

Effects of spatial resolution on predicting the distribution of aquatic invasive species in nearshore marine environments

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ABSTRACT: The most appropriate range of spatial resolutions of environmental data with which to accurately delimit potential distributions of aquatic invasive species (AIS), in shallow nearshore marine environments, using species distribution models (SDM), is currently unknown. This study used SDM to determine the optimal range of spatial resolutions of temperature and salinity data with which to predict the potential distribution of vase tunicate *Ciona intestinalis* on the Canadian east coast and European green crab *Carcinus maenas* on the Canadian west coast. Both of these problematic AIS have spread rapidly in temperate nearshore coastal waters. As the invasion success of these species in temperate seasonal environments is constrained by temperature and salinity, we used SDM, specifically MaxEnt, to correlate these environmental variables at a range of spatial resolutions (100 km to 100s of metres, the latter encompassing 100 or 500 m² on east and west coasts, respectively) with both species' occurrence data. Increasing spatial resolution from 100 km to 100s of metres of temperature and salinity data generally resulted in more accurate estimates of each species' distribution, including a more realistic depiction of how salinity and temperature shape their distributions, with several caveats. First, increasing resolution of temperature and salinity data did not translate into proportional increases in model performance. Secondly, the highest resolution (100s of metres) did not result in the most accurate predictions of east coast *C. intestinalis* distribution. Finally, lower spatial resolutions (i.e. 100 km to 8 km resolution) performed worse in MaxEnt for west coast *C. maenas* than for east coast *C. intestinalis*. Overall, finer-resolution patchiness in each species' distribution was accurately resolved at or below spatial resolutions of 9 km for east coast *C. intestinalis* or 4 km for west coast *C. maenas*.

KEY WORDS: Spatial scale patterns · Species distribution · Nearshore · Risk assessment · Invasive species

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INTRODUCTION

Species distribution models (SDM) have broad utility in ecology, evolution, biogeography, and conservation (Graham et al. 2004, Peterson 2006), including predicting the potential habitat that could be invaded by non-indigenous species (Therriault & Herborg 2008a,b, Therriault et al. 2008, Jiménez-Valverde et al. 2011, Tyberghein et al. 2012). Despite widespread use in terrestrial environments, and more recently in

offshore marine environments (Robinson et al. 2011, Tyberghein et al. 2012), application of SDM in shallow (<10 m) nearshore marine waters remains relatively limited (Herborg et al. 2007, Hill et al. 2014, Marcelino & Verbruggen 2015). The choice of spatial resolution of environmental predictors likely has important implications for resolving suitable nearshore habitat using SDM (Mitchell et al. 2001), in part because different patterns emerge in spatial data at different spatial resolutions (Johnson et al.

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2002, Graham & Hijmans 2006, Basher et al. 2014) that in turn influence accuracy of predicted ranges and extrapolation into unsampled or uninhabited environments (Guisan et al. 2007, Song et al. 2013). The optimal range of spatial resolutions with which to predict the potential distribution of species in shallow nearshore marine environments has yet to be determined.

We consider 2 nearshore shallow-water marine aquatic invasive species (AIS) that have spread rapidly around the world's temperate oceans: the vase tunicate *Ciona intestinalis* on the Canadian east coast (Carver et al. 2006, Sephton et al. 2011) and the European green crab *Carcinus maenas* on the Canadian west coast (Grosholz & Ruiz 1996, Gillespie et al. 2007). Both species are considered problematic, as they disrupt benthic ecosystem structure and function (Grosholz & Ruiz 1996, Therriault et al. 2008), commercial fisheries (e.g. soft-shell clams in Maine in the case of green crabs; Carver et al. 2006), and aquaculture (e.g. blue mussel aquaculture in the case of vase tunicates; Robinson et al. 2005, Carver et al. 2006, Locke et al. 2009). The current study informs the development of risk assessments for nearshore AIS (Therriault & Herborg 2008a,b, Therriault et al. 2008), by determining the optimal range of spatial resolutions of environmental predictors to be used in SDMs.

Maps emphasizing areas of high to low probabilities of distribution (Phillips et al. 2004) generated in SDM may be used in AIS risk assessment (Therriault & Herborg 2008a,b, Therriault et al. 2008). In this application, SDM is used to delineate the multi-dimensional range of environmental conditions that predict the potential distribution within the modelled seascape. However, extensive spatiotemporal variability in the oceans can hinder SDM performance (Valavanis et al. 2008, Miller 2009), unless the spatial resolution of environmental predictors is of sufficiently high resolution to capture variations in these environments (heterogeneity) which influence species distribution (Davies & Guinotte 2011, Basher et al. 2014). Spatiotemporal variability is particularly acute in nearshore sheltered bays, estuaries, and fjords where important environmental drivers of AIS distribution (temperature and salinity) can vary over resolutions of 10s to 100s of metres, (the latter encompassing 100 or 500 m² on east and west coasts, respectively. If lower resolutions of environmental seascape data do not 'capture' this heterogeneity, species distributions will not be accurately resolved using SDM. This problem may be further exacerbated where offshore environmental data collated at

low spatial resolutions is extrapolated into nearshore coastal environments. Thus, to delimit suitable habitat in the nearshore, environmental data must be both of sufficiently high spatial resolution and representative of the actual nearshore environmental heterogeneity that influences the species living there.

The most appropriate range of spatial resolutions of temperature and salinity data with which to accurately delimit the potential distribution of nearshore AIS in SDM is unknown. We adopted a multifaceted approach to this problem by determining how spatial resolution of environmental predictors affects: (1) accuracy of predicted distributions, and (2) environmental tolerances derived from the relative contribution of predictors to model performance and resultant predicted temperature and salinity thresholds for species occurrence. In combination, accurately predicting a species distribution with well-understood environmental tolerances is required for AIS risk assessment (Pheloung et al. 1999). The availability of several environmental datasets (e.g. Tyberghein et al. 2012, M. E. Greenlaw pers. comm.), each with different spatial resolution, provided a unique opportunity to investigate the effect of spatial resolution on these evaluation metrics. We explicitly consider seasonal variations in temperature and salinity as predictors since the invasion success of both *C. maenas* and *C. intestinalis* in temperate seasonal environments is constrained by temperature thresholds for growth (Klassen & Locke 2007), reproduction (Carver et al. 2006), and survival (Carver et al. 2006, deRivera et al. 2007, Deibel et al. 2014), and salinity thresholds for survival (Klassen & Locke 2007, Vercaemer et al. 2011, Madariaga et al. 2014). Temperature and salinity are also known to affect the population dynamics of almost all marine organisms (Therriault & Herborg 2008a, Tyberghein et al. 2012). Thus, the results of our study have broader implications for delineating the potential distribution of organisms in shallow nearshore marine waters.

Application of SDM for AIS risk assessment is an evolving and rapidly advancing field (Therriault & Herborg 2008a). Our findings provide new insights as to choice of spatial resolution of temperature and salinity data to optimize predictions for AIS whose distributions are constrained by temperature and salinity in shallow nearshore marine environments. Ultimately, this information informs the development of risk assessment and cost-effective tools for monitoring and mitigation strategies (Deibel et al. 2014) that in turn can be used to manage the spread of AIS (Drake & Bossenbroek 2004, Therriault & Herborg 2008a,b, Therriault et al. 2008).

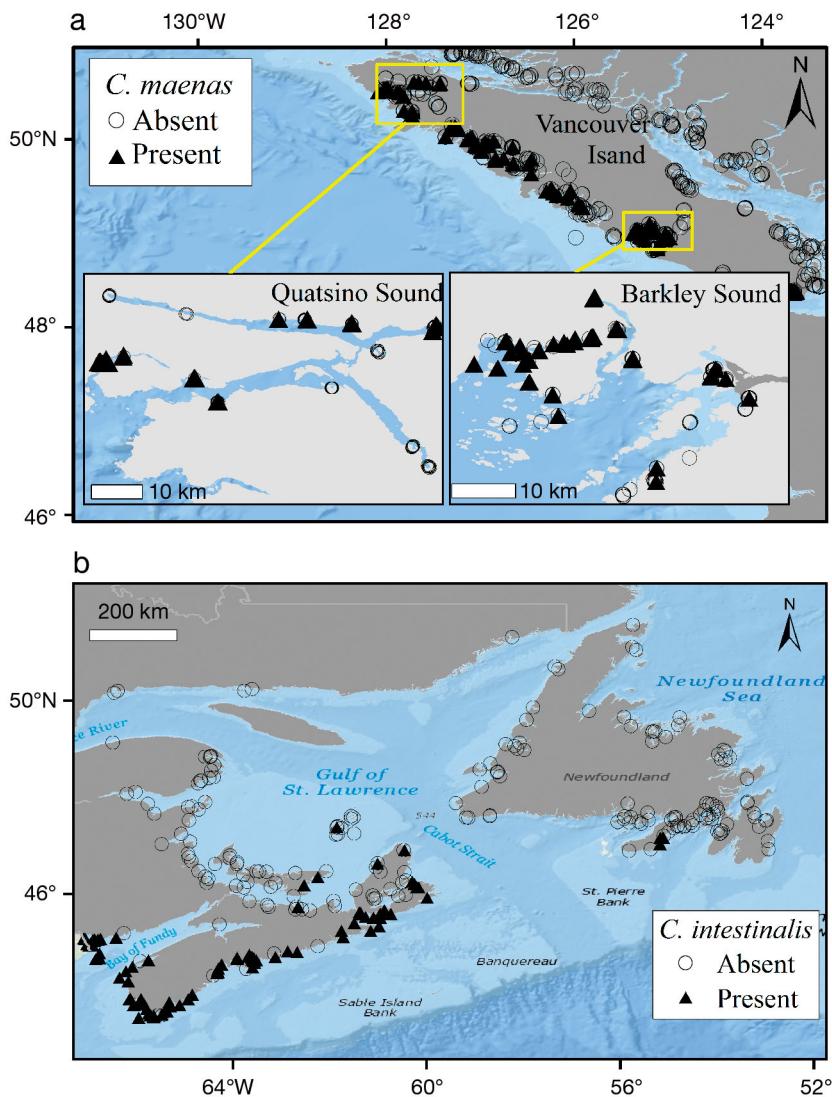


Fig. 1. Surveyed presence and absence locations for Canadian (a) west coast (*Carcinus maenas*) and (b) east coast (*Ciona intestinalis*)

MATERIALS AND METHODS

Species distributions

This area invaded by *Carcinus maenas* on the Pacific coast currently extends from San Francisco Bay, California, USA, to central British Columbia, Canada, where it has established populations on the west coast of Vancouver Island, Canada (Grosholz & Ruiz 1996, Gillespie et al. 2007). *C. maenas* occurrence data was collated from trap surveys conducted between 2007 and 2014 in British Columbia, Canada (Fig. 1). We used a subset of this occurrence data, collected during surveys of Barkley and Quatsino Sounds (Fig. 1). Survey locations were determined in

advance through examination of navigational charts and knowledge of preferred green crab habitat (Gillespie et al. 2007).

Ciona intestinalis is one of the most successful invasive species in marine systems worldwide, and is currently expanding its range northwards in the Northwest Atlantic (Carver et al. 2006, Sephton et al. 2011). It is currently found from Portland, Maine, USA, to Little Bay, in southern Newfoundland, Canada (Carver et al. 2006, Sargent et al. 2013, Deibel et al. 2014). *C. intestinalis* occurrence data was collated from the eastern Canada biofouling monitoring programme during 2006 to 2014 (e.g. Sephton et al. 2011, Simard et al. 2013) (Fig. 1).

Environmental predictors

We selected environmental variables that are known to affect the dynamics of almost all marine species and that are ecologically relevant to *C. maenas* and *C. intestinalis*, specifically temperature and salinity (Therriault & Herborg 2008a,b, Therriault et al. 2008, Madariaga et al. 2014). Environmental data layers were assembled at spatial resolutions ranging from 100s of metres to 100 km. Nearshore sea surface temperature (SST) and salinity data collected within 100s of metres of AIS survey locations on each coast from 2006 to 2014 (e.g. Sephton et al. 2011, Simard et al. 2013)

were used to generate environmental data layers interpretable to 500 m² or 100 m² spatial resolution on west and east coasts respectively (hereafter collectively referred to as 100s of metres spatial resolution). Environmental data layers (sea surface salinity and SST) interpretable at 1–100 km² resolutions were assembled from Level 3 climatological satellite data including NOAA's Advanced Very High Resolution Radiometer data (AVHRR) compiled by Fisheries and Oceans Canada for the east coast (www.bio.gc.ca/science/newtech-technouvelles/sensing-teledetection/index-en.php), or AquaModis Pacific Ocean Colour (accessed through the environmental data connector, <http://coastwatch.pfel.noaa.gov/EDC/index.html>, in ArcMAP 10.3) for the Canadian west coast, and global

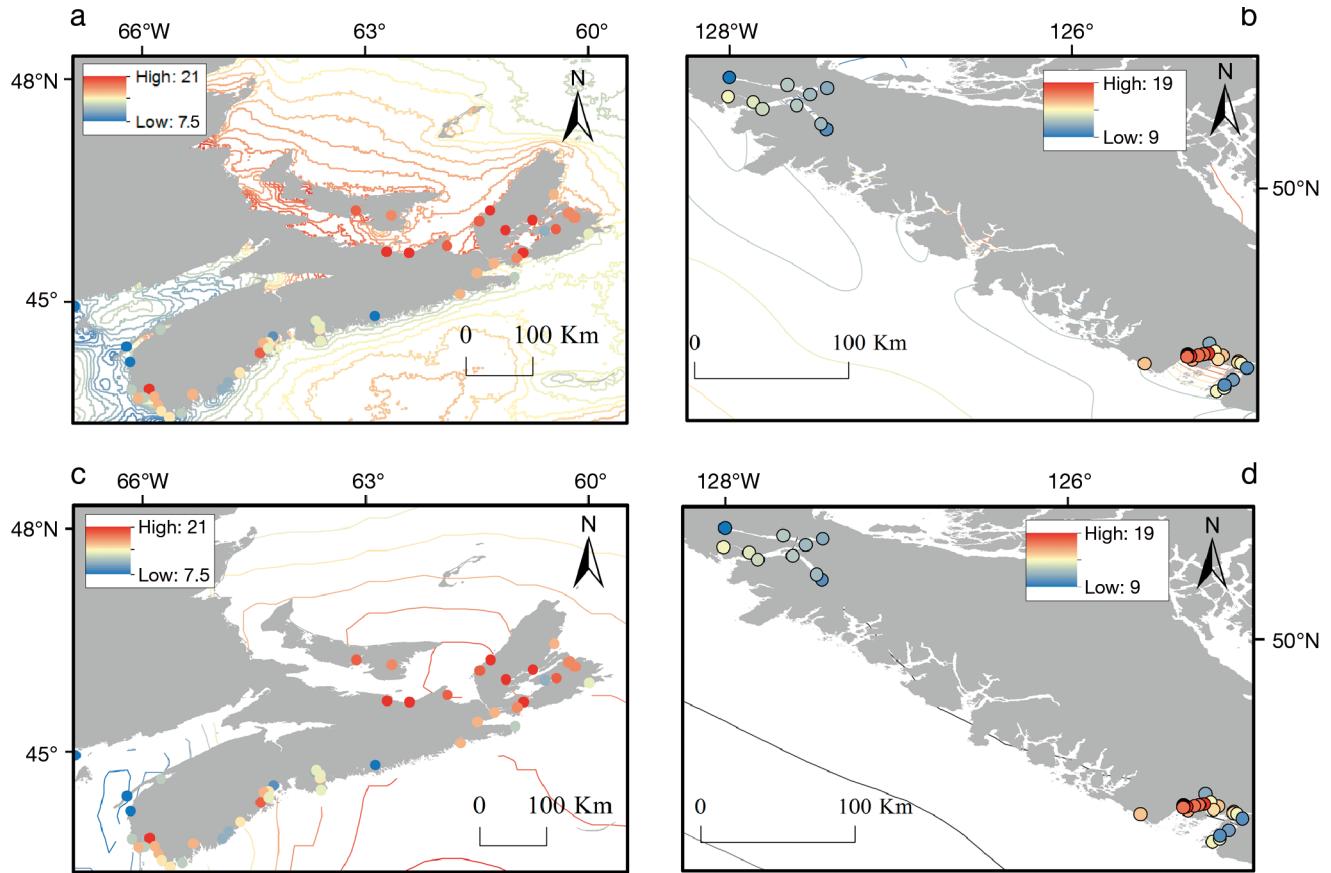


Fig. 2. Examples of differences in environmental topography (summer sea surface temperature [SST]) at lower and higher spatial resolutions for a subset of the species distribution models (SDM) domain on both the (a,c) east and (b,d) west coasts. In (a) and (b) 1 km (contours) and 100s of metres (circles) resolution summer SST is shown. In (c) and (d) lower resolution 25 km (contours) and 100s of metres (circles) resolution summer SST is shown

oceanographic climatological data composites compiled by Tyberghein et al. (2012) for both coasts.

At the highest resolution, temperature and salinity data from the west coast was converted to 4 seasonal climatological data layers, of 3 mo each (January–March, April–June, July–September, October–December). On the east coast, environmental data layers were generated as above using temperature and salinity data collected during June to October each year in tandem with AIS surveys, negating the possibility of generating seasonal data layers. At resolutions >1 km, predictor variables from the seasonal climatological composites of temperature and annual salinity collated above were upscaled (by resampling) from 1 km resolution to 8 other resolutions (2, 4, 6, 8, 16, 32, 64, and 100 km). If missing data cells were evident in our climatological composites, they were assigned the average value of 8 surrounding (nearshore) cells using the ArcGIS raster calculator during resampling. All resultant raster layers were converted to ASCII grid with WGS84 global stereo-

graphic projection and a uniform land mask applied. We also examined how poorer characterization of the nearshore environment influences predictive utility in SDM by extrapolating (25 km resolution) offshore seasonal temperature and salinity data (collated from the World Ocean Atlas 2013 v. 2 [WOA] (<https://www.nodc.noaa.gov/OC5/woa13/>) into the coastal zone using inverse distance-weighted interpolation. Differences in environmental topography using offshore data extrapolated into the coastline at 25 km resolution, versus 100s of metres and 1 km resolution are shown in Fig. 2. These differences (i.e. poorer characterization of the nearshore environment) at lower spatial resolutions are hypothesized to drive differences in prediction of suitable habitat.

Model fitting procedure and evaluation

SDMs mathematically predict the potential distribution of a species using various climatic and geo-

graphic variables (e.g. Phillips et al. 2006). A review comparing suitable habitat predictions from 16 different models on 200 taxa found that MaxEnt was preferable to presence/absence methods, where limited sampling may incorrectly classify absences (Elith et al. 2006). In our case, absences would be incorrectly classified if recently established AIS have not yet spread to suitable habitat.

The temporal (seasonal) component of this study reflects the inclusion of seasonal temperature and salinity as predictors or drivers of each species distribution in the same MaxEnt analysis (Phillips et al. 2004). This SDM predicts species distributional persistence within the seascape. For example, with unusually favourable temperatures, a species could spread, but not persist in a location. MaxEnt correlates species occurrence locations, often called presence-only data, and environmental predictors (here, seasonal temperature and salinity) within a user-defined seascape. From this seascape, MaxEnt extracts a sample of background locations which are contrasted against the presence locations to delineate the multidimensional range of environmental conditions that determine relative occurrence. Based on a species predicted ecological tolerances estimated from the environmental predictors, the final SDM map is produced by applying the calculated model to all cells in the study region, using a logistic link function to yield a relative probability of occurrence between 0 and 1 (Phillips et al. 2004).

We modelled each species distribution in MaxEnt 3.3.3k (<https://www.cs.princeton.edu/~schapire/maxent/>) (Phillips et al. 2004) at varying spatial resolutions (100s m to 100 km) for *C. maenas* and *C. intestinalis*, with each spatial resolution of seasonal temperature and salinity as predictors in consecutive runs for each model fitting procedure. Model domains encompassed the following spatial extents (in decimal degrees): latitude 46.01–56.00°N and longitude 122.30–133.00°W for west coast *C. maenas*; latitude 43.00–52.00°N and longitude 52.01–67.00°W for east coast *C. intestinalis*. As the number of occurrence records varied depending on spatial resolution, only linear, quadratic, and hinge features (Elith et al. 2011) were utilized for model fitting. The number of background points was set to 10 000. Maximum iterations in model runs were set to 1000 to allow for model convergence (Phillips et al. 2004).

Spatial autocorrelation (SAC) in occurrence data can inflate estimates of SDM performance (Dormann et al. 2007). Occurrence records were widely distributed (>100 000 km²) on both east and west coasts, which reduces the probability of SAC between

observations (Phillips et al. 2004, Mateo et al. 2010, but see also Fortin & Dale 2009). Surveys for both *C. maenas* and *C. intestinalis* were conducted such that the resultant occurrence records were not spatially clustered around areas that were easier to sample. Thus, sampling effort was relatively uniform across the seascape, further reducing the probability of SAC. Nonetheless, SAC, likely arising from clustering of samples around favourable habitat as determined by Moran's *I*-distance plot, was evident in the original distributional data.

A number of methods have recently been developed to address SAC in MaxEnt (reviewed by Dormann et al. 2007, Brown 2014, Muscarella et al. 2014), the most effective of which include spatial filtering of occurrence records, introduction of background selection via bias files, and geographically structured cross-validation to ensure models are evaluated with spatially independent data (Brown 2014, Muscarella et al. 2014). Filtering occurrence records has been shown to be a particularly effective and relatively simple way to account for SAC in MaxEnt (Kramer-Schadt et al. 2013, Fourcade et al. 2014). We applied the remove duplicate presence records in MaxEnt at each spatial resolution, a method that in our case compared well to spatial rarefying techniques employed by Brown (2014), in that filtered occurrence outputs were similar using both approaches. Further integration of a 'bias surface', using a kernel density estimate that weights the selection of background points according to sample bias (Brown 2014), followed by geographically structured cross-validation (Brown 2014, Muscarella et al. 2014), demonstrated that following cross-validation (as outlined below), the presented performance metrics are an accurate reflection of differences in model accuracy across resolutions.

To calculate final validation metrics, the spatially filtered presence data was randomly partitioned by area to create 75 % training and 25 % test datasets, with test data used to calculate the accuracy of predicted distributions (Miller 2009). This validation process was replicated 10 times, using different test data in each replicate, after which the validation metrics below were employed to quantify spatial resolution effects on estimates of *C. intestinalis* and *C. maenas* distributions.

Accuracy of predicted distributions among spatial scales was verified with the true skill statistic (TSS), sensitivity (proportion of actual presences that are accurately predicted) and specificity (proportion of actual absences that are accurately predicted), as well as false-positive and false-negative rates (Miller

2009, Merow et al. 2013, Basher et al. 2014). TSS, defined as sensitivity + specificity – 1, may vary from –1 to +1. TSS values that are negative or close to zero indicate that distributions are no better than random, while values of +1 represent perfect agreement between observed and modelled distributions. Highly accurate models exhibit a TSS greater than ~0.85 (Silva et al. 2014), sensitivity > 0.9, and an omission error (false-positive rate) of <10% (Miller 2009).

We chose not to include the area under the receiver operator characteristic curve (AUC) (Miller 2009) for evaluating predictive accuracy at varying spatial resolutions. Predictive accuracy, as determined by AUC, may be over-inflated according to prevalence of occurrence points, size of study region, and the assumption of equal costs of omission and commission errors (Lobo et al. 2008, Elith & Graham 2009, Merow et al. 2013). In combination, these biases would negate useful comparisons of models calibrated at varying spatial resolutions of seasonal temperature and salinity. Thus, the inclusion of independent validation metrics including TSS and associated sensitivity and specificity is preferable (Allouche et al. 2006, Cianfrani et al. 2010, Merow et al. 2013, Basher et al. 2014). TSS for example is indirectly estimated from MaxEnt's test and background predictions, is unbiased by prevalence of occurrence points or size of study region, and is more appropriate than AUC for models built with pseudo-absences (Barbet-Massin et al. 2012).

Continuous probability MaxEnt outputs were reclassified to binary rasters (presence or absence) using values obtained from the 10th percentile training presence threshold to evaluate spatial differences in the accuracy of predictions. MaxEnt's 10th percentile (presence value) is pertinent if presence records were collected over long time periods (Davies & Guinotte 2011), as in this study. Finally, species prevalence was calculated in ArcGIS as the proportion of the seascape in which each species was predicted present to determine if the predicted distribution was over- or underpredicted at varying spatial resolutions.

Environmental tolerances, in the context of how salinity and temperature shape each species distribution, were determined from the relative contribution of predictors to model performance, and predicted temperature and salinity thresholds for occurrence. MaxEnt provides the percent contribution of each variable to the final model. This is a heuristic approach to model importance in which the contribution values are determined by the increase in gain in the model provided by each variable. Thereby, Max-

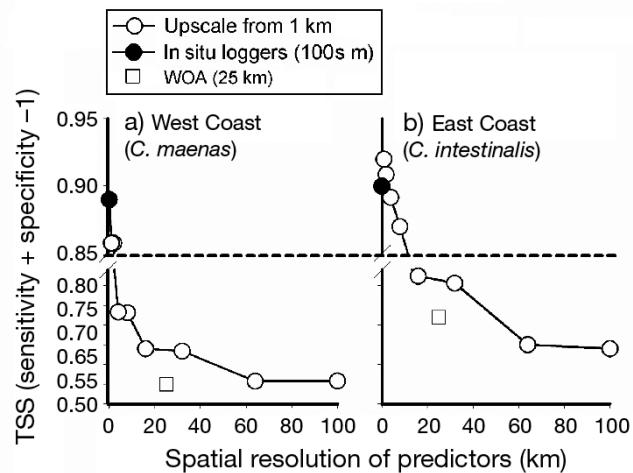


Fig. 3. Model utility as defined by the true skill statistic (TSS) for (a) west coast *Carcinus maenas* and (b) east coast *Ciona intestinalis*. Dashed black line represents the threshold TSS at which suitable habitat is accurately defined in MaxEnt (presence only), which equates to resolutions (a) between 100s of metres and 4 km resolution data or (b) 100s of metres to 8 km resolution environmental data. WOA: NOAA World Ocean Atlas

Ent provides information on the performance of each variable in the model in terms of how important each variable is at explaining the species distribution (Phillips et al. 2004). Predicted lower temperature and salinity thresholds for occurrence were estimated from response curves generated by MaxEnt.

RESULTS

Accuracy of predicted distribution

Each species distribution was accurately predicted at $TSS > 0.85$, sensitivity > 0.9 , and false-positive rate $< 10\%$, which in combination, equates to spatial resolutions of temperature and salinity below 4 km for west coast *Carcinus maenas* and 9 km for east coast *Ciona intestinalis* (Figs. 3–5). Evidently, the highest resolution (100s of metres) did not result in the most accurate predictions of east coast *C. intestinalis* distribution, which was most accurately predicted at 1 km resolution, whereas the highest resolution (100s of metres) resulted in the most accurate predictions of west coast *C. maenas* distribution. A higher resolution was also required to achieve a comparable probability of identifying suitable habitat in west coast *C. maenas* versus east coast *C. intestinalis* (Figs. 3–5). Additionally, an increase in resolution of temperature and salinity data did not translate into proportional increases in model performance (Figs. 3–5). Overall, the

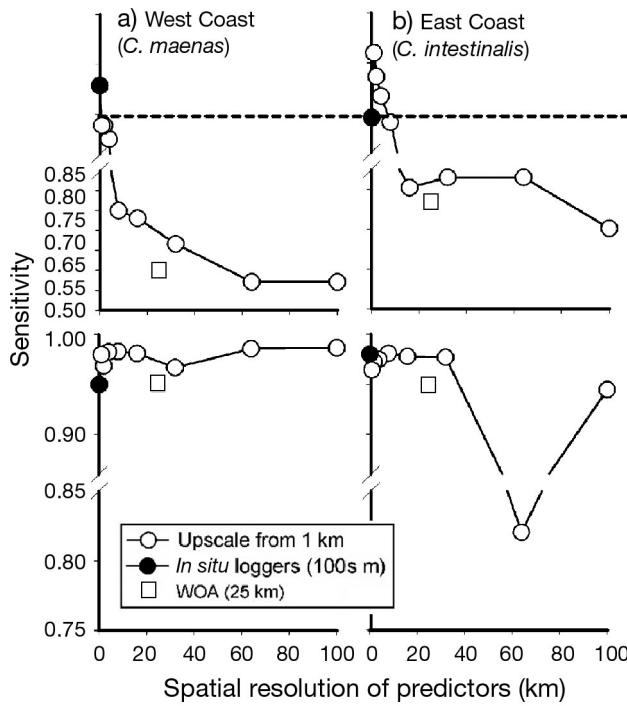


Fig. 4. Sensitivity (proportion of actual presences that are accurately predicted; upper graphs) and specificity (proportion of actual absences that are accurately predicted; lower graphs) for (a) west coast *Carcinus maenas* and (b) east coast *Ciona intestinalis*. Dashed black line represents the threshold sensitivity at which suitable habitat is accurately defined in MaxEnt (presence only), which equates to resolutions (a) between 100s of metres and 4 km resolution data and (b) 100s of metres to 8 km resolution environmental data. WOA: NOAA World Ocean Atlas

probability of accurately delineating each species distribution generally increased with the spatial resolution of temperature and salinity in the modelled seascape (Figs. 3–5).

Increasing sensitivity of predictions, or conversely, decreasing false-positive rates, with increasing spatial resolution accounted for most of the observed variation in TSS (Figs. 4 & 5). In other words, the percentage of actual presences accurately predicted increased with the spatial resolution of environmental layers. Moreover, models based on offshore environmental data collated at low spatial resolutions (25 km NOAA WOA) that were subsequently extrapolated to nearshore coastal habitats performed much more poorly for both west coast *C. maenas* and east coast *C. intestinalis* than our upscaled environmental composites at comparable resolutions (Figs. 3–5).

Observed prediction error at lower resolutions is also clearly reflected in projected distribution maps. For example, at lower spatial resolutions of environmental layers (e.g. 64 km), predictions failed to ac-

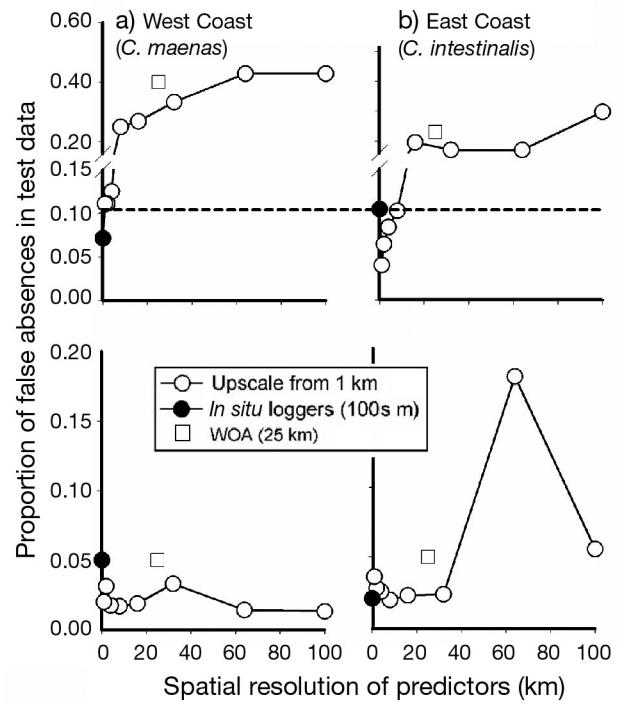


Fig. 5. Reliability of predictions as defined by false-positive (upper graphs) and false-negative rates (lower graphs) for (a) west coast *Carcinus maenas* and (b) east coast *Ciona intestinalis*. Dashed black line represents the threshold omission rate (proportion of false presences in the test data) at which suitable habitat is accurately defined in MaxEnt (presence only), which equates to resolutions (a) between 100s of metres and 4 km resolution data and (b) 100s of metres to 8 km resolution environmental data. WOA: NOAA World Ocean Atlas

curately resolve fine-resolution heterogeneity (e.g. 1 km resolution) in the distribution of *C. intestinalis* on the east coast (Fig. 6). Correspondingly, the nearshore environment (e.g. SST) was poorly characterized at lower spatial resolutions (e.g. 64 vs. 1 km resolution) (Fig. 6). There was no discernible pattern between spatial resolution of upscaled environmental predictors and the prevalence of *C. maenas* within the modelled seascape (Table 1). Prevalence in east coast *C. intestinalis* remained relatively stable at 2.3% between 1 and 64 km, but increased to 4% at 100 km resolution (Table 1).

Environmental tolerances

Environmental tolerances were represented by the relative contribution of environmental variables to model performance, and predicted temperature and salinity thresholds for occurrence. Variable importance at each spatial resolution was estimated and

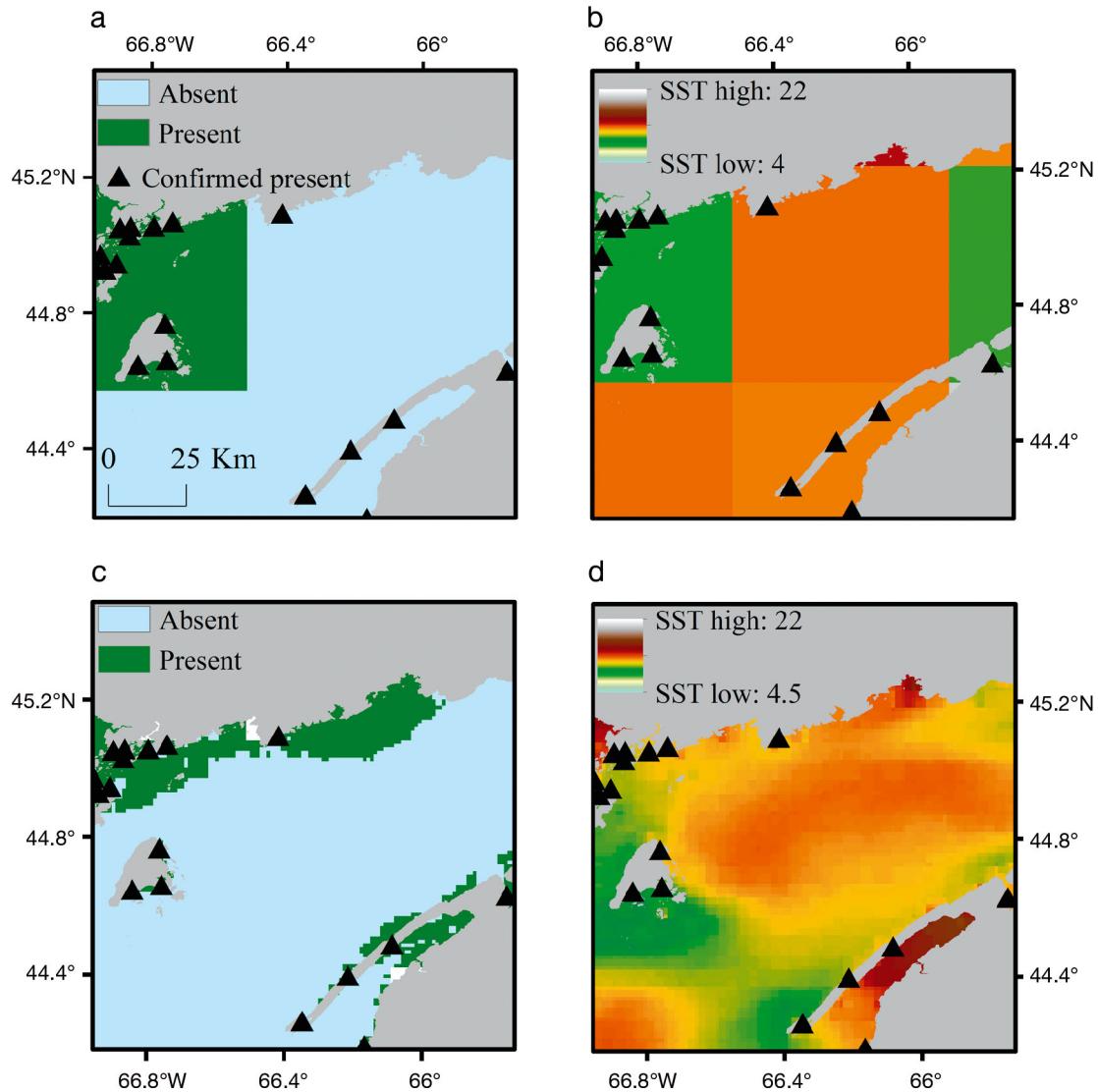


Fig. 6. Examples of high *Ciona intestinalis* omission error at 64 km vs. 1 km spatial resolution of environmental data in the Bay of Fundy, east coast of Canada. In (a), predicted absence and occurrence at 64 km resolution in species distribution models (SDM), and confirmed presence, are shown, alongside (b) summer sea surface temperature (SST, °C) at 64 km spatial resolution. In (c), predicted absence and occurrence at 1 km resolution in SDM, and confirmed presence, are shown, alongside (d) summer SST at 1 km spatial resolution. Note that SDM predictions at 1 km spatial resolution more accurately reflect the observed patchy mosaic distribution of *C. intestinalis*

compared after upscaling predictors (seasonal temperature and salinity) at 1 km to 2, 4, 6, 8, 16, 32, 64, and 100 km spatial resolutions. Variable importance remained relatively unchanged in west coast *C. maenas* and east coast *C. intestinalis* at spatial resolutions of 1–6 km or 1–8 km respectively; but not at lower spatial resolutions of temperature and salinity data (Table 1). In combination, spring and fall temperature and annual salinity accounted for ~85 % of model performance at 1–16 km spatial resolution in east coast *C. intestinalis* but contributed between 75 and 93 % to model performance at lower resolutions (32–100 km) (Table 1). Considerable variation in the

contribution of summer, fall, and winter SST was evident at 32–100 km when compared with resolutions at 1–16 km (Table 1). At 1–8 km spatial resolution on the west coast, salinity was the single most important variable, accounting for ~50 % of model performance for *C. maenas*, followed by spring (24–44 %) and winter SST (12–16 %) (Table 1). At lower resolutions (>16–100 km), percent contribution of spring, summer, and fall SST, and salinity deviated considerably from corresponding estimates for these predictors at 1–8 km resolutions (Table 1).

Spatial resolution of seasonal temperature and annual salinity seascape data strongly affected pre-

Table 1. Characterization of how seasonal temperature and salinity shape potential distributions of west coast *Carcinus maenas* and east coast *Ciona intestinalis* as defined by percentage contribution (Contrib.) of sea surface temperature (SST) and sea surface salinity to model performance, lower thresholds (Thresh.) for detection based on seasonal temperature and salinity tolerances, and prevalence

Resolution (km ²)	SST								Salinity		Pre- valence (%)
	Spring		Summer		Fall		Winter		Annual Contrib.	Thresh. (psu)	
	Contrib.	Thresh.	Contrib.	Thresh.	Contrib.	Thresh.	Contrib.	Thresh.	(%)	(psu)	
West coast <i>C. maenas</i>											
1	24	11	3	14	7	10	16	7	51	25	5.5
2	44	11	2	14	1	9	11	7	42	25	3.5
4	32	11	4	14	2	9	15	7	48	25	4.9
6	30	11	4	14	2	9	15	7	49	25	2.3
8	24	11	6	15	6	9	12	7	53	25	1.9
16	67	11	1	17	1	9	3	6	29	25	4.0
32	55	12	2	17	1	10	4	7	38	27	3.0
64	3	8	60	11	15	11	8	7	14	30	2.0
100	16	10	2	10	7	11	16	8	60	31	1.0
East coast <i>C. intestinalis</i>											
1	27	2	4	10	26	11	12	1	31	24	2.3
2	26	2	3	10	28	11	12	1	30	24	2.4
4	27	2	4	10	26	11	12	1	31	24	2.3
6	24	2	4	10	27	11	14	1	31	24	2.2
8	26	1	4	10	27	11	12	1	30	24	2.2
16	30	1	4	11	20	11	15	1	31	22	2.1
32	22	2	7	13	19	10	17	3	35	23	2.5
64	25	3	12	13	17	11	10	3	35	23	2.8
100	22	4	2	16	45	11	4	4	27	29	4.1

dicted temperature and salinity thresholds for occurrence (Table 1). Estimated lower temperature thresholds of occurrence in west coast *C. maenas* in the summer increased from ~14°C at <16 km resolution to 17°C at 16–32 km resolutions, after which it dropped to 10–11°C at 64–100 km resolutions (Table 1). Estimated lower salinity thresholds for occurrence of west coast *C. maenas* increased steadily from 25 psu at 1–16 km spatial resolution to a maximum of 30–31 psu at 64–100 km spatial resolution (Table 1). Temperature thresholds for occurrence of west coast *C. maenas* in spring, fall, and winter remained relatively unaffected by spatial resolution (Table 1).

Temperature thresholds of occurrence in east coast *C. intestinalis* in the summer increased from 11°C at 1–16 km resolution to a maximum of 16°C at 100 km resolution. In contrast, in the spring, they increased from 2°C at 1–16 km resolution to a maximum of 4°C at 100 km resolution. During winter, temperature thresholds increased from 1°C at 1–16 km resolution to a maximum of 4°C at 100 km resolution (Table 1). Temperature thresholds for occurrence of east coast *C. intestinalis* remained stable across each of the tested spatial resolutions in the fall (Table 1). Finally, salinity thresholds of occurrence in east coast *C. intestinalis* increased from 22 to 24 psu at 1–64 km resolutions to a maximum of 29 psu at 100 km resolution (Table 1).

DISCUSSION

Increasing spatial resolution of seasonal temperature and salinity data resulted in progressively more accurate predictions of the distribution of west coast *Carcinus maenas* and east coast *Ciona intestinalis*, with several important caveats. First, the highest resolution (e.g. 100s of metres) was not necessarily the most accurate, as hypothesized by Lecours et al. (2015), and recently demonstrated by Ross et al. (2015). Secondly, an increase in the resolution of environmental seascape data did not translate into proportional increases in model performance. Finally, lower spatial resolutions (i.e. 100–8 km resolution) performed worse in MaxEnt for west coast *C. maenas* than east coast *C. intestinalis*. Overall, the probability of accurately delimiting each species distribution improved considerably at or below resolutions of 8 km on the east coast for *C. intestinalis* or 4 km on the west coast for *C. maenas*.

Increasing sensitivity of predictions, or conversely, decreasing false-positive rates, with increasing spatial resolution accounted for most of the observed variation in SDM accuracy (i.e. TSS). In other words, the percentage of actual presences accurately predicted increased at higher spatial resolutions. Incorrectly predicting a known presence (i.e. omission error) represents a serious failing of the model that

has consequences for delineating core habitat (Miller 2009). Omission error at progressively lower spatial resolutions was clearly evident in projected distribution maps (Fig. 6). Consequently, observed fine-resolution patchiness in AIS distributions was resolved only at spatial resolutions < 9 km for *C. intestinalis* on the east coast and ~4 km to 100s of metres for *C. maenas* on the west coast.

Evidently, important habitat heterogeneity shaped by variations in temperature and salinity within shallow nearshore marine bays and inlets are not 'captured' by lower resolutions of environmental data, as in other more homogeneous marine environments (Valavanis et al. 2008, Miller 2009, Davies & Guinotte 2011, Basher et al. 2014). This problem may be exacerbated where offshore environmental data collated at coarse spatial resolutions (e.g. 25 km NOAA WOA) is extrapolated into coastal regions where environmental variation in nearshore environments at higher spatial resolutions (100s of metres strongly affects the identification of suitable habitat). Thus, there are potentially 2 key issues with the use of lower resolutions in SDM for our study of AIS that could account for reduced predictive accuracy, e.g. extrapolating offshore data to nearshore environments and not satisfactorily resolving inherent nearshore environmental heterogeneity.

Differences in the shape and topography of nearshore environments (e.g. embayments) between the east and west coasts may also have a significant impact on characterizing important site-specific habitat. Within our study extents, the west coast was more topographically complex than the east coast by virtue of an extensive system of fjords throughout the study area. Predicting suitable micro-habitat required more detailed (i.e. higher resolution) temperature and salinity data, as reflected in the higher resolution threshold observed (4 km). This in turn helps to explain why lower spatial resolutions (i.e. 100–8 km resolution) performed worse in MaxEnt for west coast *C. maenas* than east coast *C. intestinalis*. Differences in the way each species responds in MaxEnt at each spatial resolution of salinity and temperature also may not account for differences in predictive accuracy on each coast. Temperature and salinity constrain the distribution of both species (Carver et al. 2006, Klassen & Locke 2007). Thus, spatial resolution of these predictors strongly influenced predictive accuracy in SDM for both species. Consequently, differences in resolving nearshore temperature and salinity habitat heterogeneity in each coast could manifest as differences in SDM accuracy as observed here (e.g. in TSS).

Differences in length of pelagic larval stages and subsequent potential for dispersal among our study species in relation to hydrographic or other physical barriers on each coast (Carver et al. 2006, Klassen & Locke 2007, Collin et al. 2013) could also influence SDM predictions if dispersal is constraining or facilitating the observed distribution of each species (Robinson et al. 2005, Guisan et al. 2007). This is especially true where an invasive species has only recently established and is likely restricted in its potential to disperse due to small and/or fragmented populations or lack of dispersal vectors/opportunities (Rouget & Richardson 2003, Robinson et al. 2011). Our study species have established and are widely dispersed in each study extent, which in turn helps to generate more reliable predictions of distribution in SDM (Rouget & Richardson 2003, Robinson et al. 2005).

Widespread anthropogenic dispersal vectors on both the east and west coasts have also been attributed to the rapid spread of each species in the last 10 yr (Carver et al. 2006, Klassen & Locke 2007). Here, anthropogenic dispersal helps to negate natural differences in each species' ability to disperse to, and subsequently colonize, favourable habitat, arising from differences in length of larval stages (Carver et al. 2006, Klassen & Locke 2007), in addition to natural physical/hydrographic barriers to dispersal on both coasts. In this context, nearshore coastal environments might be considered dispersal-neutral in SDM because both species can disperse great distances and overcome natural physical or hydrographic barriers to dispersal.

Over-prediction of suitable habitat at progressively lower spatial resolutions may also be evident (Guisan et al. 2007, Miller 2009, Basher et al. 2014). There was no discernible pattern between spatial resolution of environmental predictors and prevalence of *C. maenas* within the modelled seascape. Prevalence in east coast *C. intestinalis* remained relatively stable between 1 and 64 km spatial resolutions, but increased abruptly at 100 km spatial resolution compared with 1–64 km spatial resolutions. Over-prediction of a species' range indicates the need for caution when using such data for identifying core habitat in AIS risk assessment, because an overly large predicted range could lead to inappropriate characterization of current and future areas at risk of invasion.

In addition to identifying potential habitats at risk of invasion, quantifying a species' environmental tolerances is useful (Pheloung et al. 1999, Therriault & Herborg 2008a). Here, information as to environmental drivers of species distributions (or variable

contribution), and thresholds in occurrence for temperature and salinity, provides an ecological context and justification for identifying sites at risk of invasion. Selection of an appropriate spatial resolution is critical because different environmental tolerances emerge in spatial data at different resolutions (Johnson et al. 2002, Graham & Hijmans 2006), further supported by our results. For example, percentage contribution of temperature and salinity remained relatively stable at higher resolutions (1–16 km for east coast *C. intestinalis* or 1–8 km for west coast *C. maenas*), but not at lower resolutions, where important site-specific habitat was poorly predicted. Key drivers of *C. intestinalis* distribution at higher resolutions (1–8 km) included spring and fall SST, and salinity, and to a lesser extent, winter SST. At 1–8 km spatial resolution on the west coast, salinity was the single most important environmental driver of *C. maenas* distribution, followed by spring and winter SST.

Ecologically, the importance of spring or fall SST can be attributed to the seasons in which *C. maenas* and *C. intestinalis* develop and reproduce. Extending the growing season during a warmer spring and fall increases the probability of reproductive success and thus their invasion success. Warmer winter temperatures on the other hand result in higher survival and increased growth rate (Carver et al. 2006, Klassen & Locke 2007). Low salinities further act to constrain these species' coastal distributions (deRivera et al. 2007, Vercaemer et al. 2011). At lower resolutions, the ranking of these variables changes, likely as a result of important habitat heterogeneity, shaped by variations in temperature and salinity, not being accurately captured. Salinity thresholds for occurrence at lower spatial resolutions (30–31 psu at 64–100 km in west coast *C. maenas*, or 29 psu at 100 km resolution in east coast *C. intestinalis*) also did not match published salinity thresholds for survival of any life stage, whilst salinity thresholds estimated at higher spatial resolutions did (e.g. 22–24 psu for settling *C. intestinalis* larvae in Carver et al. 2006; or 25 psu for *C. maenas* larvae, reviewed by Klassen & Locke 2007). Temperature thresholds for occurrence in *C. maenas* and *C. intestinalis* were also over-estimated at lower resolutions, while the reverse was true for winter thresholds for *C. intestinalis* on the east coast.

In summary, seascape data with high resolution and ecological relevance for the species improved model reliability and utility, making it easier to detect an effect of increasing spatial resolution of environmental predictors on model performance as noted by

Guisan et al. (2007) and Becker & Encarnaçāo (2015). Ultimately, these findings improve risk assessments for AIS. Predicting suitable habitat of a species with well understood environmental tolerances is required for AIS risk assessment (Pheloung et al. 1999). We demonstrate that inclusion of higher spatial resolution temperature and salinity data that is collected locally (i.e. within embayments) better represents limiting nearshore habitat heterogeneity and significantly improved SDM predictability, including a more realistic depiction of how salinity and temperature shape these distributions.

Temperature and salinity constrain and shape the distribution of many temperate ecotherms, including a suite of problematic AIS in nearshore coastal waters (Tyberghein et al. 2012). In these waters, considerable spatiotemporal variability in temperature and salinity over fine spatial scales (i.e. 10s to 100s of metres) is evident. By accurately capturing fine-scale temperature and salinity variability, we have demonstrated for the first time the limitations and range of spatial resolutions required to accurately resolve fine-scale patchiness and develop useful predicted distributions (at least for AIS using SDM based on temperature and salinity data). Doubtless, other factors interact to further constrain species distributions. For example, temperature and salinity anomalies, or perturbation events could be considered that either disrupt (e.g. freshwater runoff; Lambert & Lambert 1998, Carver et al. 2006, Madariaga et al. 2014) or enhance (e.g. warm water 'masses'; Patanasatienkul et al. 2014) invasive potential in *C. maenas* or *C. intestinalis*. Biotic interactions, both among native species, or other invasive species, have also been under-studied and may further constrain AIS ranges (Carver et al. 2006, Klassen & Locke 2007).

While many known problematic AIS in the coastal zone are constrained by temperature and salinity (Tyberghein et al. 2012), the resolutions of environmental data at which they are constrained may differ from the current study species, depending on thermal and salinity tolerances, and the extent to which other environmental factors drive their distribution and the resolution at which they are important. In this context, consideration of whether the target AIS is a habitat specialist or generalist should be made (Pandit et al. 2009) to determine *a priori* the types of environmental predictors to include in SDM, preferably across a range of spatial resolutions. This could resolve instances where important environmental predictors might constrain a species distribution at different spatial scales, a topic that requires more attention. Despite these caveats, our

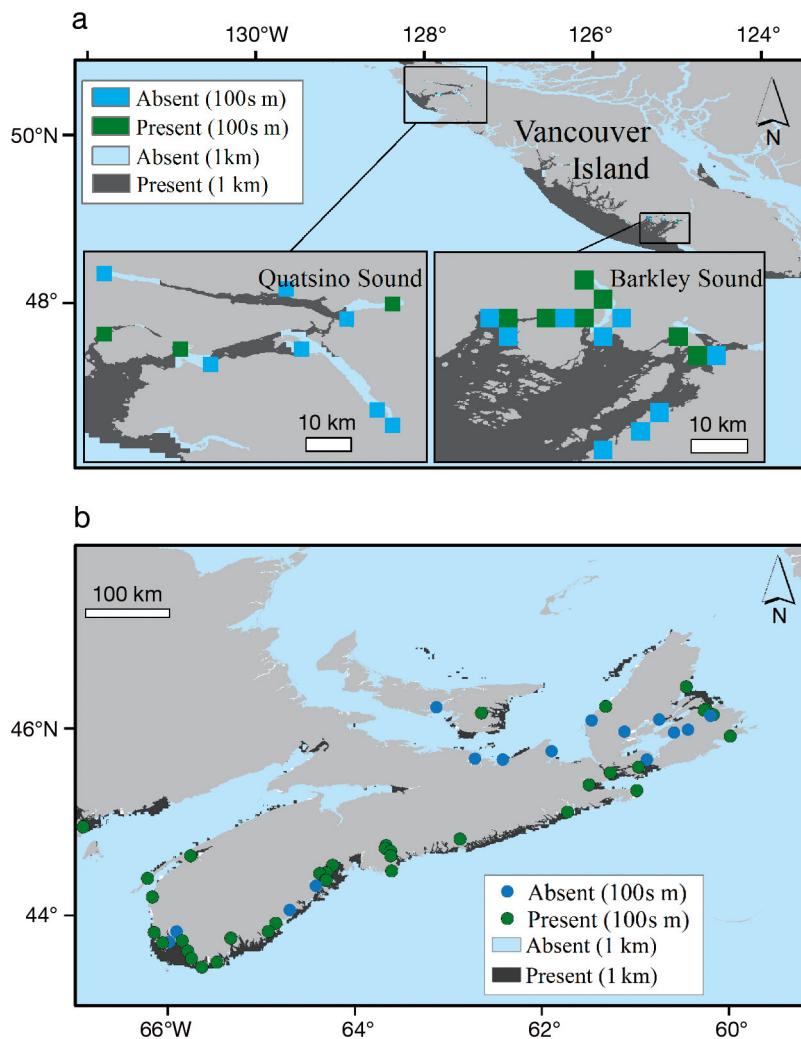


Fig. 7. Examples of predictions of distribution (i.e. presence/absence) at optimal spatial resolutions of environmental data in species distribution models (SDM) for (a) west coast *Carcinus maenas* and (b) east coast *Ciona intestinalis*. Here, SDM models derived from (a) 100s of metres to 1 km resolution data and (b) 100s of metres to 1 km resolution environmental data reliably predicted the distribution of aquatic invasive species (AIS) in this study. Predicted absence and occurrence at 1 km resolution in SDM is shown alongside predicted absence and occurrence at 100s of metres resolution

findings highlight the importance of bridging the gap between observational scale (e.g. fine-scale patchiness in distribution) and ecological scale (based on SDM predictions), by employing a range of spatial resolutions of limiting temperature and salinity data to characterize site-specific habitat for nearshore AIS in SDM. Critically, the highest resolution may not always be needed to accurately predict potential distributions, as outlined in Lecours et al. (2015), Ross et al. (2015), and the current study. However, the relatively high-resolution data (i.e. <4–9 km) required to define temperature and salinity habitats that constrain our study species distribu-

tions in the nearshore on each coast could prove challenging to obtain elsewhere.

Based on our results, optimal spatial resolutions for SDM-based risk assessment encompassed 100s of metres to 8 km resolution environmental data for east coast *C. intestinalis* and 100s of metres to 4 km resolution data for west coast *C. maenas*. Subsequent maps of potential distributions generated in SDM at these resolutions can be used to guide monitoring activities towards vectors that transport AIS to these favourable environments (Theriault & Herborg 2008a,b, Therriault et al. 2008, Deibel et al. 2014; e.g. our Fig. 7). An important caveat is that the increased effort, in terms of sampling the nearshore environment, to obtain higher resolution environmental data with *in situ* instrumentation does not necessarily translate into proportional increases in predictive utility for risk assessment, an argument raised by Lecours et al. (2015). On the other hand, readily available climatological composites provide excellent spatial coverage between latitudes 50° S and 50° N, albeit at resolutions generally not less than 1 km in marine coastal environments (Tyberghein et al. 2012, M. E. Greenlaw et al. pers. comm.). Here, a key advantage was that predictions of potential distribution were not constrained to sites where *in situ* instrumentation had been deployed. The use of readily available multi-year datasets at 1–8 km spatial resolution (Tyberghein et al. 2012, M. E. Greenlaw et al. unpubl.) could save time and money when compared with extensive sampling of the nearshore with *in situ* instrumentation.

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