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INVASIVE SPECIES - ORIGINAL PAPER

Forecasting at the edge of the niche: *Didemnum vexillum* in Southeast Alaska

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Abstract Controlling the spread of marine invasive species is a challenging and costly task. Maps that predict the potential spread of an invader based on known habitat preferences can be extremely valuable for assessing invasion risk and prioritizing management actions for invasion control or prevention. Most maps are developed by using environmental data on the species' known distribution to map the potential niche of the species in a new location. However, this approach is complicated when a species spreads to an area where environmental conditions are much different than in other places it is known to exist. *Didemnum vexillum* was discovered in Southeast Alaska in 2010, marking the northernmost known range of this species. A self-organizing map (SOM) was used to assess potential habitat for *D. vexillum* in other parts of Southeast Alaska using summer and winter temperature and salinity as controlling factors. This research highlights the uncertainty of using the species' current distribution to evaluate potential spread to an environment at the edge of a species' environmental tolerances. It also identifies gaps in our knowledge of *D. vexillum* thermal and salinity tolerances, including potential synergistic and additive effects of both low temperature and low salinity, which limit investigation of mechanistic modeling methods.

Introduction

Maps that predict the potential spread of an invasive species to new locations can be extremely valuable for assessing invasion risk and prioritizing management actions for invasion control or prevention. Most of these maps are created using species distribution modeling methods that identify suitable habitat based on the environmental conditions in the species home range or in areas to which the species has already spread (Jiménez-Valverde et al. 2011; Verbruggen et al. 2013). However, as has been noted elsewhere (Václavík and Meentemeyer 2009; Jiménez-Valverde et al. 2011) dispersal mechanisms, whether natural or anthropogenic, may limit the environments into which the species has been introduced with the result that the environmental conditions in the locations where the species is currently distributed are unlikely to represent the full suite of conditions under which the species can thrive (Gallien et al. 2012). Mechanistic models that incorporate information on species' life history may provide a more accurate method for assessing a species' potential habitat, but these models require a substantial amount of data on environmental tolerances that are not available for many species. When a species moves into an entirely new area, the challenge of risk assessment modeling is to evaluate how much the environment in the new location differs from, or is similar to, other locations where the species is known to occur and determine whether reliable predictions of potential spread can be made.

The invasive ascidian *Didemnum vexillum* is a species of global concern. Molecular evidence suggests that *D.*

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vexillum originated in Japan (Stefaniak et al. 2012) and has been spread to Eastern and Western North America, New Zealand, Europe. This species has a history of rapid expansion in some of the areas where it has been introduced (Bullard et al. 2007; Valentine et al. 2007b). It is capable of overgrowing and potentially dominating the substrate and can also overgrow sessile fauna (Bullard et al. 2007; Lambert 2009). These characteristics raise the concern that *D. vexillum* could adversely affect benthic communities and species which rely on benthic habitat and food during at least a portion of their life (Daniel and Therriault 2007; Valentine et al. 2007a).

In 2010, *D. vexillum* was first identified in Southeast Alaska following an invasive species bioblitz (Cohen et al. 2011). The species was found associated with an abandoned aquaculture facility in a man-made bay near Sitka, AK, where large amounts of *D. vexillum* covered lantern nets and docks and had spread to a portion of the adjacent rocky shoreline. This population is the northernmost colony of this species currently on record (Cohen et al. 2011). Worldwide, *D. vexillum* is primarily found in association with anthropogenic habitats (Bullard et al. 2007; Simkanin et al. 2012; Forrest et al. 2013) including mariculture facilities, docks, marinas, and adjacent structures (Bullard et al. 2007; Herborg et al. 2009). Anthropogenic vectors are implicated in the majority of introductions of this species (Daley and Scavia 2008; Tagliapietra et al. 2012), but *D. vexillum* also has the potential to spread via water dispersal of fragments broken off by waves (Bullard et al. 2007; Daley and Scavia 2008) and through spawning. Laboratory experiments also suggest that *D. vexillum* could be transported as a fouling organism on slow-moving vessels (Clarke Murray et al. 2012). *Didemnum vexillum* has broad temperature and salinity tolerances; however, extended periods of high or low temperature or low salinity can cause degeneration and death (Mccarthy et al. 2007; York et al. 2008; Gröner et al. 2011).

Although *D. vexillum* has been positively identified in only one location in Alaska, based on this species' history of rapid expansion, there is concern that it may spread to other sites. *Didemnum vexillum* only grows on hard substrates (Bullard et al. 2007), and Southeast Alaska has 36,000 km of complex, rocky coastline: nearly a quarter of the coastline of the entire USA. The region is sparsely populated with few roads, and most transport is by boat or float plane. Less than 1 % of the coastline is anthropogenic shoreline such as harbors, piers, docks, aquaculture farms, or pilings, and in 2014 there were only 47 shellfish mariculture farms in the region. However, shellfish mariculture is a growing industry: Alaska has one of the few state-managed mariculture zoning programs in the nation and the State leases tidelands and submerged lands for mariculture operations mostly in remote locations. All of these factors create concern that Southeast Alaska shorelines may provide suitable habitat for *D. vexillum* if temperature and salinity conditions are also favorable.

To assess how similar or dissimilar the Southeast Alaska environment is to other infested sites worldwide, a self-organizing map (SOM) was used to model summer and winter water temperature and salinity averages. Additionally, a map predicting potential habitat for *D. vexillum* in Southeast Alaska was developed using model output and data from the literature. This research highlights the uncertainty of using the species' current distribution to evaluate potential spread to an environment at the edge of a species' tolerance. It also identifies gaps in our knowledge of *D. vexillum* thermal and salinity tolerances, including potential synergistic and additive effects of both low temperature and low salinity, which limit investigation of mechanistic modeling approaches.

Methods

Study area

Southeast Alaska is an archipelago of approximately 1000 mountainous islands extending from approximately 59°N to 54.5°N. The coastline is generally steep and depths within several meters of the shoreline often exceed 30 m. The entire archipelago is a temperate rainforest with average annual precipitation in excess of 2000 mm/year (Neal et al. 2002). Precipitation varies locally and regionally with a general gradient of lower precipitation in the northwest and higher precipitation in the southeast. Much of the precipitation is released directly into the marine waters via numerous small streams and wetlands. Stream flow is highly seasonal and influenced by precipitation and by snow and ice melt. The highest stream flows and runoff tend to occur in October when precipitation rates are high and are lowest in February as a result of freezing. Annual runoff to the coastal waters from precipitation alone has been estimated at 15,000 $m^3\ s^{-1}$ (Royer 1998). Sea surface salinity varies in relation to freshwater inflow ranging from 0 in the vicinity of freshwater discharges to 32 PSU at the mouth of bays and along coastal areas (Weingartner et al. 2009). Nearshore water temperatures are influenced by air temperatures and by runoff from glaciers, snowmelt, and precipitation. In addition, Southeast Alaska has several tidewater glaciers with ice extending into the marine environment. Temperature generally increases westward and southward from inshore to coastal habitats with cooler temperatures in inner channels and adjacent to freshwater inflow.

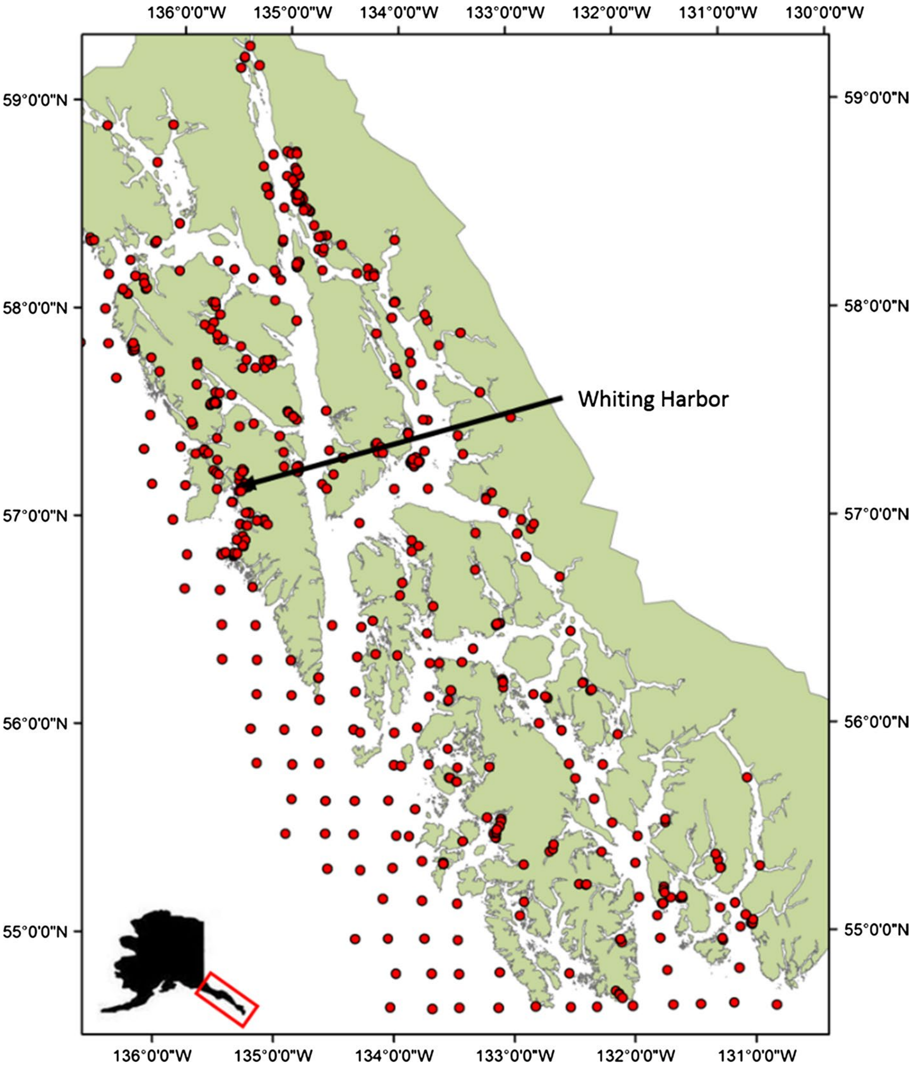

Fig. 1 Location of sea surface temperature and salinity sampling stations in Southeast Alaska

Temperature and salinity data

Measured summer temperature and salinity data for Southeast Alaska were compiled from 617 stations sampled between 1998 and 2011 (Fig. 1). Station data included the average conductivity and temperature from the top 5 m of the water column from profiles collected by the International Pacific Halibut Commission in Southeast Alaska for 2010 and 2011 (Iphc 2011). Additional nearshore data were compiled from a database of nearshore seine surveys undertaken between 1998 and 2009 (Johnson et al. 2005): the latest availability for these data. All data were collected between June and August and are presented as summer temperature and salinity. Winter temperature data were compiled from thermographs from 16 bays in Southeast Alaska (Johnson et al. 2005) and from NOAA tide and current stations for December–February (NOAA 2013b). Winter salinity was compiled from winter seine surveys throughout the region (Johnson et al. 2005).

Since Whiting Harbor is currently the only known location of *D. vexillum* in Alaska, the Alaska temperature and salinity data were evaluated to create three scenarios for use in the SOM modeling. Environmental conditions in Whiting Harbor were in the higher range of temperature and salinity values, so Whiting Harbor was selected as the high scenario. The moderate value scenario used average temperature and salinity values from the Alaska data, and the low value scenario used the lower range of values from Alaska (Table 1).

Worldwide locations of *D. vexillum* infestation were obtained from the United States Geological Survey (USGS) Woods Hole Coastal and Marine Science Center website (http://woodshole.er.usgs.gov/project-pages/stellwagen/didemnum). Locations of colonies in the species' native range in Japan were also identified. In lieu of in situ average temperature and salinity information, which was not available for any of these locations, average surface (0–5 m) summer and winter temperature and salinity data were

Table 1 Average temperature and salinity variables used in the SOM model

Location	SOM code	Summer (°C)	Summer salinity	Winter (°C)	Winter salinity
Whiting Harbor, AK (high)	AK-WHIT	12.8	32	5.0	31
Alaska—moderate	AK-1	9.0	27	4.5	29
Alaska—low	AK-2	7.0	23	3.0	27
Nootka Pt., BC	BC-1	15.5	29	7.2	26
Entrance Island, BC	BC-2	17.1	24	7.8	28
Sisters Island, BC	BC-3	16.9	26	7.6	29
Chrome Island, BC	BC-4	17.1	26	8.3	29
Belgium	BEL	16.6	34	5.7	34
San Francisco, CA	CA-SF	14.1	30	10.9	29
Mission Bay, CA	CA-1	19.5	34	14.8	34
Bodega Bay, CA	CA-2	13.1	33	11.4	33
Humboldt, CA	CA-3	13.0	33	10.7	33
Sausalito, CA	CA-4	14.4	32	9.9	32
Le Havre, France	FR-1	16.4	35	8.3	35
Brest, France	FR-2	16.4	35	10.8	35
Perros-Guirec, France	FR-3	16.0	35	10.2	35
Carlingford, Ireland	IRE-1	13.9	34	8.0	34
Clew Bay, Ireland	IRE-2	16.4	34	5.2	34
Venice, Italy	ITLY	23.8	37	12.3	37
Sagami Bay	JP-1	26.2	34	18.0	35
Otsuchi Bay	JP-2	20.8	34	7.5	34
Mutsu Bay	JP-3	22.1	34	8.3	34
Chatham, MA	MA-1	15.8	32	3.4	32
Oak Bluffs, MA	MA-2	19.4	33	7.4	33
Narragansett Bay, MA	MA-3	19.9	33	6.5	33
Rockport, ME	ME-1	14.4	32	3.0	32
Bremen, Maine	ME-2	12.8	32	2.8	32
Whiting Bay, ME	ME-3	12.4	32	1.9	32
Bremen, ME	ME-4	13.5	32	3.7	32
Damariscotta River, ME	ME-5	14.9	32	4.0	32
Oosterschelde, Netherlands	NED	17.1	34	6.7	34
Montauk, NY	NY	20.2	33	5.6	33
Whangamata Harbour, NZ	NZ-1	20.8	35	16.0	35
Shakespeare Bay, NZ	NZ-2	17.7	35	13.1	35
Shakespeare Bay, NZ	NZ-3	17.8	35	13.2	35
Umpqua, OR	OR	14.4	32	9.9	32
Holyhead Harbor, UK	UK	15.8	35	10.0	35
Gallagher Cove, WA	WA-1	14.8	28	8.6	27
Manchester, WA	WA-2	12.2	29	8.7	30
Edmonds, WA	WA-3	12.3	29	10.0	30
Des Moines, WA	WA-4	13.6	29	10.1	30

obtained from the National Ocean Data Center (NODC) World Ocean Database (NOAA 2013a) for stations close to the infested areas. Data from the NODC database were not available for interior waters of British Columbia (BC), Canada, Puget Sound, Washington USA, and San Francisco Bay, California, USA. Data for British Columbia came from the Fisheries and Oceans Canada BC Lighthouse database (DFO 2013). Data for Puget Sound came from the Puget Sound Regional Synthesis Model cruises (Prism 2006). Data for San Francisco Bay were obtained from the National Estuarine Research Reserve Centralized Data Export System (NOAA 2015).

Self-organizing map (SOM) model

Self-organizing maps are unsupervised neural networks used to visualize clusters in multidimensional data while preserving the similarity between samples (Kohonen 2001). The SOM analysis method has been described in detail elsewhere (see Brosse et al. 2001; Giraudel and Lek 2001; Kohonen 2001) so only a brief description is provided here. The SOM is composed of two parts: an input layer holding vectors (nodes) from the input data, and an output or computational layer which is a two-dimensional lattice with a predetermined number of neurons. Each neuron of the output layer is linked to the nodes of the input layer by weighted connections. The neurons of the output layer are also connected to adjacent neurons by a neighborhood relation, in this case a Gaussian function. The output lattice is initialized by populating each neuron with a random weight vector with the same dimension as the input vectors. The SOM learning then proceeds through a recursive process in which an input vector is randomly selected from the input layer and the distance (e.g., Euclidean distance) between that vector and each neuron of the output layer is computed. The best matching unit (BMU) is the neuron that is most similar to the input vector. The weights of the BMU, and units within the neighborhood around the BMU, are updated in accordance with the neighborhood function. This process repeats from the random selection of the input variable. At each time step, the size of the neighborhood function is decreased. Over numerous iterations, the learning process optimizes the output layer so that similar input vectors are placed in the same or adjacent units on the map. For this analysis, the process was stopped when no further changes could be made to optimize the map.

For this research, summer and winter temperature and salinity for the 35 data stations adjacent to *D. vexillum*-infested locations were used as the SOM input layer (Table 1). Since the objective is to evaluate the warm and cold conditions under which *D. vexillum* is currently found, winter temperatures and salinities for locations in the southern hemisphere were included as summer (warm season) values, and summer temperatures and salinities were included as winter (cold season) values for direct comparison between equivalent seasons. Measured summer and winter temperatures and salinities from Whiting Harbor, AK, and two sites representing moderate and low environmental conditions were also included. The size of the output layer (map) was composed of 20 neurons. Conventional wisdom holds that the number of units in the map should not be $<5 \times \mathrm{sqrt}(N)$, where N is the number of observations (Sarkisian 2008, Ramos 2015, Park 2003). Several iterations of the SOM were run to select the final map size of 40 units. This map size had low quantization and topological errors as well as a low number of empty nodes. The final SOM map provides a qualitative visualization of differences in temperature and salinity between the stations.

The distance between neurons on the map was calculated, and hierarchical clustering was used to group similar locations to produce a quantitative description of station differences. The optimal number of clusters (k) was determined by selecting the k with the maximum average silhouette width, which is a measure of the difference between intra-cluster similarity and similarity with the next closest cluster. Analysis was performed in R using the Kohonen package (Wehrens and Byuydens 2007).

Map development

Potential habitat maps were created in ArcGIS™ by evaluating the presence of suitable substrate with *D. vexillum* temperature and salinity tolerance ranges from the literature. Geomorphic characteristics of the intertidal coastline were obtained from the Alaska ShoreZone dataset (http://fakr.noaa.gov/shorezone/default.htm). ShoreZone is a mapping and classification system that uses oblique, low altitude aerial video and still images to classify segments of the shoreline according to natural breaks in geomorphic, sedimentary, and biological features (Harney et al. 2008). ShoreZone intertidal habitat data for hard substrates and anthropogenic structures were selected as potential habitat (Lengyel et al. 2009; Simkanin et al. 2012). Hard substrates included boulders, cobbles, rocks, and angular blocks, but excluded pebbles and sand. Anthropogenic structures include breakwaters, bulkheads, jetties, sheet piles, wharfs, and non-structural elements such as fishing nets and other debris. The mouths of perennial streams were extracted from the Tongass National Forest streams dataset (USDA 2002). This dataset lacks information on stream flow or stream size and so does not differentiate between large rivers and small streams. As a surrogate for near-zero nearshore salinity adjacent to the stream mouths, a 100 foot buffer was placed around the mouths of all streams.

Relatively little information is available on low-temperature tolerance limits for *D. vexillum* over extended periods of time. Research on *D. vexillum* in an intertidal site in Massachusetts, USA, over the course of a year observed degeneration in colonies when water temperatures decreased below 9 °C (Valentine et al. 2007a). A similar pattern has also been observed in the Netherlands where colony growth occurs at 9 °C (Gittenberger 2010), although the period over which these observations were made is not discussed. Using this information, the minimum summer temperature below which *D. vexillum* would fail to grow was set at 9 °C. Waters with summer temperatures below 8 °C were designated as Very Unlikely to facilitate *D. vexillum*, waters with temperatures between 8 and 9 °C were designated as Unlikely to facilitate *D. vexillum*, waters

Table 2 Comparison of average and low summer and winter temperature and salinity values for Southeast Alaska and worldwide locations of *Didemnum vexillum* infestation

	Southeast Alaska	Worldwide
Temperature		
Summer low	7 °C	12.2 °C
Average summer	10.2 °C ± 2.5	16.5 °C ± 3.3
Winter low	3.0 °C	3.4 °C
Average winter	4.1 °C ± 0.5	8.6 °C ± 3.7
Salinity		
Summer low	23 PSU	23.6 PSU
Average summer	29 PSU ± 2.8	32.3 PSU ± 2.9
Winter low	27 PSU	26.3
Average winter	31 PSU ± 2.3	32.5 PSU ± 2.6

with temperatures between 9 and 10 °C were designated as Possible *D. vexillum* habitat, and waters with temperatures above 10 °C were designated as Likely *D. vexillum* habitat.

D. vexillum tolerance to low salinity has also received little study. Research by Bullard and Whitlatch (2009) evaluated *D. vexillum* growth at three salinity levels (26–30, 15–28, and 10–26 ppt) in the Thames River estuary, CT, USA. Unfortunately, substantial overlap between the treatments limits the use of this research for establishing tolerance limits. The only study to directly evaluate salinity tolerance of *D. vexillum* in the laboratory observed a 20 % decline in survival for *D. vexillum* colonies held at 27 PSU and a 40 % decline in colonies held at 20 PSU for 2 weeks. Using this information, the minimum salinity below which *D. vexillum* would fail to thrive was set at 27 PSU (Gröner et al. 2011). Waters with salinity below 23 PSU were identified as Unlikely to facilitate *D. vexillum*, waters between 23 and 27 PSU were designated as Possible *D. vexillum* habitat, while waters with salinity above 27 PSU were designated as Likely *D. vexillum* habitat.

Temperature and salinity surfaces were created for Southeast Alaska waters by interpolating across the 617 Alaska data stations using inverse weighted distance in ArcGIS. The surfaces were joined to suitable shoreline habitat features, and maps were created for each temperature and salinity scenario (Fig. 5). For the lowest limiting factor analysis, the temperature and salinity habitat maps were overlaid on each other and the habitat was designated as Very Unlikely, Unlikely, Possible, or Likely based on the lowest value of either temperature or salinity. For example, habitats with salinity in the Likely range but temperatures below 8 °C were classified as Very Unlikely based on the low temperature. Similarly, habitats with temperatures between 9 and 10 °C but salinity below 23 PSU were designated as Unlikely based on the low salinity (Fig. 6).

Results

Temperature and salinity data for locations where *D. vexillum* is currently found differed substantially from temperature and salinity data for much of Southeast Alaska. For the 35 worldwide locations that were analyzed, average summer water temperature was 16.5 ± 3.3 °C, and average summer salinity was 32.3 PSU ± 2.9 (Table 2). Average winter temperatures for these locations were 8.6 °C ± 3.7 with average salinity of 32.58 PSU ± 2.6. For infested locations in British Columbia, Canada, which are closest to Alaska, average summer temperatures and salinities were 14.9 ± 2.0 °C and 27 PSU ± 2.1, while average winter temperatures and salinity were 8.5 ± 1.1 °C and 28 PSU ± 1.4

In contrast, summer water temperatures in the study area ranged from 3.8 to 17.7 °C with an average of 10.2 ± 2.5 °C. The highest recorded surface water temperature was in Tenakee Inlet, an area with numerous warm springs. Low temperatures occurred throughout northern Southeast Alaska, especially in the inland channels inlets. Temperatures were generally warmer in southern Southeast Alaska near the Canadian border and along the outer coast. Comparing with minimum values for *D. vexillum* survival and growth from the literature, only 9 % of the sampling stations had summer temperatures below 8 °C, but nearly a quarter (22 %) of the stations had summer temperatures below 10 °C. Average summer temperature in Whiting Harbor was 13 °C. Summer salinity in Southeast Alaska varied from 3 PSU to 34 PSU with an average of 29 PSU ± 2.8. A third of the sampling stations had salinities below 23 PSU, while nearly half of all stations (48 %) had salinities below 27 PSU. Summer salinity in Whiting harbor was 32 PSU. Winter temperatures in Southeast Alaska were less variable than summer temperatures ranging from 2.5 to 6.5 °C with an average of 4.1 °C ± 0.5. Winter salinity ranged from a low of 8 PSU to a high of 33 PSU with an average value of 31 PSU ± 2.3.

The results of the SOM can be visualized by coloring map units based on the distance between each unit and its neighbors (Fig. 2). Units that are closer together are darker in color, while units that are farther apart are lighter. Thus, groups of lighter-colored units can be used to distinguish clusters in the data. By labeling units with the corresponding input vectors, it is easy to see relationships between the temperature and salinity characteristics of *D. vexillum*-infested sites. Dark lines between cells indicate cluster boundaries identified by using hierarchical clustering performed on the unit distance matrix. Clusters and cluster membership are also shown in Fig. 3. The contribution of each variable in the input data to the weight vector of each SOM unit can be visualized using a fan diagram (of Fig. 4).

The size of each blade on the fan is proportional to the magnitude of the variable in the corresponding SOM unit.

The moderate and low Alaska scenarios form their own cluster (Cluster 1) on the upper left of the map having temperature and salinity values lower than most of the other locations where *D. vexillum* is found. The Alaska Whiting Harbor site clusters with sites in Maine and Massachusetts (Cluster 2), which have very low winter temperatures, low summer temperatures and moderate winter and summer salinity. Cluster 3 is composed of locations from Washington State and BC, which are characterized by moderate winter and summer temperatures. Three of the BC sites have lower salinities than the other sites in this cluster. Cluster 4 is a small group of sites in the lower right corner of the map comprised of locations from New Zealand, Japan, Italy and California. These sites have larger temperature and salinity values than any other units. Cluster membership in this cluster appears to be primarily associated with high winter and summer salinity values and high winter temperatures. Units in the final cluster (Cluster 5) have relatively low winter temperature values, but high summer temperatures and high values of summer and winter salinity.

In the SOM modeling, Whiting Harbor was the only location in Alaska that clustered with other known locations where *D. vexillum* occurs, suggesting that locations in Southeast Alaska with moderate and low environmental conditions are at relatively low risk from *D. vexillum*

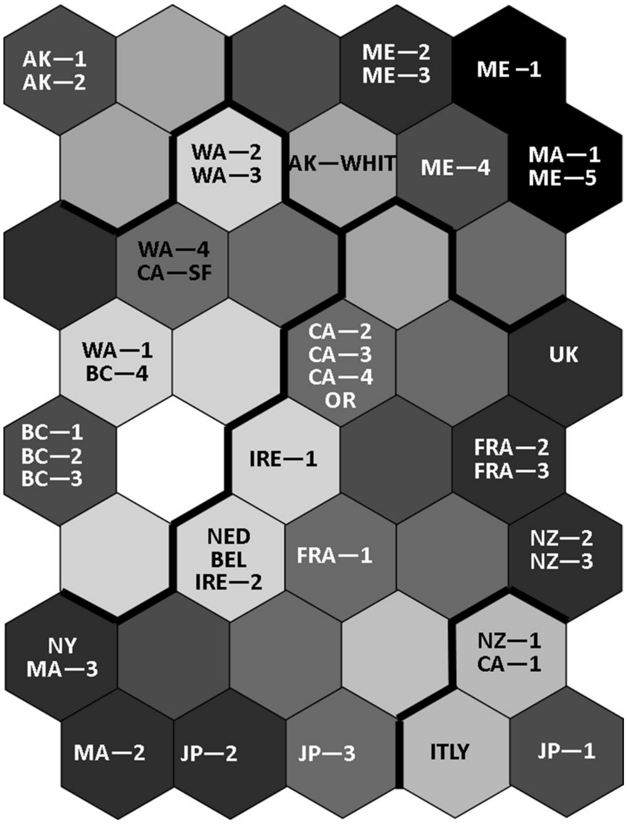

Fig. 2 SOM *shaded* to show distances between units. *Dark lines* denote cluster boundaries. Description of abbreviations is given in Table 1

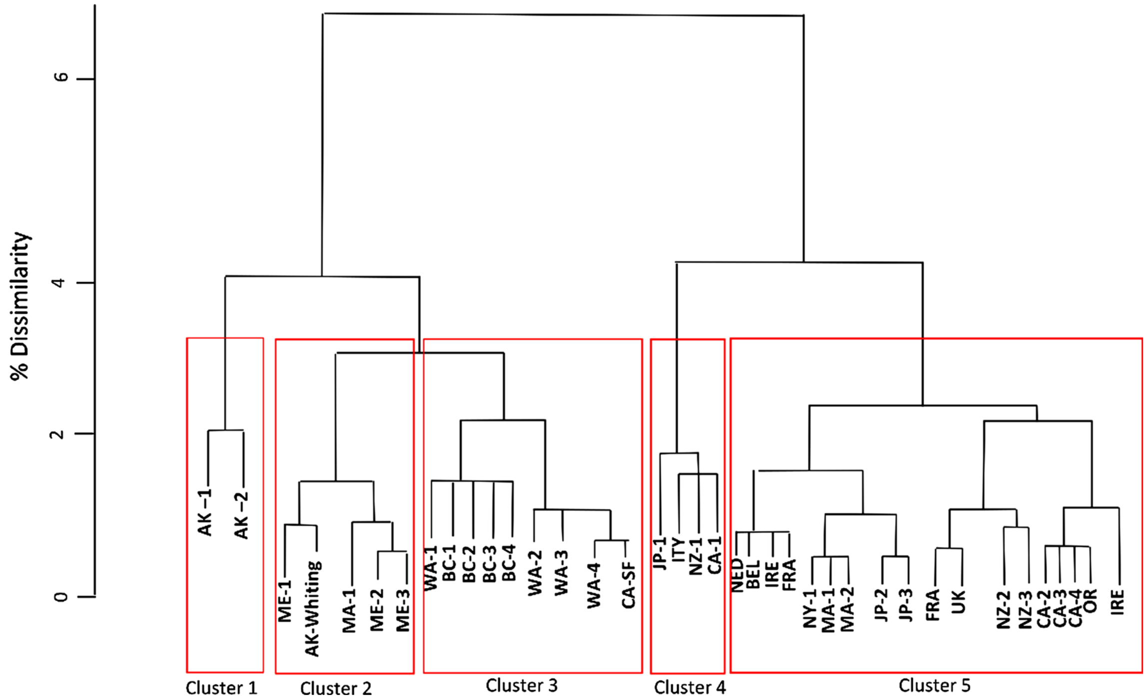

Fig. 3 Clusters and cluster membership. Description of abbreviations is given in Table 1

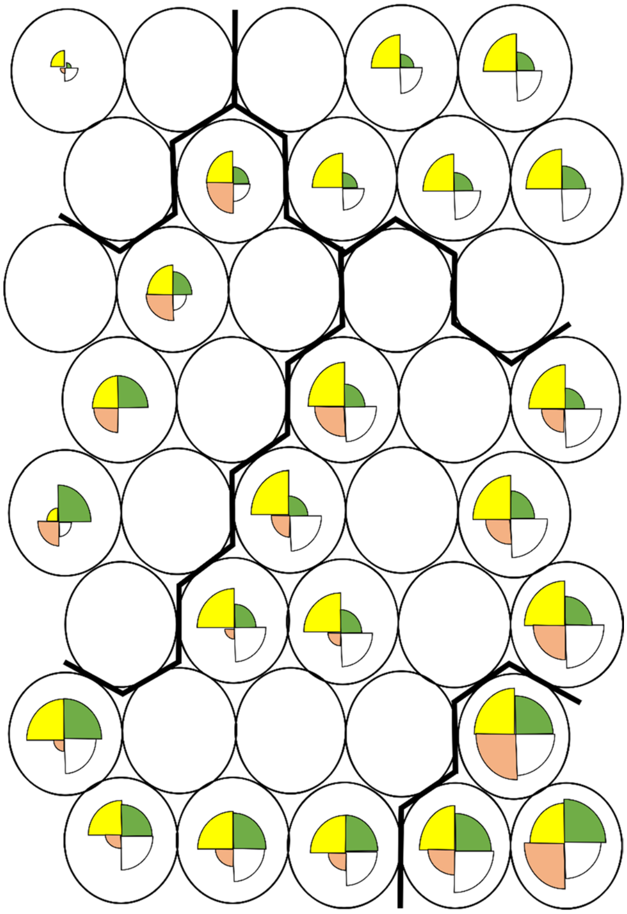

Fig. 4 Fan diagram showing magnitude of variables in each SOM unit. *Green* summer temperature (°C), *yellow* summer salinity, *orange* winter temperature (°C), *white* winter salinity

infestation. However, the average temperature and salinity values used in the SOM may not accurately represent the extreme environmental conditions in some locations where *D. vexillum* has been documented. To develop a broader assessment of risk than shown by modeling alone, potential habitat maps were created in ArcGIS™ by evaluating the presence of suitable substrate with *D. vexillum* temperature and salinity tolerance ranges from the literature. These maps show the most likely habitat for *D. vexillum* occurring in southern Southeast Alaska adjacent to the border with BC and along the outer coast (Fig. 6). Areas that are least likely to provide habitat are locations within Glacier Bay, in interior channels and fjords with large, often glacially fed, streams, and in the rain shadow of the interior mountains. Habitat suitability in the overall risk map is highly patchy with areas of low or moderate habitat interspersed with areas of potentially high vulnerability.

Discussion

The ability to develop accurate predictive maps of potential invasive species habitat requires detailed information on the habitat preferences and tolerances of the species in question. In the absence of species-specific data, it may be possible to rely on information on the habitats where the species is known to occur to evaluate the potential for spread to new locations. In the case of Southeast Alaska, conditions are much different in a large portion of the study areas than in currently known *D. vexillum*-infested locations. Since most of the shoreline in Southeast Alaska is composed of

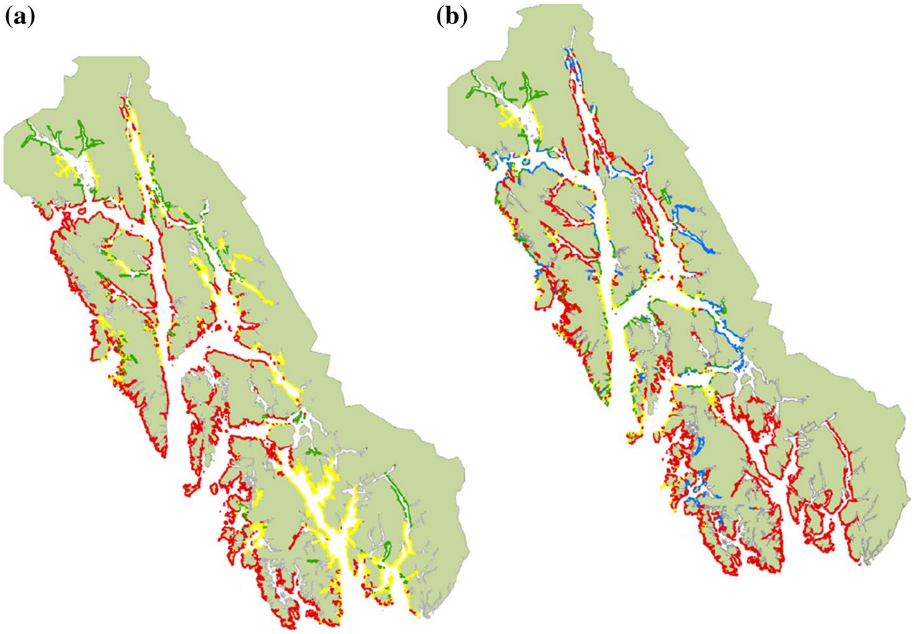

Fig. 5 Salinity (**a**) and temperature (**b**) risk maps. *Red* high potential (>10 °C or >27 PSU), *yellow* moderate potential (9–10 °C or 23–27 PSU), *green* low potential (8–9 °C or <23 PSU), *blue* very low potential (<8 °C), and *gray* no data

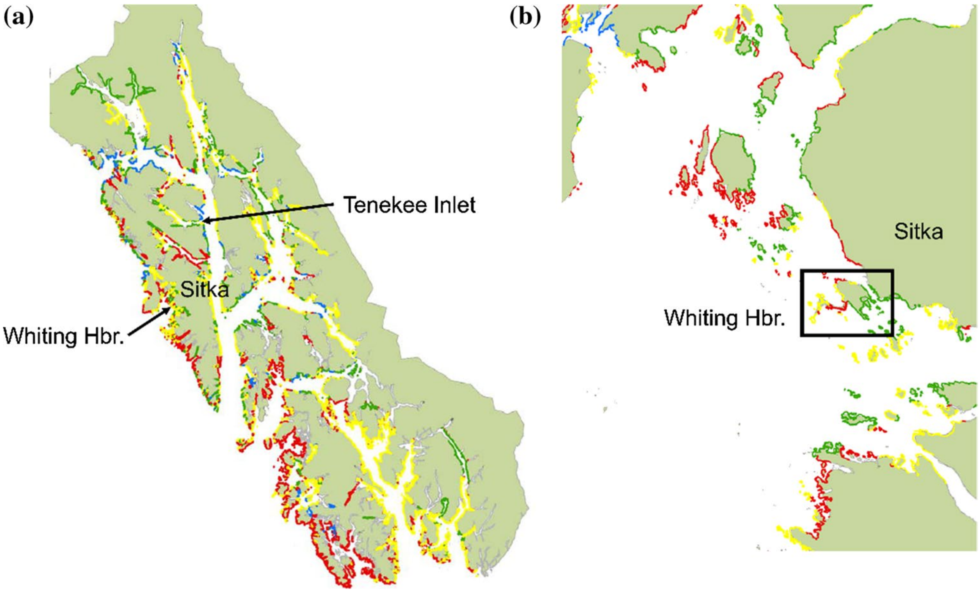

Fig. 6 Lowest limiting factor risk maps **a** for the region and **b** in the vicinity of Whiting Harbor, AK. *Colors* are the same as in Fig. 5

hard substrates, the analysis was primarily driven by the consideration of temperature and salinity. This research has shown that for much of Southeast Alaska, average summer and winter temperature and salinity values are substantially lower than average values in known locations of *D. vexillum* infestation. Only the high temperature and salinity Alaska scenario (Whiting Harbor) clustered with other known locations of infestation in the SOM model.

The risk maps accurately designated the area in Whiting Harbor as having a high potential to support *D. vexillum* under all three scenarios (Figs. 5, 6). In terms of the risk factors used in this analysis, Whiting Harbor has a number of features that make it susceptible to *D. vexillum* infestation. It is almost entirely composed of anthropogenic material that forms the Fort Rousseau Causeway. It has no source of freshwater input, which not only prevents dilution of the surface water but also limits cooling. Average summer temperature is approximately 13 °C, which is close to the optimal growth range for *D. vexillum* reported elsewhere (Gittenberger 2007; Daley and Scavia 2008). Finally, Whiting Harbor is somewhat isolated from the waters of Sitka Sound by a relatively shallow (15 m) sill in the entrance that likely inhibits exchange of water with the adjacent deeper (30 m) channel. This has the effect of increasing subsurface salinity and temperature.

While the conditions in Whiting Harbor are by no means unique in the region, they may not be representative of the majority of the coastline. In particular, the lack of freshwater is unusual in an area that is classified as a temperate rainforest. Annual runoff from Southeast Alaska to the coastal waters from precipitation has been estimated at 15,000 $m^3\ s^{-1}$ (Royer 1998), slightly less than the discharge from the Mississippi river. This estimate does not include input from rivers and streams, many of which are glacially fed. The density of streams for the land area surrounding Sitka and Whiting Harbor is shown in Fig. 7.

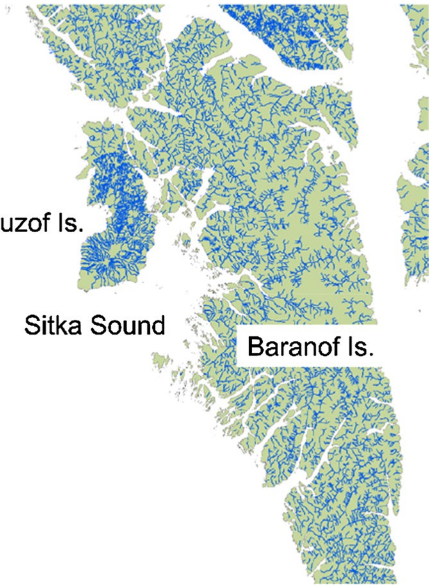

Fig. 7 Perennial streams in the vicinity of Sitka and Whiting Harbor, AK (USDA 2002)

Freshwater flow into the fjord-type bays that dominate this region results in a stratified surface layer, especially in fall and summer (Weingartner et al. 2009). This surface layer is approximately 15 m deep with salinities that vary spatially and seasonally from 0 at the head of the bay to between 28 and 31 PSU at the mouth (Weingartner et al. 2009). *D. vexillum* growth is arrested below salinities of 28 PSU (Bullard and Whitlatch 2009; Gittenberger 2010;

Gröner et al. 2011), and Gröner et al. (2011) observed a 20 % decline in survival for *D. vexillum* colonies held at 27 PSU and a 40 % decline in colonies held at 20 PSU for 2 weeks. The salinity data used in this analysis are primarily from offshore or mid-channel sampling stations, which may not accurately represent salinities closer to shore where *D. vexillum* is most likely to be found. This suggests that the patchwork nature of potential habitats is likely to be much higher at fine spatial scales due to the high density of input from coastal watersheds. In contrast to areas with higher salinity where *D. vexillum* has demonstrated explosive growth (Valentine et al. 2007b), new colonies of this species in Southeast Alaska may tend exist as small, isolated populations similar to the population in Whiting Harbor.

The outer coastal areas of Southeast Alaska, like Whiting Harbor, tend to have higher average surface temperatures than locations in the inner channels because of their proximity to the warmer ocean waters of the Gulf of Alaska. Average temperature at outer coast stations was 12 ± 1.9 °C compared with a regional average of 10.2 ± 2.5 °C. Observations of *D. vexillum* seasonal cycles indicate that the species begins to grow when temperatures are between 8 and 10 °C (Valentine et al. 2007b) with optimal growth occurring between 15 and 20 °C (Gittenberger 2007; Mccarthy et al. 2007). Based on the data used in this research, all of the worldwide locations where *D. vexillum* is currently resident have average summer water temperatures above 12 °C with the majority of them having average summer temperatures in excess of 15 °C. In Southeast Alaska, 83 % of the stations sampled had average summer water temperatures below 14 °C. Although we set the temperature for Likely *D. vexillum* habitat at 9 °C for the development of the risk maps, it is not clear whether this temperature would result in sustained growth of *D. vexillum* if it is the highest temperature that the water reaches during the year. *Didemnum vexillum* colonies in the inter and sub-tidal areas of the eastern USA begin to degenerate when fall or early winter temperatures reached 15 °C (Daley and Scavia 2008), suggesting that populations in areas with sustained lower temperatures may be marginal. This might partially explain the apparently lack of growth or expansion of the Whiting Harbor population, which may have existed since 2001 (Cohen et al. 2011). It also suggests that the lower temperature limit for sustaining populations of *D. vexillum* may be closer to 12 °C rather than the 8–10 °C at which existing populations begin to regenerate in warm water areas.

The moderate and low Alaska scenarios are differentiated from the known infestation areas by having a combination of low temperature and low salinity in both summer and winter. Maximum near-surface water temperature in the region is highest in mid-summer and lowest in spring. Salinity is lowest in August as a result of snowmelt and maximum near April when water temperatures are at a minimum (Danielson 2012). The risk maps in this research used average summer values, which represent the range of higher temperatures but lower salinities. Since salinity and temperature are out of phase, areas that provide marginal habitat for *D. vexillum* based on either temperature or salinity will tend to remain marginal as improvement in one variable through the seasons would be accompanied by a lowering of the other as the year progresses.

The synergistic or additive effects of combined low temperature and low salinity on this species have not been explored. In situ studies of low-temperature tolerance have all occurred at salinities above 28 PSU (Auker and Oviatt 2008; Carman et al. 2014) while evaluation of low salinity effects has occurred at temperatures above 15 °C (Bullard and Whitlatch 2009; Gröner et al. 2011). Synergistic or additive effects of multiple stressors have been demonstrated in *D. vexillum* (Ordóñez et al. 2015) and other invertebrates (Coles and Jokiel 1978; Anlauf et al. 2011; Thiyagarajan and Ko 2012), and it is possible that evaluating environmental factors separately may overestimate species resilience to extreme conditions. In the case of *D. vexillum*, stress from low or marginal salinity could reduce the species' ability to grow at temperatures at the lower end of its tolerance range, thereby diminishing the potential for explosive invasion. This analysis used the lowest limiting factor of temperature or salinity to create the final habitat risk map as if each factor was operating independently. How combined low temperature and low salinity might change habitat suitability cannot be evaluated at this time.

Using conditions within the known range of a species to predict future distribution does not necessarily take into account the entire range of conditions in which the species can occur and thrive. The existing distribution, or realized niche, is potentially much smaller than the fundamental niche, which includes all the possible conditions that affect species fitness (Tingley et al. 2014). For invasive species, movement to a new environment is generally facilitated through anthropogenic means. As a result, the realized niche may be more representative of the habitats conducive to the anthropogenic activity responsible for introduction than the conditions limiting species survival and growth. There is also the possibility that the niche for species introduced into a very new environment may shift or expand as the species adapts (Gallardo et al. 2013; Tingley et al. 2014; Parravicini et al. 2015). Phenotypic plasticity has been observed in tunicates (Grosberg 1988; Newlon et al. 2003; Bates 2005), and some studies have shown climate warming to be potentially advantageous to invasive tunicate populations (Dijkstra et al. 2011; Lenz et al. 2011). There has been no similar research on tunicate adaptation to cooler temperatures. In the absence of niche adaptation, climate warming could increase temperatures in the region to levels within the *D. vexillum's* thermal tolerance; however, warming projections for Alaska predict a 30–50 % increase in precipitation (UAF 2007), which could result in salinity decreases to levels below *D. vexillum's* salinity tolerance.

Despite the unknowns, this analysis provides a first look at where *D. vexillum* might establish in Southeast Alaska and gives managers information with which to prioritize invasive species surveys, education efforts and potential control measures. The sheer size and remoteness of the study area limit the ability to detect marine invaders, making predictive analyses such as these extremely important tools. When enhanced with site-specific environmental information, risk maps can guide management decisions on locating or permitting facilities such as dock, marinas, and shellfish farms, which are implicated in many *D. vexillum* introductions. As the literature on *D. vexillum* continues to evolve, it may be possible to refine this analysis using mechanistic modeling methods.

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