

Forecasting the potential distribution of the invasive tunicate *Didemnum vexillum*

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Summary

1. Invasive species are a major threat to global biodiversity and their introduction can have significant economic consequences. The invasive tunicate *Didemnum vexillum* is a notorious invader with significant negative impacts on cultured shellfish and natural benthic communities, including commercially important ones.

2. We conducted an expert survey, identifying the five most important transport vectors for *D. vexillum* along the west coast of North America. We determined the spatially explicit vector density for all vectors in order to identify introduction hotspots. Additionally, we developed an environmental niche model based on 46 occurrence points and nine environmental variables to identify areas suitable for *D. vexillum*.

3. Spatial distribution of the most important transport vectors (slow-moving vessels, aquaculture, fishing vessels, small vessels, and large commercial vessels) identified several hotspots with high vector densities. These proved to be a very good predictor of current *D. vexillum* occurrence in British Columbia (BC). Ecological niche modelling (Genetic Algorithm for Rule-set Prediction) predicted suitable environments in southern BC, parts of central BC and along the east coast of the Queen Charlotte Islands. Independent validation of the model based on the current distribution in BC indicated good predictive accuracy. Additional analytical steps confirmed that no environmental variable dominated the predictions and we identified ranges of environmental conditions predicted suitable by the model.

4. We identified areas of high establishment probability for *D. vexillum* by combining the vector model and environmental niche model. Parts of central BC, the west coast of Vancouver Island and the Strait of Georgia are areas where *D. vexillum* is most likely to establish.

5. *Synthesis and applications.* Spatially explicit predictions of the potential distribution of biological invaders are crucial for informing risk assessments, development of management strategies, and resource allocation. While most studies only focus on one step in the invasion process, we successfully combined the likelihood of introduction and establishment. Results from this study are informing the Canadian risk assessment of invasive tunicates, guiding current monitoring efforts, and providing a basis for potential intervention/mediation measures.

Key-words: Aquatic invasive species, *Didemnum vexillum*, environmental niche modelling, Genetic Algorithm for Rule-set Predictions (GARP), invasive tunicate, vector/pathway analysis

Introduction

Invasive species can have economic and ecological impacts on a global scale (Pimentel *et al.* 2000; Sala *et al.* 2000), and with increased global trade, the number of non-indigenous species

introduced into new locations continues to increase (Cohen & Carlton 1998; Ruiz *et al.* 2000). This poses a growing challenge for governments and conservation agencies to identify non-indigenous species that represent the greatest threat to the environment or economy, to allow focused management responses and efficient resource allocation. Predictive modelling of the series of filters a non-indigenous species must overcome (transport, survival, and establishment) to successfully establish and/or spread can inform management

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decisions based on the potential distribution of a new or recent invader.

Here we focus on the invasive colonial tunicate *Didemnum vexillum* Kott, 2002, a global invader that has spread to Europe (Gittenberger 2007), New Zealand (Kott 2004), and both coasts of North America (Bullard *et al.* 2007). On the east coast of North America the species is currently only found in US waters, including a 230-km² area on Georges Bank. Coverage is > 50% where it changes native benthic invertebrate communities (Bullard *et al.* 2007; Valentine *et al.* 2007b). On the west coast of North America it is found along the entire US coastline and into southern British Columbian waters, where it has been discovered recently (Bullard *et al.* 2007; Daniel & Therriault 2007). The species is a major concern for shellfish aquaculture because it grows on cultured mussels and oysters, potentially causing mortality and increased processing costs (Coutts & Sinner 2004; Bullard *et al.* 2007; Valentine *et al.* 2007b). Although a widespread invader in many marine environments, *D. vexillum* has a limited ability for natural dispersal since the pelagic larvae only remain in the water column for a short time; generally less than 1 day (Osman & Whitlatch 2007). Unlike some other colonial tunicate invaders, there is no information relating to the ability of this species to spread naturally by drifting on floating debris. Thus, human-mediated transport is the most important vector for long-distance dispersal (Svane & Young 1989; Osman & Whitlatch 2007). The most likely transport scenarios are either the direct transport of colonies fouled on aquaculture equipment, boat hulls or other mobile structures or the indirect transport of colony fragments where small parts of a colony break off during transport or disturbance (e.g. dredging, trawling) and subsequently find suitable conditions for establishment and growth. *D. vexillum* tolerates a wide range of conditions including temperature, salinity, and water quality (Millar 1971; Lambert 2002; Lambert 2005a), allowing it to overgrow large areas of seabed (Valentine *et al.* 2007b) and subtidal communities where it often dominates (Valentine *et al.* 2007a). It readily fouls boat hulls, aquaculture structures, and cultured shellfish, making it a major concern for aquaculture operations (Valentine *et al.* 2007a). The ability of *D. vexillum* to overgrow cultured shellfish in New Zealand led to a failed eradication attempt after a cost–benefit analysis indicated a significant economic impact on this industry (Coutts & Forrest 2007).

The likelihood of transport of a non-indigenous species like *D. vexillum* to a new location can be predicted by the spatial distribution and frequency of vector traffic, and has been used to identify high-risk areas for aquatic invasions via ballast water (Drake & Lodge 2004), boat trailering between freshwater lakes (MacIsaac *et al.* 2004), and coastal small craft traffic (Floerl & Inglis 2005; Floerl *et al.* 2009). Once the non-indigenous species arrives in a new location, survival and establishment are the next steps in the invasion process. Ecological niche modelling has been used successfully to identify suitable environments for a variety of invaders, based solely on occurrence data and relevant environmental variables. Recent studies have used this approach to predict the

potential distribution of Asian longhorn beetle (*Anoplophora glabripennis*; Peterson & Vieglais 2001), zebra mussels (*Dreissena polymorpha*; Drake & Bossenbroek 2004), and Asian carp and snakehead fishes (Herborg *et al.* 2007b). It is particularly suited to species like *D. vexillum* for which there is limited biological information. Among the continuously evolving methods of ecological niche modelling (Guisan & Zimmerman 2000; Elith *et al.* 2006), the Genetic Algorithm for Rule-set Prediction (GARP) has been used widely (Peterson & Vieglais 2001). While GARP's performance was deemed moderate compared with other methods (Elith *et al.* 2006), several recent studies have tested GARP's predictions of invasive ranges with independent data sets and found high predictive accuracy (Iguchi *et al.* 2004; Herborg *et al.* 2007c), suggesting this approach is more effective than initially thought. Despite the widespread use of models predicting potential distributions based on vector data or suitable habitat, rarely have both approaches been combined (Herborg *et al.* 2007a).

Here we present a spatially explicit prediction for the potential distribution of *D. vexillum* along the coastline of British Columbia (BC). We used the spatial distribution of five potential transport vectors in BC waters to predict dispersal pathways. Suitable environments were identified using environmental niche modelling based on occurrence data from the west coast of North America together with nine environmental variables. By overlaying both predictions, we identified potential hotspots for future establishment of *D. vexillum* in BC waters.

Materials and methods

SPECIES DISTRIBUTION DATA

We compiled 46 occurrence reports for *D. vexillum* along the west coast of North America (Valentine 2003; Cohen 2005; deRivera *et al.* 2005; Lambert 2005b; Bullard *et al.* 2007; Daniel & Therriault 2007). Since the taxonomy of this genus has long been uncertain (see Daniel & Therriault 2007) and the species of *Didemnum* invading North America has just been confirmed as *D. vexillum* (Stefaniak *et al.* 2008), we considered all reports for what used to be labelled *Didemnum* sp. or *Didemnum* sp. A in this study. All points were geo-referenced and entered in a data base.

EXPERT SURVEY

Since the literature on natural and human-mediated dispersal for *D. vexillum* is limited, we conducted an expert survey via an online questionnaire. This survey was sent to 520 experts and three mailing lists associated with either tunicates or invasive species (Therriault & Herborg 2008). Each expert was asked for their level of expertise: species-specific, group-specific (colonial tunicates vs. solitary tunicates), or tunicates in general. Based on their reply, the questionnaire prompted them with questions regarding the importance of 10 potential vectors for dispersal including: larval drift, dispersal of adults attached to flotsam, ballast water, movement of aquaculture gear and stock, fragments in fishing gear, releases from private or public aquaria, intentional release to establish a food source, hull fouling on slow-moving barges, and hull fouling of large (> 50 m) or small (< 50 m) vessels. Respondents were asked to provide an

Table 1. Definitions of the importance of transport vectors provided in the expert survey

Vector importance	Definition
Very low	Tunicates have not been demonstrated or believed to utilize this vector; does not require management
Low	Tunicates are unlikely to spread by this vector. May require efforts to minimize spread
Moderate	Tunicates can spread by this vector in favourable circumstances. Management could provide a reduction of spread
High	Tunicates have extensively used this vector. Management would be important for a reduction of spread, but none has been attempted
Very high	Tunicates have extensively used this vector despite extensive management efforts

estimate of importance (very low, low, medium, high, and very high) for each vector and the uncertainty associated with their reply. Definitions were provided for vector importance (Table 1). However, the questionnaire did not ask for a separate estimate of vectors for primary introduction and secondary dispersal. Due to the limited knowledge of *D. vexillum* dispersal pathways, the reason for conducting this survey in the first place, such a separation would most likely have provided limited additional information.

VECTOR DATA

The spatial distribution for all shellfish and finfish aquaculture leases and processing plants along the BC coast were based on geo-referenced data provided by the BC Government. Distribution of small craft traffic was estimated using locations of ports, small craft harbours, marinas and anchorages in BC. The distribution of commercial vector traffic was based on the location of vessels monitored by the Canadian Marine Communications and Traffic Services for 2003. The location and type of each vessel destined for a Canadian port within the Canadian Economic Exclusive Zone was recorded every 4 min (O'Hara & Morgan 2006). The data were separated according to reported vessel type (fishing vessels, slow-moving vessels such as tugs and barges, and all other commercial traffic).

Geo-referenced point data for the potential vectors were transformed into density maps using Spatial Analyst in ArcMAP 9.1 (ESRI), creating a continuous surface for the whole study area indicating areas with relative higher densities (hotspots) for each vector. All resulting density layers were standardized on a scale from 0–1 before further processing. We limited all our analysis to BC coastal waters within the 200-m depth contour as *D. vexillum* has not been reported beyond this depth.

VECTOR RISK MAP

Based on the results of the expert survey, a vector-based map of introduction risk was generated. We received 132 responses to our survey with 28 to 30 respondents answering questions specific to *D. vexillum*. Spatial density maps for the five most important vectors, slow-moving vessels, aquaculture, fishing vessels, small vessels, and commercial vessels, were each standardized on a scale between 0–1. Of the 10 potential vectors identified initially, we included the top five in subsequent analyses, and we compiled spatial data for each of these vectors. The risk associated with each transport vector as identified by the *D. vexillum* experts was converted into ordinal values (very low = 1, low = 2, medium = 3, high = 4, very high = 5) and a mean was calculated. Each of the five vector density maps were then multiplied by the mean risk value for each vector type, weighing the different vector types by the risk estimates provided by the experts ('Spatial Analyst' extension in ArcMAP 9.1). The resulting five

weighted vector risk maps were then summed together for the final vector risk map using the same tool.

OCEANOGRAPHIC DATA

We extracted salinity, temperature and dissolved oxygen data from the NOAA World Ocean Database (<http://www.nodc.noaa.gov/OC5/indprod.html>) to a depth of 50 m, based on the species occurrence from subtidal to deeper waters (Valentine *et al.* 2007a,b). Salinity and temperature data were divided into four seasons based on sampling month (January–March, April–June, July–September, October–December) using Ocean Data View 3.2.0. Seasonal salinity and temperature, and annual oxygen data were converted into a continuous data layer by calculating the mean value of each variable over the 50-m depth using inverse distance weighting (Geostatistical Wizard within ArcMAP 9.1). Annual surface chlorophyll *a* data were obtained from the 'Integrating Multiple Demands on Coastal Zones with Emphasis on Aquatic Ecosystems and Fisheries' project (<http://www.incofish.org/>). Due to data paucity, only annual (rather than seasonal) oxygen and chlorophyll *a* could be included in the predictions. The resulting 10 environmental layers: January–March temperature, April–June temperature, July–September temperature, October–December temperature, January–March salinity, April–June salinity, July–September salinity, October–December salinity, annual oxygen, annual chlorophyll *a*, all at 0.01° resolution, were then compared with occurrence data for *D. vexillum* using an environmental niche model.

ENVIRONMENTAL NICHE MODEL

We predicted potential suitable environments based on the current distribution of *D. vexillum* along the west coast of North America using the GARP model (Stockwell & Peters 1999) based on 10 environmental variables (above) and 46 occurrence points on the west coast of North America. An initial GARP model using all possible combinations of environmental variables allowed us to determine the effect of each variable on model accuracy. Only environmental variables that had a significant negative correlation ($P < 0.05$, multiple linear regression) with omission errors (false negatives, or negative predictions of occurrence points) were included in the final model (Drake & Bossenbroek 2004). All variables except annual surface chlorophyll *a* fulfilled this criterion and were used in the final prediction model that was run using a maximum of 1500 iterations and a 0.001 convergence limit following the best subset approach (Anderson, Lew & Peterson 2003). This method uses a < 5% rate of false negatives or omission errors and < 50% of false positives or commission errors to select 100 predictions fulfilling these criteria. These final predictions were then combined into a single environmental suitability map using ArcMAP 9.1.

Table 2. Results of an expert survey on the importance of a range of vectors to the spread *D. vexillum*. The five vectors with the highest importance for tunicate dispersal are highlighted in bold. Responses for vector importance were ranked as: very low = 1, low = 2, medium = 3, high = 4, very high = 5

Potential vectors	Vector importance	Numerical vector risk \pm standard deviation
Natural larvae dispersal	Moderate	2.83 \pm 1.26
Natural adult dispersal by drift	Moderate	3.27 \pm 1.08
Ballast water release	Low	2.28 \pm 0.92
Hull fouling large vessels (> 50 m)	Moderate	3.44 \pm 0.85
Hull fouling small vessels (< 50 m)	High	3.57 \pm 1.07
Hull fouling slow moving vessels	High	4.39 \pm 0.69
Aquaculture transfers	High	4.18 \pm 0.77
Commercial fishing	High	3.59 \pm 0.95
Aquarium releases	Very low	1.44 \pm 0.65
Intentional releases to establish a food source	Very low	1.12 \pm 0.43

We included two additional analytical steps into the environmental niche modelling process to increase transparency. Hierarchical partitioning identifies the contribution of each environmental variable to prediction accuracy in the final model (Peterson & Cohoon 1999). Here, the contribution of each environmental layer included in the final model to increase prediction accuracy is tested in additional GARP predictions using all possible combinations of environmental layers. Environmental strips determine the actual range of each environmental variable predicted suitable by the model. This method is based on the insertion of columns containing 100 increments of the full range of values for each environmental layer into a test section of the environmental coverage file. The number of models that predict each particular value of each variable range as suitable gives an indication at the suitable range for each environmental variable (Elith *et al.* 2005).

TEST VALIDATION

As an independent test of model performance, we included an Area Under the receiver operator Curve (AUC) calculation (Hanley & McNeil 1982) for the environmental niche model and the vector distribution model. This widely used test for environmental niche models (Wiley *et al.* 2003; Elith *et al.* 2006) compares the predicted environmental suitability or vector density for *D. vexillum* reports with an equal number of random points within the analysis area. If the AUC value is 0.5 or lower, the model does not predict *D. vexillum* occurrence better than the random points, while if it is above 0.5, the prediction is increasingly accurate, with 1.0 representing a perfect model. We calculated the AUC using the 'verification' package within the R software package, version 2.5.0 (R Development Core Team 2008).

OVERALL RISK MAP

The environmental niche model predictions and the vector model were combined into an overall risk map to identify where *D. vexillum* could be introduced and subsequently survive and establish. The vector risk prediction was converted to the same scale as the environmental niche model (0–100) to assure equal weighting of both variables. The overall risk map was determined by multiplying the environmental niche model output with the adjusted vector model output using the Spatial Analyst extension within ArcMap 9.1.

Results

VECTORS

We received 132 completed surveys, of which 28 identified themselves as *D. vexillum* experts. Since the risk predicted for each vector by respondents with different levels of expertise was within one category for all vectors, additional analysis were based on responses by self-identified *D. vexillum* experts. They identified the five vectors with the highest potential for future dispersal of *D. vexillum* as slow-moving vessels, aquaculture, fishing vessels, small vessels, and commercial vessels (Table 2). Each of these vectors was judged to have a high or moderate risk associated with them (risk value of 3.44 or greater, where moderate = 3 and high = 4). The uncertainty associated with these rankings was low with the exception of fishing, where uncertainty was deemed moderate. Of the other potential dispersal vectors included in our survey, natural larval dispersal and drift of adult colonies were predicted to have the next lowest risk (both moderate), followed by ballast water which was classified as low risk. Aquarium releases and intentional releases of this species were considered to pose a very low risk as a potential vector of introduction by our expert survey.

Spatially explicit vector risk was unevenly distributed along the BC coastline (Fig. 1). Aquaculture-associated activities were concentrated in the Strait of Georgia and Johnston Strait between Vancouver Island and the mainland, and to a lesser extent in inlets along the west coast of Vancouver Island. Very few aquaculture facilities exist along the central and northern coastline of BC. Small craft traffic was also concentrated in these areas, but indicated potential vectors to the less populated central and northern coasts of BC, including the Queen Charlotte Islands. Slow-moving vessels and fishing vessels were mainly concentrated in the Strait of Juan de Fuca, Johnstone Strait and the Strait of Georgia, as well as parts of the 'inside passage'; a series of channels and passages that provides a relatively protected route through the central coast region of BC between southern and northern waters. Very

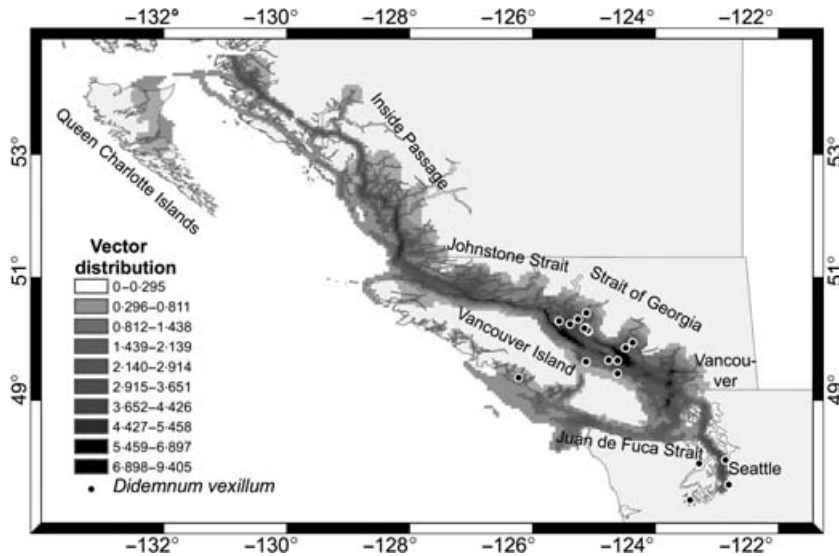


Fig. 1. Risk of *D. vexillum* transport along the BC coastline. The vector density combines aquaculture sites, recreational boating facilities, and the movements of slow-moving vessels, fishing vessels, and large commercial vessels. Each vector is weighted according to its potential to carry *D. vexillum*. Black dots represent current locations with *D. vexillum*.

Table 3. Hierarchical partitioning of the environmental niche modelling quantifies the contribution of each environmental variable to model accuracy. The environmental suitability range predicted by the model represents the conditions which were predicted as most suitable for each variable

Variable	Hierarchical partitioning (%)	Environmental suitability
January–March temperature (°C)	13	5–13
April–June temperature (°C)	5	22–31
July–September temperature (°C)	3	11–15
October–December temperature (°C)	11	8–14
January–March salinity (‰)	17	23–34
April–June salinity (‰)	15	10–15
July–September salinity (‰)	13	23–33
October–December salinity (‰)	17	22–33
Annual dissolved oxygen (mL L ⁻¹)	6	4.1–5.6

limited traffic occurred around the Queen Charlotte Islands or along the northwest coast of Vancouver Island (Fig. 1). This could represent under-sampling due to limited radar facilities in these locations or limited use of these areas by vessels as these are not major shipping or fishing areas. Other commercial traffic was concentrated between Vancouver and Seattle and through the Strait of Juan de Fuca into the Pacific Ocean, while few ships travelled the northern BC coastline. The combined vector risk map identified the Strait of Georgia and Johnstone Strait as the areas with the highest risk, followed by parts of the inside passage along the central BC coastline. The combined vector risk map predicted known *D. vexillum* reports in BC waters very successfully (AUC = 0.9246, $P < 0.001$), with a mean vector risk extracted for each occurrence point of 3.165 (SD = 1.882).

ENVIRONMENTAL NICHE MODELLING

Environmental niche modelling predicted high environmental suitability in the Strait of Georgia and along the west coast of Vancouver Island (Fig. 2). Medium to high environmental

suitability was forecast both for nearshore and offshore waters in central BC and around the Queen Charlotte Islands. The Strait of Juan de Fuca and Johnstone Strait were predicted as environmentally unsuitable. The environmental niche model performed very well (AUC = 0.757, $P < 0.001$). Environmental variables contributed relatively evenly to test accuracy (Table 3) with the most important variables being October–December salinity, January–March salinity, and April–June salinity. January–March temperature and October–December temperature also were important. In contrast, annual dissolved oxygen concentrations and April–June and July–September temperatures had limited (but significant) contributions. Based on the evaluation strips, the suitable ranges for *D. vexillum* included temperatures between 5–31 °C and salinities from 10–33‰, regardless of season (Table 3).

OVERALL RISK MAP

A combination of vector traffic and environmental suitability identified three main areas of higher risk for future invasion by *D. vexillum* along the BC coastline (Fig. 3). The primary

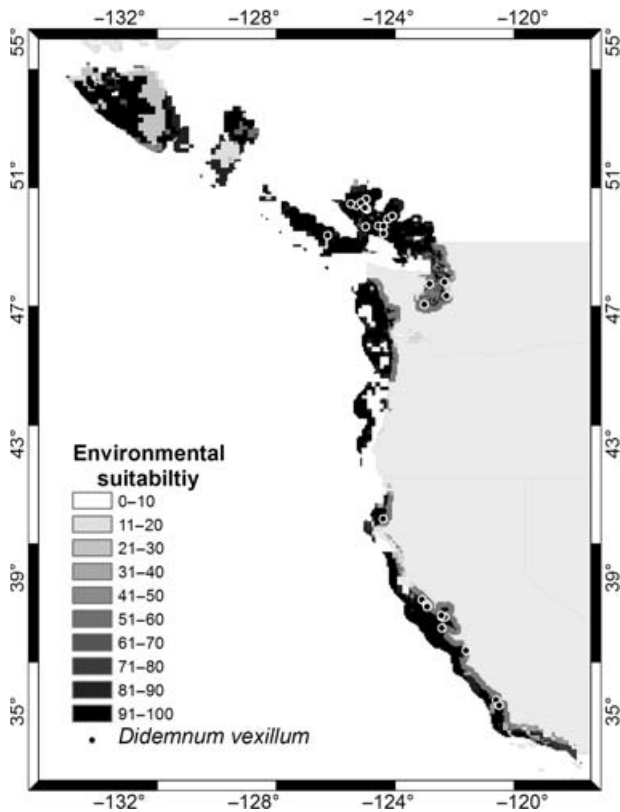


Fig. 2. Environmental niche model for *D. vexillum* based on its current distribution on the west coast of North America. Environmental suitability is presented as the cumulative result of 100 separate niche models. Black dots represent current locations with *D. vexillum*.

hotspot is the Strait of Georgia and Puget Sound where most *D. vexillum* has been found. Another area at higher risk is part of the central BC coastline including a section of the inside passage. The third hotspot is along the east coast of the Queen Charlotte Islands in the shallower waters of Dogfish Bank.

Discussion

VECTORS

A spatially explicit vector risk analysis predicted the current distribution of *D. vexillum* with a high level of accuracy in BC. Whereas most predictions of marine transport as potential vectors for species introductions just consider a single pathway (Drake & Lodge 2004; Floerl & Inglis 2005), we were able to include the five most important transport vectors potentially responsible for dispersing *D. vexillum* within BC waters using an expert survey to inform our decision making. These five vectors represented 50% of those considered in our survey, and are the ones most likely to spread invasive tunicates. The vectors not included in the model each had a lower risk of transporting tunicates. While adult colonies of some tunicates can be found attached to floating material, the probability that they sink into in a suitable environment is limited, especially

for strictly subtidal species such as *D. vexillum*. In addition, the short larval dispersal period of *D. vexillum*, generally lasting only a few hours (Osman & Whitlatch 2007), makes dispersal via this pathway or through ballast water release unlikely. There are no reports of *D. vexillum* being present in the aquarium trade, or seafood trade, making aquarium releases and intentional releases to establish food sources unlikely introduction pathways.

This survey made use of the knowledge of a large number of experts that would have been unavailable otherwise. This approach has become a common tool for conducting invasive species' risk assessments (Pheloung, Williams & Halloy 1999) where published literature on transport vectors for these organisms is limited. Of the few existing reports on transport vectors, all agree with our survey results, identifying barges (Courtts & Forrest 2007) as a key vector. Hull fouling of small and large vessels, as well as aquaculture-related movements are other high-risk vectors (Dijkstra, Harris & Westerman 2007), while ballast water is of lesser importance due to the very short larval phase of *D. vexillum* and its limited tolerance to siltation (Lambert & Lambert 1998; Lambert 2005a).

ENVIRONMENTAL NICHE MODELLING

Environmental niche modelling is a useful tool in invasion biology, especially for species like *D. vexillum* where information is limited. While there are some reports on thermal tolerances for the species on the east coast of North America and in Europe, the ongoing taxonomic debate confounds species identification and associated tolerances. Hence, we based the predictions here only on the current distribution along the west coast of North America, clearly representing the absolute minimum of its potential range; the area of suitable environments will increase as the invaded range expands. While our risk model will most probably result in an underestimation of potentially suitable environments, we chose this conservative approach for several reasons. The taxonomy of the species remains unresolved, making the use of other invaded ranges to predict the west coast distribution questionable due to potential species-specific differences in tolerances. Additionally, the extent of its presumed native range remains uncertain, and thus, it is not possible to predict a potential invaded range using this approach (Bullard *et al.* 2007).

Environmental niche modelling is becoming more widespread as a tool in invasion biology (e.g. Peterson & Vieglais, 2001; Iguchi *et al.* 2004; Herborg *et al.* 2007b; Therriault & Herborg 2008), helping to identify the potential range of an invader and allowing prioritization before an introduction. Environmental niche models are sometimes criticized as a 'black box', but by incorporating additional analytical steps like hierarchical partitioning and environmental strips, predictions become more transparent. Hierarchical partitioning identifies the contribution of each oceanographic variable to the final prediction, thereby providing a safeguard against predictions where a single variable determines the final result. In our model, six environmental variables contributed

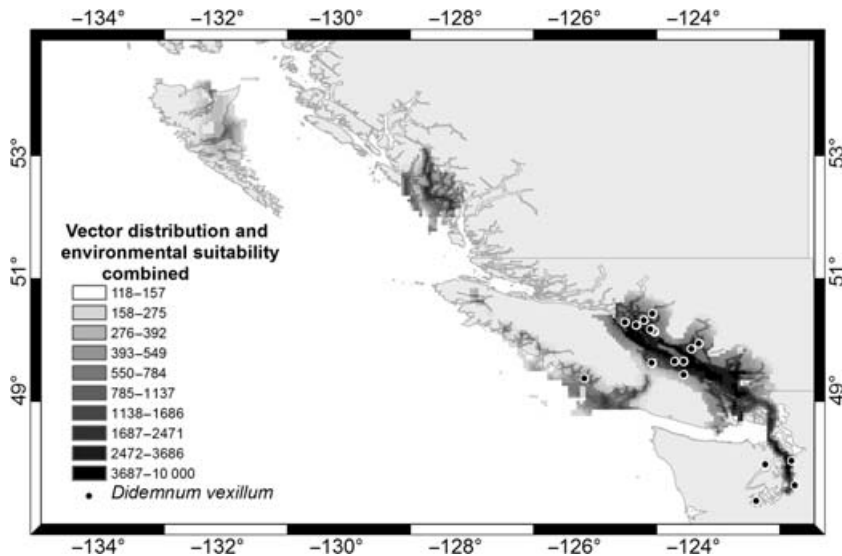


Fig. 3. The overall risk of *D. vexillum* introduction to a particular area, based on the combined risk of vector density and environmental suitability (Figs 1 & 2). Black dots represent current locations with *D. vexillum*.

between 11–17%, indicating an even contribution among variables to the final prediction. The evaluation strips method (Elith *et al.* 2005) provides further insight into the ranges of different environmental tolerances extracted by the model. The temperature limits predicted by our models (5 to 31 °C) were similar to reported thermal tolerances based on field observations of 1 to 24 °C (Lambert 2005a; Valentine *et al.* 2007a) and observations of colony degeneration below 4 °C (Gittenberger 2007). The similarity between the environmental strip results and other studies provides support for the accuracy of this model. The salinity tolerances for all seasons were within the higher salinity requirements reported for this species, except April–June which indicated lower salinity levels (10–15‰) than previously reported in the literature (> 24‰) (Vázquez & Young 2000; Lambert 2005a). This discrepancy could be caused by the relatively low resolution of this environmental variable due to the density of available data and the large study area, causing low salinity areas in estuaries to lower the mean salinity of the entire pixel. While our model predicts successfully where *D. vexillum* could survive on a large scale based on salinity, temperature, and oxygen; light and hydrodynamics are also important variables in determining overall environmental suitability for tunicates (Lambert 2005a), but are not available at the spatial scale of this study.

OVERALL RISK PREDICTIONS

The overall risk map for *D. vexillum* in BC clearly highlights key areas at risk in the Strait of Georgia and central sections of the inside passage. By combining a measure of propagule pressure with predictions of suitable environments, we were able to forecast three main stages in the invasion process: arrival, survival/establishment, and subsequent spread. However, since our environmental suitability is based on the current distribution of *D. vexillum*, areas currently predicted to be unsuitable could actually be suitable for this species (see previous section on the conservative approach taken here).

Regardless, combining vector and environmental data to predict the future spread of invasive species is rarely done. One study used the volume of ballast water released and environmental suitability to predict the relative risk of mitten crab (*Eriocheir sinensis*) introductions into US ports (Herborg *et al.* 2007a).

CONTRIBUTIONS TO RESEARCH AND MANAGEMENT

Predictions incorporating the first three steps of the invasion process provide important information for managers and can guide future research. First, we were able to highlight that there are at least two sections of the BC coastline at high risk from future *D. vexillum* introduction. While *D. vexillum* is well established inside the Strait of Georgia, and is present on the west coast of Vancouver Island, it has not been reported from the predicted high-risk areas along the inside passage and the east coast of the Queen Charlotte Islands. In Canada, an Introduction and Transfers Committee assesses the risk associated with aquaculture-related movements among areas, thereby limiting the future risk of *D. vexillum* dispersal via this pathway. However, other key vectors such as slow-moving vessels remain unchecked and our research highlights the importance of determining the risk posed by hull fouling. This includes both commercial shipping activities such as barge movements in BC and recreational activities. It is important to characterize the movement of these vessels to estimate the likelihood of moving *D. vexillum* to un-invaded areas. Potential management options to reduce the risk of *D. vexillum* introductions by intercontinental or trans-oceanic commercial shipping should focus on hull fouling. For example, ship and barge hulls should be cleaned and treated with anti-fouling paint at certain intervals to reduce the probability of *D. vexillum* fouling on hulls and the overall risk of introduction.

In addition to informing management options, this study can be used to inform research and monitoring activities for *D. vexillum* and non-indigenous species in general. For

example, the predictions both of invasion hotspots based on vector data and environmental hotspots based on oceanographic data can provide guidance for establishing monitoring sites. We used the predictions generated in this study to identify sites where tunicate settlement collectors should be deployed to gather detailed distribution data for several species. Finally, our predictions of environmental suitability are providing direct input into a Canadian risk assessment of invasive tunicates, assessing the likely distribution and spread of five species, including *D. vexillum* along both the east and west coast of Canada.

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