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Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic

Jesica Goldsmit  · Philippe Archambault · Guillem Chust · Ernesto Villarino · George Liu · Jennifer V. Lukovich · David G. Barber · Kimberly L. Howland

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Abstract A rise in Arctic shipping activity resulting from global warming and resource exploitation is expected to increase the likelihood of aquatic invasive species (AIS) introductions in the region. In this context, the potential threat of future AIS incursions at a Canadian Arctic regional scale was examined. Habitat suitability under current environmental conditions and future climate change scenarios was projected for a subset of eight potential invaders ranked as having a high risk of establishment in the Canadian Arctic based on dispersal pathways/donor regions, biological attributes and invasion history: (1) *Amphibalanus improvisus*, (2) *Botrylloides violaceus*, (3) *Caprella mutica*, (4) *Carcinus maenas*, (5)

Littorina littorea, (6) *Membranipora membranacea*, (7) *Mya arenaria* and (8) *Paralithodes camtschaticus*. Habitat modelling was performed using MaxEnt based on globally known native and non-native occurrence records and environmental ranges for these species. Results showed that under current environmental conditions the habitat is suitable in certain regions of the Canadian Arctic such as the Hudson Complex and Beaufort Sea for *L. littorea*, *M. arenaria* and *P. camtschaticus*. Under a future climate change scenario, all species showed poleward gains in habitat suitability with at least some regions of the Canadian Arctic projected to be suitable for the complete suite of species modelled. The use of these models is helpful in understanding potential future AIS incursions as a result of climate change and shipping at large spatial scales. These approaches can aid in the identification

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of high risk regions and species to allow for more focused AIS monitoring and research efforts in response to climate change.

Keywords Arctic · Biological invasions · Climate change · MaxEnt · Ship-mediated invasive species · Species distribution modelling

Introduction

Aquatic invasive species (AIS) have become a serious threat to biodiversity and to the structure and functioning of ecosystems causing damages and losses of billions of dollars per year (Pimentel et al. 2005; Ehrenfeld 2010). Most aquatic invaders have been introduced through ballast water and/or hull fouling vectors due to shipping activity (Drake and Lodge 2007; Bailey 2015; Ruiz et al. 2015). Since commercial shipping makes up 90% of global cargo (Minchin 2006), shipping patterns can be expected to have implications for marine ecosystems with respect to non-indigenous species introductions. The Arctic is becoming more prone to AIS introductions due to the increase in shipping activity, together with global warming and resource exploitation (Niimi 2004; Smith and Stephenson 2013; Miller and Ruiz 2014; Ware et al. 2014). Shipping in the Canadian Arctic mainly consists of community re-supply, bulk shipments of raw materials and supplies, exploration activity for resource development operations, and tourism (Arctic-Council 2009). In 10 years, the number of ships transiting the Canadian Arctic has more than doubled (from 121 in 2005 to 302 in 2014) (Guy and Lasserre 2016), with the main ports receiving domestic and international vessels being located in Iqaluit, Deception Bay and Churchill (Chan et al. 2012). The major developments in the region are oil and gas, mineral and infrastructure mainly concentrated in Nunavut, Quebec, and Labrador (Gavrilchuk and Lesage 2014). Under current regulations, domestic ballast water can be transported from Canadian temperate regions and released in Canadian Arctic waters without treatment or exchange, thus facilitating transfer and potential introduction of NIS in Arctic waters (Chan et al. 2012; Goldsmit 2016). The Arctic Ocean covers approximately 10 million km², 20% of which is in Canada (CAFF 2013). Moreover, Canada

has the longest coastline of any country in the world (approximately 16% of the world coastline), the majority of which is located in Arctic waters (Archambault et al. 2010). Given that most known marine AIS are of coastal and estuarine origins (Ruiz et al. 2000), having a vast coastline could provide the proper habitat for new species to establish.

Sea surface temperature in high-latitude regions is warming at faster rates than other parts of the globe (Doney et al. 2012; Stammerjohn et al. 2012) and their coasts are highly susceptible to a combination of climate change impacts and sea-level rise (Larsen et al. 2014). In the Arctic, the seasonal minimal sea ice extent has decreased by 45,000 km²/year over the past 20 years and the decrease in summer sea ice is estimated at 12.4% per decade (Stroeve et al. 2007, 2012). There has also been a commensurate reduction in perennial sea ice and subsequent increase in annual forms of sea ice (Barber et al. 2009, 2014). Climate simulations project future scenarios ranging from mean reductions of 31% of the annually averaged sea ice area in the Arctic by 2100 (Solomon 2007), to more extreme projections of complete disappearance of summer sea ice by 2037 (Hoegh-Guldberg and Bruno 2010) and a complete open water season lasting half of the year by 2070 (Barnhart et al. 2016). While these predicted changes may sound extreme, they may be conservative given that actual reductions in sea ice are happening faster than model predictions (Meier et al. 2014). With these changes, it is forecasted that by mid-century, shipping routes such as the Northwest Passage, which crosses the Canadian Arctic, will become more viable, linking the Atlantic and Pacific oceans (Smith and Stephenson 2013). Since high-latitudes have not yet experienced significant introductions of non-indigenous species, only predictions of the potential changes and impacts can be studied (Ruiz and Hewitt 2009; Ware et al. 2014).

Predicting which species have higher probabilities of introduction and survival is essential for the development of effective pro-active management strategies (de Rivera et al. 2011; Ware et al. 2014, 2015). Ideally, management should include a pre-invasion planning phase, since once an introduced species is established, eradication is difficult and in many cases, impossible (Locke and Hanson 2009; Floerl 2014). Managers need to identify vulnerable habitats, and determine where and how to monitor species of concern (Locke and Hanson 2009; Reiss

et al. 2014). Species distribution modelling (SDM) is a powerful tool that can be very effective in making predictions regarding potential geographic distributions for species of concern (Peterson 2003) based on the environmental conditions and known occurrences of both native and introduced populations (Phillips et al. 2006; Elith and Leathwick 2009; Elith et al. 2011). These models provide an approximation of a species' ecological niche based on the examined environmental dimensions (Phillips et al. 2006).

Given that the majority of known introduced marine species are benthic (Streftaris et al. 2005), it is of particular interest to study these organisms and forecast which species could potentially be introduced in the Canadian Arctic. A minimum of ten AIS are known to be established in Alaskan waters (Hines et al. 2000; Ruiz and Hewitt 2009), and new arrivals and introductions have been reported in recent years in the North Atlantic and other higher latitude regions (Ashton et al. 2008; Svavarsson and Dungal 2008; Lambert et al. 2010; Gíslason et al. 2014; Chan et al. 2015). Moreover, new species have been discovered in the Arctic but their origin is uncertain (MacDonald et al. 2010; Goldsmit et al. 2014). There is currently only one known introduced marine species, the red algae *Dumontia contorta* (Mathieson et al. 2010) and seven recently identified cryptogenic species (i.e., new species that could be either native or introduced) in the Canadian Arctic (Goldsmit et al. 2014). However, this region is under sampled as few systematic surveys have been conducted (Archambault et al. 2010; Piepenburg et al. 2011; CAFF 2013), thus new or introduced species may remain undiscovered.

The establishment of ship-mediated invasive species is expected to increase with the projected changes in the Arctic which include warmer, less saline ocean conditions and increased shipping activity (Carmack and McLaughlin 2011). Increasing temperatures are also expected to result in shifts in aquatic communities with southern species expanding their ranges to more northern locations (Beaugrand et al. 2010; Villarino et al. 2015; Wisz et al. 2015). It is within the context of this changing environment that the objective of this study is to predict the extent of suitable habitat within the Canadian Arctic under current and projected future environmental conditions for a suite of known AIS in globally connected ports.

Methods

Study region and shipping activity

Shipping plays a key role in supporting Arctic communities and the economy by transporting resources via domestic and international pathways. The Canadian Arctic includes eight ecoregions as delineated by Spalding et al. (2007), from the Beaufort Sea East to Southern Labrador. The majority of vessel arrivals in the Canadian Arctic are destined for ports in the Hudson Complex region, which includes Hudson Strait, Hudson Bay, Foxe Basin, James Bay and Ungava Bay (Chan et al. 2012) (see Fig. S1 for detail on ecoregions and arrival ports). Although relatively few ballast water discharges occur in the Canadian Arctic, the risk associated with individual discharges, in particular by international transoceanic vessels, is considered to be high (Casas-Monroy et al. 2014). Any increase in vessel traffic (for example due to the opening of new shipping routes) (Smith and Stephenson 2013; Meier et al. 2014; Miller and Ruiz 2014) will magnify overall risk to the region.

Selection of species for modelling

Potential invaders were screened and ranked for modelling using a two-step process that considered the number of barriers to introduction and establishment with respect to environmental conditions, and potential connections through shipping (Fig. S2). A combination of data sources were used to make a robust and complete search of documented records. These included published articles (Hines et al. 2000; Ruiz et al. 2006; Molnar et al. 2008; Chan et al. 2012), grey literature and the following global invasive species lists available on the web: National Exotic Marine and Estuarine Species Information System NEMESIS (www.invasions.si.edu/nemesis/), Invasive Species Compendium (www.cabi.org/isc), the European Network on Invasive Alien Species NOBANIS (www.nobanis.org/) and the Global Invasive Species Database GISD (www.issg.org/database). The first step in the process involved a pre-screening analysis to select known invasive species with biological/ecological features that could allow for survival in arctic conditions. For example, temperature and salinity tolerances of species needed to coincide with the range of environmental conditions present in the Arctic. The

potential for being transported through ballast water and/or hull fouling from connected ports was also considered (Chan et al. 2012) to identify species with a higher likelihood of introduction via shipping traffic (Fig. S2). The second step involved ranking the potential species following Ricciardi and Rasmussen (1998). This methodology involves evaluating the potential barriers to invasion success of different aquatic organisms based on documented information regarding: (1) potential donor regions and dispersal pathways of future invaders, (2) biological characteristics of selected potential invaders (e.g., abundance in native range, growth rate, reproductive capacity, mechanisms for dispersal, etc.) and (3) invasion history (Fig. S2). Species were ranked as low moderate or high risk if they had either \geq two, one or zero barriers, respectively (Fig. S2, Table S1). Of sixteen species that were identified after the first pre-screening step, a subset of eight potential invaders ranked as having high risk for the Canadian Arctic were selected for modelling (Table S1).

The final species list included: (1) Bay Barnacle *Amphibalanus improvisus*, (2) Violet Tunicate *Botrylloides violaceus*, (3) Japanese Skeleton Shrimp *Caprella mutica*, (4) Green Crab *Carcinus maenas*, (5) Periwinkle *Littorina littorea*, (6) Coffin Box Bryozoan *Membranipora membranacea*, (7) Soft-shell Clam *Mya arenaria* and (8) Red King Crab *Paralithodes camtschaticus*. These species are known invaders that are present in ports connected to Canadian Arctic ports, either by domestic and/or international shipping (Turcotte and Sainte-Marie 2009; Jørgensen and Nilssen 2011; Chan et al. 2012) and could potentially be transported through ballast water or biofouling (Table S1).

Environmental data

The environmental variables used for modelling were those that are typically the most important limiting factors for benthic aquatic species and included temperature and salinity (bottom and sea surface), ice concentration and bathymetry (Wagner 1977; Barnes 1999; Cusson et al. 2007; Belanger et al. 2012). The model was built, trained and validated using monthly climatological values based on global scale environmental data at a 1° resolution. Sea surface and bottom temperature and salinity, together with bathymetry were obtained from the World Ocean

Atlas 2013 v.1 (Boyer and Mishonov 2013). These monthly objectively-analysed mean climatological values (one mean value per month based on all raw data from 1951 to 2012) were used to determine the maximum and minimum temperature and salinity based on the coldest/warmest and least/most saline months, respectively. The annual mean salinity and temperature at surface and bottom was then calculated from the mean monthly climatological values ($N = 12$). Sea ice cover information (1981–2010) was obtained from the Sea Ice Index (Fetterer et al. 2002) and from the Met Office Hadley Centre (Rayner et al. 2003). The average sea ice coverage over the 30-year period was calculated from the annual length (in months) of open water period at 15% (Sea Ice Index and Hadley Centre) and 50% (Hadley Centre) ice coverage on a global scale. Ocean currents were not included in the present model since high resolution models of oceanographic currents and an ice-ocean modelling system are not available for nearshore coastal areas of the Canadian Arctic where ports are located. Substratum type was not included in the analysis due to the lack of accessibility to a global scale database.

Distributional data

Larger sampling sizes have been shown to result in better models (Guisan et al. 2007a, b) and efforts should be focused on improving the number and quality of occurrence records (Lobo 2008; García-Roselló et al. 2015). Hence, in this study there was an emphasis on finding the highest number of occurrence records possible for each species. Native and invaded ranges were pooled together given that the inclusion of both can improve prediction of the extent of invasion (Broennimann and Guisan 2008). Global scale occurrence data were compiled for each species to cover the majority of native and invaded ranges using the global databases Global Biodiversity Information Facility GBIF (www.gbif.org), and Ocean Biogeographic Information system OBIS (www.iobis.org), as well as invasive species lists with available coordinate location information and specific literature (Table S2). To decrease the possibility of over prediction, only one presence record was counted per grid cell (1° resolution) (García-Roselló et al. 2015) with the assumption that a given sample unit was equal to the same resolution of the corresponding environmental variables.

With this approach, the total occurrence records ranged from 81 (*C. mutica*) to 189 (*M. arenaria*) (Table S2). The ecoregion names used in the text were according to the ecoregions described by Spalding et al. (2007).

Habitat suitability modelling

MaxEnt 3.3.3k (<http://www.cs.princeton.edu/~schapire/maxent/>) (Phillips et al. 2006), one of the most widely utilized SDM algorithms (Elith et al. 2011), was used to conduct habitat suitability modelling for the above-described suite of benthic AIS. This machine learning method based on maximum entropy relates presence-only species occurrence information and corresponding environmental variables to approximate the niche and potential geographic distributions for a given species of interest (Phillips et al. 2006). MaxEnt has been found to outperform other methods, show a high predictive accuracy and is known to be efficient in modelling range shifts under future climate change scenarios (Elith et al. 2006; Hijmans and Graham 2006; Pearson 2007).

Correction for spatial bias is highly recommended when projecting future trends in SDM to avoid sampling habitat outside the species' known occurrence and to account for sample collection bias (Brown 2014; Hertzog et al. 2014). Hence, bias files were included during model building using the SDMtoolbox package in ArcGIS (Brown 2014), whereby background points were compared with presence data and differentiated from the environmental conditions under which a species can potentially occur. Cross-validation was used to evaluate the predictive power of the model with 70% of the occurrence points chosen randomly and used to train the model, while the other 30% were used to test it (Araújo et al. 2005). During this *k*-fold validation procedure, *k* iterations of training and validation were performed splitting data by a random process. During each iteration, a different fold of the data was held-out for validation while the remaining folds were used for model fitting (Hijmans 2012). The convergence threshold was set at 0.00001, 500 iterations were made and random seeding was used to select training points. The hinge feature was used since it produces complex but smoothed and ecologically meaningful response curves and improves model performance (Phillips and Dudík 2008; Merow et al. 2013). Suitable *versus* not suitable habitat was identified through transformation of continuous values

using the maximum training sensitivity plus specificity threshold. This threshold is known to produce the most accurate predictions, especially for presence-only datasets (Jiménez-Valverde and Lobo 2007; Liu et al. 2013).

The model was constructed using a small suite of environmental predictors at a coarser resolution rather than increasing the number of variables and the resolution with a corresponding loss of data quality. The use of coarse resolution was balanced with the utilization of high quality data for the region of study by trying to minimize the quantity of grids with missing data, and the quantity of extrapolated data. While increased spatial resolution generally results in more accurate predictions, the best resolution to use can depend on the species/location and using the highest resolution does not necessarily always increase accuracy and model performance (Lowen et al. 2016). Accordingly, from the complete set of environmental variables only the most important ones were included in the models for each species (Table 1). These were identified by evaluating the combination of: (1) the response curves for each species indicating the suite of variables that most closely corresponded to a biologically realistic situation (i.e. unimodal shape as outlined in the Hutchinson (1957) niche theory framework); (2) a species-specific Jackknife test built with all the variables alone and by excluding each variable sequentially for testing the contribution of the different parameters and analysing the variable importance; and (3) the estimates of the contribution of each variable to the model prediction. The area under the curve (AUC) was used to evaluate the performance of the models. In presence-only models, the AUC is the probability that the model correctly ranks a random presence site *versus* a random site from the study area (Phillips et al. 2009). It ranges from 0 to 1 (values closer to 1 indicate better prediction in the discrimination of sites, 0.5 indicate a prediction equal to random and values lower than 0.5 indicate performance worse than random). The model runs were corrected using a mask for maximum depths each species could inhabit according to their ecological requirements (Table S1).

Prior to model fitting, autocorrelation between environmental variables was checked to prevent inclusion of other correlated variables. This was calculated using the SDMtoolbox (Brown 2014). In cases where multiple variables were highly correlated

Table 1 Variables used to build the habitat suitability model for each species

	SST			SSS			BT			BS			Sea ice			Bathym.
	Max*	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	15 ^a	50 ^a	15 ^b	
<i>Amphibalanus improvisus</i>		X		X									X			X
<i>Botrylloides violaceus</i>	X		X										X			X
<i>Caprella mutica</i>	X	X		X							X		X			X
<i>Carcinus maenas</i>		X											X			X
<i>Littorina littorea</i>	X	X											X			X
<i>Membranipora membranacea</i>	X	X		X									X			X
<i>Mya arenaria</i>	X	X				X									X	X
<i>Paralithodes camtschaticus</i>				X			X				X		X			X

* Max SST removed from models due to high correlation with sea ice concentration

SST sea surface temperature, SSS sea surface salinity, BT bottom temperature, BS bottom salinity

^aSea ice: Met Office Hadley Centre database (Rayner et al. 2003)

^bSea ice: Sea Ice Index database (Fetterer et al. 2002)

(coefficients greater than or equal to 0.7, Dormann et al. 2013) for a given species, only one of them was retained for model construction.

Future projection under climate change scenario

Once the global SDMs were built and validated under present environmental conditions, forecasts of habitat suitability were undertaken using future projected environmental layers for the Arctic and North Atlantic for the same set of variables used to build the model under current conditions (Table 1). Future environmental variables were generated from projections of the ocean-sea ice model from the Nucleus for European Modelling of the Ocean (NEMO) forced with the input from the Model for Interdisciplinary Research on Climate (MIROC5) (Madec 2008; Watanabe et al. 2010). In this study, an RCP4.5 emission scenario was selected since it represents an intermediate greenhouse emission (temperature anomaly of 2.4 °C by 2100) (Moss et al. 2008) and stabilization scenario resulting from the implementation of appropriate mitigation strategies (Clarke et al. 2007). The environmental variables generated through this climate model had higher resolution (1/4° in general, ~1/8° in Hudson

Bay and ~1/18° in the Canadian Archipelago) than the ones used for building and training the SDMs'. The climate model begins in 2006 and projects environmental changes in the ocean and sea ice until 2050. Two-time series were used in the SDMs: the average across years for 2006–2015 to represent the present, and 2045–2050 to project into the future.

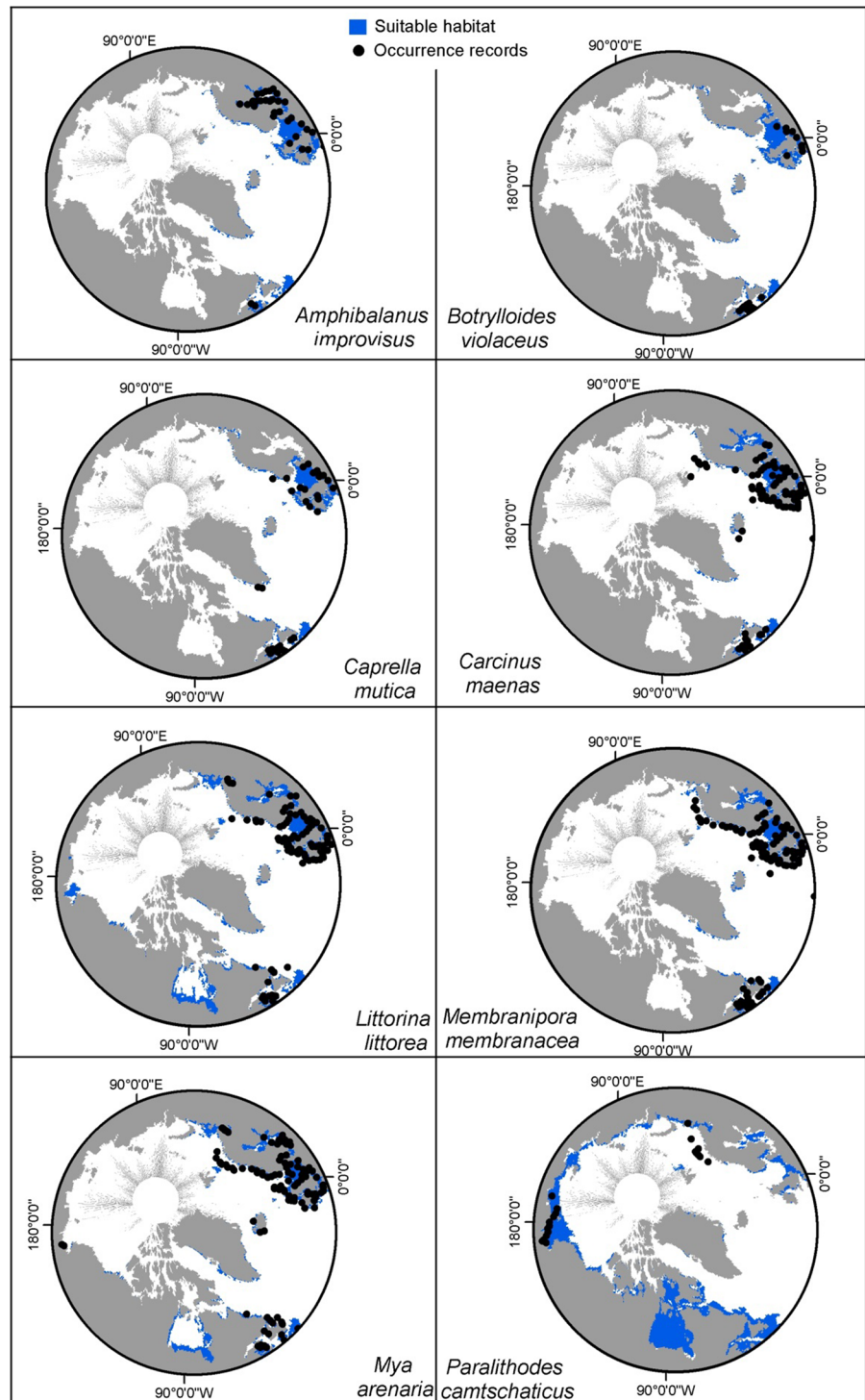
Latitudinal shifts in forecasted suitable habitat between present and future were spatially analyzed using ArcMap v10.2 to calculate percentage change in the area of habitat suitability (km²) and illustrate suitable areas in: (i) only the present, (ii) only the future and (iii) both present and future timeframes.

Results

Habitat suitability in the present

Based on model projections, all species had suitable habitat in their known ranges. Suitable habitat for all eight species was also projected in other locations where the species are not known to currently occur, indicating that existing environmental conditions are suitable for those species elsewhere, particularly in

Fig. 1 Habitat suitability projected for the Arctic and North Atlantic Oceans under current environmental conditions. Suitable habitat (shown in *blue*) is based on threshold values and occurrence records are shown as *black dots*



more northerly locations including Greenland, northern Asia, Iceland, and in some cases, northern Europe and the Canadian Arctic (Fig. 1). Under current

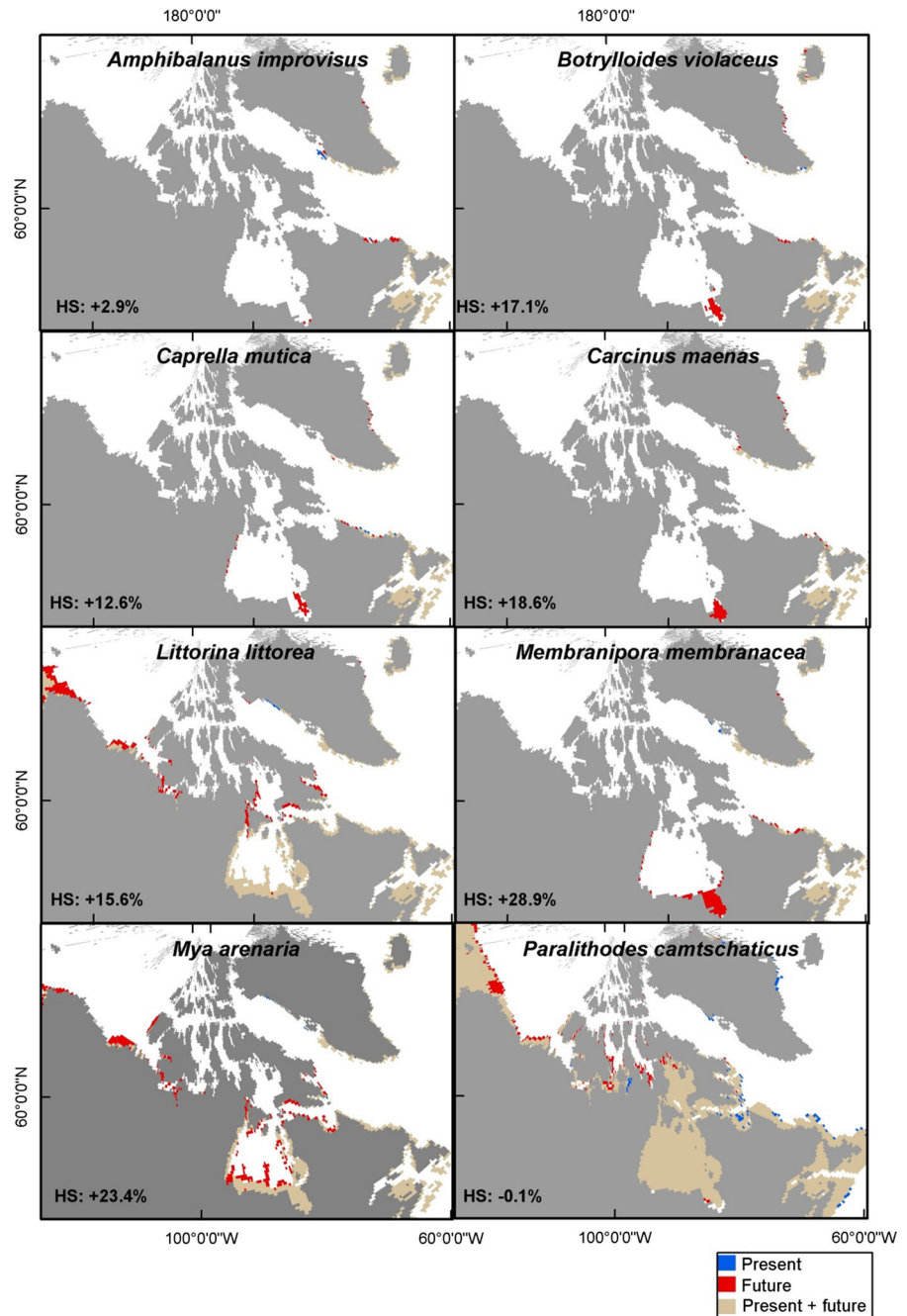
environmental conditions, the Hudson complex and Beaufort Sea regions of the Canadian Arctic are predicted to be suitable for *L. littorea*, *M. arenaria* and

P. camtschaticus, however suitable habitat for *M. membranacea* and *C. mutica* only extended to just north of Labrador and for the remaining species to south eastern Labrador (Fig. 1).

Latitudinal shifts in the future

Based on estimated potential latitudinal changes in habitat suitability under future climate warming, suitable habitat was projected to increase for all species towards the Canadian Arctic (Fig. 2). Even though all species showed a poleward shift, there were species-

Fig. 2 Habitat suitability projected for the Canadian Arctic under current and future environmental conditions. Percentage of gain (+) or loss (−) in habitat suitability (HS) is shown for each species. Suitable habitat is based on threshold values. Blue, red, and light brown areas correspond to suitable habitats in the present, future, and both in the present and in the future, respectively



specific differences in the magnitude and regions of distributional shifts. For example, future suitable habitats for *L. littorea*, *M. arenaria* and *P. camtschaticus*, were mostly extensions of regions that were already predicted to be suitable under present environmental conditions. In contrast, for the remaining species, new suitable habitats were forecasted in the Canadian Arctic and other northern regions only in the future, together with some extended regions of suitable habitat where they are already present. The Hudson Complex was one of the most prominent new suitable regions under future environmental conditions.

All species showed gains in habitat suitability in the future with the exception of *P. camtschaticus*. The percentage gain in area of suitable habitat between the present and future models was highest for *M. membranacea* and *M. arenaria* (+28.9 and +23.4% respectively), and the lowest for *P. camtschaticus* (−0.1%), which showed a small loss in percentage of suitable habitat (Fig. 2). Values of loss and gain in habitat are restricted to the region that can be seen in Fig. 2.

Model evaluation

All models had high values of AUC (>0.9) and low values of error rates (Table 2) providing a high confidence in their predictive power. The maximum training sensitivity plus specificity thresholds used were also low for all species ($P < 0.0001$) (Table 2). The analysis of unimodal shape environmental response curves indicated that environmental conditions were within suitable ranges for each of the species modelled.

Table 2 Model parameters and evaluation indicators

Species	AUC	SD	Threshold
<i>Amphibalanus improvisus</i>	0.958	0.023	0.1641
<i>Botrylloides violaceus</i>	0.975	0.017	0.0802
<i>Caprella mutica</i>	0.985	0.014	0.1986
<i>Carcinus maenas</i>	0.935	0.024	0.1694
<i>Littorina littorea</i>	0.978	0.008	0.039
<i>Membranipora membranacea</i>	0.975	0.006	0.1505
<i>Mya arenaria</i>	0.968	0.018	0.0591
<i>Paralithodes camtschaticus</i>	0.984	0.005	0.0364

AUC area under the curve, SD standard deviation, and threshold values obtained for each species

Most of the environmental variables were found to be inside their training ranges, with the exception of two regions, the Baltic Sea and the high Arctic Circle, where sea surface temperature and salinity were outside the range present in the training data. Predictions in these locations should be treated with caution.

The variables that were the most important for the majority of species were mean and maximum sea surface temperature, sea ice concentration and in several cases maximum sea surface salinity, but *P. camtschaticus* differed from other species with maximum bottom temperature and mean bottom salinity being most important (Table 1). However, maximum sea surface temperature and sea ice concentration were highly correlated ($R > 0.7$). A decision was made to retain sea ice over maximum sea surface temperature given that other sea surface temperature values were considered important and thus already included in the models.

Discussion

Regional and species-specific models like the one used in the present study can aid in the identification of areas of suitable habitat for high threat species to allow for more focused AIS monitoring and research efforts. The SDM performed in this study identified suitable habitat for a suite of potential ship-mediated aquatic invasive species in locations where these species are not currently known to occur. Suitable areas for establishment in the Canadian Arctic, especially in the Hudson Complex, were identified for three of the eight species modelled. This indicates current potential for successful introduction of high risk AIS in this region. With projected changes in climate, habitat was forecasted to be suitable for all eight species in at least some regions of the Canadian Arctic by 2050. Although the complete suite of species used in this study showed a poleward latitudinal shift in suitable habitat by mid-century, the extent varied among species. These results, based solely on environmental factors affecting habitat suitability, indicate that there is a probability of establishment for a subset of cold-adapted AIS that will increase with time in Arctic regions in general and in the Canadian Arctic in particular. Although overall introduction risk for the Canadian Arctic is currently low compared to higher traffic regions such as the Atlantic or Pacific coasts, it

has been predicted to be relatively high on a per transit basis (Casas-Monroy et al. 2015), particularly when considered in light of coastal domestic sources in the Arctic and Northwest Atlantic (Chan et al. 2013; Tremblay 2017). This risk will be further accentuated if we consider that maritime shipping activity is increasing in the Canadian Arctic (Pizzolato et al. 2014) and that at wider scale, future Arctic shipping is predicted to grow, increasing propagule pressure and the likelihood for transport of new species to accessible areas (Smith and Stephenson 2013; Miller and Ruiz 2014).

Suitable habitats for all modelled species were identified in locations outside their occurrence records, predominantly to the north, in agreement with other studies (Cheung et al. 2009, 2011; Chust et al. 2013). These results suggest that habitat conditions are suitable not only where the species have been recorded, but also beyond it. This may be due to limitations in extent of surveyed areas, sampling effort and/or under-reporting of occurrences (Rocchini et al. 2011), however it may also be partly explained by biotic interactions, dispersal limitation of species and niche size (Pulliam 2000). This finding is also consistent with the fact that invasive populations are frequently able to occupy new environments relative to their native ranges (Compton et al. 2010). In the present study, habitat was projected to be suitable in the Canadian Arctic under current environmental conditions for the Periwinkle *L. littorea*, the Soft-shell Clam *M. arenaria* and the Red King Crab *P. camtschaticus*. The former is well established in the Gulf of St-Lawrence as well as in cooler waters along Newfoundland's coast, and there are records of the species along the Northeastern coast of North America since the 1800 s (Chapman et al. 2007). The most supported hypotheses of introduction of the Periwinkle in North America is the transport by rock ballast and intentional transportation as a food resource (Brawley et al. 2009). In the case of *M. arenaria*, there are coastal distribution records in other cold water regions such as Labrador, Iceland and Alaska (Morgan et al. 1978). The Soft-shell Clam has become a successful invader by natural migration, through aquaculture and transportation by ballast water (Strasser 1998). Both of these species have long-lived feeding planktonic larvae in their life cycles and are currently present in ecoregions connected to the Canadian Arctic via vessels that may transport

organisms through hull fouling and/or ballast water (Chan et al. 2012). In contrast, *P. camtschaticus* has been intentionally released in areas where it is currently established to create an economic resource (Orlov and Ivanov 1978) and there are no known records of ballast water transport to date. Nevertheless, larvae could be transported in ballast water (Jørgensen and Nilssen 2011). Given that this species is distributed in the North Pacific and Bering Sea (Jørgensen and Nilssen 2011) there is potential for future transport and introductions to the Canadian Arctic through new expected shipping routes such as the Northwest Passage (Smith and Stephenson 2013; Miller and Ruiz 2014). Also of concern is that the projected habitat suitability for this species encompasses a vast portion of the study area.

The present study is difficult to compare with others given that Arctic regions have not been widely addressed concerning threats of specific AIS and projected habitat suitability. For most of the AIS considered here, this is the first time that SDM has been done for the Arctic. However, the Green Crab *C. maenas* and the Bay Barnacle *A. improvisus* have been more extensively studied and can be considered here for discussion. Concurrent with the findings in the present study, Ware et al. (2015) also forecasted that by mid-century the environmental conditions will be suitable in the southern region of Hudson Bay for both of these species. Similarly, de Rivera et al. (2011) also found wide ranges of suitable habitat for both species north of their current distribution when modelled for Alaskan coasts under global warming conditions. However, at a global scale, it has been predicted that at least for the Green Crab, the introduction likelihood is very low given that the species is likely to die in transit due to the long distances between major world ports and most high-latitude ports (Crafton 2014). Though, at a regional scale, Canadian Arctic ports receive domestic ships that come from nearby regions where the species is present (e.g., Atlantic Canada – Eastern Arctic) (Chan et al. 2012), thus likelihood of survival during transport is expected to be higher. Moreover, risk is expected to increase in the future due to greater shipping activity linked with global warming, a longer open water period, and expanded resource exploitation (Smith and Stephenson 2013; Gavrilchuk and Lesage 2014; Pizzolato et al. 2014; Ware et al. 2014; Casas-Monroy et al. 2015). Indeed, the number of shipping transits in the Canadian Arctic

has already increased substantially in the last few years (Ruffilli 2011).

Global warming could also provide new opportunities for species introductions to areas where they are not able to survive currently (Walther et al. 2009). Poleward shifts in habitat suitability for all modelled species were projected by mid-century with new regions becoming suitable, especially in the Hudson Complex of the Canadian Arctic. This increases the likelihood of introduction in the future given that most of the species modelled in this study are present or established in ports that are connected to the major Canadian Arctic ports (Chan et al. 2012). These findings are consistent with other studies that have forecasted future poleward shifts of marine fish, zooplankton, seagrass and benthic invertebrates (Cheung et al. 2009; Beaugrand et al. 2010; Chust et al. 2013; Valle et al. 2014; Villarino et al. 2015; Wisz et al. 2015). Forecasted poleward shifts in the current modelling study could be even more extreme than our predictions in cases where species have thermo-tolerances that are greater than what known occurrences would suggest. For example experimental evidence on thermo-tolerance of *C. maenas* has shown that it can tolerate thermal conditions year round beyond what its current range limits would suggest (Kelley et al. 2013). Similar testing and modelling in other invasive species has shown that temperature is the most influential factor for habitat suitability (Capinha and Anastácio 2011). This is consistent with the results of the present study, where temperature was one of the environmental variables with most influence on the SDMs.

Seven of the eight modelled species were forecasted to have positive increases in the total areal extent of the studied region of future suitable habitat, consistent with estimated shifts for other marine organisms under climate change scenarios (Cheung et al. 2009; Valle et al. 2014). The only exception was *P. camtschaticus* which exhibited a loss in future habitat suitability of 0.1% or essentially no net difference between the projected habitat suitability in the present compared to the future. The small decrease in habitat suitability of the Red King Crab may be explained by the extensive predicted habitat suitability under current environmental conditions for this species and that being cold-water adapted, warming waters due to climate change may decrease suitable habitat (Cheung et al. 2009, 2011). There

are also other factors such as physical barriers and food availability than could limit distribution and contribute to loss of suitable habitat (Gerasimova 1997; Weinert et al. 2016), but they have not been included in the present study.

The use of SDM is valuable for evaluating how climate change can affect future biodiversity. These models should be viewed as a first approximation of the potential impact of climate-induced habitat change on biodiversity (Pearson and Dawson 2003). MaxEnt has been applied broadly in terrestrial species (Graham and Hijmans 2006; Monterroso et al. 2009; Young et al. 2009; Yates et al. 2010), but its use in marine species is recent and limited (Reiss et al. 2011; Robinson et al. 2011; Meißner et al. 2014; Lowen et al. 2016; Weinert et al. 2016), particularly for forecasting benthic invertebrate species distributions under climate change scenarios (de Rivera et al. 2011; Weinert et al. 2016). The use of predictive modelling methods in the marine environment has increased thanks to the recent improvements in the availability of global environmental data. The use of this tool can provide information to help manage resources in the face of increasing anthropogenic pressures affecting the marine realm (Reiss et al. 2014). However, it should be recognized that modelling studies are limited by the factors that are included in the analysis. Understanding the restrictions of SDMs can highlight the utility and the applicability of results in marine systems. Given that the projections of our study were in a different region from the species source area and that the results were projected into the future, there were several considerations in interpretation of the model results including: (1) the use of abiotic factors only, (2) the selection of environmental variables used, (3) the choice of the model used for the SDM analysis, and (4) the climate change projection models used to predict future environmental conditions.

Biotic interactions were not addressed in our SDMs since they only related species occurrence to abiotic factors (Guisan and Zimmermann 2000). Even though the importance of the biotic interactions in shaping the spatial distributions of a species is recognized (Wisz et al. 2013), it was not possible to include this variable in the present study due to lack of information. Much more research effort on basic ecology and biogeography is required to cover the inclusion of biological factors in general, and an even higher effort is needed for coastal Arctic marine communities given the

paucity of data (Reiss et al. 2014). Since the objective of the present study was to project species distributions into a new environment as well as into the future, it was difficult to predict what the possible future interactions might be. Furthermore, there are studies indicating that at a wider scale, species distributions are dominated and influenced mainly by abiotic factors (Pearson and Dawson 2003). In fact, Snickars et al. (2014) found that hydrographic variables were the most important predictors for modelling benthic species.

The selection of environmental variables is an important step in model building for each species. Including all available variables can result in a lower predictive power (Bradie et al. 2015) due to collinearity and model overparameterization (Tyberghein et al. 2012). In this study, correlation between variables was calculated and accounted for in the analysis of each species. For example, only a few variables (mean sea surface temperature, sea ice concentration and bathymetry) contributed to explaining known distribution patterns for *C. maenas*, thus only these variables were included in the model for this species. For the majority of species in the current study, temperature and ice cover were the main variables included for modelling. This is supported by experimental and modelling studies showing that temperature is the most important variable in predicting the locations where invasive species, such as the Green Crab, may establish (Compton et al. 2010; Kelley et al. 2013). In contrast, our modelling results only occasionally showed salinity as an important variable in predicting invasive ranges. This is not surprising given that we modelled mainly euryhaline species for which salinity has been shown to play only a minor role (Compton et al. 2010). Furthermore our study only encompassed marine habitat which has a relatively narrow range of salinities so this variable would be expected to have less importance in the modelling of saltwater adapted species.

MaxEnt is one of the best algorithms for projecting species range shifts under future climate change scenarios (Hijmans and Graham 2006). However, predicted distributions should be treated with caution since they involve extrapolation to novel combinations of environmental variables (Merow et al. 2013). Projecting future changes inevitably comes with a degree of uncertainty (Wenger et al. 2013). Clearly, the selected emission scenario(s) and prediction

year(s) can influence the outcomes of SDMs. The NEMO coupled ocean-sea ice model also has limitations, including those associated with horizontal spatial resolution. Further, both the coupled ocean-sea ice and the atmospheric forcing models are expected to have limitations in future projections particularly in the areas of hydrological forcing of the system and the response of sea ice type and concentration. The version of NEMO used in this study is considered appropriate for processes with horizontal spatial scales exceeding 10 km, however, the low spatial resolution of the atmospheric variables used to force NEMO may introduce bias in high-resolution ice-ocean simulations (Hu and Myers 2014).

Studies in prediction of invasive species in the Arctic are rare (de Rivera et al. 2011; Ware et al. 2015), making this study a valuable contribution to the prediction and understanding of the future changes in this region. Predictive studies like this one can provide information for early warning systems, help identify vulnerable habitats in marine environments associated with shipping activity and direct invasive species monitoring efforts when information is scarce (Reiss et al. 2014). The use of distribution models such as MaxEnt have been shown to perform well in the marine environment (Reiss et al. 2011; Meißner et al. 2014; Gallardo et al. 2015; Weinert et al. 2016) and thus provide a tool with results that can be of great utility. This study reveals that the Canadian Arctic and northern high-latitudes in general are already suitable for some potential high risk non-indigenous species and that this suitability will only continue to increase. These findings provide an excellent foundation for further work including more detailed risk assessment studies that combine habitat suitability results with information on port activity, shipping patterns and vectors (Goldsmit 2016). Future efforts should combine potential for establishment together with propagule pressure for more precise estimates of likelihood of arrival via shipping and potential impact of individual species. These types of assessments can provide valuable information regarding where and how to monitor species of concern.

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