which have altered the function of marine ecosystems, and fishing industry sectors (Pershing et al., 2015). As fisheries management seeks to adapt to wide variabilities in the geographic distribution and seasonal cycles of fisheries stocks due to warming temperatures (Mills et al., 2013), the restoration of wild oyster populations poses unique opportunities for social ecological systems adapting through fisheries diversification (Steneck et al., 2011).

As preliminary evidence of the reintroduction of shellfish species resulting from larval spillover from aquaculture, this study posits the potential for larval spillover to be considered an ecosystem service with direct market value. The socioecological implications of larval spillover should thus be of significant interest to marine resource managers, fishers, aquaculture producers, and conservation agencies seeking to restore, and enhance the function of coastal and estuarine ecosystems. Natural resource management strategies which blend the interests of numerous industries with the focus on ecosystem restoration have the potential to reinvent the current extractive, user-interest focus, towards a reciprocal conservation paradigm.

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