Management of Biological Invasions (2016) Volume 7, Issue 2: 141–155
DOI: http://dx.doi.org/10.3391/mbi.2016.7.2.02
© 2016 The Author(s). Journal compilation © 2016 REABIC
Open Access

Research Article

Development and validation of a habitat suitability model for the non-indigenous seagrass *Zostera japonica* in North America

Deborah J. Shafer[1], Todd M. Swannack[1,*], Christina Saltus[1], James E. Kaldy[2] and Austin Davis[1]

[1]*US Army Corps of Engineers, Engineer Research and Development Center, 3909 Halls Ferry Rd, Vicksburg, MS 39180, USA*
[2]*US EPA, Western Ecology Division, 2111 SE Marine Science Dr., Newport, OR 97365, USA*

E-mail: Todd.M.Swannack@erdc.dren.mil (TMS), DrDeborahShafer@gmail.com (TJS), ChristinaSaltus@erdc.dren.mil (CS), Austin.V.Davis@erdc.dren.mil (AD), kaldy.jim@epa.gov (JEK)*

**Corresponding author*

Received: 27 January 2015 / Accepted: 7 August 2015 / Published online: 19 October 2015

Handling editor: Marnie Campbell

Abstract

We developed a spatially-explicit, habitat suitability model that can be used to identify and predict areas at higher risk for non-native dwarf eelgrass (*Zostera japonica*) invasion. The niche-based model uses simple readily available environmental parameters (depth, near shore slope, and salinity) to quantitatively describe habitat suitable for *Z. japonica* invasion based on ecology and physiology from the primary literature. Habitat suitability is defined with values ranging from zero to one, where one denotes areas most conducive to *Z. japonica* and zero denotes areas not likely to support *Z. japonica* growth. Functional forms and equations for the ZJHSM were developed a priori, and the model was validated by comparison with multiple years of independent field-collected spatial *Z. japonica* maps from Yaquina Bay, Oregon, USA, an area that has well documented *Z. japonica* expansion over the last two decades. Sensitivity analysis performed to evaluate the contribution of each parameter to the model prediction revealed that depth was the most important factor. The highest suitability values for *Z. japonica* occurred in the mid to upper portions of the intertidal zone, with larger expanses occurring in the lower estuary. While the upper estuary did contain suitable habitat, most areas were not as large as in the lower estuary, due to inappropriate depth, a steeply sloping intertidal zone, and lower salinity. The lowest suitability values occurred below the lower intertidal zone, within the Yaquina River channel. Shallow sloping intertidal soft-bottom sediments appear to provide optimum habitat for this species. This model would allow resource managers to identify those areas at risk for future invasion, and develop proactive plans for limiting the opportunities for further introduction and spread in areas where it does not currently occur.

Key words: seagrass, *Zostera japonica*, invasive species management, habitat suitability, modeling

Introduction

Background

Two of the biggest alterations of estuarine and marine biodiversity and ecosystem function are likely to be driven by climate change (e.g. temperature and pH) and anthropogenic species introductions. It is likely that the impacts of these separate processes may work in a non-linear manner, thus climate change may exacerbate the spread of non-native species resulting in alterations of ecosystem services (Bierwagen et al. 2008; Hershner and Havens 2008). Consequently, there is intense interest in modeling the distribution of non-native species with respect to their ecological and physiological tolerances. Descriptive and mechanistic modeling approaches have been used to predict distributions. The descriptive approach uses habitat suitability models which relate species occurrences to a suite of environmental variables. Habitat suitability models are based on ecological niche theory and describe the relationships between species occurrence or abundance and a set of environmental data (Guisan and Thuiller 2005). This type of model can be used as a screening or risk assessment tool by resource management agencies in order to efficiently utilize limited resources. The mechanistic model approach focuses on predicting invasion dynamics or ecosystem response (Gallien et al. 2010) via empirically derived relationships. Mechanistic models may be inherently more satisfying from an ecological perspective but they tend to be site

specific and data intensive. Often the physical and biological data required to drive these models are not readily available and expensive to collect. Consequently, the large scale application of numerical mechanistic ecosystem response models for invasion ecology is generally more limited. Previous efforts to develop a spatially explicit numerical population model (Almasi and Eldridge 2008) of *Zostera japonica* Ascherson and Graebner colonization was plagued by limited data availability for model development and validation. Although the Almasi and Eldridge (2008) model output suggests that disturbance, competition and survival were important variables, most of these parameters were not well constrained by empirical or physiological data, and the model was subjected to limited validation. Consequently, the predictive capacity of the Almasi and Eldridge model has not been verified over interannual time scales and as a result has not been adopted for resource management.

Niche-based habitat suitability models have been widely used as management screening and risk assessment tools to predict the potential distributions of invasive species over large spatial scales (Thuiller et al. 2005; Inglis et al. 2006; Gallien et al. 2010; Jimenez-Valverde et al. 2011). Here we present a niche-based habitat suitability model of the non-native seagrass *Zostera japonica* that is expanding its range along the Pacific coast of North America (Shafer et al. 2014).

Zostera japonica is believed to have been unintentionally introduced with aquaculture products to North America, and is currently distributed in bays and estuaries in British Columbia (Canada), and Washington, Oregon and northern California (USA). A recent review on the science and management of *Z. japonica* in North America (Shafer et al. 2014) noted that invasion of new areas is continuing at a rapid pace. Although several studies have documented *Z. japonica* expansion (Gaeckle et al. 2001; Young et al. 2008; Young et al. 2015), the underlying factors responsible for the rapid increase in areal extent have not been identified. Moreover, several studies suggest that this species has only colonized a small fraction of the available suitable habitat throughout its potential range in North America (Harrison and Bigley 1982; Shafer et al. 2008; Shafer et al. 2011). Recent research has focused on the physiological ecology of *Z. japonica*. For example, it has been determined that *Z. japonica* is eurythermal with optimal growth at 20 °C (Shafer et al. 2008) and a lethal thermal threshold at 35 °C (Kaldy and Shafer 2012). North American *Z. japonica* populations have optimal growth at salinity 20 but are euryhaline, and can tolerate daily freshwater immersion (Kaldy 2006; Shafer et al. 2011). Recent work suggests that vertical zonation patterns can be controlled by temperature, not light limitation (Shafer and Kaldy 2014; Kaldy et al. 2015). The potential for interaction with the native seagrass *Z. marina* has also been explored. Some work suggests negative interactions (e.g. Bando 2006), but more recent work suggests that the scale of competitive interactions is limited to specific microtopographic features (Hannam and Wyllie-Echeverria 2015). Although some aspects of plant ecophysiology are better understood, the ecological consequences (e.g. ecosystem metabolism) and economic impact of *Z. japonica* colonization are poorly understood (Shafer et al. 2014). The transition from bare mudflat to a non-native seagrass habitat alters the physical and biogeochemical process (e.g. net primary productivity, nutrient cycling, etc.) associated with the habitat; additionally negative economic impacts to intertidal Manila Clam aquaculture have been documented (Patten 2014). Consequently, understanding the potential for continued colonization of unvegetated mudflat in North America is important from both an ecosystem conservation and economic perspective.

Management of *Z. japonica* in North America varies between States and Countries and has changed over time (see Shafer et al. 2014 for review). Recent management actions in the USA have been predominantly geared toward control or eradication but have generally been unsuccessful at the estuarine scale (Shafer et al. 2014). One aspect that has hampered effective management of this non-native species has been a lack of predictive tools to identify potential areas at risk for invasion which has suppressed the ability to develop early detection and monitoring protocols. Development of a model to identify areas at risk of *Z. japonica* colonization would allow resource agencies to focus limited monitoring funds on areas susceptible to colonization, thereby utilizing those resources in a more efficient manner. Rapid discovery of new populations of non-native species greatly increases the probability of eradication or elimination (Myers et al. 2000; Simberloff 2003).

Our objective was to develop and test a simple niche-based habitat suitability model for *Zostera japonica* as a risk assessment tool to predict areas expected to be susceptible to colonization. The model was specifically developed to utilize three

relatively simple environmental variables (salinity, depth and bathymetric slope) that are widely available or can be readily calculated for many estuaries. The simple data requirements allow application of the model to areas where there are insufficient data available to develop more complex mechanistic models.

Model Overview

The *Zostera japonica* Habitat Suitability Model (*ZJHSM*) model is a spatially-explicit, grid-based model that was developed to predict suitable locations for the invasion and growth of dwarf eelgrass (*Z. japonica*). The terminology and model evaluation techniques were adapted from Pollack et al. (2012). The model assumes that the three driving variables (depth, bathymetric slope and salinity) quantitatively describe suitable habitat for *Z. japonica* invasion. Each variables is assigned a dimensionless suitability index value that represents the relationship between the environ-mental variable and the habitat requirements of *Z. japonica* (noted as ZSI_n). Each *ZSI* is represented quantitatively as a series of linear suitability curves, with a minimum value of 0 for unsuitable to 1.0 for optimal habitats. The shape of each suitability curve was based on the expert opinions of the co-authors, reviews of the relevant peer-reviewed literature, and more than a decade of research on the physiological tolerances of *Z. japonica*, collected from multiple locations within its introduced range in North America (Kaldy 2006; Shafer 2007; Kaldy and Shafer 2012; Shafer and Kaldy 2014; Shafer et al. 2008, 2011, 2014; Kaldy et al. 2015a, 2015b). Suitability curves are formulated as step-functions with linear approxi-mations between each step. An overall suitability index is calculated as the geometric mean of the *ZSI* values and represents the overall suitability for invasion (noted as *HSI*). Data and equations are imported into a GIS and applied to specific geo-referenced locations within Yaquina Bay, Oregon, where the distribution of *Z. japonica* has been well studied.

A portion of the Yaquina River, located in Oregon between its confluence with the Pacific Ocean and river mile 14 south of Toledo, was selected as the model domain area (Figure 1). This area was chosen due to the documented expansion of *Z. japonica* (Young et al. 2008) and the large number of habitat surveys and related environmental data available to build and evaluate the model hypothesis (Young et al. 2015).

Methods

Suitability Indices

Depth (ZSI_{Depth})

Depth is one of the most important factors affecting seagrass distribution worldwide, due to their dependence on light to drive photosynthetic processes (Dennison 1987; Duarte 1991; Koch 2001). In its native range, *Z. japonica* has been reported to grow as deep as 3–7 m, although it typically grows at depths < 1 m (Hayashida 2000; Nakaoka and Aioi 2001; Abe et al. 2010). Unfortunately, very few (if any) of the publications on *Z. japonica* from Asia report the tidal datum; consequently the actual depth distribution in Asia is somewhat unclear. Throughout its established range in North America, *Z. japonica* is found primarily in mid- to upper- intertidal zones (Shafer et al. 2014; Young et al. 2015). Although there are currently no documented cases of *Z. japonica* growing below mean sea level in North America (Shafer et al. 2014), *Z. japonica* should be able to grow to a similar depth as *Z. marina* based on photosynthetic characteristics (Kaldy et al. 2015). The lower depth margin for *Z. marina* in Yaquina Bay is ~ -2 Mean Lower Low Water (MLLW), with most biomass centered around 0 m MLLW (Young et al. 2015). Consequently, we chose the depth interval between 0 m MLLW and the High tide mark (+ 2.3 m MLLW) to represent the potential *Z. japonica* colonization zone.

The relationship between Depth and its *ZSI* is formulated as a linear step function (Figure 2A). Breakpoints in the step-functions were determined according to the depth distributions described in Kaldy (2006). Values between the step-functions were linearly interpolated (that is, we calculated a linear equation between neighboring steps). Equations one through eight (Table 1) calculate ZSI_{Depth} values for the model domain.

Percent Slope ($ZSI_{\%\ slope}$)

Field observations suggest that the zonation patterns of *Z. japonica* are related to the slope of the intertidal zone; steeply sloping intertidal zones will provide less potential habitat than broad, relatively flat areas (Shafer et al. 2014). In the *ZJHSM*, we represented this phenomenon as the percent slope calculated between the upper limit of the bathymetry data (+2.3 m MLLW) and the mean lower low water lines (*% Slope*).

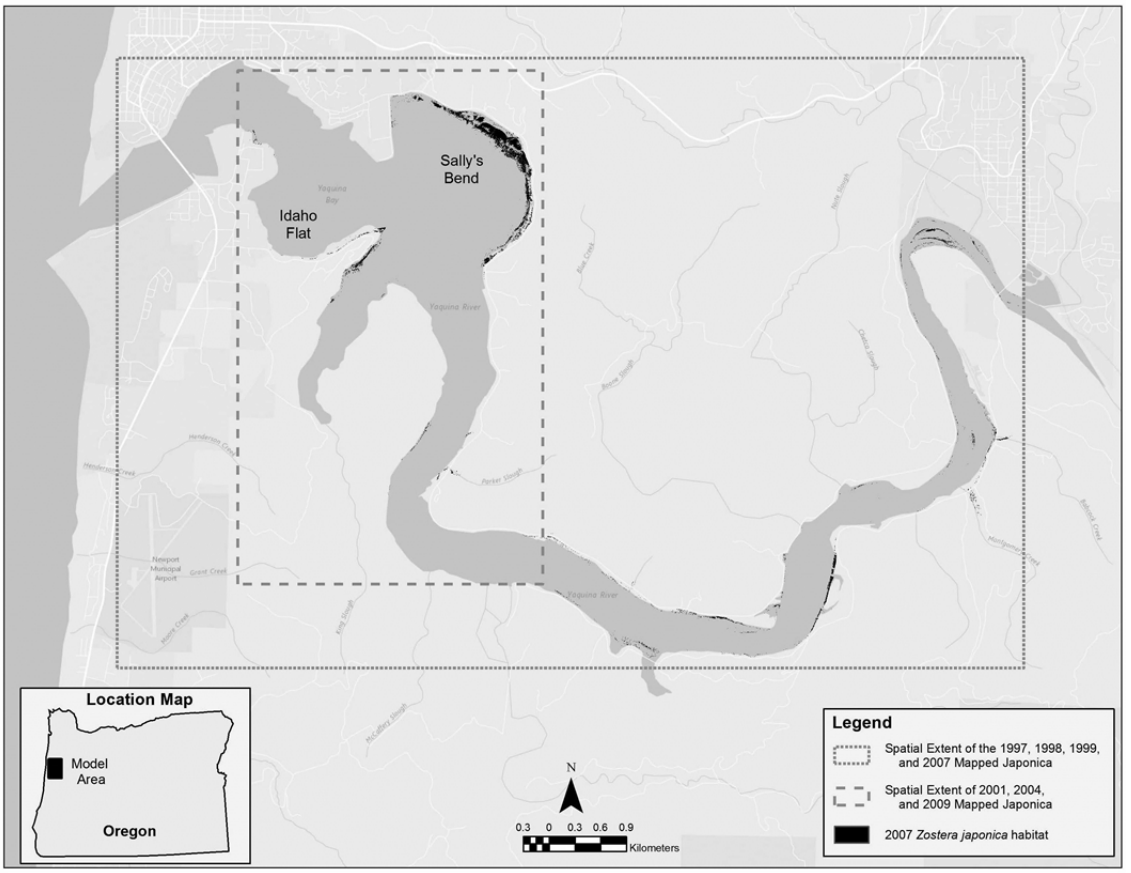

Figure 1. Mapped distribution of *Zostera japonica* in Yaquina Bay, Oregon in 2007.

Table 1. Equations for used for calculating *ZSI* values for each of the variables in the *ZJHSM*.

Variable	Equation	Eq#
Depth (m)		
Depth≤ 0.6 or *Depth*> 2.4	$ZSI_{Depth} = 0$	(1)
0.6 <*Depth* ≤ 0.7	$ZSI_{Depth} = -3 + (5 * Depth)$	(2)
0.7 <*Depth* ≤ 0.9	$ZSI_{Depth} = -0.2 + (Depth)$	(3)
0.9 <*Depth* ≤ 1.0	$ZSI_{Depth} = -2 + (3 * Depth)$	(4)
1.0 <*Depth* ≤ 1.9	$ZSI_{Depth} = 1$	(5)
1.9 <*Depth* ≤ 2.0	$ZSI_{Depth} = 6.7 - (3 * Depth)$	(6)
2.0 <*Depth* ≤ 2.3	$ZSI_{Depth} = 2.033 - (0.67 * Depth)$	(7)
2.3 <*Depth* ≤ 2.4	$ZSI_{Depth} = 12 - (5 * Depth)$	(8)
Slope		
Slope ≤ 0.5%	$ZSI_{\%\ Slope} = 1$	(9)
0.5% <*Slope* ≤ 1%	$ZSI_{\%\ Slope} = 1.5 - Slope$	(10)
1% <*Slope* ≤ 2%	$ZSI_{\%\ Slope} = 1.5 - (0.25 * Slope)$	(11)
2.0% <*Slope*	$ZSI_{\%\ Slope} = 0.25$	(12)
Salinity		
0 ≤ *Salinity* ≤ 10	$ZSI_{Salinity} = 0.1 * Salinity$	(13)
Salinity> 10	$ZSI_{Salinity} = 1$	(14)

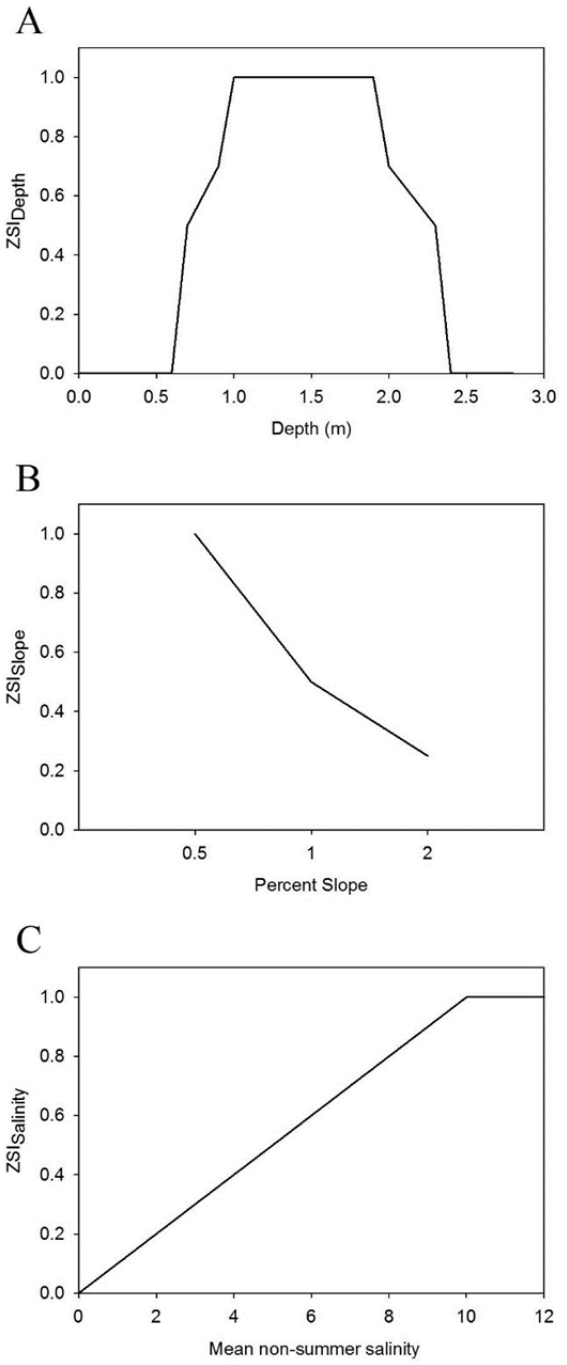

Figure 2. Relationship between *Zostera japonica* habitat suitability indices and (A) depth within Yaquina Bay (*Depth*), (B) degree of elevational change from mean high water to mean low water (% *Slope*), and (C) mean salinity during non-summer months.

The relationship between *% Slope* and its *ZSI* is formulated as a linear step function (Figure 2B). Breakpoints in the step-functions were determined by expert opinion based on field surveys and observations (Shafer 2007). Values between the step-functions were linearly interpolated (that is, we calculated a linear equation between neighboring steps). Equations nine through twelve (Table 1) calculate $ZSI_{\%\ slope}$ values for the model domain.

Salinity ($ZSI_{salinity}$)

Experimental research on *Z. japonica* physiology has shown that this species is extremely euryhaline, although it does have optimal growth and photosynthesis at salinity 20 (Shafer 2007; Shafer et al. 2011; Kaldy and Shafer 2012). Although *Z. japonica* is capable of tolerating short-term fluctuations in salinity over the course of daily tidal cycles, sustained periods of salinities under 10 may stress *Z. japonica* (Shafer et al. 2011; Kaldy and Shafer 2012). We hypothesized that sustained exposure to low salinity conditions over three to four months would limit *Z. japonica* growth. Because salinity values change seasonally, we categorized the salinity data into two seasons: October through April (the rainy season) and May through September (dry season), and calculated an average salinity value during each season from daily modeled values. The relationship between *Salinity* and its *ZSI* is formulated as a linear step function (Figure 2C). Values between the step-functions were linearly interpolated (that is, we calculated a linear equation between neighboring steps). Equations 13 and 14 (Table 1) calculate $ZSI_{salinity}$ values for the model domain.

Habitat Suitability (*HSI*)

The suitability of a particular location for *Z. japonica* invasion (Habitat Suitability Index*: HSI*) is determined as the geometric mean of the *ZSI* values for the three component variables (similar to the restoration suitability index calculated by Pollack et al. (2012). If any component *ZSI* is 0 (unsuitable), then *HSI* is 0 and the habitat is considered unsuitable for invasion. *HSI* is calculated as:

$$HSI = \left(\prod_{i=1}^{n} ZSI_i \right)^{1/n} \qquad (1)$$

Data Collection and Preparation

Several data sets developed by the US EPA, Western Ecology Division, Newport, OR were used in preparation and standardization of the three environmental variables (depth, percent slope and salinity) to be utilized in the creation of habitat suitability index raster files. The Yaquina Bay Topobathy Digital Elevation Model (DEM) was compiled using the Topogrid command in Arcinfo workstation 7.2.1 based on the ANUDEM 4.6.3 method for hydrologically correcting digital elevation models (Young et al. 2008). Model data were interpolated from soundings and independent verification found intertidal the DEM bathymetry was accurate to ± 0.25m (P. Clinton, US EPA unpublished data, Young et al. 2008). Depth values used in the model were derived from the topobathy-metric digital elevation model (DEM) of Yaquina Bay, Oregon at a horizontal resolution of 2 m and a vertical resolution of 0.25 m (USEPA 2003). Maintaining the high level of detail provided by the DEM was important for this model since observed seagrass distribution is coincident with slight variations in elevation which provide a good indicator of suitable *Z. japonica* habitat (Shafer 2007; Hannam and Wyllie-Echeverria 2015).

The percent slope values were determined by calculating the degree of maximum elevation change from the topobathy DEM using the Slope tool in ArcGIS®, and the resultant values were stored as a percent for each cell within the raster file (ESRI 2011 and USEPA 2003). The percent slope raster was output to a 2 m horizontal resolution for model data consistency.

Salinity variable values were derived by modeling the tidal range within Yaquina River study area by (1) the collection of South Beach sonde tidal data, (2) the division of the project area into five zones, and (3) the application of salinity information from three separate sonde locations throughout the Yaquina Bay study area (Critesers, Oregon oyster, and Oregon State University (OSU) Dock) (Figure 3)) to those zones. Tidal data from the South Beach sonde were originally obtained in 1hr increments from NOAA (2013) and documented the tidal state at the mouth of the Yaquina Bay estuary. The tidal data from a series of diurnal cycles were then graphed together with the 2004 temperature data from a series of temperature stations located in Yaquina Bay. Details of the sediment temperature dataset are described in Specht (2013). Continuous records of sediment temperature at 15 min intervals were made with in-situ solid-state temperature loggers (Onset Stowaway® TidbiT® Temperature Logger) placed at 5 cm depth. The temperature peaks and troughs were compared to the tidal peaks and troughs to estimate the tides occurring throughout the bay. This was done to increase the fitness of a bathtub-type tide modeling approach which uses only two variables, elevation and tidal data, to map inundation levels (NOAA 2010; Schmid et al. 2013). Next, five zones were derived for the model area by calculating river distances from the mouth of the bay to the project area extent, and dividing the area into equidistant sections (Figure 3).

Finally, continuous records of water column salinity collected every 15 min during 2007 at OSU dock, Oregon Oyster and Critesers (Figure 3) using YSI 6000 and YSI 6600 sondes were used as model inputs. Pre- and post-deployment calibrations ensured that sonde data met quality assurance requirements. Since only three sonde locations were available in the model area, the salinity data for each sonde were grouped and averaged to 1 hour temporal resolution and mapped to the appropriate zone based on following calculations. The salinity values were then divided into two separate datasets based on the temporal range for the dry season (a) Season 1 = May-Sept 2007, and the rainy season (b) Season 2 = Jan-April 2007 and Oct-Dec 2007 (Kaldy 2006). Then, the salinity data in each zone was averaged for the season based on weekly salinities. A raster dataset was then generated from the polygons for each seasonal salinity range using the same spatial extent, horizontal resolution (2 meters), and projection as the depth and percent slope variable raster files.

Habitat Suitability Index Model Variables

Raster files were created for each environmental variable (*Depth*, *Salinity*, *%Slope*) by applying the respective *ZSI* curves to each grid cell. The spatial domain was limited to study sites where *Z. japonica* is known to occur. Subsequently, all individual environmental *ZSI* raster were clipped to the model area as shown in Figure 1 and output to the geographic coordinate system; UTM, Zone 10, North NAD 1983. The *HSI* output values were calculated by applying equation 1 to the *HSI* rasters via ArcGIS® Raster Calculator. *HIS* results were divided into four categories: $0 \leq HSI \leq 0.25$, $0.25 < HSI \leq 0.50$, $0.50 < HSI \leq 0.75$, and $0.75 < HSI \leq 1.0$, representing low, low-medium, medium-high, and highly suitable habitat, respectively.

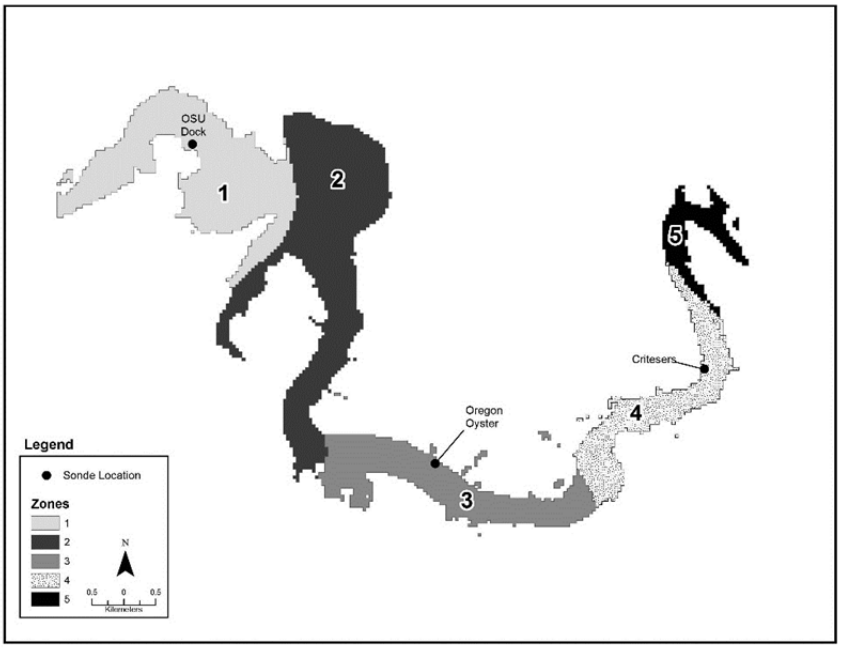

Figure 3. Five designated zones used to calculate Salinity HSI (SHSI) values in Yaquina Bay, Oregon. Salinity derived from sonde(s): Zone 1 = OSU dock; Zone 2 = (Oregon Oyster + OSU Dock) / 2; Zone 3 = Oregon Oyster; Zone 4= Critesers; Zone 5 = Critesers * (1.0–0.2).

Model Evaluation and Statistical Analyses

Observed *Z. japonica* habitat distribution was mapped by EPA for each of the following seven years: 1997, 1998, 1999, 2001, 2004, 2007, and 2009 (Clinton et al. 2007) and was used to determine if the *ZJSHM* habitat quality estimates were associated with *Z. japonica* presence (our hypothesis was that cells with higher HSI scores would be associate with *Z. japonica* presence). The spatial extent of the mapped distributions for 1997, 1998, 1999, and 2007 comprise the entire model area, while the spatial extent in 2001, 2004, and 2009 was smaller, and did not cover the central to eastern portion of the model area (Figure 1).

We evaluated our model using known presence/ absence data for *Z. japonica* collected in Yaquina Bay by developing several contingency tables (=confusion matrices) that explored associations between actual *Z. japonica* occupancy, and the HSI values our model generated. We used field data collected in 2007 for our analysis since it was the most extensive dataset. First, we developed a 2 × 2 contingency table that tested the conditional independence of habitat quality and *Z. japonica* occupancy. The modeled HSI values were aggregated and summarized into two categories: high quality habitat (HSI ≥ 0.5) or low quality habitat (HSI < 0.5). The presence or absence of *Z. japonica* was recorded for each cell and aggregated across the spatial domain. A Pearson's χ^2 goodness of fit test was used to determine if *Z. japonica* occupancy was conditionally independent of habitat quality. Next, using a 2 × 4 contingency table (Agresti 2012), we determined if each HSI bin was conditionally independent of seagrass presence or absence. Pearson's χ^2 goodness of fit test was used to determine conditional independence of *Z. japonica* and habitat quality. This method provided a quantitative method to further evaluate whether our model could determine a relationship between model-generated HSI values, and field-collected *Z. japonica* distributions. Methods followed Agresti (2012) and Simonoff (2003), statistical analyses used $\alpha = 0.10$, and all analyses were conducted in JMP Pro 11.0.0 (SAS Institute).

Model Sensitivity Analyses

In order to determine how robust the overall HSI equation was to the variables and parameter values included in the model, three levels of sensitivity analyses were conducted. First, overall model sensitivity was determined by applying

Equation (1) to two scenarios: 1) increasing all the variables by 10%, and 2) then again by decreasing all the variables by 10%. The amount of area (in ha) for each of HSI bins was recorded for the altered models, and statistical differences between each altered model and the baseline model were determined using a χ^2 goodness of fit test.

Second, we systematically removed a parameter from the model in order to determine how the predicted model index values responded to the exclusion of specific model parameters. The sensitivity analysis evaluates how the total area occupied by specific *HSI* bins changed value from a 3-parameter model to a 2-parameter model scenario. Specifically, we determined the total area of *HSI* values affected by removing one parameter (e.g., XX hectares of suitable habitat (*HSI*-values from 0.75–1.0) changed to unsuitable with the removal of one parameter), which reflects the relative importance of each parameter to the model structure. We increased the spatial domain of the model to include the channel and surrounding areas so that we could have a larger area over which to test the model. This method quantifies the importance of each parameter to overall model performance and allows for a more rigorous evaluation of model outputs (Pollack et al. 2012; Swannack et al. 2014). We chose a representative year (2007) for our sensitivity analysis to explore general trends in model sensitivity.

Finally, in order to determine how sensitive overall HSI values were to variable inclusion, each possible combination of 2-parameter model was run (e.g., salinity and slope, depth and salinity, etc.), and results were compared to the baseline model using a χ^2 goodness of fit test a specific variable to model performance. All statistical analyses used $\alpha = 0.10$ and were conducted using JMP Pro 11.0.0 (SAS Institute).

Results

In the Yaquina Bay model area, depth ranged from -12.5 to +2.3 m MLLW (Figure 4), percent slope ranged from 0% to 64.2% (Figure 5), and the average weekly salinity conditions for the 2007 rainy season (October-April) ranged from 7.0 to 27.4 (Figure 6). Salinities were only limiting for *Z. japonica* from October through April (the rainy season). During the dry season (May – September), $ZSI_{salinity}$ values were all 1, so we limited our analyses to include only the time period from October – April. The general trend shows lower and more variable salinities in the upper part of the Yaquina Bay, as well as steeper slopes and narrower intertidal zones. Whereas, the central and lower portions of the estuary transition into wider, more shallow intertidal zones with higher salinities due to the hydrologic connection between the Yaquina River and the Pacific Ocean.

The higher *HSI* values generally occurred throughout the model area within the mid to upper portion of the intertidal zone with larger expanses occurring mostly in the lower estuary within Sally's Bend and Idaho Flat (Figure 7). While the upper estuary did contain some suitable habitat, most areas were not as large as those in the lower estuary due to inappropriate depth, a steeply sloping intertidal zone, and lower salinity. The lowest *HIS* values occurred below the lower intertidal zone, specifically within the Yaquina River channel. Although salinity conditions were suitable, it ranked low as a result of increased depth.

Z. japonica is consistently more prevalent in the lower estuary model area than in the upper estuary. The largest distribution of mapped *Z. japonica* was 22.25 ha during 2007 (Figure 1), while the smallest areal extent occurred in 1999 which contained 1.07 ha (Table 2). Even though some years cover a smaller extent, mapped *Z. japonica* in 2009, 2004, and 2001 represents the second (9.06 ha), third (7.26 ha) and fourth (3.17 ha) largest distributions respectively.

For each of the seven years, we superimposed the *ZJHSM* to distinguish the habitat suitability among sites (Brooks 1997). Comparison between model results and the field-collected distributions of *Z. japonica* indicated that the habitat suitability rankings of the *ZJHSM* were relatively accurate at predicting spatial distribution of *Z. japonica* in Yaquina Bay (Table 2). For example, in 2007 there was 22.25 ha of *Z. japonica* mapped, and the *ZJHSM* projected that 89.8% was in medium to highly-suitable habitat (i.e., *HSI* values from 0.5–1), and 10.17% was present in the low-medium category. Most of the mapped *Z. japonica* distributions (45.3 ha or 94.5%) was found within the med-high and high *HIS* value zones, which supports the model's ability to identify and predict areas at risk for *Z. japonica* invasion. Very little of the mapped *Z. japonica* distributions (2.6 ha or 5.5%) was found within the low-medium and low *HIS* value zones. For all years except 2007, less than 0.3 ha of *Z. japonica* was mapped in areas predicted to be low quality habitat ($0<HSI<0.25$) (Table 2).

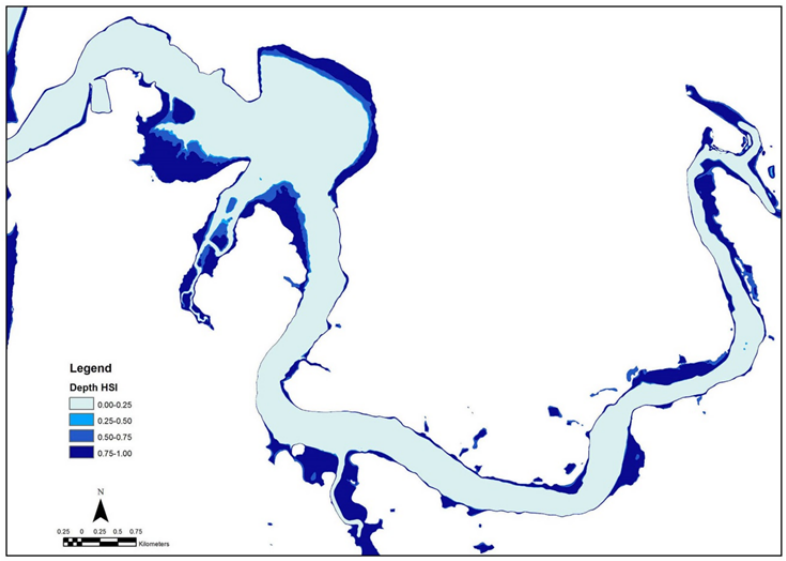

Figure 4. Depth HSI (DH_{SI}) value raster for Yaquina Bay, Oregon.

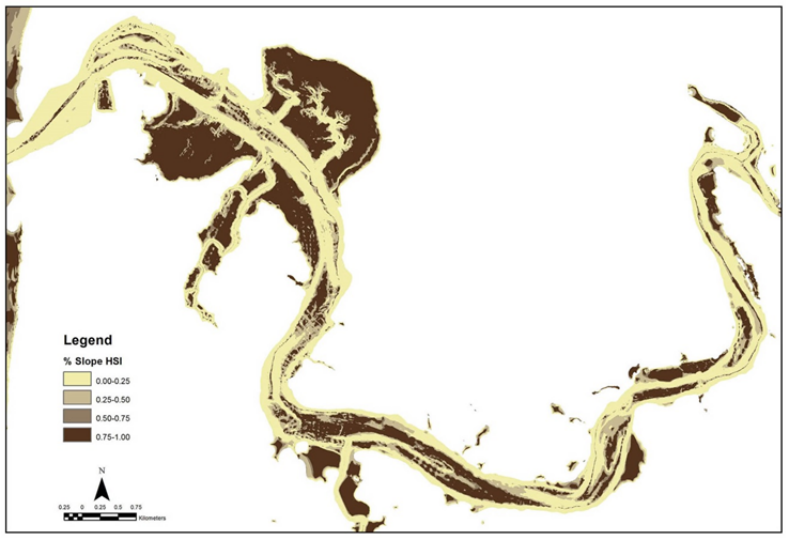

Figure 5. Percent Slope ($\%SH_{SI}$) value raster for Yaquina Bay, Oregon.

The highest mean *HSI* values were observed in the 2001, 2004, and 2009 distributions due to the mapping of seagrass mainly in the western portion of the model where ample habitat was predicted (Table 2). The more representative mapping years 1997, 1998, 1999 and 2007 which cover the entire model area range from a mean *HSI* value of 0.77 to 0.79 with the 2007 mapped year containing the largest mapped dataset (Table 2). The contingency analysis of the 2 × 2 table (performed on the 2007 data) indicated that there was an association of *Z. japonica* with habitat quality ($\chi^2_{df=3}$= 10.916, p = 0.001) (Figure 8A). Likewise, a 2-tailed Fisher's Exact Test indicated that the probability of absence was greater for low-medium quality habitat than for the higher quality habitat (p = 0.0214). Model results were not perfectly predictive. Specifically, ten percent of *Z. japonica* occupied the low-medium habitat category (Figure 8A). Further, there were over 97 ha of unoccupied high quality habitat in Yaquina Bay. When the model results were sub-divided into four bins based on HSI score (low: < 0.25, low-med: 0.25–0.5, med.-high: 0.5–0.75, and high > 0.75), the test of independence was rejected ($\chi^2_{df=3}$= 12.669, p = 0.0054), indicating that high quality habitat was more associated with *Z. japonica* presence than absence (Figure 8B).

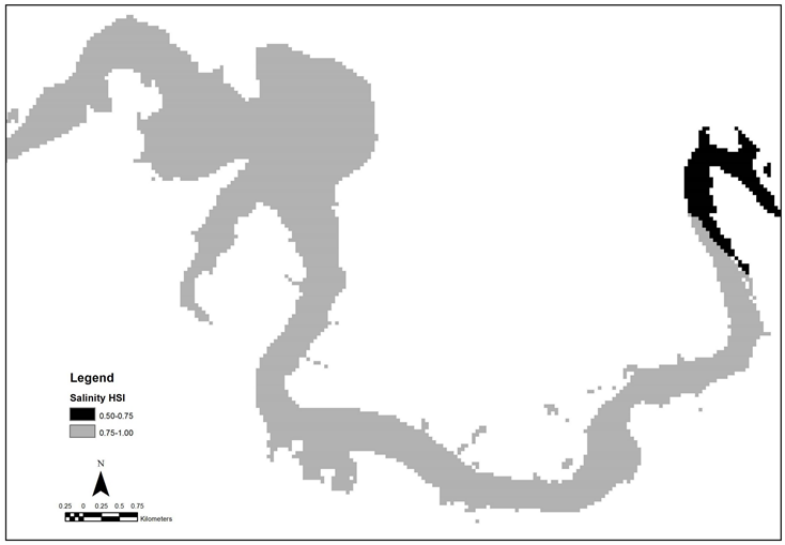

Figure 6. Salinity (S_{HSI}) value raster for Yaquina Bay, Oregon.

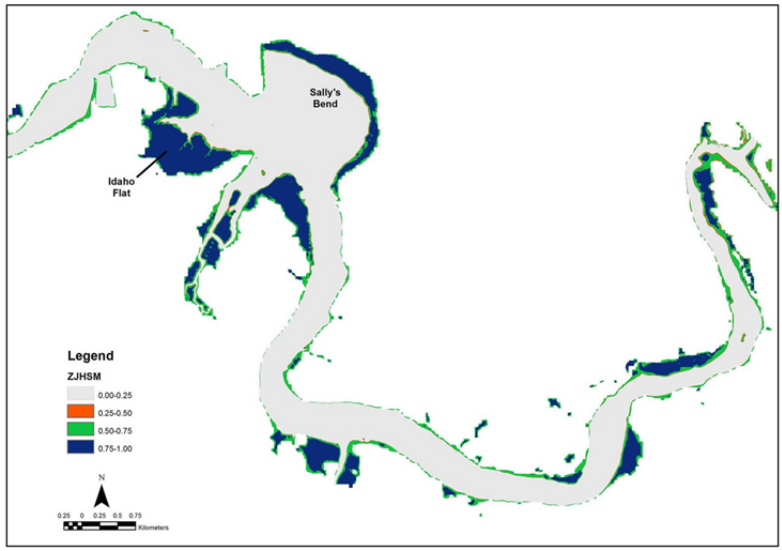

Figure 7. Results from *Zostera japonica* Habitat Suitability Index Model (ZJHSM).

The collective sensitivity analyses indicated that the *low-med.* category was the most influenced by changes in parameter values, and that *Depth* had the most influence on model results, which was expected given the correlation between depth and aquatic vegetation (Table 3). When *Depth* was increased by 10%, the *low-med.* category increased by 29.9% (Figure 9A), but other categories did not change much (< 10%), when Depth was decreased by 10%. Likewise when *Depth* removed from the model, 1,056 ha of low quality habitat was reallocated to better habitat and overall values of *HIS* increased (Table 3). Specifically, there was a 3,266% increase in low-medium habitat (an increase from 19 ha to 662 ha), a 260% increase in medium-high (168 ha to 260 ha), and a 132% increase in highly suitable habitat (242 ha to 564). In contrast, *HIS* values were less sensitive to the removal of *Salinity* or *%Slope* (Table 3, Figures 9B and C). The *low-med* category increased by 14% when *Salinity* was decreased by 10%, and increased by 15% when *Salinity* was increased. When *Salinity* was removed, a total of 115 ha changed, and overall *HIS* decreased. There was a negligible increase in low quality habitat (0.52%, 6 ha). Highly suitable habitat decreased by 14% (35.8 ha), and medium-high habitat decreased by 47% (79.5 ha). These reductions of higher quality habitats were all repartitioned into the low-medium category (Table 3). When *%Slope* was altered by

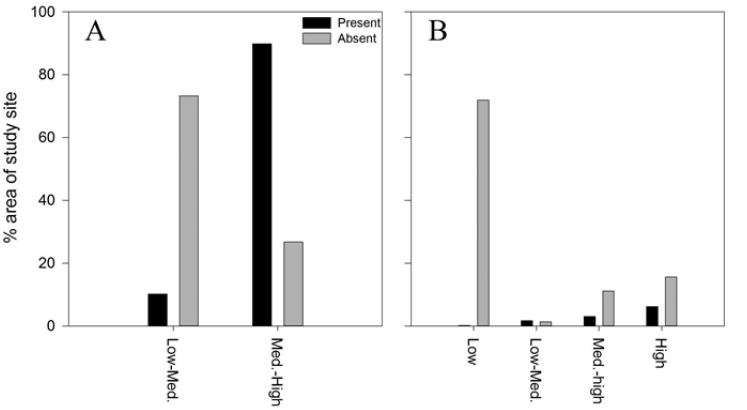

Figure 8. Area (in % of total) of model domain occupied (black bars) or not occupied (gray bars) by *Zostera japonica* divided into (A) two habitat types: low-medium quality habitat (HSI < 0.5), or medium-high quality habitat (HSI ≥ 0.5), and (B) four habitat types (Low: HSI < 0.25, Low-Medium: 0.25 ≤ HSI < 0.5, Medium-High 0.5 ≤ HSI < 075, and High ≥ 0.75).

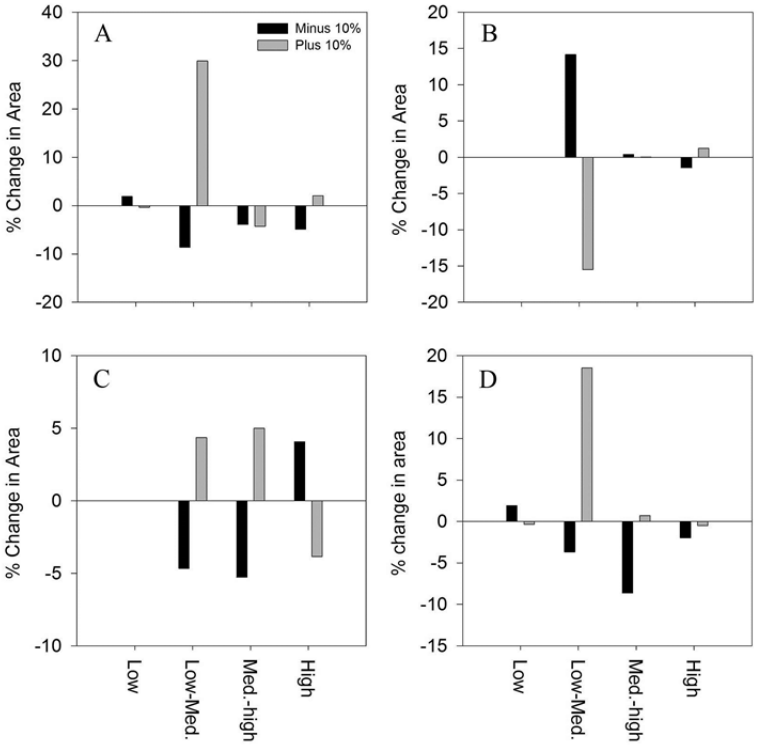

Figure 9. Results of sensitivity analyses quantifying differences in area affected by altering combinations of parameter values. Results are reported as % change from the baseline model. (A) (B), and (C) represent results from changing one variable (*Depth*, *Salinity*, and *%Slope,* respectively) by +10% (gray bars), or -10% (black bars) while leaving the other two unaltered. (D) represents a paramterization where all variables were altered by +10% (gray bars) or -10% (black bars)Sensitivity analyses was performed for 2007 and applied throughout the entire modeled region.

±10%, there was less than 6% change in overall area across all categories, with the least change in low quality habitat (Figure 9C). When *%Slope* was removed, 123 ha of habitat changed and overall suitability increased; eight and 115 ha of low-medium and medium-high habitat, respectively, were converted to 121 ha of highly suitable habitat, resulting in a 50% increase of highly suitable habitat. When the model was applied after each variable was increased by 10%, the Low-Med category increased by 18%, whereas there was a negligible shift (< 1%) in the other categories (Figure 9D). Decreasing the value of each variable by 10% decreased habitat in each of the four habitat categories, except Low, which increased by 1%.

Table 2. Equations (A) Comparison of seven years of the total number of hectares of *HSI* values divided into four suitability categories compared to total area of field-mapping efforts and (B) mean ± 1 S.D. of overall *HSI* values across years.

ISI values	Area (ha)						
	1997	**1998**	**1999**	**2001**	**2004**	**2007**	**2009**
(**A**) 0–0.25 (low)	0.03	<0.01	0	<0.01	0	1.93	0.34
0.25–0.5 (low-med)	<0.01	0	0	<0.01	0	0.33	0.01
0.5–0.75 (med-high)	1.09	1.41	0.50	1.27	1.01	5.04	1.61
0.75–1.0 (high)	1.09	1.54	0.57	1.90	6.25	14.95	7.10
Total Mapped Area	2.21	2.95	1.07	3.17	7.26	22.25	9.06
(B) Mean *ISI* (± 1SD)	0.77±0.17	0.78±0.15	0.79±0.15	0.81±0.15	0.92±0.13	0.79±0.29	0.87±0.21

Table 3. Results from sensitivity analysis comparing the number of hectares occupied in each of four ISI bin of the full 3-parameter model (Full Model) and respective 2-parameter models where one variable was removed (e.g., -Depth is the model with *Depth* removed). The numbers in parentheses are the percent change in area from the full model to the 2-parameter.

ISI bin	Full Model	-*Depth*	-*Salinity*	-*Slope*
0.00 – 0.25	1056.63	0 (100%)	1062.16 (0.52%)	1058.67 (0.19%)
0.25 – 0.50	19.69	662.93 (3266%)	129.49 (557%)	11.58 (-41%)
0.50 – 0.75	168.75	260.23 (260%)	89.22 (-47%)	53.18 (-68%)
0.75 – 1.00	242.56	564.47 (132%)	206.76 (-14%)	364.20 (50%)
Mean *ISI*	0.23 ± 0.37	0.69 ± 0.22	0.24 ± 0.36	0.26 ± 0.41

Discussion

For natural resource agencies faced with combatting the spread of invasive species, understanding where and how these species will disperse is crucial. This issue is further complicated when species habitat is dynamic and influenced by large scale processes such as climate change. These rapid and stochastic drivers can make it difficult to effectively target areas for monitoring of population expansion. The *ZJHSM* is a generalized model for determining potential locations suitable for colonization by *Z. japonica*, including those areas where the actual distribution of the species is unknown. Our approach focused on identifying the spatial continuum of habitat quality for *Z. japonica,* and we were able to elucidate an association between *Z. japonica* presence and higher quality habitat, doing so with a three parameter HSI model, representing critical important factors controlling its distribution of this species. It was intentionally designed as a simple model incorporating the basic physiology and habitat requirements (i.e., the minimum factors) necessary to accurately predict *Z. japonica* habitat suitability. The model is flexible enough that it can easily be applied to other locations, and the minimum data needed to drive the model (e.g. bathymetry and salinity) are available for other Pacific coast estuaries. The *ZJHSM* is designed to be flexible with regard to data inputs and spatial scales, and can incorporate new information as it becomes available, provided that sufficient data exist. Because *ZJHSM* captured general trends in *Z. japonica* habitat suitability, we believe this model could prove useful to resource managers for targeting monitoring efforts to areas at greater risk for potential *Z. japonica* invasion. Furthermore, *ZJHSM* has a wide variety of potential applications to anthropogenic or natural processes which modify depth, salinity, or slope in ways that alter habitat sufficiently to facilitate invasion.

Model Variables and Sensitivity

Although many environmental variables influence seagrass growth and distribution, we were able to utilize a minimal subset and accurately predict *Z. japonica* distribution. However it is critically important to quantify the impact of variables by thoroughly exploring the parameter space through rigorous evaluative techniques, such as sensitivity analysis (Brooks 1997; Pollack et al. 2012). Our sensitivity analyses concluded that *Depth* was the most important model factor controlling the predicted distribution, and that marginal habitat is the most likely to change if

parameter values change. Depth is recognized as a critical factor for the growth and distribution of submerged aquatic vegetation due to limited light availability at greater depths (Dennison 1987; Duarte 1991; Koch 2001). The *ZJHSM* was most sensitive to *Depth* being removed or altered. When *Depth* was removed, the overall amount of suitable habitat increased because of the increased number of cells that had suitable slopes and salinity values. Likewise, increasing *Depth* by as little at 10% can increase lower quality habitat by 30%. Since *Z. japonica* is confined to the mid- and upper intertidal zones (Kaldy 2006; Shafer et al. 2014; Young et al. 2015), and since the habitat quality projections are sensitive to changes in depth, it is essential to include water depth in order to accurately project the spatial distribution of the species.

Z. japonica populations are physiologically tolerant of a wide salinity range (Shafer et al. 2011; Kaldy and Shafer 2012) and can be seasonally exposed to and tolerate low salinity from direct precipitation and from flood events (Kaldy et al. 2015b).Removing *Salinity* did not greatly affect overall HSI values since salinity was in the highly suitable range throughout most of the study area, except in the upper reaches of the Yaquina River. Although salinity gradients may not strongly contribute to *Z. japonica* suitability in Yaquina Bay, salinity is known to be an important factor affecting plant distributions in estuarine environments, so it is likely an important driver for the spatial dynamics of the species at larger scales. Experimental data indicate that seasonal exposure to pulses of low salinity or fresh water could stimulate germination of the *Z. japonica* seed bank (Kaldy et al. 2015b), suggesting that periodic exposure to low salinity conditions could be important in initiating new populations from seed.

Although the model accurately predicts the associations between habitat quality and *Z. japonica* distribution in Yaquina Bay, there are numerous caveats. Several reviews highlight the impact of omission and commission errors that can influence ecological niche modeling and geographic prediction efforts (Fielding and Bell 1997; Peterson et al. 1999). Omission of areas actually inhabited represents a failure of the modeling effort to extend to all ecological conditions which support populations. Commission errors are the erroneous inclusion of areas actually uninhabited. Commission error includes two components: real commission error, in which combinations of ecological conditions not actually within the species' niche are included, and apparent commission error, resulting from species' absences owing to interspecific interactions and historical factors, including limited colonization ability, speciation patterns, and local extinction (Peterson et al. 1999). Apparent commission error represents a real feature of species' distributional ecology: not all habitable areas are inhabited (Peterson et al. 1999).More recent work suggests that for models involving invasive species, model testing and evaluation should focus on predicting presence with a high level of confidence and place less emphasis on efficient predictions of species absence (Jimenez-Valverde et al. 2011). Consequently, our focus has been centered on developing a model that provides robust and accurate distribution predictions. We attempted to reduce error by using a multi-year dataset, and also by including the entirety of Yaquina Bay in our model domain. Our results did show that *Z. japonica* inhabited poorer quality habitats (HSI < 0.5), but it is not clear if those areas are actually high quality habitat misclassified as poor quality, or if *Z. japonica* can survive across a gradient of habitat quality. Further, *ZJHSM* returned high quality habitat where no *Z. japonica* was present – these results could be a misclassification of habitat quality, or could represent areas of high quality habitat that have not been colonized. If the latter is accurate, our model can be used as a screening tool to identify areas that are at higher risk for invasion.

Although this model was developed to try to accurately quantify *Z. japonica* habitat quality as parsimoniously as possible, it is flexible and other variables could easily be integrated into the model framework as data become available. For example, physiological studies have shown that temperature is an important factor affecting *Z. japonica* distribution (Shafer et al. 2008; Kaldy and Shafer 2012), and a previous model used temperature to predict occurrence of *Z. japonica* in Humboldt Bay, CA (Weltz 2012). Temperature has recently been suggested to provide a control on *Z. japonica* growth rates (Kaldy et al. 2015a). However, due to the limited spatial coverage of existing temperature data in Yaquina Bay (Specht 2013), temperature data were not directly used in this model, but were used to validate the close correlation between temperature and tidal elevation (e.g. depth).

Incorporating a temperature duration dependent growth factor (Kaldy et al. 2015a), or salinity

dependent seed germination (Kaldy et al. 2015b) may be future refinements that increase the model predictive capacity. Shoreline orientation may also influence *Z. japonica* distribution through an indirect effect on temperature; south-facing shorelines would likely be warmer than shorelines oriented in other directions. Substrate type could also be considered as an additional variable in future versions of the model. Most seagrasses, including *Z. japonica*, inhabit soft, unconsolidated sediments. Within the Yaquina estuary, there are relatively few areas that exhibit a rocky substrate that would preclude *Z. japonica* colonization, therefore the inclusion of this variable would have added little discriminatory capability. However, in other areas with more heterogeneous substrates, including this parameter in the model could be a useful addition.

Future research could also explore the functional forms of the component HSI relationships as well as considering weighting different components.

At this point, the model does not include a recruitment/colonization component. Although we acknowledge the importance of propagule dispersal and recruitment in the establishment of new populations and potential range expansions, we know very little about the processes of seed dispersal and recruitment in seagrasses (Orth et al. 2006). Wind, currents and migratory waterfowl have been suggested as possible mechanisms of *Z. japonica* seed dispersal (Shafer et al. 2014). Ongoing research is being conducted to investigate the factors affecting seed germination in *Z. japonica*, and it might be possible to add a seed recruitment component in the model in the future.

Acknowledgements

The authors wish to acknowledge EPA contributors T.C. Mochon-Collura for his work in obtaining and processing YSI Sonde data; P. Clinton developed the topobathy DEM and D. Specht obtained and processed the sediment temperature data records. Additionally, D. Young and P. Clinton provided access to unpublished *Z. japonica* maps for model validation. The authors also thank L. Nelson and M. Kjelland for valuable comments and discussion on previous versions of this manuscript. The information in this document has been funded in part by the U.S. Army Corps of Engineers Aquatic Plant Control Research Program and the US Environmental Protection Agency. It has been subjected to review by the US Army Corps of Engineers, Engineering Research and Development Center and by the National Health and Environmental Effects Research Laboratory's Western Ecology Division and approved for publication. Approval does not signify that the contents reflect the views of the agencies, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

References

Abe M, Yokota K, Kurashima A, Maegawa M (2010) Estimation of light requirement for growth of *Zostera japonica* cultured seedlings based on photosynthetic properties. *Fisheries Science* 76: 235–242, http://dx.doi.org/10.1007/s12562-009-0203-0

Agresti A (2012) Categorical data analysis, third edition. John Wiley and Sons, Inc., New York

Almasi KN, Eldridge PM (2008) A dynamic model of an estuarine invasion by a non–native seagrass. *Estuaries and Coasts* 31: 163–176, http://dx.doi.org/10.1007/s12237-007-9024-5

Bando KJ (2006) The roles of competition and disturbance in a marine invasion. *Biological Invasions* 8: 755–763, http://dx.doi.org/10.1007/s10530-005-3543-4

Bierwagen BG, Thomas R, Kane A (2008) Capacity of management plans for aquatic invasive species to integrate climate change. *Conservation Biology* 22: 568–574, http://dx.doi.org/10.1111/j.1523-1739.2008.00954.x

Brooks RP (1997) Improving habitat suitability index models. *Wildlife Society Bulletin*: 163–167

Clinton PJ, Young DR, Specht DT, Lee II H (2007) A guide to mapping intertidal eelgrass and nonvegetated habitats in estuaries of the Pacific Northwest USA. EPA/600/R-07/062, US Environmental Protection Agency, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Newport, OR

Dennison WC (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27: 15–26, http://dx.doi.org/10.1016/0304-3770(87)90083-0

Duarte CS (1991) Seagrass depth limits. *Aquatic Botany* 40: 363–377, http://dx.doi.org/10.1016/0304-3770(91)90081-F

ESRI (2011) ArcGIS® Desktop: Release 10. Redlands, CA: Environmental System Research Institute

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49, http://dx.doi.org/10.1017/S0376892997000088

Gaeckle J, Dowty P, Berry H, Ferrier L (2011) Puget Sound Submerged Vegetation Monitoring Project 2009 Report. Olympia, Washington State Department of Natural Resources Nearshore Habitat Program. http://www.dnr.wa.gov/ResearchScience/Topics/AquaticHabitats/Pages/aqr_nrsh_eelgrass_monitoring.aspx

Gallien L, Munkemuller T, Ambert CH, Boulangeat I, Thuiller W (2010) Predicting potential distributions of invasive species: where to go from here? *Diversity and Distributions* 16: 331–342, http://dx.doi.org/10.1111/j.1472-4642.2010.00652.x

Guisan A, Thuiller W (2005) Predicting species distribution: offering more that simple habitat models. *Ecology Letters* 8: 993–1009, http://dx.doi.org/10.1111/j.1461-0248.2005.00792.x

Hannam M, Wyllie-Echeverria S (2015) Microtopography promotes coexistence of an invasive seagrass and its native congener. *Biological Invasions* 17: 381–395, http://dx.doi.org/10.1007/s10530-014-0736-8

Harrison PG, Bigley RE (1982) The recent introduction of the seagrass *Zostera japonica* Aschers and Graebn to the Pacific coast of North America. *Canadian Journal of Fisheries and Aquatic Science* 39: 1642–1648, http://dx.doi.org/10.1139/f82-221

Hayashida F (2000) Vertical distribution and seasonal variation of eelgrass beds in Iwachi Bay, Izu Peninsula, Japan. *Hydrobiologia* 428: 179–185, http://dx.doi.org/10.1023/A:1004036003521

Hershner C, Havens KJ (2008) Managing invasive aquatic plants in a changing system: strategic consideration of ecosystem services. *Conservation Biology* 22: 544–550, http://dx.doi.org/10.1111/j.1523-1739.2008.00957.x

Inglis GJ, Hurren H, Oldman J, Haskew R (2006) Using habitat suitability index and particle dispersion models for early detection of marine invaders. *Ecological Applications* 16: 1377–1390, http://dx.doi.org/10.1890/1051-0761(2006)016[1377:UHSIAP]2.0.CO;2

Jimenez-Valverde A, Peterson AT, Soberon J, Overton J M, Aragon P, Lobo JM (2011) Use of niche models in invasive species risk assessments. *Biological Invasions* 13: 2785–2797, http://dx.doi.org/10.1007/s10530-011-9963-4

Kaldy JE (2006) Production ecology of the non-indigenous seagrass, dwarf eelgrass (*Zostera japonica* Aschersand Graebn) in a Pacific Northwest estuary, USA. *Hydrobiologia* 553: 210–217, http://dx.doi.org/10.1007/s10750-005-5764-z

Kaldy JE, Shafer DJ (2012) Effects of salinity on survival of the exotic seagrass *Zostera japonica* subjected to extreme high temperature stress. *Botanica Marina* 56: 75–82

Kaldy JE, Shafer DJ, Magoun AD (2015a) Duration of temperature exposure controls growth of *Zostera japonica*: implications for zonation and colonization. *Journal of Experimental Marine Biology and Ecology* 464: 68–74, http://dx.doi.org/10.1016/j.jembe.2014.12.015

Kaldy JE, Shafer DJ, Ailstock S, Magoun AD (2015b) Effects of Temperature, Salinity and Seed Age on Induction of *Zostera japonica* Germination in North America. *Aquatic Botany* 126: 73–79, http://dx.doi.org/10.1016/j.aquabot.2015.06.006

Koch EW (2001) Beyond light: physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24: 1–17, http://dx.doi.org/10.2307/1352808

Myers JH, Simberloff D, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution* 15: 316–320, http://dx.doi.org/10.1016/S0169-5347(00)01914-5

Nakaoka M, Aioi K (2001) Ecology of seagrasses *Zostera* spp. (Zosteraceae) in Japanese waters: A review. *Otsuchi Marine Science* 26: 7–22

National Oceanographic and Atmospheric Administration (NOAA) (2010) Mapping Inundation Uncertainty. NOAA Coastal Services Center, Charleston, SC, 10 pp

National Oceanographic and Atmospheric Administration (NOAA) (2013) NOAA Tides and Currents, South Beach Sonde Station number 9435380, http://tidesandcurrents.noaa.gov/waterlevels.html?id=9435380

Orth RJ, Harwell MC, Inglis GJ (2006) Ecology of seagrass seeds and dispersal strategies. In: Larkum AWD, Orth RJ, Duarte CM (eds), Seagrasses: biology, ecology, and conservation. Springer, New York, pp 111–133

Patten K (2014) The impacts of nonnative Japanese eelgrass (*Zostera japonica*) on commercial shellfish production in Willapa Bay, WA. *Agricultural Sciences* 5: 625–633, http://dx.doi.org/10.4236/as.2014.57066

Peterson AT, Soberón J, Sánchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. *Science* 285: 1265–1267, http://dx.doi.org/10.1126/science.285.5431.1265

Pollack JB, Cleveland A, Palmer TA, Reisinger AS, Montagna PA (2012) A restoration suitability index model for the eastern oyster (*Crassostrea virginica*) in the Mission-Aransas estuary, TX, USA. *PLoS ONE* 7: e40839, http://dx.doi.org/10.1371/journal.pone.0040839

Schmid K, Hadley B, Waters K (2013) Mapping and portraying inundation uncertainty of bathtub-type models. *Journal of Coastal Research* 30: 548–561

Shafer DJ (2007) Physiological factors affecting the distribution of the nonindigenous seagrass *Zostera japonica* along the Pacific coast of North America. PhD Dissertation, University of South Alabama, Mobile, AL, USA, 134 pp

Shafer DJ, Wyllie-Echeverria S, Sherman TD (2008) The potential role of climate in the distribution and zonation of the introduced seagrass *Zostera japonica* in North America. *Aquatic Botany* 89: 297–302, http://dx.doi.org/10.1016/j.aquabot.2008.03.005

Shafer DJ, Kaldy JE, Sherman TD, Marko KM (2011) Effects of salinity on photosynthesis and respiration of the seagrass *Zostera japonica*: A comparison of two established populations in North America. *Aquatic Botany* 95: 214–220, http://dx.doi.org/10.1016/j.aquabot.2011.06.003

Shafer DJ, Kaldy JE (2014) Comparison of Photosynthetic Characteristics of the Seagrass Congeners *Zostera marina* and *Zostera japonica*. *Aquatic Botany* 112: 91–97, http://dx.doi.org/10.1016/j.aquabot.2013.09.002

Shafer DJ, Kaldy JE, Gaeckle J (2014) Science and Management of the Introduced Seagrass *Zostera japonica* in North America. *Environmental Management* 53: 147–162, http://dx.doi.org/10.1007/s00267-013-0172-z

Simberloff D (2003) Eradication – preventing invasions at the outset. *Weed Science* 51: 247–253, http://dx.doi.org/10.1614/0043-1745(2003)051[0247:EPIATO]2.0.CO;2

Simonoff JS (2003) Analyzing categorical data. Springer, New York, New York, USA, http://dx.doi.org/10.1007/978-0-387-21727-7

Specht DT (2013) Yaquina Bay, Oregon, Intertidal sediment temperature database, 1998–2006. US Environmental Protection Agency, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Newport, OR, http://www.epa.gov/wed/pages/models/SedimentTemp.htm

Swannack TM, Reif MK, Soniat TM (2014) A robust, spatially-explicit model for identifying oyster restoration sites: case studies on the Atlantic and Gulf Coasts. *Journal of Shellfish Research* 33: 395–408, http://dx.doi.org/10.2983/035.033.0208

Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234–2250, http://dx.doi.org/10.1111/j.1365-2486.2005.001018.x

United States Environmental Protection Agency, USEPA (2003) Yaquina Bay, Oregon Topobathy Digital Elevation Model, United States Environmental Protection Agency Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Pacific Coastal Ecology Branch. Newport, OR

Weltz AE (2012) Using a temperature-based GIS model to identify potential habitat for *Zostera japonica* in Humboldt Bay, CA. MS thesis. Humboldt State University, Humboldt, CA, USA, 29 pp

Young DR, Clinton PJ, Specht DT, DeWitt TH, Lee H II (2008) Monitoring the expanding distribution of nonindigenous dwarf eelgrass *Zostera japonica* in a Pacific Northwest USA estuary using high resolution digital aerial photography. *Journal of Spatial Science* 53: 87–97, http://dx.doi.org/10.1080/14498596.2008.9635138

Young D, Clinton P, Specht D, Mochon-Collura TC (2015) Comparison of non-native dwarf eelgrass (*Zostera japonica*) and native eelgrass (*Zostera marina*) distributions in a northeast Pacific estuary: 1997–2014. *Botanica Marina* 58: 239–250, http://dx.doi.org/10.1515/bot-2014-0088