USING A TEMPERATURE-BASED GIS MODEL TO IDENTIFY POTENTIAL HABITAT FOR ZOSTERA JAPONICA IN HUMBOLDT BAY, CA

HUMBOLDT STATE UNIVERSITY

By

Andrew Edward Weltz

A Thesis
Presented to
The Faculty of Humboldt State University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science in Biology

May 10, 2012
USING A TEMPERATURE-BASED GIS MODEL TO IDENTIFY POTENTIAL HABITAT FOR ZOSTERA JAPONICA IN HUMBOLDT BAY, CA

HUMBOLDT STATE UNIVERSITY

By

Andrew Edward Weltz

We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Master of Science:

Dr. Frank J. Shaughnessy, Major Advisor

Dr. Erik Jules, Committee Member

Dr. Steven J. Steinberg, Committee Member

Dr. Robert VanKirk, Committee Member

Dr. Michael Mesler, Graduate Coordinator

Dr. Jená Burges, Vice Provost
ABSTRACT

A geographic information system allows for the ability to predict potential distributions of spreading non-native species by identifying suitable, unoccupied habitat. *Zostera japonica* (Asch. and Grabn.), a non-native seagrass from the subtropical western Pacific, has expanded its distribution in the NE Pacific since its introduction in the mid-1900s. Humboldt Bay in northern California and the nearby Eel River estuary now represent the southern extent of its non-native range. In this study, *in situ* intertidal temperature data were used to predict optimal *Z. japonica* habitat in Humboldt Bay. Kriging analysis was used to produce an interpolated temperature map of the Humboldt Bay intertidal mudflat during the 2010 growth season, and the scenario of a warmer growth season was examined. Optimal habitat was identified by the amount of time a given section of mudflat spends within a temperature range that is optimal for *Z. japonica* growth (20°C – 30°C). The spatial extent of native eelgrass (*Zostera marina*, Linnaeus) habitat was used to exclude areas of intertidal that, due to interspecific competition, would not provide suitable *Z. japonica* habitat. The model identifies large areas of upper-intertidal mudflat as optimal potential *Z. japonica* habitat, especially in northern Humboldt Bay where *Z. japonica* has been spreading since 2001, and describes southern Humboldt Bay, where the non-native is absent, as less optimal than northern Humboldt Bay. Additionally, the warmer scenario predicts a substantial increase in optimal *Z. japonica* habitat in South Bay’s upper intertidal and an increase in relative habitat suitability in
unvegetated North Bay mudflat as compared to the cooler scenario. The predictions generated by this model have important implications for resource managers monitoring spread and attempting local eradication of this species.
ACKNOWLEDGEMENTS

Thanks to Dr. Frank Shaughnessy, Dr. Erik Jules, Dr. Stephen Steinberg, and Dr. Robert VanKirk for overseeing and advising this project. Funding was provided by grants from the United States Fish and Wildlife Service and Humboldt State University’s Department of Biological Sciences. Deborah Shafer made invaluable contribution to the direction of the analysis. Roxanne Robertson, Marcus Jones, Kirby Morejohn, Christopher Steenbock, Steve Monk, and the California Department of Fish and Game provided assistance in the field. Special thanks to Annie Eicher and Kirsten Ramey.
# TABLE OF CONTENTS

ABSTRACT .......................................................................................................................... iii

ACKNOWLEDGEMENTS .................................................................................................... v

LIST OF TABLES ............................................................................................................. vii

LIST OF FIGURES .......................................................................................................... viii

INTRODUCTION ............................................................................................................. 1

METHODS ......................................................................................................................... 9

RESULTS ........................................................................................................................... 14

DISCUSSION ..................................................................................................................... 21

LITERATURE CITED ...................................................................................................... 25
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>For each data logger site (alphabetical) and <em>Z. japonica</em> site (numerical) across the 2010 growth period, the mean of the daily maximum temperatures (Mean Max.) with the corresponding standard deviation (Max. SD), the mean of the daily minimum temperatures (Mean Min.) and standard deviation (Min. SD), and the proportion of time during the growth period that each site spent within the optimal growth temperature range.</td>
<td>16</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Study location of Humboldt Bay in Northern California. Lettered symbols are random temperature logger sites, numbered symbols are sites where <em>Z. japonica</em> does or used to exist. The positions of the CeNCOOS water quality sites are indicated in central and southern Humboldt Bay.</td>
</tr>
<tr>
<td>2</td>
<td>Representative water temperatures from 2010 (a) and 2009 (b) from two CeNCOOS water quality sites (Fig. 1) in central and southern Humboldt Bay.</td>
</tr>
<tr>
<td>3</td>
<td>Comparison of representative temperatures from low and high intertidal mudflat data loggers during the June to July 2010 sampling period. Tide heights were recorded by the CeNCOOS Dock B sonde (Fig. 1).</td>
</tr>
<tr>
<td>4</td>
<td>The cooler 2010 scenario showing interpolated distributions of mudflat areas experiencing different time lengths of optimal growth temperatures for <em>Z. japonica</em> and the existing habitat footprint for <em>Z. marina</em>.</td>
</tr>
<tr>
<td>5</td>
<td>The warm scenario showing interpolated distributions of mudflat areas experiencing different time lengths of optimal growth temperatures for <em>Z. japonica</em> and the existing habitat footprint for <em>Z. marina</em>.</td>
</tr>
</tbody>
</table>
INTRODUCTION

Natural ecosystems provide humans with numerous goods and services that we depend on for food, recreation, trade, and aesthetic purposes, and biodiversity in those natural ecosystems is a direct source of these goods and services (Daily et al. 1997). Non-native, invasive species have the potential to threaten biodiversity by disrupting natural ecosystem processes in these systems, which in turn may have negative consequences for native species, economies, and even human health (Ruiz et al. 1997). Furthermore, estuarine and bay ecosystems are among the most affected by invading non-native species (Ruiz et al. 1997). *Zostera japonica* (Asch. and Grabn.) is an example of a non-native aquatic plant that is currently invading bays and estuaries in the North-East Pacific. An understanding of how *Z. japonica* grows and reproduces, the characteristics of its native niche, as well as the habitat it has come to occupy in its non-native range suggest how the plant will further spread in North America.

*Z. japonica* is native to the cool to subtropical northern-pacific coast of East Asia, from Vietnam in the south to Sakhalin and Kamchatka, Russia in the north (Shin and Choi 1998, Aioi and Nakoa 2003). There, it forms monotypic beds in the mid-intertidal zone of estuaries and sheltered bays on a variety of substrates (Lee 1997, Yamada 2007). Patches increase in size by horizontal growth of a rhizome (Lee 1997). These beds are perennial with peak flowering during the summer (June and July) and minimal biomass during the winter (October - January).
Flowering shoots and leaves can reach lengths of 0.30 m, although they are commonly less than 0.15 m long (Lee 1997, Shin and Choi 1998).

Percent cover of Z. japonica is negatively correlated with suspended sediment and water salinity, and high solar irradiance during summer months may limit production in the subtropical portion of its native range (Lee 1997). Temperature, on the other hand, has been found to correlate positively with Z. japonica growth; leaf productivity and flowering shoot density have been shown to coincide with maximum air and water temperatures on the west coast of Korea (Lee et al. 2005). Air temperature has the greater effect on annual changes in biomass with production peaking from 19° - 29° C (Lee et al. 2006).

Z. japonica was first reported in North America in Washington State in 1957, although it may have been present as early as 1902, and separate introduction events have been suggested (Harrison and Bigley 1982). Z. japonica was likely introduced from Japan via shipments of oysters (Crassostrea gigas) that were packed in the Asian seagrass (Harrison 1976). Bulthuis (1995) suggests that the population of Z. japonica in Padilla Bay, Washington is one of the oldest on the West Coast of North America.

The phenological and habitat characteristics of Z. japonica in its non-native range, the NE Pacific, are similar to those in its native range. In North America, Z. japonica occupies the mid- to upper- intertidal mudflats, grows rapidly, and puts a large proportion of its resources into flowering, which peaks in August
(Harrison 1979). It typically behaves as an annual plant, overwintering as buried seed, although some vegetative individuals may survive perennially in sheltered areas. These, however, typically die the following spring when seeds begin to germinate (Harrison and Bigley 1982). Above-ground biomass persists year round in Yaquina Bay, Oregon, suggesting that the phenology and intensity of Z. *japonica*’s sexual reproduction in the southern part of its range may differ from northern portions of its non-native range (Kaldy 2006).

Leaf elongation rates for NE Pacific plants are strongly correlated with maximum sediment temperature (Kaldy 2006), and plants taken from populations at opposite ends of its non-native range have varying responses to different water temperature treatments in an experimental setting (Shafer et al. 2008). Individuals from Yaquina Bay, Oregon exhibit maximum leaf elongation, growth and aerial productivity rates in the 20°-30° C range whereas plants from Padilla Bay exhibit declining maximum leaf elongation, growth and aerial productivity rates in treatments above 20° C (Shafer et al. 2008). These differences in physiology suggest some degree of ecotypic differentiation, and indicate that Z. *japonica* is able to spread further south where the temperatures are warmer and would also be capable of expanding within northern estuaries that are warming faster than the oceans (Largier et al. 2010).

Since its introduction in Washington, Z. *japonica* has spread north to the vicinity of Vancouver, British Columbia and south to Humboldt Bay and the Eel River Estuary in northern California (Wyllie-Echeverria and Ackerman 2003, Ramey
2008). *Z. japonica* was first detected in Humboldt Bay during June 2002 and in the McNulty slough of the Eel River Estuary, just south of Humboldt Bay, in April 2008 (Schlosser and Eicher\(^1\), Ramey \(^2\)). The Eel River Estuary population of *Z. japonica* is the southernmost known extent of the species in its non-native range.

One concern for managers about a spreading exotic seagrass is its potential for negative interactions with the native eelgrass *Zostera marina*. However, *Z. japonica* has not been demonstrated to negatively impact *Z. marina* where the congeners co-occur in the NE Pacific (Wyllie-Echeverria and Ackerman 2003, Mach et al.\(^3\)). Once established, *Z. japonica* occupies the mid- to upper-intertidal zone where it is immersed only during high tides (Kaldy 2006). *Z. marina*, on the other hand, occurs lower in the intertidal and subtidal and is abundant only where it remains inundated with water at low tide (Harrison 1987). Thus, *Z. japonica* and *Z. marina* typically occupy separate niches in estuaries where they co-occur, although overlap between the two has been observed (Thom 1990, Harrison 1979). *Z. marina* canopy has been shown to suppress *Z. japonica* shoot density, and in the absence of disturbance, *Z. marina* out-competes the *Z. japonica* (Nomme and Harrison 1991a,b, Bando 2006). Additionally, physical stresses

---

\(^1\) Schlosser, S and A Eicher. 2007. Humboldt Bay Cooperative Eelgrass Project report to the National Fish and Wildlife Foundation. *UC Sea Grant Extension Program*.

\(^2\) Ramey, K 2008. Humboldt Bay Harbor, Recreation and Conservation District Permit No. 03-03: *Zostera japonica* Eradication Project annual report. *California Department of Fish and Game*

may be involved in the differences in zone-preferences between the two species, as optimal *Z. japonica* growth has been shown to occur at high temperature that stress *Z. marina* and *Z. japonica* grows very slowly at the low temperatures where *Z. marina* thrives (Shafer et al. 2008). This may explain why *Z. japonica* is not known to extend below 1.0 m mean-lower-low water (MLLW) even in areas where *Z. marina* is absent (Kaldy 2006).

Despite the low potential for negative interactions with native eelgrass, there may be cause for concern with a clonal organism that spreads across high intertidal mudflats that previously lacked vascular plants and were characterized by bare mud, ulvoid algae and microalgae, and an infaunal community that supports a diverse bird community (Barnhart et al. 1992). There is the potential for *Z. japonica* shoots to trap different kinds of sediments and therefore alter the infaunal community structure. For example, average sediment grain size declined significantly within *Z. japonica* patches as patch age increased (Posey 1988), and the abundance of the native burrowing shrimp *Neotrypea* (formerly *Callianassa*) declined in areas of the southwest coast of British Columbia where both *Z. japonica* and *Z. marina* spread (Harrison 1987). Additionally, the non-native seagrass may affect how organisms utilize mudflats by decreasing seawater flow rates relative to unvegetated mudflats, although specifics regarding *Z. japonica*’s effects on ecosystem function are not well documented.
Since *Z. japonica* can potentially increase rates of sedimentation to the mudflat habitat, it has also been suggested that non-native salt marsh species, such as *Spartina densiflora* in Humboldt Bay, will be able to spread out on to what was mudflat habitat as the latter raises in elevation via accretion (Schlosser and Eicher). Managers need to predict how non-native species, particularly those that can alter an entire habitat, will spread. This ability informs decisions regarding development and implementation of policy designed to protect vulnerable habitat and, if necessary, remove the non-native species. To predict the spread of non-native organisms, a modeling approach is typically employed. Models are produced which incorporate biotic and/or abiotic limiting factors into mathematical algorithms, include spatially explicit population models (e.g. Almasi and Eldridge 2008) and, more recently, habitat-based spatial models using a geographic information system (GIS).

In Humboldt Bay, local managers have pursued early detection and eradication of new and existing patches of *Z. japonica* since April of 2003 (Schlosser and Eicher, Ramey). Although this effort seemed successful initially, *Z. japonica* has

---


6 Ramey, K 2008. Humboldt Bay Harbor, Recreation and Conservation District Permit No. 03-03: *Zostera japonica* Eradication Project annual report. *California Department of Fish and Game*
since established itself at various sites in the upper mudflats of northern Humboldt Bay, and new patches are discovered in this general area every year (Weltz, pers. obs.). Z. japonica’s potential distribution in Humboldt Bay has been modeled using a bathymetric approach (Kauffman et al.)\(^7\). In this approach, suitable habitat was modeled in a GIS as a function of bottom depth using a digital elevation model (DEM). The resulting prediction maps defined all areas of mudflat between 0.6 and 1.6m above MLLW as suitable future habitat for Z. japonica (Kauffman et al.) A major limitation of this approach is that it does not account for variation in physical and biological factors that limit the spread of the plant within a given bathymetric range, and thus may overestimate potential habitat. This has been the only previous attempt to predict potential Z. japonica habitat in an estuary where it has not already become fully established. However, given the limitations of the bathymetric approach, there remains a need to develop predictive maps that account for available knowledge concerning limiting biotic and abiotic factors.

The first objective of this study, therefore, was to move beyond bathymetry and to use intertidal temperature in conjunction with established Z. marina habitat to identify those areas of Humboldt Bay mudflat that are the most optimal for Z. japonica’s growth, and thus most likely to be sites for future colonization. The groundwork for this temperature-based approach has been laid by Shafer et al. (2008), who identified 20°-30°C as physiologically optimal for growth of Z.

*japonica* plants in the southern portion of its NE Pacific distribution. Since temperatures in this range are reached in the intertidal only during periods of emersion on warm days, and since *Z. marina* occupies much of the lower intertidal in Humboldt Bay, we expected that the model would identify upper intertidal mudflat habitat as the most optimal growth locations. While these areas have been previously identified as potential habitat by Kauffman et al. (2007), it was our hope that, by accounting for physical and biological limiting factors, we would be able to produce a more precise predictive model.
METHODS

Bay Temperatures for Mapping Optimal Growth Zones

Humboldt Bay is an estuarine embayment located approximately 370 km north of San Francisco Bay and 137 km south of the California-Oregon border (Fig. 1). In order to describe temperatures of bay mudflats, temperature loggers were deployed in the bay’s intertidal. A GIS was used to generate random temperature sampling locations. Portions of the bay that would be exposed during low tides were identified using a digital elevation model. Fifteen random sites were then identified within each end of the bay for a total of 30 sites initially, but site accessibility issues and loss of logger units resulted in only twenty-six sites (thirteen in North Bay, thirteen in South Bay) being included in the analysis (Fig. 1). Additionally, nine former and contemporary Z. japonica sites in North Bay were added to the sampling scheme to determine the thermal range experienced by the plant in Humboldt Bay (Fig. 1). Polyvinyl chloride (PVC) pipes were fashioned into 1.2 m length stakes with holes midway for attachment of Thermochron iButton® temperature loggers. Marine epoxy was applied to the seam on the body of each iButton to render the units waterproof. These units were deployed to both the random sites and the Z. japonica sites. PVC stakes were inserted into the mud so that logger units rested on the surface of the mud. All sites were accessed by shore or by boat during minus tides.
Figure 1. Study location of Humboldt Bay in Northern California. Lettered symbols are random temperature logger sites, numbered symbols are sites where Z. japonica does or used to exist. The positions of the CeNCOOS water quality sites are indicated (*) in central and southern Humboldt Bay.
Loggers recorded temperatures every half hour from May through August 2010. Sites were accessed every thirty days to download temperature data, in order to ensure that ample memory was available for each iButton to continue recording temperature throughout the sampling period. The failure of some units resulted in gaps in the temperature data. Therefore, to ensure complete temporal overlap of the data, only temperatures from mid-June through mid-July 2010 were analyzed, a period which corresponded reasonably well with the peak of the plant’s summer growing season (Lee 1997).

In order to produce a GIS layer of interpolated *in situ* temperatures, the twice-hourly temperature data were sorted from lowest to highest temperature value for each temperature logger site. The proportion of time spent in the 20-30 °C range was determined for each site by dividing the number of temperature readings within that range for a particular site by the total number of readings for that site. Proportion values from random mudflat sites were then imported into a GIS as a table, which was joined with a shapefile representing their locations. Values from these locations were used to interpolate values for the proportion of time spent in the 20-30 °C range for the rest of the Humboldt Bay mudflat habitat using ordinary kriging (van Horssen et al. 1999, Valley et al. 2005). Ordinary kriging interpolation was performed using default parameters in ESRI ArcMap® version 9.3.1 in Spatial Analyst. Interpolated proportions were classified into nine classes using the natural breaks (Jenks) method, which sorted the data into bins according to natural groupings within the data. In order to generate a prediction
map for optimal *Z. japonica* habitat, a shapefile representing continuous *Z. marina* habitat in Humboldt Bay (derived from the Humboldt Bay and Eel River Estuary Coastal and Marine Ecological Classification Standard Habitats shapefile, accessed via NOAA Coastal Service Center’s Digital Coast\(^8\)) was overlaid on the map of interpolated proportions. This excludes areas that, due to interspecific competition, would not likely provide suitable habitat for *Z. japonica* even if the location was within the 20-30 °C range.

**Bay Temperatures for the Warmer Scenario**

To compare the mudflat temperatures collected during the 2010 growing season, to another year, continuous (every 15 min) summer water temperature data collected at two sites in the bay by the Central North Coast Ocean Observing System (CeNCOOS) were examined for 2009 and 2010. Both sites (‘Dock B’ and ‘Kramer Dock’, Fig. 1) indicated that SST measured during the June -July 2010 growing season was about 2° C cooler than the previous summer (Fig. 2). Therefore, a scenario of optimal *Z. japonica* habitat based on a warmer growing season was also modeled. *In situ* temperatures from random logger locations during the 2010 growing season (‘cooler scenario’) were artificially increased by adding 2° C to each reading. The prediction map for *Z. japonica* habitat was then developed using the previously described methods.

---

\(^8\) [http://www.csc.noaa.gov/digitalcoast/data/benthiccover/download.html](http://www.csc.noaa.gov/digitalcoast/data/benthiccover/download.html)
Figure 2. Representative water temperatures from 2010 (a) and 2009 (b) from two CeNCOOS water quality sites (Fig. 1) in central and southern Humboldt Bay.
RESULTS

*In situ* logger temperatures from random mudflat locations ranged from less than 10°C at low-elevation sites in South Bay to greater than 25°C at high-elevation sites in both North Bay and South Bay during the June to July 2010 sampling period (Fig. 3). Temperature minima for each site corresponded to flood tide water whereas maximum temperatures are due either to direct heating while emerged or ebbing tidal water (Fig. 3). Mean daily temperature minima for random logger sites ranged from 9.7° C to 15.8° C, while mean daily temperature maxima for these sites ranged from 14.6° C to 24.1° C (Table 1). *Z. japonica* mean daily maximum temperatures ranged from 18.35° C to 26.13° C, and mean daily minimum temperatures for *Z. japonica* sites ranged from 10.02° C to 14.37° C (Table 1). Random mudflat sites spent between 0.1% and 21.6% of the June-July 2010 growing season in the optimum temperature range. All *Z. japonica* sites spent between 10.0% and 40.0% of the sampled period in the 20°-30°C range except site 8, which spent only 0.5% of the time in the optimal growth range (Table 1).

The model for the cooler scenario, based on 2010 *in situ* temperature data, predicted areas of North Bay to experience longer periods of the optimal growth temperature range (i.e. 20°-30°C) than areas in South Bay (Fig. 4). Mudflat regions in the north-eastern reaches of the bay were predicted to spend 8.5%-14.4% of the time in *Z. japonica*’s optimal thermal range. Much of the middle portion of North Bay was predicted to spend from 5.6% to 8.4% of the time in the
Figure 3. Comparison of representative temperatures from low and high intertidal mudflat data loggers during the June to July 2010 sampling period. Tide heights were recorded by the CeNCOOS Dock B sonde (Fig. 1).
Table 1. For each data logger site (alphabetical) and *Z. japonica* site (numerical) across the 2010 growth period, the mean of the daily maximum temperatures (Mean Max.) with the corresponding standard deviation (Max. SD), the mean of the daily minimum temperatures (Mean Min.) and standard deviation (Min. SD), and the proportion of time during the growth period that each site spent within the optimal growth temperature range.

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean Max.</th>
<th>Max. SD</th>
<th>Mean Min.</th>
<th>Min. SD</th>
<th>Prop. time 20-30 °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>20.13</td>
<td>1.59</td>
<td>12.74</td>
<td>1.29</td>
<td>0.064</td>
</tr>
<tr>
<td>B</td>
<td>18.37</td>
<td>1.08</td>
<td>13.15</td>
<td>1.22</td>
<td>0.006</td>
</tr>
<tr>
<td>C</td>
<td>21.08</td>
<td>2.10</td>
<td>13.35</td>
<td>1.25</td>
<td>0.078</td>
</tr>
<tr>
<td>D</td>
<td>20.10</td>
<td>1.82</td>
<td>12.29</td>
<td>1.04</td>
<td>0.064</td>
</tr>
<tr>
<td>F</td>
<td>22.60</td>
<td>1.93</td>
<td>12.13</td>
<td>1.62</td>
<td>0.168</td>
</tr>
<tr>
<td>G</td>
<td>24.08</td>
<td>1.76</td>
<td>12.77</td>
<td>2.12</td>
<td>0.400</td>
</tr>
<tr>
<td>H</td>
<td>18.42</td>
<td>1.06</td>
<td>15.53</td>
<td>1.12</td>
<td>0.003</td>
</tr>
<tr>
<td>J</td>
<td>21.29</td>
<td>2.02</td>
<td>12.74</td>
<td>1.52</td>
<td>0.115</td>
</tr>
<tr>
<td>K</td>
<td>18.76</td>
<td>0.96</td>
<td>15.82</td>
<td>1.26</td>
<td>0.024</td>
</tr>
<tr>
<td>L</td>
<td>21.95</td>
<td>1.77</td>
<td>13.87</td>
<td>1.60</td>
<td>0.216</td>
</tr>
<tr>
<td>M</td>
<td>18.54</td>
<td>1.13</td>
<td>14.43</td>
<td>1.35</td>
<td>0.014</td>
</tr>
<tr>
<td>N</td>
<td>21.95</td>
<td>1.92</td>
<td>11.93</td>
<td>1.09</td>
<td>0.184</td>
</tr>
<tr>
<td>O</td>
<td>19.27</td>
<td>2.67</td>
<td>12.21</td>
<td>1.28</td>
<td>0.021</td>
</tr>
<tr>
<td>P</td>
<td>20.82</td>
<td>2.85</td>
<td>9.66</td>
<td>1.15</td>
<td>0.050</td>
</tr>
<tr>
<td>R</td>
<td>17.27</td>
<td>2.40</td>
<td>12.40</td>
<td>1.07</td>
<td>0.007</td>
</tr>
<tr>
<td>S</td>
<td>14.61</td>
<td>1.49</td>
<td>10.48</td>
<td>1.03</td>
<td>0.001</td>
</tr>
<tr>
<td>T</td>
<td>21.76</td>
<td>2.43</td>
<td>12.35</td>
<td>0.82</td>
<td>0.099</td>
</tr>
<tr>
<td>Site</td>
<td>Mean Max.</td>
<td>Max. SD</td>
<td>Mean Min.</td>
<td>Min. SD</td>
<td>Prop. time</td>
</tr>
<tr>
<td>------</td>
<td>-----------</td>
<td>---------</td>
<td>-----------</td>
<td>---------</td>
<td>------------</td>
</tr>
<tr>
<td>U</td>
<td>19.5</td>
<td>3.96</td>
<td>12.05</td>
<td>0.84</td>
<td>0.035</td>
</tr>
<tr>
<td>V</td>
<td>19.71</td>
<td>2.56</td>
<td>11.76</td>
<td>0.91</td>
<td>0.042</td>
</tr>
<tr>
<td>W</td>
<td>17.77</td>
<td>3.17</td>
<td>11.69</td>
<td>0.82</td>
<td>0.012</td>
</tr>
<tr>
<td>X</td>
<td>18.79</td>
<td>1.56</td>
<td>12.18</td>
<td>0.99</td>
<td>0.013</td>
</tr>
<tr>
<td>Z</td>
<td>20.63</td>
<td>2.99</td>
<td>13.39</td>
<td>1.06</td>
<td>0.066</td>
</tr>
<tr>
<td>AA</td>
<td>23.27</td>
<td>3.26</td>
<td>13.05</td>
<td>1.25</td>
<td>0.180</td>
</tr>
<tr>
<td>BB</td>
<td>15.50</td>
<td>2.14</td>
<td>10.32</td>
<td>1.12</td>
<td>0.002</td>
</tr>
<tr>
<td>CC</td>
<td>13.92</td>
<td>0.87</td>
<td>10.52</td>
<td>0.69</td>
<td>0.001</td>
</tr>
<tr>
<td>DD</td>
<td>16.58</td>
<td>1.08</td>
<td>11.98</td>
<td>1.59</td>
<td>0.001</td>
</tr>
<tr>
<td>1</td>
<td>24.08</td>
<td>1.76</td>
<td>12.77</td>
<td>2.12</td>
<td>0.400</td>
</tr>
<tr>
<td>2</td>
<td>22.37</td>
<td>1.97</td>
<td>10.02</td>
<td>1.86</td>
<td>0.135</td>
</tr>
<tr>
<td>3</td>
<td>23.65</td>
<td>1.72</td>
<td>13.47</td>
<td>1.20</td>
<td>0.313</td>
</tr>
<tr>
<td>4</td>
<td>23.90</td>
<td>1.73</td>
<td>12.87</td>
<td>1.26</td>
<td>0.298</td>
</tr>
<tr>
<td>5</td>
<td>23.21</td>
<td>1.78</td>
<td>13.53</td>
<td>1.52</td>
<td>0.271</td>
</tr>
<tr>
<td>6</td>
<td>26.13</td>
<td>2.47</td>
<td>13.94</td>
<td>1.26</td>
<td>0.344</td>
</tr>
<tr>
<td>7</td>
<td>25.56</td>
<td>2.12</td>
<td>14.37</td>
<td>1.21</td>
<td>0.403</td>
</tr>
<tr>
<td>8</td>
<td>18.35</td>
<td>1.25</td>
<td>12.74</td>
<td>0.71</td>
<td>0.005</td>
</tr>
<tr>
<td>9</td>
<td>21.90</td>
<td>1.61</td>
<td>11.18</td>
<td>0.90</td>
<td>0.100</td>
</tr>
</tbody>
</table>
Figure 4. The cooler 2010 scenario showing interpolated distributions of mudflat areas experiencing different time lengths of optimal growth temperatures for *Z. japonica* and the existing habitat footprint for *Z. marina*.
optimal range, but most of this area is occupied by continuous beds of Z. marina (Fig. 4). The peripheral mudflats of South Bay were projected to experience optimal temperatures from 1.5% to 5.5% of the time in the cooler scenario, and while this was also the case for the northern and central parts of South Bay, these areas are dominated by Z. marina (Fig. 4).

The model for the warmer scenario, based on increased in situ mudflat temperatures, projected large increases in more optimal habitat area for both portions of Humboldt Bay, but especially in North Bay (Fig. 5). There, all of the mudflat area above Z. marina was predicted to experience optimal Z. japonica temperatures from 12.7% to 45.0% of the growth period (Fig. 5). Additionally, in South Bay, upper intertidal areas in the southern-most regions were predicted to spend the same proportion of time in the optimal temperature range for Z. japonica growth. The rest of the mudflat areas of South Bay above Z. marina were predicted to occur in the optimal temperature range 5.6% to 12.6% of the time (Fig. 5).
Figure 5. The warm scenario showing interpolated distributions of mudflat areas experiencing different time lengths of optimal growth temperatures for *Z. japonica* and the existing habitat footprint for *Z. marina*. 
DISCUSSION

In both the cool scenario, based on in situ 2010 mudflat temperatures, and the hypothetical warm scenario, North Bay was the warmer of the two subregions of Humboldt Bay. The greatest proportions of time spent in *Z. japonica*’s optimal temperature range are predicted to occur in the northern and eastern-most portions of North Bay that are the least proximal to input of cool water from the entrance channel. Thus, these unvegetated high-intertidal regions of North Bay are predicted to provide the most optimal *Z. japonica* habitat in Humboldt Bay, and in fact, with the exception of the Indian Island populations, all currently-known sites of *Z. japonica* establishment in Humboldt Bay occur in this region. Indian Island is on the southern end of North Bay, and its intertidal regions are among the coolest in North Bay. The fact that *Z. japonica* has established there despite the less-optimal thermal conditions may give important clues as to its mode of spread, as the Indian Island sites are in close proximity to oyster aquaculture operations and migrating Brant geese (*Branta bernicula*), both of which have the potential to play a role as vectors for *Z. japonica* spread.

South Bay was comparatively cooler than North Bay, with the lowest predicted proportions of time spent in the 20°-30°C temperature range, and thus is predicted by the model to provide less optimal potential habitat for *Z. japonica*. Also, continuous beds of *Z. marina* occupy a greater portion of South Bay than they do of North Bay, further reducing the potential for *Z. japonica* to become established there. However, in the warmer scenario, some regions of
unvegetated mudflat that are peripheral to the continuous *Z. marina* habitat experience thermal conditions as optimal as those in the North Bay for both scenarios. Thus, South Bay, although less optimal than North Bay from a thermal standpoint, may provide adequate habitat for the non-native as it spreads.

The unvegetated, upper-intertidal areas identified by this model as potential habitat for *Z. japonica* correspond with those predicted by the Kaufman et al.\(^9\) elevation-based model. However, this temperature-based model differs from theirs in describing these areas of potential habitat as more or less optimal for the spreading plant. Therefore, although the elevation-based model identified portions of North Bay and South Bay as equally suitable for *Z. japonica* to become established, this temperature-based model identifies high-elevation mudflat in North Bay as more suitable than mudflat at the same elevation in South Bay, and thus more likely to experience invasion by the plant in the near future. By breaking up mudflat within the acceptable elevation range into areas that are more or less likely to provide optimal growth conditions to *Z. japonica* as it spreads, this model provides resource management authorities with an important tool for assessing potential impacts on the local ecosystem.

From a management perspective, Humboldt Bay is unique in that it is the only place in *Z. japonica*'s non-native range where eradication of the plant has been

---

attempted by resource managers (Schlosser and Eicher\textsuperscript{10}, Ramey\textsuperscript{11}). Based on the predictions generated by this study, local managers seeking to identify and remove new infestations of the invading plant are recommended to concentrate their search efforts on the portions of North Bay identified as being most optimal for \textit{Z. japonica} growth, especially those adjacent to currently-existing patches of \textit{Z. japonica}, which provide sources for dispersal of the plant. However, the entire perimeter of Humboldt Bay contains portions of unvegetated intertidal mudflat that spend at least some of the summer growing season in \textit{Z. japonica}'s optimal temperature range. Additionally, the warm-scenario model characterizes the majority of South Bay mudflat as equally optimal habitat as the entirety of North Bay in the cooler 2010 scenario. Thus, in attempting to identify new patches of \textit{Z. japonica} as they become established, it is important for managers to include the South Bay intertidal mudflats in their survey protocols. As global climate change effects warm our bays and estuaries, the likelihood of \textit{Z. japonica}'s establishment in South Bay will increase, and monitoring changes in sea-surface temperature in South Bay may become an important management strategy for appropriate application of \textit{Z. japonica} removal effort.

An important step in the development of a model for predicting species spread is model validation. While no actual validation was attempted as part of this study, a

\textsuperscript{10} Schlosser, S and A Eicher. 2007. Humboldt Bay Cooperative Eelgrass Project report to the National Fish and Wildlife Foundation. \textit{UC Sea Grant Extension Program}.  

\textsuperscript{11} Ramey, K 2008. Humboldt Bay Harbor, Recreation and Conservation District Permit No. 03-03: \textit{Zostera japonica} Eradication Project annual report. \textit{California Department of Fish and Game}
certain amount of 'soft validation' is apparent in the fact that all former and present patches of *Z. japonica* in Humboldt Bay occur on mudflat areas identified by the model as experiencing relatively long periods of optimal growth temperature. To validate the general method employed in developing this model, a combination of presence-absence and temperature data from a fully invaded estuary (e.g. Willapa Bay, WA) could be used to determine whether variation in the proportion of time spent in the 20°-30°C temperature range is a significant predictor of *Z. japonica* presence on a given piece of mudflat. Additionally, since local managers continue to document new patches of *Z. japonica* in Humboldt Bay, further validation could be achieved by quantifying the number of new patch locations that occur on areas of more optimal habitat (as identified by this model) and comparing that to the number of new patches identified in less optimal mudflat.

As *Z. japonica* continues to spread southward in its NE Pacific range (Shafer et al. 2008), the method employed in this study will provide managers with a valuable tool for assessing potential *Z. japonica* habitat in the bays and estuaries to the south of its current NE Pacific range. By identifying optimal *Z. japonica* habitat in these areas, managers will be able to make informed decisions on the potential for impacts to sensitive habitat and species, as well as potential conflicts with mariculture industry in areas such as Tomales Bay and Drakes Estero. This method could also be adapted for use in determining habitat optima for any invading species where temperature is a known limiting factor to spread.
LITERATURE CITED


Yamada, K, M Hori, Y Tanaka, N Hasegawa and M Nakaoka. 2007. Temporal and spatial macrofaunal community changes along a salinity gradient in