What and where? Predicting invasion hotspots in the Arctic marine realm

Abstract:	The risk of aquatic invasions in the Arctic is expected to increase with climate warming, greater shipping activity and resource exploitation in the region. Planktonic and benthic marine aquatic invasive species (AIS) with the greatest potential for invasion and impact in the Canadian Arctic were identified and the 23 riskiest species were modelled to predict their potential spatial distributions (using Maximum Entropy) at pan-Arctic and global scales. Modelling was conducted under present environmental conditions and two intermediate future (2050 and 2100) global warming scenarios. Hotspots – regions of the Arctic where habitat is predicted to be suitable for a high number of potential AIS – were located in Hudson Bay, Northern Grand Banks/Labrador, Chukchi/Eastern Bering Seas, and Barents/White Seas, suggesting that these regions could be more vulnerable to invasions. Most benthonic and planktonic organisms showed a trend for a positive poleward shift in suitable habitat in the future. At a pan-Arctic scale, planktonic and, in particular, benthic organism, showed positive predicted suitable habitat gains under future conditions. However, at the global scale, habitat loss was predicted in more tropical regions for some taxa, particularly planktonic species. Results from the present study can help prioritize management efforts in the face of climate change in the Arctic marine ecosystem. Moreover, this particular approach provides information to identify present and future high-risk areas for AIS in response to global warming.

1   **What and where? Predicting invasion hotspots in the Arctic marine realm**

2   **Running head:** Arctic marine invasion hotspots

3   **Authors:** Jesica Goldsmit1[1,2], Christopher W. McKindsey[1], Philippe Archambault[2], Kimberly L.

4   Howland[3]

5

6   [1] Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, Quebec, Canada.

7   [2] Quebec-Ocean, Takuvik, Laval University, Department of Biology, Science and Engineering
8   Faculty, Quebec City, Quebec, Canada

9   [3] Fisheries and Oceans Canada, Arctic Research Division, Freshwater Institute, Winnipeg,
10   Manitoba, Canada

11

12   **Corresponding author**: jesica.goldsmit@dfo-mpo.gc.ca, jesicagoldsmit@gmail.com

13

14   **Keywords**: Aquatic invasive species, risk of invasion, shipping, species distribution model, habitat

15   suitability, MaxEnt, climate warming.

16

17   **Paper type:** Primary research article

18

19

20

21

Abstract

The risk of aquatic invasions in the Arctic is expected to increase with climate warming, greater shipping activity and resource exploitation in the region. Planktonic and benthic marine aquatic invasive species (AIS) with the greatest potential for invasion and impact in the Canadian Arctic were identified and the 23 riskiest species were modelled to predict their potential spatial distributions (using Maximum Entropy) at pan-Arctic and global scales. Modelling was conducted under present environmental conditions and two intermediate future (2050 and 2100) global warming scenarios. Hotspots – regions of the Arctic where habitat is predicted to be suitable for a high number of potential AIS – were located in Hudson Bay, Northern Grand Banks/Labrador, Chukchi/Eastern Bering Seas, and Barents/White Seas, suggesting that these regions could be more vulnerable to invasions. Most benthonic and planktonic organisms showed a trend for a positive poleward shift in suitable habitat in the future. At a pan-Arctic scale, planktonic and, in particular, benthic organism, showed positive predicted suitable habitat gains under future conditions. However, at the global scale, habitat loss was predicted in more tropical regions for some taxa, particularly planktonic species. Results from the present study can help prioritize management efforts in the face of climate change in the Arctic marine ecosystem. Moreover, this particular approach provides information to identify present and future high-risk areas for AIS in response to global warming.

Introduction

Invasive species are considered to be one of the main drivers of biodiversity loss and recent extinctions (Bellard, Cassey, & Blackburn, 2016; Blackburn, Bellard, & Ricciardi, 2019). In

44   addition, they may cause great ecological and economic impacts and, in some cases, even impact

45   human health (Cook, Payne, MacLeod, & Brown, 2016; Hewitt, Campbell, & Gollasch, 2006;

46   Ricciardi, Hoopes, Marchetti, & Lockwood, 2013; Simberloff et al., 2013). Estimates suggest that

47   their presence may entail costs of up to 12% of the gross domestic product of affected countries

48   (Marbuah, Gren, & McKie, 2014).

49   The greatest numbers of aquatic invasions have been documented in temperate regions (Ruiz &

50   Hewitt, 2009). However, high latitude areas are generally warming at a faster rate than other areas

51   (Overland et al., 2018) and various climate change scenarios predict that the ice-free season will

52   continue to lengthen (Barnhart, Miller, Overeem, & Kay, 2016; Jahn, 2018; Niederdrenk & Notz,

53   2018; Sigmond, Fyfe, & Swart, 2018). If warming is limited to 1.5 °C, as proposed in the Paris

54   Agreement, ice-free summers in the Arctic will continue to rise even if global warming ceases

55   (Screen, 2018). Moreover, temperature extremes at regional scales could be much greater than the

56   global mean with some models predicting a rise greater than 7°C in the Arctic with a global average

57   increase of only 1.5°C at peak warming (Seneviratne et al., 2018). Aquatic invasions in Arctic

58   ecosystems have thus been identified as an emerging issue (Ricciardi et al., 2017) as the area is

59   becoming increasingly susceptible due to regional climate change and associated increases in

60   shipping activity and resource exploitation (Melia, Haines, & Hawkins, 2016; Miller & Ruiz, 2014;

61   Niimi, 2004; Smith & Stephenson, 2013).

62   One of the leading causes of increasing invasion risk is the expansion of transportation networks

63   (Early et al., 2016). Aquatic transportation, in particular, is highly relevant given that the shipping

64   network is responsible for 90% of global trade (Kaluza, Kölzsch, Gastner, & Blasius, 2010; Xu et

65   al., 2014), with ballast water and biofouling being the main vectors for transport of organisms

66   (Bailey, 2015; Drake & Lodge, 2007; Ruiz, Fofonoff, Steves, & Carlton, 2015). Consequently,

67   marine taxa are one of the dominant groups that are unintentionally introduced at a global scale

68   (Turbelin, Malamud, & Francis, 2017), and are predicted to contribute up to a 3- to 20-fold increase

69   in global invasion risk (Sardain, Sardain, & Leung, 2019). In the Arctic, almost half of all known

70   marine invasions to date have been due to shipping activities as a single-pathway means of

71   transport (Chan et al., 2019). Greater opportunities for aquatic invasive species (AIS) transport are

72   expected in the future as shipping traffic is also projected to grow given predicted ice-free

73   conditions that will allow a more direct shipping corridor between the Pacific and the Atlantic

74   oceans (Melia et al., 2016; Miller & Ruiz, 2014; Smith & Stephenson, 2013), reducing transit

75   distances by up to 24% relative to current shipping routes (Buixadé Farré et al., 2014).

76   A recent study tallied a total of 34 non-indigenous species for the entire Arctic, with shipping

77   activity being one of the main purported vectors (Chan et al., 2019). In addition, non-indigenous

78   species have been identified from both ships *en route* to the Arctic and in the environment to which

79   they arrive, highlighting the risk of new invasions in this region (Ashton, Riedlecker, & Ruiz,

80   2008; Chan, MacIsaac, & Bailey, 2015; Dispas, 2019; Gíslason et al., 2014; Golder, 2018; Laget,

81   2017; Lambert, Shenkar, & Swalla, 2010; Svavarsson & Dungal, 2008; Tremblay, 2017; Zimina,

82   2014). Further, the origin of many newly observed species in Arctic locations is unknown and they

83   have thus been classified as cryptogenic (Goldsmit, Howland, & Archambault, 2014; MacDonald,

84   Bluhm, Iken, Gagaev, & Strong, 2010). These numbers are high compared to the other polar

85   environment – the Antarctic – where there are no established AIS populations to date and only five

86   non-indigenous marine species have potentially arrived through human activities (McCarthy,

87   Peck, Hughes, & Aldridge, 2019). Although Hughes et al. (2020) suggest marine taxa pose the

88   greatest potential invasion risk to the Antarctic Peninsula relative to other types of organisms.

89   Commercial shipping is not expected to increase in the region and resource exploitation is

90   restricted under the Antarctic Treaty. However, the shortening sea ice season and increased

91   shipping traffic due to tourism may increase risks of invasions (Ruiz & Hewitt, 2009; Hughes &

92   Ashton, 2017; Jabour, 2017).

93   Given the vast size and remoteness of the Arctic, few baseline studies have been conducted

94   (Archambault et al., 2010; CAFF and PAME, 2017; Piepenburg et al., 2011) and the resident fauna

95   are thus poorly described relative to more accessible locations elsewhere in the world (Costello et

96   al., 2017). Consequently, simply identifying newly arriving species can be challenging. To

97   improve this detection gap, new methods and identification techniques are being used in remote

98   regions, such as environmental DNA and metabarcoding (E. A. Brown, Chain, Zhan, MacIsaac,

99   & Cristescu, 2016; Chain, Brown, MacIsaac, & Cristescu, 2016; Lacoursière-Roussel et al., 2018;

100 Leduc, 2019). In addition, methods such as species distribution modelling (SDM) may be used to

101 predict the potential distribution of suitable habitat for AIS (Barbosa & Schneck, 2015; Barbosa,

102 Schneck, & Melo, 2012), including for high risk AIS in areas of concern such as in high latitude

103 regions (Byrne, Gall, Wolfe, & Agüera, 2016; de Rivera, Steves, Fofonoff, Hines, & Ruiz, 2011;

104 Goldsmit et al., 2018; Ware et al., 2016). Modelled results can inform pre-invasion management

105 policies to avoid new arrivals and, potentially, subsequent issues with the establishment of the

106 species and the consequent need to deal with eradication actions (Floerl, 2014; Locke & Hanson,

107 2009).

108 Although future invasions are expected to be enhanced by climate change (Bellard et al., 2013),

109 predicted SDM-modelled distributions of environmental suitability for invasive species have been

110 understudied in this context (Bellard, Jeschke, Leroy, & Mace, 2018), particularly for marine

111 ecosystems (Barbosa et al., 2012; Bellard et al., 2018). Nevertheless, SDM tools such as MaxEnt,

112 have been successfully applied to marine species (Lowen, McKindsey, Therriault, & DiBacco,

113   2016; Meißner et al., 2014; Reiss, Cunze, König, Neumann, & Kröncke, 2011; Robinson et al.,

114   2011; Weinert et al., 2016; Robinson, Nelson, Costello, Sutherland, & Lundquist, 2017), including

115   forecasting distributions under global change scenarios in high latitude regions (de Rivera et al.,

116   2011; Goldsmit et al., 2018; Jueterbock, Smolina, Coyer, & Hoarau, 2016).

117   Regions where many species coincide are known as biodiversity hotspots and may provide

118   information about species richness, endemism and/or threatened taxa, and may be of importance

119   for conservation (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Based on this

120   concept, potential invasion hotspots may be identified as areas that are hospitable to and thus at

121   risk to invasion by a greater than average numbers of AIS for a given region (Ruiz, Fofonoff,

122   Steves, Foss, & Shiba, 2011). The use of a biological invasions hotspot approach has been limited

123   to date (but see Bellard, Leroy, Thuiller, Rysman, & Courchamp, 2016; Catford, Vesk, White, &

124   Wintle; 2011; Ibanez, Silander Jr, Allen, Treanor, & Wilson, 2009, O'Donnell et al., 2012; Torres

125   et al., 2018) with few studies in marine environments. Most analyses of AIS hotspots in marine

126   ecosystems have focused on vectors (Davidson et al., 2010; Drake & Lodge, 2004; Pearce, Peeler,

127   & Stebbing, 2012; Semmens, Buhle, Salomon, & Pattengill-Semmens, 2004; Tidbury, Taylor,

128   Copp, Garnacho, & Stebbing, 2016) and current AIS richness (Edelist, Rilov, Golani, Carlton, &

129   Spanier, 2013; Katsanevakis et al., 2014; Kelly, Leach, Cameron, Maggs, & Reid, 2014; Rilov &

130   Galil, 2009; Ruiz et al., 2011; Verlaque, 2001), although a few have also predicted hotspots of

131   potential marine biological invasions (Cheung et al., 2009; Gallardo, Zieritz, & Aldridge, 2015;

132   Jones & Cheung, 2015).

133   This study aims to identify potential high risk AIS and predict hotspots of invasion for these under

134   current and projected future environmental conditions in Arctic environments. Cold-tolerant

135   planktonic and benthic AIS were scored to produce a list of the top species with the highest relative

136   likelihood of invasion and impact, since these ecological groups include the dominant known

137   highest risk marine invasive species (Molnar, Gamboa, Revenga, & Spalding, 2008). The

138   distribution of suitable habitats for this set of species was then modelled to predict regions of

139   overlap under current and future projected conditions, thus identifying hotspots of potential

140   biological invasions. Although all analyses were done globally, there was an emphasis at the

141   Canadian and pan-Arctic scales.

142

143   **Materials and methods**

144   <u>Study region</u>

145   Distribution model outputs were produced with global coverage to allow evaluation of global and

146   pan-Arctic patterns although analyses were focussed on the potential highest-risk species for the

147   Canadian Arctic. The rationale for this approach is the vast expanse of the Canadian Arctic

148   (Archambault et al., 2010), its vulnerability to invasion (Chan, Bailey, Wiley, & MacIsaac, 2013;

149   Chan, MacIsaac, & Bailey, 2016; Goldsmit et al., 2018; Goldsmit, McKindsey, Archambault, &

150   Howland, 2019), the ambiguous status of new species that have potentially arrived through human

151   transport (Goldsmit et al., 2014), and the unprecedented warming that it has experienced over the

152   last decade (Bush & Lemmen, 2019). The region is immense, accounting for eight of 19 Arctic

153   ecoregions (Figure 1) (Spalding et al., 2007). In fact, Canada has the longest coastline in the world,

154   the majority of which is situated in the Arctic (it accounts for almost 2,000,000 km^2 of the

155   territorial sea) (Archambault et al., 2010). Even though few AIS have been identified in Canada

156   relative to other Arctic regions, Chan et al. (2019) suggest that this accounts for ca. 20% of all AIS

157   recorded from marine Arctic waters. At the same time, additional species have been identified for

158   the first time in the Canadian Arctic using molecular tools (E. A. Brown et al., 2016; Chain et al.,

159 <mark>2016; Lacoursière-Roussel et al., 2018</mark>) or identified as cryptogenic as their origin is unclear

160 (Goldsmit et al., 2014). Moreover, Canadian Arctic ports (especially those in the Hudson

161 <mark>Complex</mark>) (Figure <mark>1</mark>) have been identified as being of moderate to high ecological risk of invasion

162 since they could provide suitable habitat for various AIS (Goldsmit et al., 2018; Goldsmit, Nudds,

163 et al., 2019) and there is evidence that a number of <mark>non-indigenous</mark> species are already being

164 transported by shipping traffic into the region (Chan et al., 2015; Dispas, 2019; Laget, 2017;

165 Tremblay, 2017).
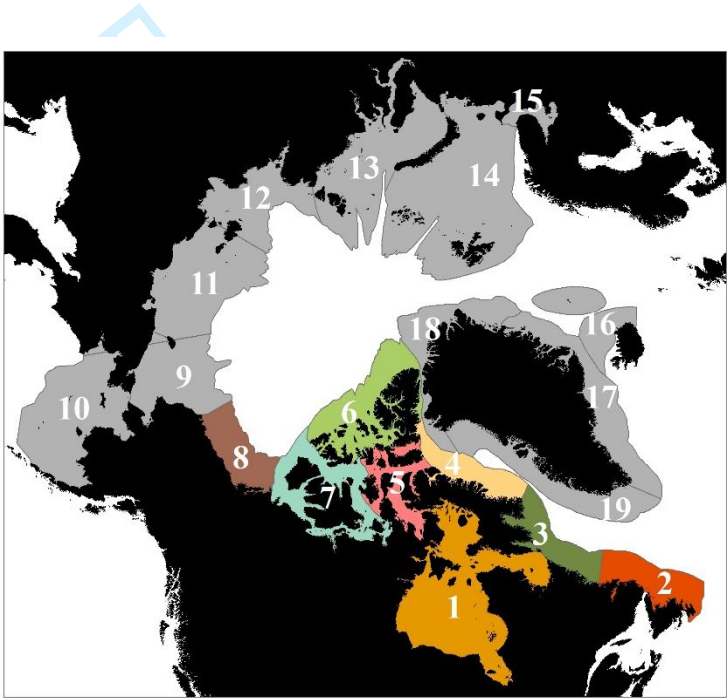

166

167 <mark>Figure 1: Arctic ecoregions as delineated by Spalding et al. (2007). Canadian Arctic ecoregions</mark>
168 <mark>are coloured. 1: Hudson Complex; 2: Northern Grand Banks-Southern Labrador; 3: Northern</mark>
169 <mark>Labrador; 4: Baffin Bay-Davis Strait; 5: Lancaster Sound; 6: High Arctic Archipelago; 7:</mark>
170 <mark>Beaufort-Amundsen-Viscount Melville-Queen Maud; 8: Beaufort Sea-continental coast and shelf;</mark>
171 <mark>9: Chukchi Sea; 10: Eastern Bering Strait; 11: East Siberian Sea; 12: Laptev Sea; 13: Kara Sea;</mark>
172 <mark>14: Northern and East Barents Sea; 15: White Sea; 16: North and East Iceland; 17: East Greenland</mark>
173 <mark>Shelf; 18: North Greenland; 19: West Greenland Shelf.</mark>

174

175

176

177   Species selection

178   A three-step procedure was used to select potential marine AIS (zoobenthos, phytobenthos and

179   zooplankton) for modelling (Figure S1). The majority were species that are considered AIS in

180   other regions of the world and have the possibility of being transported through shipping to the

181   Canadian Arctic; several other AIS had been previously detected in other Arctic environments.

182   These steps included: 1) pre-screening analysis and selection; 2) ranking a subset of these species

183   using a semi-quantitative screening-level risk assessment tool, the Canadian Marine Invasive

184   Screening Tool (CMIST) (Drolet et al., 2016); and 3) selecting a final list of higher risk species

185   based on CMIST.

186   The first step of the pre-screening analysis considered biological and ecological characteristics that

187   could allow a given organism to survive Arctic conditions (e.g., temperature and salinity tolerance

188   of the species needed to generally fall within the range of expected Arctic conditions) and

189   information on the potential of it arriving in the region via shipping (Figure S1.1). One hundred

190   species were thus pre-screened using a combination of data sources including published articles

191   (Chain et al., 2016; Chan et al., 2012; Chan et al., 2015; Chan et al., 2016; Geller & Ruiz, 2013;

192   Hines, Ruiz, & Fofonoff, 2000; Molnar et al., 2008; Ruiz et al., 2006; Turbelin et al., 2017; Ware

193   et al., 2016; Young, 2016), grey literature and web-based global invasive species databases such

194   as the National Exotic Marine and Estuarine Species Information System (NEMESIS;

195   www.invasions.si.edu/nemesis/), Invasive Species Compendium (www.cabi.org/isc), the

196   European Network on Invasive Alien Species NOBANIS (www.nobanis.org/) and the Global

197   Invasive Species Database GISD (www.issg.org/database).

198   A total of 31 species were identified as being of potential risk to the area using this pre-screening

199   process (Figure S1.2a). These species were then ranked to evaluate risk of invasion using CMIST

200 (Drolet et al., 2016) – a rapid screening-level risk assessment tool to quantify the risk of existing

201 or potential marine invaders in a given area. The semi-quantitative tool uses existing information

202 and expert opinion to evaluate the potential for arrival, establishment, spread, and impact by a

203 given species and has been applied in a number of eco-regions within Canada (DFO, 2017; Drolet

204 et al., 2016; A. M. Moore, Lowen, & DiBacco, 2018; Therriault et al., 2018). CMIST scores are

205 computed based on responses to 17 questions related to the likelihood and impact of invasion (see

206 Figure S1.2a). The information used to answer CMIST questions included published articles,

207 governmental reports, grey literature, and the global invasive species websites listed above for

208 each species. Expert assessor knowledge on the risk assessment areas was used to score the

209 potential impact of a given species based on its known impacts observed elsewhere and the

210 availability of suitable habitats and environmental conditions. Uncertainty is scored for each risk

211 question by assigning a qualitative score reflecting the quality of information available to answer

212 each CMIST question. A Monte Carlo randomization procedure is then used to obtain adjusted

213 risk scores that include uncertainty (Drolet et al., 2016).

214 CMIST-ranked species with medium and high mean risk scores (N=18; Table 1) were retained for

215 more detailed assessment using SDM. To this list, five potentially harmful phytoplankton species

216 were added (Table 1, Figure S1.2b). These dinoflagellate species have been found in ballast water

217 tanks and/or in ballast water exchange zones of Canadian domestic ships that discharge their water

218 in Canadian Arctic ports (Laget, 2017). All are known to have the capacity to produce toxins and

219 have been implicated in harmful algal events throughout the world (Harmful Algal Information

220 System, from the Intergovernmental Oceanographic Commission of UNESCO,

221 http://haedat.iode.org/).

222   The final species list for modelling ==thus included== a total of 23 known marine AIS or harmful algal

223   species ==from 4 ecological groups== (zoobenthos, ==phytobenhtos==, zooplankton and phytoplankton) that

224   pose potential risks for invasion in the Canadian Arctic. To simplify terminology, hereafter when

225   referring to this suite of species they will be termed as 'AIS'. (See Table S1 for information on

226   species' characteristics and impacts). ==Likewise, the term "invasion" is used to make reference to==

227   ==the complete process of a species transitioning all invasion stages (transport, arrival, establishment,==

228   ==and spread) (Lockwood, Hoopes, & Marchetti, 2007).==

229

230   Table 1: List of modelled species and the methodology for species selection. ==Ecological== groups
231   were classified as zoobenthos, ==phytobenthos==, zooplankton, and phytoplankton. Selection methods
232   were the Canadian Marine Invasive Screening Tool (CMIST) (Drolet et al., 2016), and harmful
233   dinoflagellate species found in ballast of vessels discharging in the Canadian Arctic (Laget, 2017).
234

Species	Common name	Taxa	Ecological group	Selection method	Predictors included in SDM
Amphibalanus eburneus	Ivory barnacle	Crustacea	Zoobenthos	CMIST	
Botrylloides violaceus	Violet tunicate	Tunicata	Zoobenthos	CMIST	
Botryllus schlosseri	Golden star tunicate	Tunicata	Zoobenthos	CMIST	
Carcinus maenas	Green crab	Crustacea	Zoobenthos	CMIST	
Chionoecetes opilio	Snow crab	Crustacea	Zoobenthos	CMIST	Bottom temperature
Ciona intestinalis	Vase tunicate	Tunicata	Zoobenthos	CMIST	Sea surface temperature
Littorina littorea	Common periwinkle	Mollusca	Zoobenthos	CMIST	Bottom salinity
Membranipora membranacea	Coffin box bryozoan	Bryozoa	Zoobenthos	CMIST	Sea surface salinity
Molgula manhattensis	Sea grape	Tunicata	Zoobenthos	CMIST	Ice thickness / Depth
Mya arenaria	Soft shell clam	Mollusca	Zoobenthos	CMIST	Distance to land
Paralithodes camtschaticus	Red king crab	Crustacea	Zoobenthos	CMIST	

Codium fragile **spp.** *fragile*	Dead man's fingers	Chlorophyta	Phytobenthos	CMIST	Bottom temperature Sea surface temperature Bottom salinity Sea surface salinity Ice thickness Depth Distance to land Photosynthetically active radiation Dissolved oxygen pH Minerals and nutrients (calcite, iron, nitrate, phosphate, and silicate)
Dumontia contorta	Dumont's tubular weed	Rhodophyta	Phytobenthos	CMIST	
Sargassum muticum	Japanese wireweed	Phaeophycea	Phytobenthos	CMIST	
Undaria pinnatifida	Wakame	Phaeophycea	Phytobenthos	CMIST	
Acartia (Acanthacartia) tonsa	No common name found	Copepoda	Zooplankton	CMIST	Sea surface temperature Bottom salinity Sea surface salinity Ice thickness Depth Distance to land Chlorophyll concentration Dissolved oxygen pH
Aurelia limbata	Brown-branded moon jelly	Cnidaria	Zooplankton	CMIST	
Mnemiopsis leidyi	Warty comb jelly	Ctenophora	Zooplankton	CMIST	
Alexandrium tamarense	No common name found	Dinoflagellata	Phytoplankton	Laget (2017)	Sea surface temperature Sea surface salinity Ice thickness Distance to land Photosynthetically active radiation Dissolved oxygen pH Minerals and nutrients (iron, nitrate, phosphate, and silicate)
Dinophysis caudata	No common name found	Dinoflagellata	Phytoplankton	Laget (2017)	
Dinophysis dens	No common name found	Dinoflagellata	Phytoplankton	Laget (2017)	
Gonyaulax polygramma	No common name found	Dinoflagellata	Phytoplankton	Laget (2017)	
Kryptoperidinium triquetrum	No common name found	Dinoflagellata	Phytoplankton	Laget (2017)	

235

236   Species data

237   Global scale occurrence data of marine invaders selected for modelling was compiled for both

238   native and invaded ranges using global biodiversity databases such as the Global Biodiversity

239   Information Facility (GBIF - www.gbif.org), Ocean Biogeographic Information System (OBIS -

240   www.obis.org), and invasive species lists with coordinate location information and specific

241   literature (Table S1). An effort was made to maximize the number and quality of occurrence

242   records to best predict potential distributions by doing a vast and complete search of occurrence

243   records and by checking information to find the original source of those records (García-Roselló

244   et al., 2015; Guisan, Graham, Elith, & Huettmann, 2007; Guisan, Zimmermann, et al., 2007; Lobo,

245   2008). The inclusion of both native and invaded ranges was used to improve predictions for the

246   extent of suitable habitat (Broennimann & Guisan, 2008). A single presence record was counted

247   per grid cell to decrease the possibility of over-prediction, hence, occurrence points were

248   considered at the same resolution as the corresponding environmental layers (García-Roselló et

249   al., 2015). All points were verified to ensure that they were in sea grids (and not over land). When

250   necessary, points were moved to the closest sea grid using the Near Proximity tool in ArcMap

251   v10.2.2.

252   <u>Environmental data</u>

253   Marine data layers, prepared specifically for ecological modelling, were used as environmental

254   predictors and downloaded at a global scale from Bio-ORACLE v2 (http://www.bio-oracle.org/).

255   These layers were produced with climate data describing monthly averages for the period from

256   2000 to 2014 representing recent (hereafter referred to as present) conditions (Assis et al., 2018).

257   They were obtained from pre-processed global ocean re-analyses combining satellite and *in situ*

258   observations at regular two- and three-dimensional spatial grids (Assis et al., 2018). A set of 37

259   environmental layers was used from this source comprising bottom and sea surface temperature

260   and salinity, ice thickness, chlorophyll, dissolved oxygen, pH, photosynthetically active radiation,

261   and minerals and nutrients (iron, calcite, nitrate, phosphate, and silicate) (Table 1 and Table S2).

262   Long-term maximum, minimum and mean values were used for most of the predictors when

263   available (Table S2). For example, the layer of long-term maximum temperature takes the average

264   of records that correspond to the average of the warmest months between 2000 and 2014 (Assis et

265   al., 2018). Resolution of environmental layers was 5 arcmin (approximate 9.2 km at the equator).

266   Bathymetry and land distance obtained from Aquamaps (http://www.aquamaps.org/) (Kaschner et

267   al., 2016), were also added as layers, but with a resolution of 30 arcmin (approximate 55 km at the

268   equator) (Table S2). Bottom substratum type was not included in the analysis due to the lack of

269   availability of a high-resolution global scale database, however suitable benthic habitat was

270   assumed to be present within each study region.

271   <u>Habitat suitability model</u>

272   Habitat suitability for selected AIS was modelled using MaxEnt v3.3.3k (Phillips, Anderson, &

273   Schapire, 2006), a machine learning method based on maximum entropy. It predicts the potential

274   geographic distribution of suitable habitat for species using species occurrence data (presence-

275   only) and various potential combinations of environmental data layers as input. MaxEnt is one of

276   the most widely used SDM algorithms because of its high predictive accuracy and efficiency in

277   modelling range shifts under future climate change scenarios (Bucklin et al., 2015; Elith et al.,

278   2006; Elith et al., 2011; Hijmans & Graham, 2006; Pearson, 2007). In addition, it has recently been

279   shown to outperform other modelling techniques to accurately predict the distributions of invasive

280   species (Battini, Farías, Giachetti, Schwindt, & Bortolus, 2019).

281   A limitation of using presence-only data in SDM is the effect of sample selection bias whereby

282   sampling is more intensive in some areas than others (Phillips et al., 2009). To control for this, the

283   Gaussian kernel density of sampling localities tool was used to reduce spatial sampling biases (J.

284   L. Brown, 2014). Bias files were included in model building using the SDMtoolbox package in

285 ArcGIS (J. L. Brown, 2014). This method assigns a higher weighting to presence-only data points

286 with fewer neighbors in the geographic landscape for inclusion in the SDM.

287 Model predictive power was evaluated using cross-validation with 70% of the occurrence points

288 chosen randomly and used to train the model and the other 30% to test it (Araújo, Pearson, Thuiller,

289 & Erhard, 2005). In this validation procedure, data were partitioned by a random process of k=500

290 iterations of training and validation (Hijmans, 2012). Both native and invaded ranges were used

291 for training and evaluating the models (Verbruggen et al., 2013), since invaded area provides

292 valuable information on species' tolerance to climatic conditions that may not be present in its

293 native range (Marcelino & Verbruggen, 2015). Training points were selected by random seeding

294 with the convergence threshold set at 0.00001. The hinge feature was used as it produces complex

295 yet smoothed and ecologically meaningful response curves and has been shown to improve model

296 performance (Merow, Smith, & Silander, 2013; Phillips & Dudík, 2008). MaxEnt generates

297 background data to compare with known presence points. This study used the default option, which

298 generates 10000 random background points.

299 Initial models were run for each species individually with pre-selected environmental layers. The

300 selected layers were those known to typically be the most important limiting factors for each type

301 of taxa, to have been used in other modelling studies (Table 1) (Barnes, 1999; Belanger et al.,

302 2012; Chust et al., 2016; Cusson, Archambault, & Aitken, 2007; Gallardo et al., 2015; Jensen,

303 Mousing, & Richardson, 2017; Leidenberger, Obst, et al., 2015; Wagner, 1977), or that were

304 identified as being important by personal communications with taxonomic experts (G. Winkler

305 pers. comm. 2017, and A. Rochon pers. comm. 2018). After the first run, layers with a relative

306 contribution score of <4% were excluded (Jueterbock et al., 2016). Special attention was made to

307 layers that were highly correlated (correlation coefficient $\geq$ 0.7) (Dormann et al., 2013), as

308   correlated predictors can lead the model to produce erroneous response curves to layers that do not

309   reflect species physiological tolerances (Marcelino & Verbruggen, 2015). Correlation was

310   calculated using the SDMtoolbox (J. L. Brown, 2014) (Table S2) and only one such correlated

311   predictor – that with the highest contribution to the modelling exercise – was retained for model

312   construction. As per Goldsmit et al. (2018), predictors were identified by evaluating the

313   combination of: a) the response curves for each species – to evaluate if the predictor behaves in a

314   biologically meaningful way in the model (Marcelino & Verbruggen, 2015); b) a species-specific

315   Jackknife test – to evaluate the contributions of the various parameters and analyse importance of

316   variables; and c) the estimates of the contribution of each variable to model prediction. A minimum

317   of three environmental layers was included in each model. Each species was then modelled again

318   with the selected layers (Table S3). Model performance was evaluated as the area under the curve

319   (AUC) and true skill statistic (TSS). In presence-only models, AUC is the probability that the

320   model correctly ranks a random presence site versus a random site from the study area (Phillips et

321   al., 2009). Values close to 1 indicate good prediction in site discrimination, while a value of 0.5

322   indicates a prediction equal to random and values lower than 0.5 indicate a performance that is

323   worse than random predictions. TSS assesses the accuracy of predictions using sensitivity

324   (proportion of correctly predicted presences) and specificity (proportion of correctly predicted

325   absences) in its equation (TSS= sensitivity + specificity – 1). TSS is an appropriate evaluation

326   alternative for model predictions converted to binary (presence–absence) maps using a threshold

327   (Allouche, Tsoar, & Kadmon, 2006). It ranges from −1 to +1, where values between 0 and -1

328   indicate performance no better than random, while a statistically reliable model performance is

329   indicated by values > 0.4, excellent models by a minimum of 0.7, and 1 indicates perfect agreement

330   with the model (Allouche et al., 2006).

331   Model runs were replicated five times and the averages of those runs used as the outcome of the

332   modelling exercise. Continuous values were transformed to binary values to identify predicted

333   suitable and unsuitable habitat since continuous model projections may present some difficulties

334   for interpretation. In addition, binary presence/absence maps are more useful for risk assessment

335   exercises. This transformation was done using the maximum training sensitivity plus specificity

336   threshold, which has been shown to produce the most accurate predictions, especially for presence-

337   only datasets (Jiménez-Valverde & Lobo, 2007; Liu, White, & Newell, 2013). All binary models

338   were then delimited using a threshold for the maximum depth each species could inhabit according

339   to their ecological requirements (Goldsmit et al., 2018) (Table S4). An exception was made for

340   phytoplankton as they were all surface dinoflagellates; thus, there was no need to consider

341   maximum depth for their distribution (A. Rochon pers. comm. 2018). Heat maps showing the total

342   number of modelled AIS that may find suitable habitat in a region – hereafter AIS richness – were

343   then created using combined maps representing the cumulative number of species (of the 23

344   modelled) predicted to find suitable habitat in a given grid cell at global and pan-Arctic scales. It

345   should be kept in mind that, at a global scale, richness includes native and invaded ranges of all

346   species modelled, while at pan-Arctic scale, richness includes mainly predicted invaded ranges.

347   <u>Future projections</u>

348   Once all models were run, tested, and validated, predicted habitat suitability was evaluated under

349   projected global change scenarios at global and pan-Arctic scales. The same set of environmental

350   layers that were used for contemporary models were used for projected future models although

351   only temperature, salinity, and ice layers were available for projected future scenarios (Table S3).

352   Future environmental layers were obtained from Bio-ORACLE v2 for RCP4.5 emission scenario

353   for the years 2050 and 2100. The average and range of climatic anomalies for temperature, salinity

354   and sea ice thickness of this scenario at the end of the century are given in Assis et al. (2018). In

355   short, it represents an intermediate greenhouse emission (temperature anomaly of 2.4 °C by 2100)

356   (Moss et al., 2008) and stabilization scenario resulting from the implementation of appropriate

357   mitigation strategies (Clarke et al., 2007). This anomaly also coincides approximately with the

358   expected increase in temperature in Arctic regions under the proposed efforts of the Paris

359   Agreement in 2015 (Solecki et al., 2018). Future layers were produced for 2040–2050 and 2090–

360   2100 by averaging data from distinct atmosphere–ocean general circulation models provided by

361   the Coupled Model Intercomparison Project 5, which was developed by the World Climate

362   Research Programme's Working Group on Coupled Modelling (see Assis et al. 2018 for more

363   information).

364   Resulting distribution models of each individual species were compiled by ecological groups

365   (zoobenthos, phytobenthos, zooplankton and phytoplankton) and these combined models were

366   then used to compare present with forecasted distributions for the years 2050 and 2100. This was

367   achieved by spatially analyzing species richness and distribution change between present and

368   future climate scenarios using ArcMap v10.2.2 and SDMtoolbox (J. L. Brown, 2014). Overlap of

369   regions were analyzed at both global and pan-Arctic scales, to evaluate predicted latitudinal shifts

370   in suitable habitat. Changes in the distribution of suitable habitat over time were evaluated

371   independent of natural or anthropogenic habitat overlap to identify regions of loss, gain, and no

372   change in time, for both timeframes.

373   **Results**

374   Analysis of environmental predictors and model evaluation

375   Varying combinations of predictors contributed to explaining the species distribution models of

376   the ecological groups analyzed (Figure 2). Sea surface temperature and land distance contributed

377 to models for all ecological groups, although in varying proportions. Bottom temperature and depth

378 were important in explaining models for zoobenthos and phytobenthos, in addition to ice

379 concentration for the latter. Other main predictors for zooplankton included sea surface salinity,

380 ice, and depth, whereas important phytoplankton predictors included nutrients and minerals

381 (especially iron) (Figure 2, Table S3). All environmental predictors used to construct the final

382 model for each species were within training ranges. Most AUC values were >0.91 and TSS >0.81

383 indicating good prediction in site discrimination, with the exception of four modelled species that

384 were somewhat lower (*Chionoecetes opilio*, *Dinophysis caudata*, and *Gonyaulax polygramma*

385 with AUC between 0.76 and 0.83; and *G. polygramma* and *Aurelia limbata* with TSS between

386 0.75 and 0.79), but still well above the thresholds for random site prediction (Table S5). Analysis

387 of unimodal environmental response curves indicated that environmental conditions were within

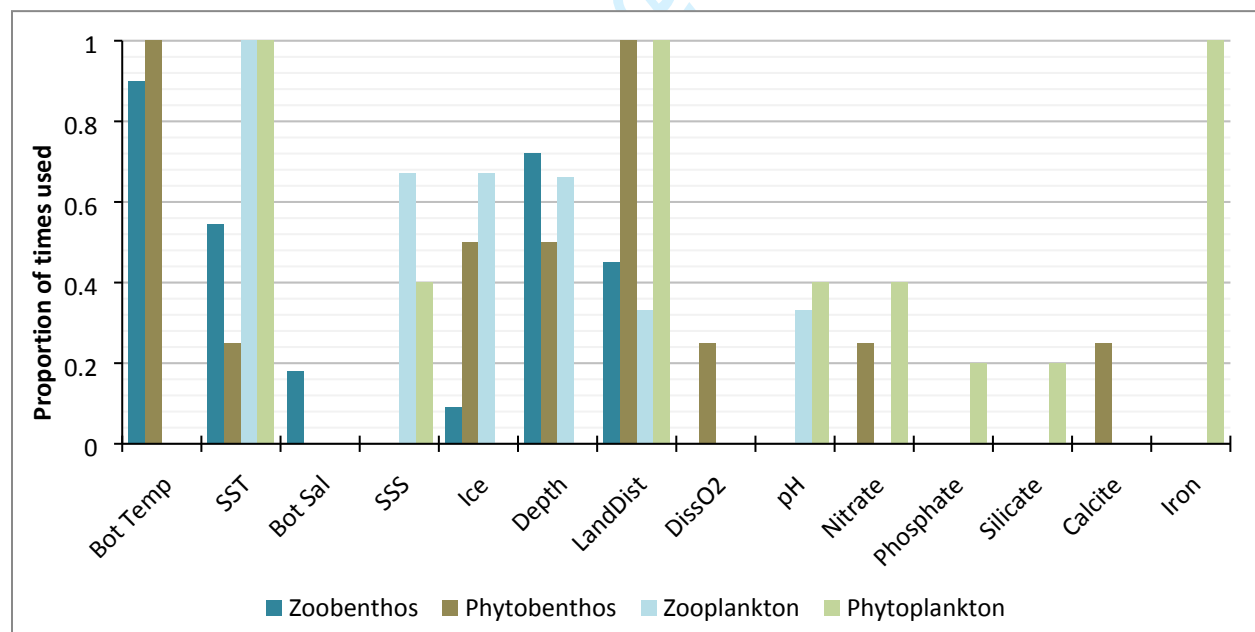388 suitable ranges for all modelled species.

389

390 Figure 2: Proportion of times individual predictors were used for model building per ecological
391 group. Bot Temp = Bottom temperature; SST = Sea surface temperature; Bot Sal = Bottom salinity;
392 SSS = Sea surface salinity; LandDist = Land distance; DissO$_2$ = Dissolved oxygen.

393

394 <u>Hotspots vulnerable to invasions</u>

395 Arctic regions with an elevated number of modelled AIS having overlapping suitable habitat were

396 located in coastal regions surrounding Hudson Bay, Northern Grand Banks/Labrador,

397 Chukchi/Eastern Bering Seas, and Barents/White Seas (Figure 3a). These hotspots are predicted

398 to have potentially greater AIS richness compared to other Arctic regions in the present and both

399 modelled future scenarios. The areal extent of hotspots vulnerable to invasion is predicted to

400 increase over time; this increase is predicted not only in total area covered, but also in the number

401 of species projected to encounter appropriate habitat there (Figure 3b).
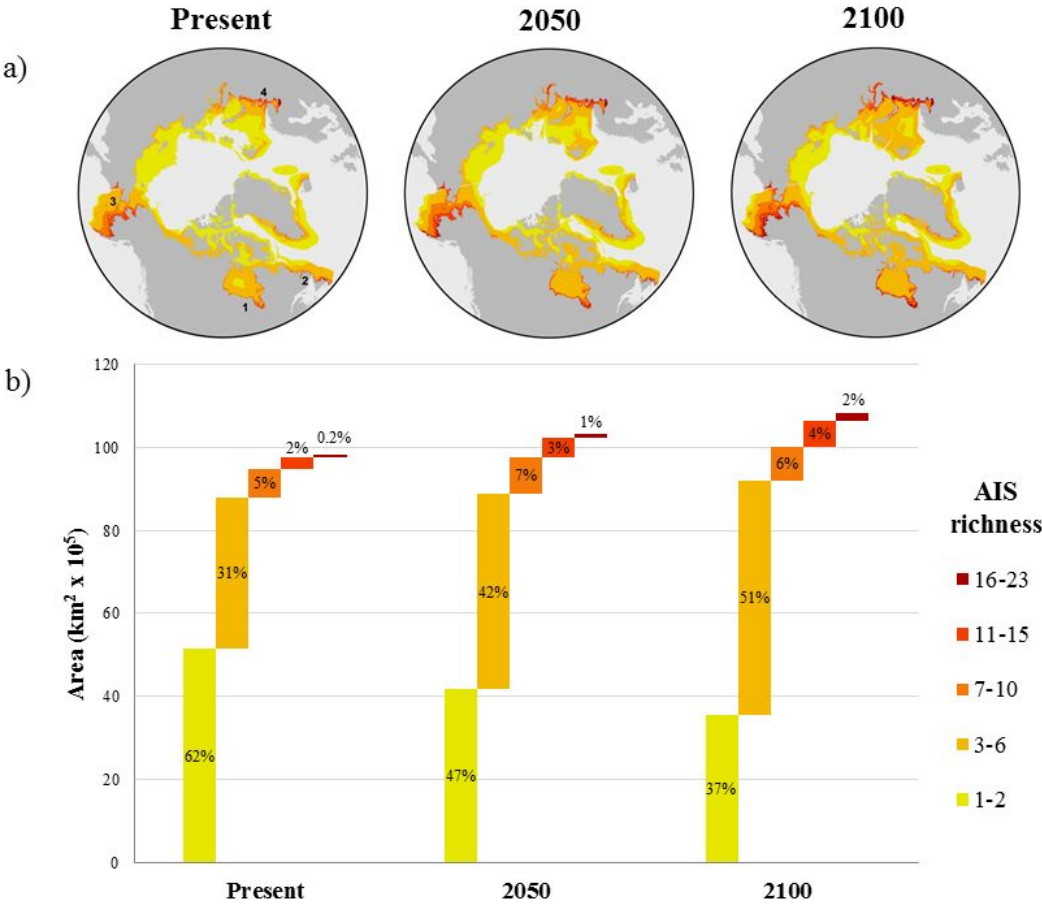
402

403

404 Figure 3: Predicted total AIS richness at an Arctic scale: a) Predicted hotspots of AIS richness for
405 present and future (2050 and 2100) conditions in the Arctic (1. Hudson Bay, 2. Northern Grand

Banks/Labrador, 3. Chukchi/Eastern Bering Seas, 4. Barents and White Seas). Colors represent the number of overlapping species with predicted suitable habitat in a given area; b) Predicted future extension of suitable habitat by area for each category (natural breaks Jenks) of AIS richness. Values shown in the bars are the net percentages of suitable habitat at each level of AIS richness within each projected time period.

These same regions are predicted to be hotspots for individual ecological groups, particularly zoobenthos, phytobenthos, and phytoplankton (Figure 4a, 4b and 4d). When evaluated independently, these groups showed the same pattern of future increased areal extent in the predicted suitable habitat, but at varying taxa-dependent scales (absolute area extent: zoobenthos and phytoplankton ~ 100×10^5 km², phytobenthos and zooplankton ~ 20×10^5 km²) (Figure 4a-d). Despite these differences in magnitude for absolute predicted future suitable habitat, at a relative scale the percentage change in suitable habitat was predicted to be greater through time for some groups (e.g., phytobenthos). Further, the relative change in predicted suitable habitat for various categories of AIS richness differed between ecological groups (Figure 4e-h). For example, zoobenthos are predicted to have greater future increases in the areal extent of habitats suitable for a high number of overlapping species (i.e., with high AIS richness).

Only one species of zooplankton (*Aurelia limbata*) was predicted to have extended suitable habitat in the Arctic; hence, no potential hotspots with overlapping species was observed (Figure 4c). It should be highlighted that few zoobenthic species have native ranges included in the area of analysis: i) *C. opilio*: Beaufort Sea, Bering Sea and Northern Grandbanks/Labrador; ii) *Littorina littorea*: White Sea; iii) *Mya arenaria*: Northern Grandbanks/Labrador; and iv) *Paralithodes camtschaticus*: Bering Sea (Figure 1, Table S1).
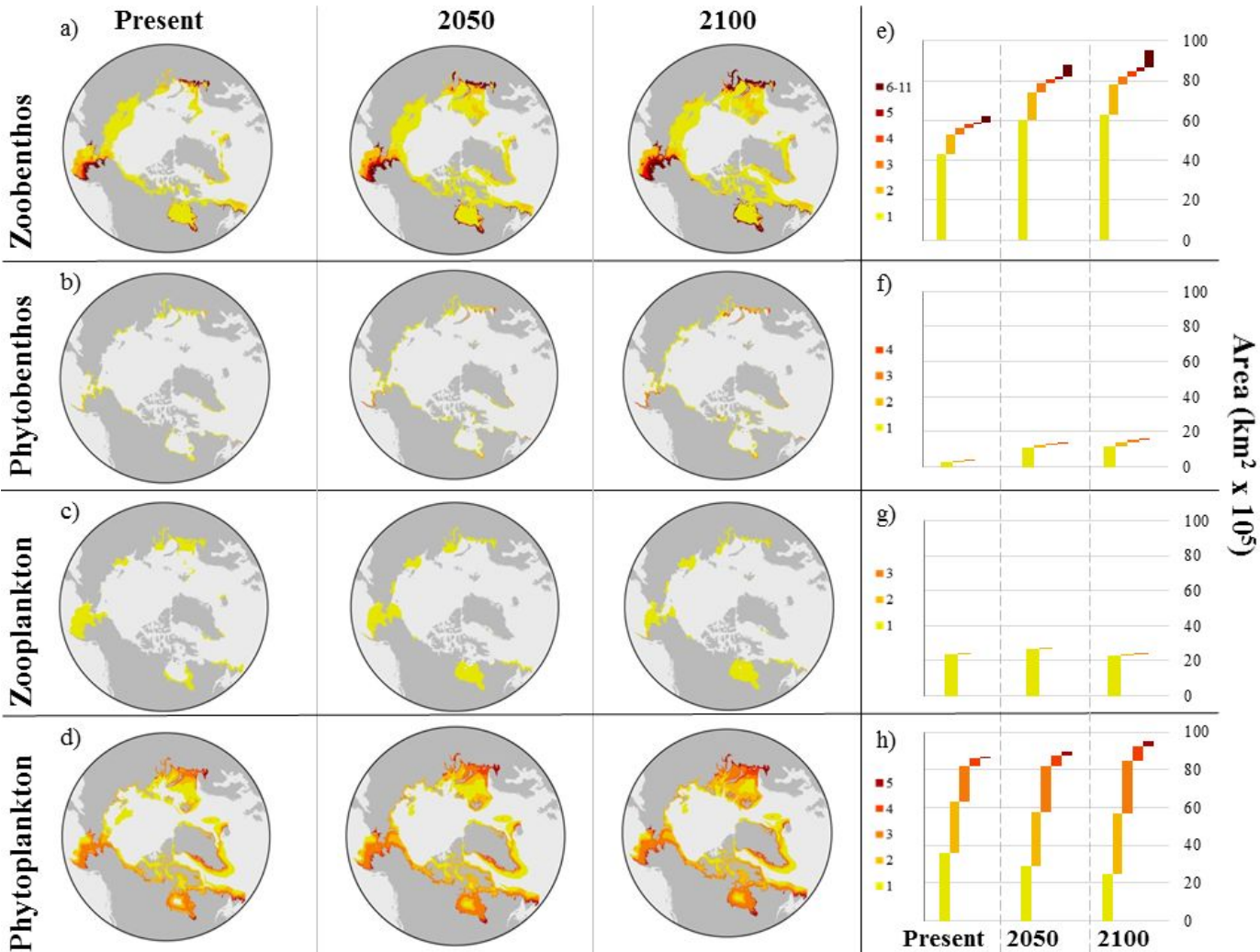
Figure 4: a-d) Predicted hotspots of AIS richness per ecological group under present and future (2050 and 2100) conditions at an Arctic scale. Colors represent the number of overlapping species with suitable habitat in a given area. e-h) Predicted future change of suitable habitat for each category of AIS richness.

At a global scale, total species richness was higher and largely concentrated on the coasts of

Northern Europe and the White Sea, Northwest Atlantic, some regions of Northwest and Northeast

Pacific, and southern regions of Temperate South America and Temperate Australasia (Figure S2).

440   Distribution change

441   Suitable habitat was projected to increase in the future for all AIS combined as well as for all

442   individual ecological groups in the Arctic realm under both climate change scenarios (Figures 5

443   and 6), although benthic species showed greater potential habitat gains (Figures 5a, 5b, and 7) than

444   did planktonic species (Figure 5c, 5d, and 7) under future climate scenarios. The overall predicted

445   future suitable habitat changes at the pan-Arctic scale for all AIS combined were net habitat gains

446   of +5.8% and +14.1% by 2050 and 2100, respectively (Figures 6 and 7). However, the same

447   analysis predicted an overall suitable habitat loss at a global scale in both future scenarios (-4% by

448   2050 and -4.2% by 2100) (Figures 6 and 7).
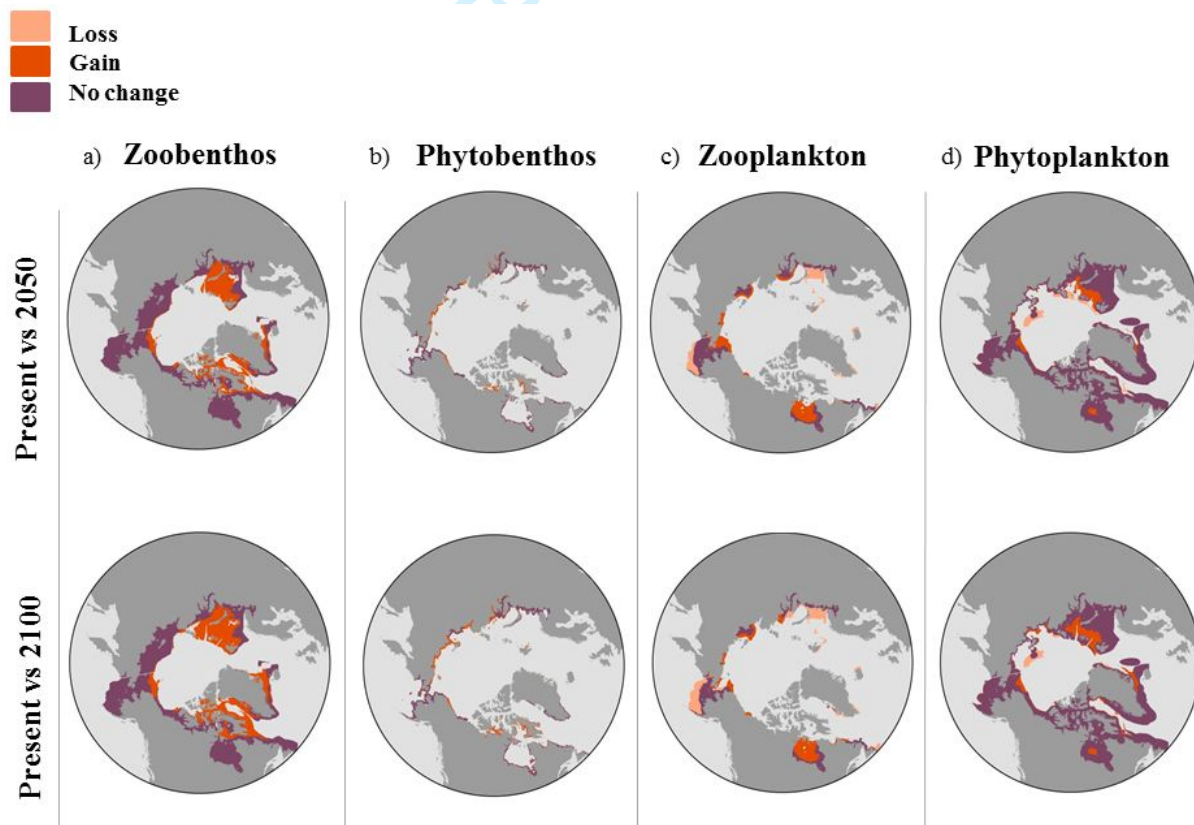

449

450   Figure 5: Overall change in predicted suitable habitat for each ecological group at an Arctic scale
451   between present and future scenarios (2050 and 2100): a) zoobenthos, b) phytobenthos, c)
452   zooplankton, and d) phytoplankton.
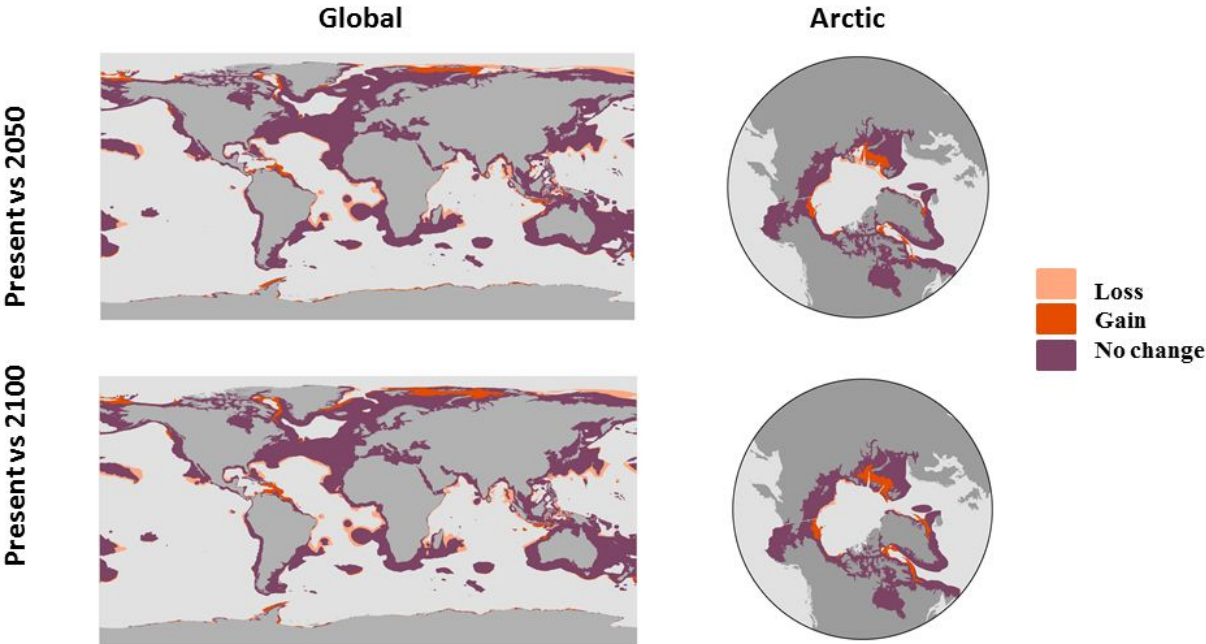
453
454   Figure 6: Overall change in predicted suitable habitat of all AIS combined at global and pan-Arctic
455   scales between present and future scenarios (2050 and 2100).

456

457   These results show that most modelled species are predicted to find suitable habitats in colder

458   regions, with a trend towards a positive pole-ward shift in future distributions, particularly in

459   northern latitudes (the pole-ward shift to the south is predicted to be lower) (Figure 6). At a global

460   scale, however, planktonic species are predicted to experience habitat loss, while benthic species

461   are predicted to have a positive and higher habitat gain (Figure 7 and S3).

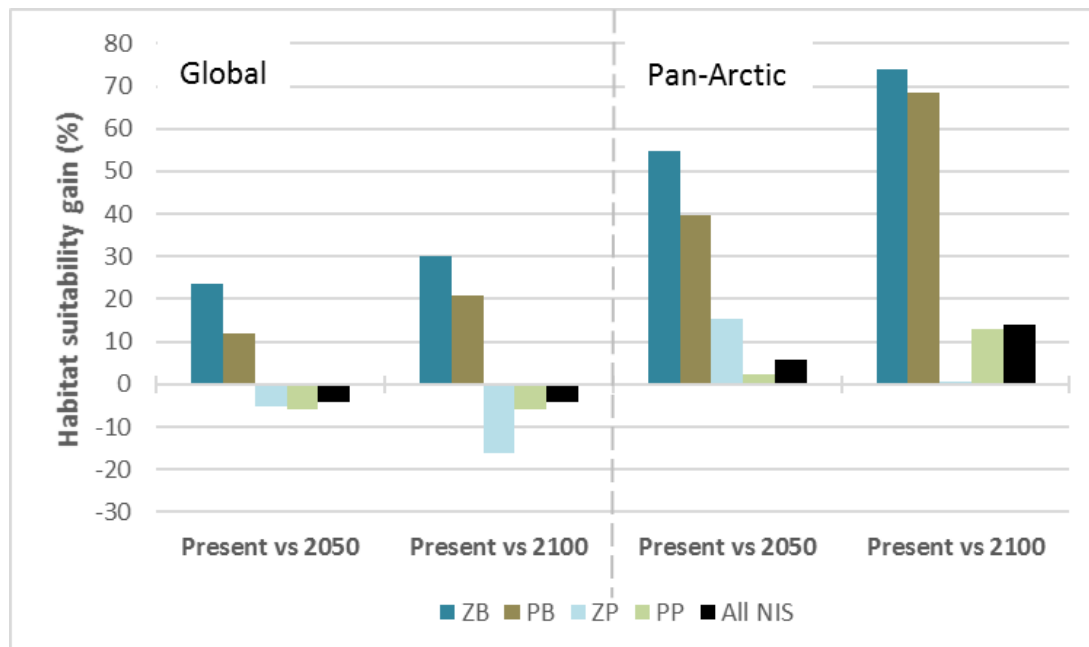Figure 7: Percentage of predicted habitat suitability change (gain or loss) for the four ecological groups and all AIS together at global and pan-Arctic scales. ZB= zoobenthos; PB= phytobenthos; ZP= zooplankton; PP= phytoplankton.

Discussion

This study predicted the distribution of suitable habitat for 23 high-risk AIS at pan-Arctic and global scales and identified hotspots of suitable habitats for multiple species. Overall, results indicate that suitability will increase over time in Arctic regions, particularly in Hudson Bay, Northern Grand Banks/Labrador, Chukchi/Eastern Bering Seas, and Barents/White Seas regions. Gradually, these regions could become more vulnerable to invasions not only due to the increased extent of suitable habitat but also due the increased number of species that may find suitable habitat there (i.e., AIS richness). This trend was observed across all assessed ecological groups which showed gains in suitable habitat in future scenarios, especially benthic organisms, which exhibited particularly high distributional changes as compared to planktonic organisms.

477   Interestingly, predicted shifts under future climate scenarios differed at pan-Arctic and global

478   scales. When all species were considered collectively, there was a predicted increase in suitable

479   habitat at the pan-Arctic scale. In contrast, the net result at a global scale was a predicted loss of

480   suitable habitat, suggesting a marked northward shift with global change. Projected future

481   scenarios considered only the direct effect of climate change. However, projected increases of

482   shipping to the area will likely exacerbate the risk as new transport routes open due to longer ice-

483   free conditions that increase opportunities for natural resource extraction (Melia et al., 2016; Miller

484   & Ruiz, 2014; Smith & Stephenson, 2013). Likewise, the Antarctic, could be affected by native

485   and invasive species in northern regions, given that environmental conditions are similar. Arctic

486   ports could act as possible sources of AIS to the Antarctic given that some ships transit between

487   poles and could act as a potential pathway of transportation, although survival and establishment

488   in such scenarios are unknown (McCarthy et al., 2019).

489   The use of CMIST as a screening tool to identify high-risk species for specific ecoregions is a

490   recent approach to stay ahead of the invasion process (Drolet et al., 2016; A. M. Moore et al.,

491   2018; Therriault et al., 2018). Although the use of CMIST combined with habitat modelling as

492   done in this study places more emphasis on the likelihood of invasion risk component of risk, the

493   tool may be used as a first step in developing a ranked watch list to guide early detection and

494   monitoring efforts and to prioritize species for detailed risk assessments and potential regulations

495   (Locke et al., 2011). CMIST provided the opportunity to identify potential AIS of greater risk to

496   the Arctic by considering known species' characteristics and impacts in other regions of the world

497   where they have already invaded. Eighty-seven percent of the species included in the present

498   modelling assessment belong to groups with the greatest numbers of known invasions in the

499   marine Arctic ecosystem (Chan et al., 2019). The uneven emphasis of organisms retained for

500   modelling (i.e., those scored as higher risk based on CMIST) from the different ecological groups

501   (maximum of 11 zoobenthic species *vs.* a minimum of 3 zooplankton species) may, in part, be

502   explained by the fact that most known introduced marine organisms are benthic species (Streftaris,

503   Zenetos, & Papathanassiou, 2005). These proportions are comparable with previous assessment

504   studies (Leidenberger, Obst, et al., 2015), although the uneven coverage does make general trends

505   more difficult to interpret.

506   Sea surface temperature and land distance were retained in all models, consistent with other studies

507   that found these predictors to contribute significantly to explaining species distributions

508   (Leidenberger, Obst, et al., 2015; Stelzer, K, Bourlat, & Obst, 2013). Water temperature has been

509   identified as the most relevant predictor of global marine species distribution and land distance of

510   moderate importance for both benthic and planktonic species (Bosch, Tyberghein, Deneudt,

511   Hernandez, & De Clerck, 2018). Depth was an important predictor, as shown by Bosch et al.

512   (2018) who suggested that bathymetry is of high relevance for modelling various taxa. Ice

513   concentration was moderately important for phytobenthos and zooplankton, perhaps reflecting

514   limits on distribution of the former due to ice abrasion, changes in light exposure and a preference

515   of ice-free waters for the latter (Clark et al., 2013; Kube, Postel, Honnef, & Augustin, 2007;

516   Pascual et al., 2015; Richardson, 1979). Iron was an important predictor for all modelled

517   phytoplankton species, likely as it is known to be important to phytoplankton growth, abundance,

518   dominance, and species distributions (Hecky & Kilham, 1988; C. M. Moore et al., 2013) and plays

519   a role in the development of harmful algal bloom species (Doucette & Harrison, 1990; Wells,

520   Mayer, & Guillard, 1991). In Arctic regions, meltwater can be a significant bioavailable source of

521   iron to surrounding coastal oceans (Bhatia et al., 2013; Tovar-Sánchez et al., 2010) and evidence

522   suggests a link between ice and iron from glacial meltwater leading to blooms in some

523   phytoplankton taxa (Aguilar-Islas, Rember, Mordy, & Wu, 2008; Joli et al., 2018). This is

524   important given that increased iron due to a shift from an ice-covered to an open water Arctic

525   Ocean (Screen, 2018; Seneviratne et al., 2018) could create favourable conditions for harmful

526   species that may arrive in the region.

527   Four Arctic regions (i.e., Hudson Bay, Northern Grand Banks/Labrador, Chukchi/Eastern Bering

528   Seas, and Barents/White Seas) were identified as potential hotspots for invasions. Invasion

529   hotspots could pose even greater risks if they coincide with major shipping routes, biodiversity

530   hotspots or areas of special interest/importance, which is the case for most of the invasion hotspots

531   predicted in the present study. The predicted invasion hotspots overlap with regions that have been

532   highlighted for being special (with regards to their uniqueness, importance for species life

533   histories, threatened species and/or habitats, biological productivity, diversity, etc.). For example,

534   some Ecologically and Biologically Significant Areas (also known as EBSAs) and Marine Refuges

535   coincide with the predicted invasion hotspots in Northern Grand Banks/Labrador, Chukchi/Eastern

536   Bering Seas and Barents/White Seas (Kenchington et al., 2011; Speer & Laughlin, 2011;

537   Templeman, 2007; www.dfo-mpo.gc.ca/oceans/oeabcm-amcepz/refuges/index-eng.html), as well

538   as in the southern part of Hudson Bay, which has been identified as being an area of high biological

539   importance (Stephenson & Hartwig, 2010). Ecoregions with a high concentration of polynyas

540   could also be at greater risk, given that they may act as important biological hotspots due to their

541   increased productivity and biodiversity (Marchese, 2015). This may be the case for the Chukchi

542   and Eastern Bering Seas, which are known to have concentrations of polynyas (CAFF, 2013). This

543   is consistent with previous studies that have identified biodiversity hotspots in marine and

544   terrestrial ecosystems as being at particular risk to future invasions (Bellard et al., 2014; Li, Liu,

545   Kraus, Tingley, & Li, 2016) and climate change (Ramírez, Afán, Davis, & Chiaradia, 2017). The

546 presence of AIS in biological hotspots could endanger native and endemic species as AIS are

547 considered to be one of the leading causes of biodiversity loss and contemporary extinctions

548 (Bellard, Cassey, et al., 2016; Blackburn et al., 2019) with impacts on ecosystem structure and

549 functioning, including changes in food webs, biomass, flux rates, etc. (Ehrenfeld, 2010). Relating

550 where invasion hotspots overlap with biological hotspots could be crucial for prioritizing

551 conservation efforts.

552 The Barents Sea has been highlighted as a region that already has a substantial number of invasions

553 and environmental conditions that increase the probability of successful establishment (Chan et

554 al., 2019). Two of the species modelled in the present study, *C. opilio* and *P. camtschaticus*, are

555 already established there (Chan et al., 2019; Dvoretsky & Dvoretsky, 2009; Hansen, 2015). The

556 former is thought to have been introduced by ballast water, while the latter was an intentional

557 introduction (Alvsvåg, Agnalt, & Jørstad, 2009; Jørgensen & Nilssen, 2011). The Barents Sea

558 appears to be in transition from a cold Arctic to warm Atlantic climate regime (Lind, Ingvaldsen,

559 & Furevik, 2018), making it particularly vulnerable to invasion. Indeed, it is predicted to suffer

560 one of the largest future habitat losses by endemic species in the Arctic (Renaud et al., 2019),

561 leaving potential niches available for novel species to occupy. Additionally, Arctic ecoregions will

562 be more exposed to potential future arrivals with further ice reduction and increased navigability

563 of the Northern Sea Route and the Northwest Passage, although much greater investment in

564 infrastructure, navigation and communications would be needed to this end (Buixadé Farré et al.,

565 2014). Nonetheless, both human activities and AIS are likely to increase over time in the Arctic,

566 as has been observed over the last few years (Chan et al., 2019; Dawson, Pizzolato, Howell,

567 Copland, & Johnston, 2018).

568   At a global scale, planktonic organisms showed a marked loss of suitable habitat that exceeded

569   predicted gains. This may be due to their being dispersive pelagic organisms which have the

570   capability of expanding rapidly and show extensive distribution changes in response to

571   temperature increases related to global warming (Poloczanska et al., 2013). Predicted future

572   changes in sea surface temperatures, in particular, which are expected to outpace shifts in bottom

573   temperature (Levitus et al., 2012) may be driving this pattern. Indeed, models in the present study

574   showed that sea surface temperature was more important for planktonic organisms whereas bottom

575   temperature was an important variable for benthic organisms. However, the pattern of predicted

576   change by taxa is different at the pan-Arctic scale where both planktonic and particularly benthic

577   AIS showed positive suitable habitat gains coinciding with other modelling studies (de Rivera et

578   al., 2011; Goldsmit et al., 2018; Jueterbock et al., 2013; Townhill et al., 2018; Villarino et al.,

579   2015; Ware et al., 2016). This could be explained by the fact that temperature increases have been

580   shown to be greater in the Arctic than in other areas (Bush & Lemmen, 2019; Pendleton et al.,

581   2019) and thus predicted gains in suitable habitat there would be expected to be relatively greater

582   than losses elsewhere.

583   A marked poleward shift was predicted, consistent with other forecasting studies for various types

584   of marine organisms, including invertebrates, algae and fish (Byrne et al., 2016; Chust et al., 2013;

585   Goldsmit et al., 2018; Jones & Cheung, 2015; Mackey et al., 2012; Townhill et al., 2018; Valle et

586   al., 2014; Wisz et al., 2015). Poleward shifts may serve as an early warning signal of ecosystem

587   change due to climate warming. Multiple studies across different taxa are showing consistency

588   between observed responses of marine organisms to climate change, particularly in high-latitude

589   regions (Poloczanska et al., 2013). Cold-adapted species typically have narrow thermal windows

590   and low energy-demand lifestyles, making them more sensitive to temperature changes

591   (Poloczanska et al., 2016). Poleward shifts in predicted future suitable habitat in the present study

592   are disproportionately located in Arctic areas, such as has been shown in Cheung et al. (2009),

593   García Molinos et al. (2015), and Jones & Cheung (2015). Invasive species in the Antarctic region

594   have been limited by physiology at cold temperatures rather than geographic limits, but global

595   warming may remove those physiological barriers and alter limitations (Aronson et al 2007).

596   However, it should be noted that a substantial number of the species modelled here are already

597   distributed in northern/cold regions, which may bias observed patterns. Although, three modelled

598   species (*C. intestinalis*, *B. schlosseri*, and *U. pinnatifida*) are among the most likely to become

599   invasive in the Antarctic Peninsula according to a recent horizon scanning study (Hughes et al.,

600   2020).

601   The locations with greater reductions of the sea ice season over the last 40 years (Stammerjohn,

602   Massom, Rind, & Martinson, 2012) coincides with the regions of predicted invasion hotspots

603   in the present study, suggesting that these areas are already experiencing changing

604   environmental conditions and that such variations are projected to continue in time, including

605   the probability of a complete ice-free Arctic during summer (Screen, 2018; Sigmond et al.,

606   2018). The combination of species invasions and predicted reductions in sea-ice cover could alter

607   reproduction/phenology timing, energy pathways, and food-web dynamics with subsequent

608   impacts on production at higher trophic levels (Ploczanska et al., 2013; Haug et al., 2017 and

609   references therein). In this context, AIS could take advantage of new habitats and resources and

610   outcompete native species, which are generally expected to be more sensitive to temperature

611   changes given that they live within a narrow low-temperature range (Peck, 2005). Invasive,

612   non-native, and native boreal species could thus expand their ranges as suitable habitats in polar

613   regions become more common (de Rivera et al., 2011; Goldsmit et al., 2018; Ware et al., 2016;

614   Renaud et al., 2019) with subsequent impacts on richness, community composition, and Arctic

615   ecosystems. However, it remains unknown whether biogeographic boundary locations will

616   change (Costello et al., 2017).

617   The model used in this study, MaxEnt, is robust and performs well to predict suitable habitats for

618   invasive species currently and to project range shifts under future climate change scenarios (Battini

619   et al., 2019; Hijmans & Graham, 2006). Special attention was taken in the selection of

620   environmental predictors for modelling. Correlation between predictors was accounted for as

621   including all available predictors may lower predictive power due to model over-parameterization

622   (Bradie, Pietrobon, & Leung, 2015; Tyberghein et al., 2012). Nevertheless, modelling studies

623   always have some restrictions and limits that should be recognized in results interpretation. One

624   main limitation of the present study is that potential species occurrences and range changes are

625   based solely on abiotic factors and do not reflect the realized distribution of a species, assuming

626   that species are in equilibrium with their environment (Bellard et al., 2018; Guisan &

627   Zimmermann, 2000). Biotic interactions, potential resources, and life history traits were not

628   included in the modelling exercise, even though they are known to be important in shaping the

629   spatial distribution of species (Wisz et al., 2013). Moreover, including physiological data such as

630   reproductive temperature to represent phenology, can significantly change SDM predictions.

631   Including this type of data has been shown to strongly limit predicted northward shifts under future

632   climate change scenarios (Chefaoui, Serebryakova, Engelen, Viard, & Serrão, 2019). However,

633   this particular aspect was somewhat offset by the fact that environmental conditions for

634   reproduction, together with conditions needed for different life stages, were considered in this

635   study during the species selection using CMIST scores. Given that the present study modelled the

636   potential distribution of suitable habitat in a new environment, biotic interactions may not be

637 realistic if applied in a different context, such as different regions or time periods (Anderson, 2017

638 and references therein). Moreover, biotic interactions are known to affect distributions at local

639 spatial scales (Pearson & Dawson, 2003). Another potential limiting factor in modelling future

640 distributions was the availability of projected environmental predictors under global warming

641 scenarios, since it has been recently shown that including projections using multi-factor models

642 can result in better performance predictions (McHenry, Welch, Lester, & Saba, 2019).

643 Temperature, salinity and sea ice thickness were the only environmental predictors available to

644 use as future projected environmental layers, although including only these factors is common

645 practice in similar modelling exercises (e.g., Goldsmit et al., 2018; Jueterbock et al., 2016;

646 Leidenberger, De Giovanni, Kulawik, Williams, & Bourlat, 2015, and Weinert et al., 2016).

647 Despite limitations and restrictions, SDM can provide valuable information to help manage

648 resources in a marine ecosystems that will face increasing anthropogenic pressures (Reiss et al.,

649 2014) and has been shown to be a useful predictive tool to assess various taxa concurrently

650 (Gallardo et al., 2015; Leidenberger, Obst, et al., 2015). SDM may also be particularly useful for

651 regions such as the Arctic, where predicting biodiversity changes under global warming effects is

652 challenging due to the paucity of baseline data for most organisms (Wassmann, Duarte, Agusti, &

653 Sejr, 2011; Renaud et al., 2019).

654 Distributional change of AIS may increase risk in previously unimpacted areas, potentially

655 creating new problems for wildlife and even human health (such as harmful algal blooms). These

656 types of episodes are being facilitated by climate change (Hallegraeff, 2010; Kordas, Harley, &

657 O'Connor, 2011; Poloczanska et al., 2013; Poloczanska et al., 2016). The present study predicts

658 changes over such an extensive area (more than 1×10^7 km², equivalent to almost 5.5 times the

659 size of Greenland) that altered community structure may be widespread. Results presented here

660   provide information on AIS that pose some of the greatest threats to the Arctic, with areas at

661   greatest risk identified as hotspots. This information is valuable given that aquatic invaders are

662   understudied in the context of climate change (Bellard et al., 2018). The Arctic is predicted to

663   be affected by increased habitat suitability for a number of potential AIS and given its vast area,

664   it could be severely impacted by AIS accumulating in specific locations under both current and

665   future environmental conditions. Identification of hotspots through SDM, predictions on habitat

666   vulnerability and particular areas of concern could guide ballast water practices and other

667   management actions, including prevention, early detection monitoring, rapid response, and

668   conservation planning. Information such as that provided by the present study should help guide

669   how best to prioritize management efforts in this unique and vast region.

670

682   High Arctic Research Station, and Quebec-Ocean. The author sequence follows the 'first-last

683   author-emphasis' norm.

684

685   **References**

686   Aguilar-Islas, A. M., Rember, R. D., Mordy, C. W., & Wu, J. (2008). Sea ice-derived dissolved
687   iron and its potential influence on the spring algal bloom in the Bering Sea. *Geophysical*
688   *Research Letters, 35*(24).
689   Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution
690   models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology,*
691   *43*(6), 1223-1232.
692   Alvsvåg, J., Agnalt, A. L., & Jørstad, K. E. (2009). Evidence for a permanent establishment of the
693   snow crab (*Chionoecetes opilio*) in the Barents Sea. *Biological Invasions, 11*(3), 587-595.
694   Anderson, R. P. (2017). When and how should biotic interactions be considered in models of
695   species niches and distributions? *Journal of Biogeography, 44*(1), 8-17.
696   Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate
697   impact models under climate change. *Global Change Biology, 11*(9), 1504-1513.
698   Archambault, P., Snelgrove, P. V. R., Fisher, J. A. D., Gagnon, J. M., Garbary, D. J., Harvey, M.,
699   . . . Poulin, M. (2010). From sea to sea: Canada's three oceans of biodiversity. *PLoS ONE,*
700   *5*(8), e12182.
701   Ashton, G. V., Riedlecker, E. I., & Ruiz, G. M. (2008). First non-native crustacean established in
702   coastal waters of Alaska. *Aquatic Biology, 3*(2), 133-137.
703   Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018).
704   Bio-ORACLE v2. 0: Extending marine data layers for bioclimatic modelling. *Global*
705   *Ecology and Biogeography, 27*(3), 277-284.
706   Bailey, S. A. (2015). An overview of thirty years of research on ballast water as a vector for aquatic
707   invasive species to freshwater and marine environments. *Aquatic Ecosystem Health &*
708   *Management, 18*(3), 261-268.
709   Barbosa, F. G., & Schneck, F. (2015). Characteristics of the top-cited papers in species distribution
710   predictive models. *Ecological Modelling, 313*, 77-83.
711   Barbosa, F. G., Schneck, F., & Melo, A. S. (2012). Use of ecological niche models to predict the
712   distribution of invasive species: a scientometric analysis. *Brazilian Journal of Biology,*
713   *72*(4), 821-829.
714   Barnes, D. K. A. (1999). The influence of ice on polar nearshore benthos. *Journal of the Marine*
715   *Biological Association of the United Kingdom, 79*(3), 401-407.
716   Barnhart, K. R., Miller, C. R., Overeem, I., & Kay, J. E. (2016). Mapping the future expansion of
717   Arctic open water. *Nature Climate Change, 6*(3), 280-285.
718   Battini, N., Farías, N., Giachetti, C. B., Schwindt, E., & Bortolus, A. (2019). Staying ahead of
719   invaders: using species distribution modeling to predict alien species' potential niche shifts.
720   *Marine Ecology Progress Series, 612*, 127-140.
721   Beaugrand, G., Conversi, A., Atkinson, A., Cloern, J., Chiba, S., Fonda-Umani, S., . . . Otto, S. A.
722   (2019). Prediction of unprecedented biological shifts in the global ocean. *Nature Climate*
723   *Change, 9*(3), 237.

724   Belanger, C. L., Jablonski, D., Roy, K., Berke, S. K., Krug, A. Z., & Valentine, J. W. (2012).
725   Global environmental predictors of benthic marine biogeographic structure. *Proceedings*
726   *of the National Academy of Sciences of the Unitet States of America, 109*(35), 14046-
727   14051.
728   Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions.
729   *Biology Letters, 12*(2), 20150623.
730   Bellard, C., Jeschke, J. M., Leroy, B., & Mace, G. M. (2018). Insights from modeling studies on
731   how climate change affects invasive alien species geography. *Ecology and Evolution,*
732   *8*(11), 5688-5700.
733   Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., & Courchamp, F. (2014).
734   Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography,*
735   *23*(12), 1376-1386.
736   Bellard, C., Leroy, B., Thuiller, W., Rysman, J. F., & Courchamp, F. (2016). Major drivers of
737   invasion risks throughout the world. *Ecosphere, 7*(3), e01241.
738   Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., & Courchamp, F. (2013). Will
739   climate change promote future invasions? *Global Change Biology, 19*(12), 3740-3748.
740   Bhatia, M. P., Kujawinski, E. B., Das, S. B., Breier, C. F., Henderson, P. B., & Charette, M. A.
741   (2013). Greenland meltwater as a significant and potentially bioavailable source of iron to
742   the ocean. *Nature Geoscience, 6*(4), 274.
743   Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of
744   recent extinctions. *Frontiers in Ecology and the Environment, 17*(4), 203-207.
745   Bosch, S., Tyberghein, L., Deneudt, K., Hernandez, F., & De Clerck, O. (2018). In search of
746   relevant predictors for marine species distribution modelling using the MarineSPEED
747   benchmark dataset. *Diversity and Distributions, 24*(2), 144-157.
748   Bradie, J., Pietrobon, A., & Leung, B. (2015). Beyond species-specific assessments: an analysis
749   and validation of environmental distance metrics for non-indigenous species risk
750   assessment. *Biological Invasions, 17*(12), 3455-3465.
751   Broennimann, O., & Guisan, A. (2008). Predicting current and future biological invasions: both
752   native and invaded ranges matter. *Biology Letters, 4*(5), 585-589.
753   Brown, E. A., Chain, F. J. J., Zhan, A., MacIsaac, H. J., & Cristescu, M. E. (2016). Early detection
754   of aquatic invaders using metabarcoding reveals a high number of non-indigenous species
755   in Canadian ports. *Diversity and Distributions, 22*(10), 1045-1059.
756   Brown, J. L. (2014). SDMtoolbox: a python-based GIS toolkit for landscape genetic,
757   biogeographic and species distribution model analyses. *Methods in Ecology and Evolution,*
758   *5*(7), 694-700.
759   Bucklin, D. N., Basille, M., Benscoter, A. M., Brandt, L. A., Mazzotti, F. J., Romanach, S. S., . . .
760   Watling, J. I. (2015). Comparing species distribution models constructed with different
761   subsets of environmental predictors. *Diversity and Distributions, 21*(1), 23-35.
762   Buixadé Farré, A., Stephenson, S. R., Chen, L., Czub, M., Dai, Y., Demchev, D., . . . Keil, K.
763   (2014). Commercial Arctic shipping through the Northeast Passage: routes, resources,
764   governance, technology, and infrastructure. *Polar Geography, 37*(4), 298-324.
765   Bush, E., & Lemmen, D. S., editors (2019). *Canada's Changing Climate Report*. Government of
766   Canada. Retrieved from: https://changingclimate.ca/CCCR2019/
767   Byrne, M., Gall, M., Wolfe, K., & Agüera, A. (2016). From pole to pole: the potential for the
768   Arctic seastar *Asterias amurensis* to invade a warming Southern Ocean. *Global Change*
769   *Biology, 22*(12), 3874-3887.

770   CAFF (Conservation of Arctic Flora and Fauna) (2013). *Arctic Biodiversity Assessment: Status*
771   *and trends in Arctic biodiversity*. Akureyri, Iceland. Retrieved from:
772   http://arcticlcc.org/assets/resources/ABA2013Science.pdf
773   CAFF (Conservation of Arctic Flora and Fauna) & PAME (Protection of the Arctic Marine
774   Environment) (2017). *Arctic Invasive Alien Species: Strategy and Action Plan*. Akureyri,
775   Iceland. (ISBN: 978-9935-431-65-3). Retrieved from: https://www.caff.is/invasive-
776   species
777   Catford, J. A., Vesk, P. A., White, M. D., & Wintle, B. A. (2011). Hotspots of plant invasion
778   predicted by propagule pressure and ecosystem characteristics. *Diversity and*
779   *Distributions, 17*(6), 1099-1110.
780   Chain, F. J. J., Brown, E. A., MacIsaac, H. J., & Cristescu, M. E. (2016). Metabarcoding reveals
781   strong spatial structure and temporal turnover of zooplankton communities among marine
782   and freshwater ports. *Diversity and Distributions, 22*(5), 493-504.
783   Chan, F. T., Bailey, S., Wiley, C., & MacIsaac, H. (2013). Relative risk assessment for ballast-
784   mediated invasions at Canadian Arctic ports. *Biological Invasions, 15*(2), 295-308.
785   doi:10.1007/s10530-012-0284-z
786   Chan, F.T., Bronnenhuber, J.E., Bradie, J.N., Howland, K., Simard, N. and Bailey, S.A. 2012. *Risk*
787   *assessment for ship-mediated introductions of aquatic nonindigenous species to the*
788   *Canadian Arctic.* Canadian Science Advisory Secretariat Research Document 2011/105.
789   vi + 93 p. Retrieved from: http://publications.gc.ca/site/eng/457830/publication.html
790   Chan, F. T., MacIsaac, H. J., & Bailey, S. A. (2015). Relative importance of vessel hull fouling
791   and ballast water as transport vectors of nonindigenous species to the Canadian Arctic.
792   *Canadian Journal of Fisheries and Aquatic Sciences, 72*(8), 1230-1242.
793   Chan, F. T., MacIsaac, H. J., & Bailey, S. A. (2016). Survival of ship biofouling assemblages
794   during and after voyages to the Canadian Arctic. *Marine Biology, 163*(12), 250.
795   Chan, F. T., Stanislawczyk, K., Sneekes, A. C., Dvoretsky, A., Gollasch, S., Minchin, D., . . .
796   Bailey, S. A. (2019). Climate change opens new frontiers for marine species in the Arctic:
797   Current trends and future invasion risks. *Global Change Biology, 25*(1), 25-38.
798   doi:10.1111/gcb.14469
799   Chefaoui, R. M., Serebryakova, A., Engelen, A. H., Viard, F., & Serrão, E. A. (2019). Integrating
800   reproductive phenology in ecological niche models changed the predicted future ranges of
801   a marine invader. *Diversity and Distributions, 25*(5), 688-700.
802   Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., & Pauly, D. (2009).
803   Projecting global marine biodiversity impacts under climate change scenarios. *Fish and*
804   *Fisheries, 10*(3), 235-251.
805   Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y., & Irigoien, X. (2013).
806   Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach.
807   *ICES Journal of Marine Science*, *71*(2), 241-253.
808   Chust, G., Villarino, E., Chenuil, A., Irigoien, X., Bizsel, N., Bode, A., . . . Fonda-Umani, S.
809   (2016). Dispersal similarly shapes both population genetics and community patterns in the
810   marine realm. *Scientific Reports, 6*, 28730.
811   Clark, G. F., Stark, J. S., Johnston, E. L., Runcie, J. W., Goldsworthy, P. M., Raymond, B., &
812   Riddle, M. J. (2013). Light-driven tipping points in polar ecosystems. *Global Change*
813   *Biology, 19*(12), 3749-3761.
814   Clarke, L., Edmonds, J., Jacoby, H., Pitcher, H., Reilly, J., & Richels, R. (2007). *Scenarios of*
815   *greenhouse gas emissions and atmospheric concentrations*. Sub-Report 2.1a of Synthesis

816   and Assessment Product 2.1 by the U.S. Climate Change Science Program and the
817   Subcommittee on Global Change Research, Department of Energy, Office of Biological &
818   Environmental   Research,   Washington   DC   Retrieved   from   :
819   http://www.climatescience.gov/Library/sap/sap2-1/finalreport/default.htm
820   Cook, E. J., Payne, R. D., MacLeod, A., & Brown, S. F. (2016). Marine biosecurity: protecting
821   indigenous marine species. *Research and Reports in Biodiversity Studies, 5*, 1-14.
822   Costello, M. J., Basher, Z., McLeod, L., Asaad, I., Claus, S., Vandepitte, L., . . . Appeltans, W.
823   (2017). Methods for the study of marine biodiversity. In: M. Walters & R. J. Scholes (Eds.),
824   *The GEO handbook on biodiversity observation networks* (pp. 129-163). Retrieved from:
825   https://link.springer.com/book/10.1007/978-3-319-27288-7.
826   Cusson, M., Archambault, P., & Aitken, A. (2007). Biodiversity of benthic assemblages on the
827   Arctic continental shelf: historical data from Canada. *Marine Ecology Progress Series,*
828   *331*, 291-304.
829   Davidson, I. C., Zabin, C. J., Chang, A. L., Brown, C. W., Sytsma, M. D., & Ruiz, G. M. (2010).
830   Recreational boats as potential vectors of marine organisms at an invasion hotspot. *Aquatic*
831   *Biology, 11*(2), 179-191.
832   Dawson, J., Pizzolato, L., Howell, S. E. L., Copland, L., & Johnston, M. E. (2018). Temporal and
833   spatial patterns of ship traffic in the Canadian Arctic from 1990 to 2015. *Arctic, 71*(1), 15-
834   26.
835   de Rivera, C. E., Steves, B. P., Fofonoff, P. W., Hines, A. H., & Ruiz, G. M. (2011). Potential for
836   high-latitude marine invasions along western North America. *Diversity and Distributions,*
837   *17*(6), 1198-1209.
838   DFO. 2017. *Screening of the Pacific Fishery Regulations (PFR) Schedule VIII Species for Risk of*
839   *Invasiveness*. DFO Canadian Science Advisory Secretariat Science Response (2017/040).
840   Retrieved from: http://publications.gc.ca/site/eng/9.847598/publication.html
841   Dispas, A. (2019). *Étude de référence sur la biodiversité du mésozooplancton dans quatre ports*
842   *de l'Arctique canadien en vue d'une augmentation de l'activité maritime, de l'exploitation*
843   *des ressources et du réchauffement climatique.* (Unpublished master's thesis), Université
844   du Québec à Rimouski, Rimouski, Canada.
845   Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., . . . Leitão, P. J. (2013).
846   Collinearity: a review of methods to deal with it and a simulation study evaluating their
847   performance. *Ecography, 36*(1), 027-046.
848   Doucette, G. J., & Harrison, P. J. (1990). Some effects of iron and nitrogen stress on the red tide
849   dinoflagellate *Gymnodinium sanguineum*. *Marine Ecology Progress Series, 62*(3), 293-
850   306.
851   Drake, J. M., & Lodge, D. M. (2004). Global hot spots of biological invasions: Evaluating options
852   for ballast–water management. *Proceedings of the Royal Society of London B: Biological*
853   *Sciences, 271*(1539), 575-580.
854   Drake, J. M., & Lodge, D. M. (2007). Hull fouling is a risk factor for intercontinental species
855   exchange in aquatic ecosystems. *Aquatic Invasions, 2*(2), 121-131.
856   Drolet, D., DiBacco, C., Locke, A., McKenzie, C. H., McKindsey, C. W., Moore, A. M., . . .
857   Therriault, T. W. (2016). Evaluation of a new screening-level risk assessment tool applied
858   to non-indigenous marine invertebrates in Canadian coastal waters. *Biological Invasions,*
859   *18*(1), 279-294.

860   Dvoretsky, A. G., & Dvoretsky, V. G. (2009). Fouling community of the red king crab,
861   *Paralithodes camtschaticus* (Tilesius 1815), in a subarctic fjord of the Barents Sea. *Polar*
862   *Biology, 32*(7), 1047-1054.
863   Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., . . . Miller,
864   L. P. (2016). Global threats from invasive alien species in the twenty-first century and
865   national response capacities. *Nature Communications, 7*, 12485.
866   Edelist, D., Rilov, G., Golani, D., Carlton, J. T., & Spanier, E. (2013). Restructuring the Sea:
867   profound shifts in the world's most invaded marine ecosystem. *Diversity and Distributions,*
868   *19*(1), 69-77.
869   Ehrenfeld, J. G. (2010). Ecosystem consequences of biological invasions. *Annual Review of*
870   *Ecology, Evolution and Systematics, 41*, 59-80.
871   Elith, J., Graham, C. H., Anderson, R. P., Dudı´k, M., Ferrier, S., Guisan, A., . . . Zimmermann,
872   N. E. (2006). Novel methods improve prediction of species' distributions from occurrence
873   data. *Ecography, 29*(2), 129-151.
874   Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical
875   explanation of MaxEnt for ecologists. *Diversity and Distributions, 17*(1), 43-57.
876   Floerl, O. (2014). Management challenges and opportunities for marine biosecurity in the Arctic.
877   In L. Fernandez, A.K. Brooks, & N. Vestergaard (Eds.), *Marine invasive species in the*
878   *Arctic* (pp. 57-67). Copenhagen, TemaNord.
879   Gallardo, B., Zieritz, A., & Aldridge, D. C. (2015). The importance of the human footprint in
880   shaping the global distribution of terrestrial, freshwater and marine invaders. *PloS ONE,*
881   *10*(5), e0125801.
882   García-Roselló, E., Guisande, C., Manjarrés-Hernández, A., González-Dacosta, J., Heine, J.,
883   Pelayo-Villamil, P., . . . Lobo, J. M. (2015). Can we derive macroecological patterns from
884   primary Global Biodiversity Information Facility data? *Global Ecology and Biogeography,*
885   *24*(3), 335-347. doi:10.1111/geb.12260
886   García Molinos, J., Halpern, Benjamin S., Schoeman, David S., Brown, Christopher J., Kiessling,
887   W., Moore, Pippa J., . . . Burrows, Michael T. (2015). Climate velocity and the future
888   global redistribution of marine biodiversity. *Nature Climate Change, 6*, 83.
889   doi:10.1038/nclimate2769
890   Geller, J. B., & Ruiz, G. M. (2013). *Marine invasive species technical support – Quantitative*
891   *survey of nonindigenous species (NIS) in Prince William Sound: Plankton*. Prince William
892   Sound Regional Citizens' Advisory Council, Contract number: 952.13.01. Retrieved from:
893   http://www.pwsrcac.org
894   Gíslason, Ó. S., Halldórsson, H. P., Pálsson, M. F., Pálsson, S., Davíðsdóttir, B., & Svavarsson, J.
895   (2014). Invasion of the Atlantic rock crab (*Cancer irroratus*) at high latitudes. *Biological*
896   *Invasions, 16*(9), 1865-1877.
897   Golder (Golder Associates Ltd.) (2018). *2017 marine environmental effects monitoring program*
898   *(MEEMP) and aquatic invasive species (AIS) monitoring program*. (Report No. 1663724-
899   048-R-Rev0). Mary River Project; submitted to Baffinland Iron Mines Corporation,
900   Oakville, ON. Available online at: http://www.baffinland.com/document-portal-
901   new/?cat=4&archive=1&lang=en.
902   Goldsmit, J., Archambault, P., Chust, G., Villarino, E., Liu, G., Lukovich, J. V., . . . Howland, K.
903   L. (2018). Projecting present and future habitat suitability of ship-mediated aquatic
904   invasive species in the Canadian Arctic. *Biological Invasions, 20*(2), 501-517.
905   doi:10.1007/s10530-017-1553-7

906   Goldsmit, J., Howland, K. L., & Archambault, P. (2014). Establishing a baseline for early detection
907   of non-indigenous species in ports of the Canadian Arctic. *Aquatic Invasions, 9*(3), 327-
908   342. doi:http://dx.doi.org/10.3391/ai.2014.9.3.08
909   Goldsmit, J., McKindsey, C., Archambault, P., & Howland, K. L. (2019). Ecological risk
910   assessment of predicted marine invasions in the Canadian Arctic. *PloS ONE, 14*(2),
911   e0211815.
912   Goldsmit, J., Nudds, S. H., Stewart, D. B., Higdon, J. W., Hannah, C. G., & Howland, K. L. (2019).
913   Where else? Assessing zones of alternate ballast water exchange in the Canadian eastern
914   Arctic. *Marine Pollution Bulletin, 139*, 74-90.
915   doi:https://doi.org/10.1016/j.marpolbul.2018.11.062
916   Guisan, A., Graham, C. H., Elith, J., & Huettmann, F. (2007). Sensitivity of predictive species
917   distribution models to change in grain size. *Diversity and Distributions, 13*(3), 332-340.
918   Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I.
919   T., . . . Mantyka-Pringle, C. (2013). Predicting species distributions for conservation
920   decisions. *Ecology Letters, 16*(12), 1424-1435.
921   Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology.
922   *Ecological Modelling, 135*(2), 147-186.
923   Guisan, A., Zimmermann, N. E., Elith, J., Graham, C. H., Phillips, S., & Peterson, A. T. (2007).
924   What matters for predicting the occurrences of trees: Techniques, data, or species'
925   characteristics? *Ecological Monographs, 77*(4), 615-630.
926   Hallegraeff, G. M. (2010). Ocean climate change, phytoplankton community responses, and
927   harmful algal blooms: a formidable predictive challenge. *Journal of Phycology, 46*(2), 220-
928   235.
929   Hansen, H. S. B. (2015). *Snow crab (Chionoecetes opilio) in the Barents Sea. Diet, biology and
930   management.* (Master's thesis). Retrieved from: https://munin.uit.no/handle/10037/7746
931   Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E. H., Høines, Å. S., . . . Knutsen,
932   T. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and
933   Barents Seas: a review of possibilities and constraints. *Fisheries Research, 188*, 38-57.
934   Hecky, R. E., & Kilham, P. (1988). Nutrient limitation of phytoplankton in freshwater and marine
935   environments: a review of recent evidence on the effects of enrichment. *Limnology and
936   Oceanography, 33*(4, part2), 796-822.
937   Hewitt, C. L., Campbell, M. L. and Gollasch, S. (2006). *Alien species in aquaculture.
938   Considerations for responsible use.* IUCN, Gland, Switzerland and Cambridge, UK.
939   Retrieved from: https://www.iucn.org/content/alien-species-aquaculture-considerations-
940   responsible-use-0
941   Hijmans, R. J. (2012). Cross-validation of species distribution models: removing spatial sorting
942   bias and calibration with a null model. *Ecology, 93*(3), 679-688.
943   Hijmans, R. J., & Graham, C. H. (2006). The ability of climate envelope models to predict the
944   effect of climate change on species distributions. *Global Change Biology, 12*(12), 2272-
945   2281.
946   Hines, A. H., Ruiz, G. M., & Fofonoff, P. W. (2000). *Summary of NIS in Prince William Sound
947   and Alaska. Biological invasions of cold-water coastal ecosystems: ballast-mediated
948   introductions in Port Valdez / Prince William Sound, Alaska.* Prince William Sound:
949   Regional Citizens' Advisory Council of Prince William Sound. Retrieved from:
950   https://www.anstaskforce.gov/EcoSurveys/tech0050.pdf

951 Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine
952   ecosystems. *Science, 328*(5985), 1523-1528.
953 Hughes, K. A., & Ashton, G. V. (2017). Breaking the ice: the introduction of biofouling organisms
954   to Antarctica on vessel hulls. *Aquatic Conservation: Marine and Freshwater Ecosystems*,
955   27(1), 158-164.
956 Hughes, K. A., Pescott, O. L., Peyton, J., Adriaens, T., Cottier-Cook, E. J., Key, G., ... & Belchier,
957   M. (2020). Invasive non-native species likely to threaten biodiversity and ecosystems in
958   the Antarctic Peninsula region. *Global Change Biology*. DOI: 10.1111/gcb.14938
959 Ibanez, I., Silander Jr, J. A., Allen, J. M., Treanor, S. A., & Wilson, A. (2009). Identifying hotspots
960   for plant invasions and forecasting focal points of further spread. *Journal of Applied
961   Ecology, 46*(6), 1219-1228.
962 Jabour, J. (2017). Case study Antarctica: Up against the ice barrier: Antarctic tourism operators
963   prepare for the polar shipping code. *Global Climate Change and Coastal Tourism:
964   Recognizing Problems, Managing Solutions and Future Expectations*, 273.
965 Jahn, A. (2018). Reduced probability of ice-free summers for 1.5° C compared to 2° C warming.
966   *Nature Climate Change, 8*(5), 409.
967 Jensen, L. Ø., Mousing, E. A., & Richardson, K. (2017). Using species distribution modelling to
968   predict future distributions of phytoplankton: Case study using species important for the
969   biological pump. *Marine Ecology, 38*(3), e12427.
970 Jiménez-Valverde, A., & Lobo, J. M. (2007). Threshold criteria for conversion of probability of
971   species presence to either–or presence–absence. *Acta Oecologica, 31*(3), 361-369.
972 Joli, N., Gosselin, M., Ardyna, M., Babin, M., Onda, D. F., Tremblay, J.-É., & Lovejoy, C. (2018).
973   Need for focus on microbial species following ice melt and changing freshwater regimes
974   in a Janus Arctic Gateway. *Scientific Reports, 8*(1), 9405.
975 Jones, M. C., & Cheung, W. W. (2015). Multi-model ensemble projections of climate change
976   effects on global marine biodiversity. *ICES Journal of Marine Science*, 72(3), 741-752.
977 Jørgensen, L. L., & Nilssen, E. M. (2011). The invasive history, impact and management of the
978   red king crab *Paralithodes camtschaticus* off the coast of Norway. In *In the Wrong Place-
979   Alien Marine Crustaceans: Distribution, Biology and Impacts* (pp. 521-536). Springer,
980   Dordrecht.Jueterbock, A., Smolina, I., Coyer, J. A., & Hoarau, G. (2016). The fate of the
981   Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling
982   approach. *Ecology and Evolution, 6*(6), 1712-1724.
983 Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J. A., Olsen, J. L., & Hoarau, G. (2013).
984   Climate change impact on seaweed meadow distribution in the North Atlantic rocky
985   intertidal. *Ecology and Evolution, 3*(5), 1356-1373.
986 Kaluza, P., Kölzsch, A., Gastner, M. T., & Blasius, B. (2010). The complex network of global
987   cargo ship movements. *Journal of the Royal Society Interface, 7*(48), 1093-1103.
988 Kaschner, K., Kesner-Reyes, K., Garilao, C., Rius-Barile, J., Rees, T., & Froese, R. (Eds.) (2016).
989   *AquaMaps: Predicted range maps for aquatic species*. Website reference:
990   www.aquamaps.org, Version 08/2016.
991 Katsanevakis, S., Coll, M., Piroddi, C., Steenbeek, J., Ben Rais Lasram, F., Zenetos, A., &
992   Cardoso, A. C. (2014). Invading the Mediterranean Sea: biodiversity patterns shaped by
993   human activities. *Frontiers in Marine Science, 1*, 32.
994 Kelly, R., Leach, K., Cameron, A., Maggs, C. A., & Reid, N. (2014). Combining global climate
995   and regional landscape models to improve prediction of invasion risk. *Diversity and
996   Distributions, 20*(8), 884-894.

997   Kenchington, E., Link, H., Roy, V., Archambault, P., Siferd, T., Treble, M., & Wareham, V.
998   (2011). *Identification of mega- and macrobenthic ecologically and biologically significant*
999   *areas (EBSAs) in the Hudson Bay Complex, the Western and Eastern Canadian Arctic.*
1000   Canadian Science Advisory Secretariat Research Document (2011/071). Retrieved from:
1001   http://publications.gc.ca/site/eng/454975/publication.html
1002 Kordas, R. L., Harley, C. D. G., & O'Connor, M. I. (2011). Community ecology in a warming
1003   world: the influence of temperature on interspecific interactions in marine systems. *Journal*
1004   *of Experimental Marine Biology and Ecology, 400*(1-2), 218-226.
1005 Kube, S., Postel, L., Honnef, C., & Augustin, C. B. (2007). *Mnemiopsis leidyi* in the Baltic Sea:
1006   distribution and overwintering between autumn 2006 and spring 2007. *Aquatic Invasions,*
1007   *2*(2), 137-145.
1008 Lacoursière-Roussel, A., Howland, K., Normandeau, E., Grey, E., Archambault, P., Deiner, K., .
1009   . . and Bernatchez, L. (2018). eDNA metabarcoding as a new surveillance tool for coastal
1010   Arctic biodiversity. *Ecology and Evolution, 8*(16), 7763-7777.
1011 Laget, F. (2017). *Transport d'espèces de dinoflagellés potentiellement non-indigènes dans*
1012   *l'Arctique canadien, suite au déversement des eaux de ballast par un navire domestique*
1013   (Master's thesis). Retrieved from: http://semaphore.uqar.ca/1342/
1014 Lambert, G., Shenkar, N., & Swalla, B. J. (2010). First Pacific record of the north Atlantic ascidian
1015   *Molgula citrina*-bioinvasion or circumpolar distribution. *Aquatic Invasions, 5*(4), 369-378.
1016 Leduc, N., Lacoursière-Roussel, A., Howland, K. L., Archambault, P., Sevellec, M., Normandeau,
1017   E., ... & Bernatchez, L. (2019). Comparing eDNA metabarcoding and species collection
1018   for documenting Arctic metazoan biodiversity. *Environmental DNA*, 1(4), 342-358.
1019 Leidenberger, S., De Giovanni, R., Kulawik, R., Williams, A. R., & Bourlat, S. J. (2015). Mapping
1020   present and future potential distribution patterns for a meso-grazer guild in the Baltic Sea.
1021   *Journal of Biogeography, 42*(2), 241-254.
1022 Leidenberger, S., Obst, M., Kulawik, R., Stelzer, K., Heyer, K., Hardisty, A., & Bourlat, S. J.
1023   (2015). Evaluating the potential of ecological niche modelling as a component in marine
1024   non-indigenous species risk assessments. *Marine Pollution Bulletin, 97*(1-2), 470-487.
1025 Levitus, S., Antonov, J. I., Boyer, T. P., Baranova, O. K., Garcia, H. E., Locarnini, R. A., . . .
1026   Yarosh, E. S. (2012). World ocean heat content and thermosteric sea level change (0–2000
1027   m), 1955–2010. *Geophysical Research Letters, 39*(10).
1028 Li, X., Liu, X., Kraus, F., Tingley, R., & Li, Y. (2016). Risk of biological invasions is concentrated
1029   in biodiversity hotspots. *Frontiers in Ecology and the Environment, 14*(8), 411-417.
1030 Lind, S., Ingvaldsen, R. B., & Furevik, T. (2018). Arctic warming hotspot in the northern Barents
1031   Sea linked to declining sea-ice import. *Nature Climate Change, 8*(7), 634.
1032 Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species
1033   occurrence with presence-only data. *Journal of Biogeography, 40*(4), 778-789.
1034   doi:10.1111/jbi.12058
1035 Lobo, J. M. (2008). More complex distribution models or more representative data? *Biodiversity*
1036   *Informatics,* 5, 14-19.
1037 Locke, A., & Hanson, J. M. (2009). Rapid response to nonindigenous species. 3. A proposed
1038   framework. *Aquatic Invasions, 4*(1), 259-273.
1039 Locke, A., Mandrak, N. E., & Therriault, T. W. (2011). *A Canadian rapid response framework for*
1040   *aquatic invasive species*. Canadian Science Advisory Secretariat Research Document
1041   (2010/114). Retrieved from: http://publications.gc.ca/site/eng/404076/publication.html

Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2007). Invasion Ecology (Blackwell Publishing: Oxford, UK.).

Lowen, J. B., McKindsey, C. W., Therriault, T. W., & DiBacco, C. (2016). Effects of spatial resolution on predicting the distribution of aquatic invasive species in nearshore marine environments. *Marine Ecology Progress Series, 556*, 17-30.

MacDonald, I. R., Bluhm, B. A., Iken, K., Gagaev, S., & Strong, S. (2010). Benthic macrofauna and megafauna assemblages in the Arctic deep-sea Canada Basin. *Deep Sea Research Part II: Topical Studies in Oceanography, 57*(1), 136-152.

Mackey, A. P., Atkinson, A., Hill, S. L., Ward, P., Cunningham, N. J., Johnston, N. M., & Murphy, E. J. (2012). Antarctic macrozooplankton of the southwest Atlantic sector and Bellingshausen Sea: Baseline historical distributions (Discovery Investigations, 1928–1935) related to temperature and food, with projections for subsequent ocean warming. *Deep Sea Research Part II: Topical Studies in Oceanography, 59*, 130-146.

Marbuah, G., Gren, I.-M., & McKie, B. (2014). Economics of harmful invasive species: A review. *Diversity, 6*(3), 500-523.

Marcelino, V. R., & Verbruggen, H. (2015). Ecological niche models of invasive seaweeds. *Journal of Phycology, 51*(4), 606-620.

Marchese, C. (2015). Biodiversity hotspots: A shortcut for a more complicated concept. *Global Ecology and Conservation, 3*, 297-309.

McCarthy, A. H., Peck, L. S., Hughes, K. A., & Aldridge, D. C. (2019). Antarctica: The final frontier for marine biological invasions. *Global Change Biology*, 25(7), 2221-2241.

McHenry, J., Welch, H., Lester, S. E., & Saba, V. (2019). Projecting marine species range shifts from only temperature can mask climate vulnerability. *Global Change Biology*, (Accepted Author Manuscript), doi:10.1111/gcb.14828

Meißner, K., Fiorentino, D., Schnurr, S., Martinez Arbizu, P., Huettmann, F., Holst, S., . . . Svavarsson, J. (2014). Distribution of benthic marine invertebrates at northern latitudes ― An evaluation applying multi-algorithm species distribution models. *Journal of Sea Research, 85*, 241-254. doi:http://dx.doi.org/10.1016/j.seares.2013.05.007

Melia, N., Haines, K., & Hawkins, E. (2016). Sea ice decline and 21st century trans-Arctic shipping routes. *Geophysical Research Letters, 43*(18), 9720-9728.

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography, 36*(10), 1058-1069.

Miller, A. W., & Ruiz, G. M. (2014). Arctic shipping and marine invaders. *Nature Climate Change, 4*(6), 413-416.

Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment, 6*(9), 485-492.

Moore, A. M., Lowen, J. B., & DiBacco, C. (2018). Assessing invasion risk of *Didemnum vexillum* to Atlantic Canada. *Management of Biological Invasions, 9*(1), 11-25.

Moore, C. M., Mills, M. M., Arrigo, K. R., Berman-Frank, I., Bopp, L., Boyd, P. W., . . . Jaccard, S. L. (2013). Processes and patterns of oceanic nutrient limitation. *Nature Geoscience, 6*(9), 701-710.

Moss, R., Babiker, W., Brinkman, S., Calvo, E., Carter, T., Edmonds, J., ... & Jones, R. N. (2008). *Towards new scenarios for the analysis of emissions: Climate change, impacts and response strategies.* Intergovernmental Panel on Climate Change Secretariat (IPCC),

1088   Geneva, Switzerland. Retrieved from: https://www.ipcc.ch/publication/ipcc-expert-
1089   meeting-report-towards-new-scenarios-for-analysis-of-emissions-climate-change-
1090   impacts-and-response-strategies/
1091 Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., & Kent, J. (2000).
1092   Biodiversity hotspots for conservation priorities. *Nature, 403*(6772), 853.
1093 Niederdrenk, A. L., & Notz, D. (2018). Arctic sea ice in a 1.5 C warmer world. *Geophysical*
1094   *Research Letters, 45*(4), 1963-1971.
1095 Niimi, A. J. (2004). Environmental and economic factors can increase the risk of exotic species
1096   introductions to the Arctic region through increased ballast water discharge. *Environmental*
1097   *Management, 33*(5), 712-718.
1098 O'Donnell, J., Gallagher, R. V., Wilson, P. D., Downey, P. O., Hughes, L., & Leishman, M. R.
1099   (2012). Invasion hotspots for non-native plants in Australia under current and future
1100   climates. *Global Change Biology, 18*(2), 617-629.
1101 Overland, J., Dunlea, E., Box, J. E., Corell, R., Forsius, M., Kattsov, V., . . . Wang, M. (2018). The
1102   urgency of Arctic change. *Polar Science (in press)*.
1103   doi:https://doi.org/10.1016/j.polar.2018.11.008
1104 Pascual, M., Fuentes, V., Canepa, A., Atienza, D., Gili, J. M., & Purcell, J. E. (2015). Temperature
1105   effects on asexual reproduction of the scyphozoan *Aurelia aurita* sl: differences between
1106   exotic (Baltic and Red seas) and native (Mediterranean Sea) populations. *Marine Ecology,*
1107   *36*(4), 994-1002.
1108 Pearce, F., Peeler, E., & Stebbing, P. (2012). *Modelling the risk of the introduction and spread of*
1109   *non-indigenous species in the UK and Ireland.* (Project report for E5405W). Centre for
1110   Environment, Fisheries and Aquaculture Science (Cefas). Retrieved from:
1111   http://www.nonnativespecies.org/downloadDocument.cfm?id=791
1112 Pearson, R. G. (2007). *Species' distribution modeling for conservation educators and*
1113   *practitioners. Synthesis.* American Museum of Natural History. Retrieved from:
1114   http://ncep.amnh.org.
1115 Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the
1116   distribution of species: are bioclimate envelope models useful? *Global Ecology and*
1117   *Biogeography, 12*(5), 361-371. doi:10.1046/j.1466-822X.2003.00042.x
1118 Peck, L. S. (2005). Prospects for survival in the Southern Ocean: vulnerability of benthic species
1119   to temperature change. *Antarctic Science, 17*(4), 497-507.
1120 Pendleton, S. L., Miller, G. H., Lifton, N., Lehman, S. J., Southon, J., Crump, S. E., & Anderson,
1121   R. S. (2019). Rapidly receding Arctic Canada glaciers revealing landscapes continuously
1122   ice-covered for more than 40,000 years. *Nature Communications, 10*(1), 445.
1123 Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species
1124   geographic distributions. *Ecological Modelling, 190*(3), 231-259.
1125 Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions
1126   and a comprehensive evaluation. *Ecography, 31*(2), 161-175.
1127 Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S.
1128   (2009). Sample selection bias and presence-only distribution models: implications for
1129   background and pseudo-absence data. *Ecological Applications, 19*(1), 181-197.
1130 Piepenburg, D., Archambault, P., Ambrose Jr, W. G., Blanchard, A. L., Bluhm, B. A., Carroll, M.
1131   L., . . . Grebmeier, J. M. (2011). Towards a pan-Arctic inventory of the species diversity
1132   of the macro-and megabenthic fauna of the Arctic shelf seas. *Marine Biodiversity, 41*(1),
1133   51-70.

1134 Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., .
1135   . . Burrows, M. T. (2013). Global imprint of climate change on marine life. *Nature Climate*
1136   *Change, 3*(10), 919.
1137 Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-
1138   Guldberg, O., . . . Schoeman, D. S. (2016). Responses of marine organisms to climate
1139   change across oceans. *Frontiers in Marine Science, 3*, 62.
1140 Ramírez, F., Afán, I., Davis, L. S., & Chiaradia, A. (2017). Climate impacts on global hot spots of
1141   marine biodiversity. *Science Advances, 3*(2), e1601198.
1142 Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., . . .
1143   Neumann, H. (2014). Benthos distribution modelling and its relevance for marine
1144   ecosystem management. *ICES Journal of Marine Science, 72*(2), 297-315.
1145   doi:10.1093/icesjms/fsu107
1146 Reiss, H., Cunze, S., König, K., Neumann, H., & Kröncke, I. (2011). Species distribution
1147   modelling of marine benthos: a North Sea case study. *Marine Ecology Progress Series,*
1148   *442*, 71-86.
1149 Renaud, P. E., Wallhead, P., Kotta, J., Włodarska-Kowalczuk, M., Bellerby, R. G., Rätsep, M., ...
1150   & Kukliński, P. (2019). Arctic Sensitivity? Suitable habitat for benthic taxa is surprisingly
1151   robust to climate change. *Frontiers in Marine Science*, 6, 538.
1152 Ricciardi, A., Blackburn, T. M., Carlton, J. T., Dick, J. T. A., Hulme, P. E., Iacarella, J. C., . . .
1153   MacIsaac, H. J. (2017). Invasion science: a horizon scan of emerging challenges and
1154   opportunities. *Trends in Ecology & Evolution, 32*(6), 464-474.
1155 Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward
1156   understanding the ecological impacts of nonnative species. *Ecological Monographs, 83*(3),
1157   263-282.
1158 Richardson, M. G. (1979). The distribution of Antarctic marine macroalgae related to depth and
1159   substrate. *British Antarctic Survey Bulletin, 49,* 1-13.
1160 Rilov, G., & Galil, B. (2009). Marine bioinvasions in the Mediterranean Sea–history, distribution
1161   and ecology. In: G. Rilov, & J. A. Crooks (Eds.) *Biological invasions in marine ecosystems*
1162   (pp. 549-575). Berlin, Springer.
1163 Robinson, L. M., Elith, J., Hobday, A. J., Pearson, R. G., Kendall, B. E., Possingham, H. P., &
1164   Richardson, A. J. (2011). Pushing the limits in marine species distribution modelling:
1165   lessons from the land present challenges and opportunities. *Global Ecology and*
1166   *Biogeography, 20*(6), 789-802.
1167 Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E., & Lundquist, C. J. (2017). A
1168   systematic review of marine-based species distribution models (SDMs) with
1169   recommendations for best practice. *Frontiers in Marine Science*, 4, 421.
1170 Ruiz, G. M., Fofonoff, P. W., Steves, B., Foss, S. F., & Shiba, S. N. (2011). Marine invasion
1171   history and vector analysis of California: a hotspot for western North America. *Diversity*
1172   *and Distributions, 17*(2), 362-373.
1173 Ruiz, G. M., Fofonoff, P. W., Steves, B. P., & Carlton, J. T. (2015). Invasion history and vector
1174   dynamics in coastal marine ecosystems: A North American perspective. *Aquatic*
1175   *Ecosystem Health & Management, 18*(3), 299-311.
1176 Ruiz, G. M., & Hewitt, C. (2009). Latitudinal patterns of biological invasions in marine
1177   ecosystems: a polar perspective. *Proceedings of Smithsonian at the poles: contributions to*
1178   *international polar year science*./ I. Krupnik, M. A. Lang, & S. E. Miller (Eds.) pp 347-
1179   358. IPY. https://doi.org/10.5479/si.097884601X.26

1180 Ruiz, G. M., Huber, T., Larson, K., McCann, L., Steves, B., Fofonoff, P., & Hines, A. H. (2006).
1181   *Biological Invasions in Alaska's Coastal Marine Ecosystems: Establishing a Baseline.*
1182   Prince William Sound: Regional Citizens' Advisory Council of Prince William Sound.
1183   Retrieved from: http://www.vliz.be/imisdocs/publications/238416.pdf
1184 Sardain, A., Sardain, E., & Leung, B. (2019). Global forecasts of shipping traffic and biological
1185   invasions to 2050. *Nature Sustainability*, 2(4), 274-282.
1186 Screen, J. A. (2018). Arctic sea ice at 1.5 and 2° C. *Nature Climate Change, 8*(5), 362.
1187 Semmens, B. X., Buhle, E. R., Salomon, A. K., & Pattengill-Semmens, C. V. (2004). A hotspot of
1188   non-native marine fishes: evidence for the aquarium trade as an invasion pathway. *Marine
1189   Ecology Progress Series, 266*, 239-244.
1190 Seneviratne, S. I., Rogelj, J., Séférian, R., Wartenburger, R., Allen, M. R., Cain, M., . . . Hoegh-
1191   Guldberg, O. (2018). The many possible climates from the Paris Agreement's aim of 1.5
1192   C warming. *Nature, 558*(7708), 41.
1193 Sigmond, M., Fyfe, J. C., & Swart, N. C. (2018). Ice-free Arctic projections under the Paris
1194   Agreement. *Nature Climate Change, 8*(5), 404.
1195 Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., . . . Pascal, M.
1196   (2013). Impacts of biological invasions: what's what and the way forward. *Trends in
1197   Ecology & Evolution, 28*(1), 58-66.
1198 Smith, L. C., & Stephenson, S. R. (2013). New Trans-Arctic shipping routes navigable by
1199   midcentury. *Proceedings of the National Academy of Sciences of the Unitet States of
1200   America, 110*(13), E1191-E1195.
1201 Solecki, W., Rosenzweig, C., Dhakal, S., Roberts, D., Barau, A. S., Schultz, S., & Ürge-Vorsatz,
1202   D. (2018). City transformations in a 1.5 C warmer world. *Nature Climate Change, 8*(3),
1203   177-181. doi: 10.1038/s41558-018-0101-5
1204 Sorte, C. J. B., Williams, S. L., & Carlton, J. T. (2010). Marine range shifts and species
1205   introductions: comparative spread rates and community impacts. *Global Ecology and
1206   Biogeography, 19*(3), 303-316.
1207 Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M. A. X., . . .
1208   Lourie, S. A. (2007). Marine ecoregions of the world: a bioregionalization of coastal and
1209   shelf areas. *Bioscience, 57*(7), 573-583.
1210 Speer, L., & Laughlin, T. L. (2011). *IUCN/NRDC Workshop to Identify Areas of ecological and
1211   Biological Significance or Vulnerability in the Arctic Marine environment: Workshop
1212   Report.* Workshop organized by International union for the Conservation of Nature,
1213   Natural Resources Defense Council. La Jolla , USA. Retrieved from:
1214   https://portals.iucn.org/library/node/12787
1215 Stammerjohn, S., Massom, R., Rind, D., & Martinson, D. (2012). Regions of rapid sea ice change:
1216   An inter-hemispheric seasonal comparison. *Geophysical Research Letters, 39*(6).
1217 Stelzer, K., Heyer, K., Bourlat, S., & Obst, M. (2013). *Application of niche modeling and earth
1218   observation for the risk assessment and monitoring of invasive species in the Baltic Sea.*
1219   MarCoast II -Marine and Coastal Environmental Information Services Ballast Water
1220   Option. Report to the European Space Agency. doi: 10.5281/zenodo.886349
1221 Stephenson, S. A., & Hartwig, L. (2010). *The Arctic marine workshop*. Canadian Manuscript
1222   Report of Fisheries and Aquatic Sciences (2934). Retrieved from: http://www.dfo-
1223   mpo.gc.ca/Library/341178.pdf

Streftaris, N., Zenetos, A., & Papathanassiou, E. (2005). Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas. *Oceanography and Marine Biology: An Annual Review, 43*, 419-453.

Svavarsson, J., & Dungal, P. (2008). *Leyndardómar sjávarins við Ísland*. Reykjavík.

Templeman, N. D. (2007). *Placentia Bay-Grand Banks large ocean management area ecologically and biologically significant areas.* Canadian Science Advisory Secretariat Research Document (2007/052). Retrieved from: http://www.icomnl.ca/files/CSAS%20Report%20PBGB%20EBSAs.PDF

Therriault, T. W., Nelson, J. C., Carlton, J. T., Liggan, L., Otani, M., Kawai, H., . . . Murray, C. C. (2018). The invasion risk of species associated with Japanese tsunami marine debris in Pacific North America and Hawaii. *Marine Pollution Bulletin, 132*, 82-89.

Tidbury, H. J., Taylor, N. G. H., Copp, G. H., Garnacho, E., & Stebbing, P. D. (2016). Predicting and mapping the risk of introduction of marine non-indigenous species into Great Britain and Ireland. *Biological Invasions, 18*(11), 3277-3292.

Torres, U., Godsoe, W., Buckley, H. L., Parry, M., Lustig, A., & Worner, S. P. (2018). Using niche conservatism information to prioritize hotspots of invasion by non-native freshwater invertebrates in New Zealand. *Diversity and Distributions, 24*(12), 1802-1815.

Tovar-Sánchez, A., Duarte, C. M., Alonso, J. C., Lacorte, S., Tauler, R., & Galbán-Malagón, C. (2010). Impacts of metals and nutrients released from melting multiyear Arctic sea ice. *Journal of Geophysical Research: Oceans, 115*(C7).

Townhill, B. L., Tinker, J., Jones, M., Pitois, S., Creach, V., Simpson, S. D., . . .Pinnegar, J. K. (2018). Harmful algal blooms and climate change: exploring future distribution changes. *ICES Journal of Marine Science, 75*(6), 1882-1893.

Tremblay, P. (2017). *Évaluation du risque potentiel d'introduction d'espèces non-indigènes de mésozooplancton suite au déversement des eaux de ballast d'un navire domestique dans l'Arctique canadien* (Mater's thesis). Retived from: http://semaphore.uqar.ca/1300/.

Turbelin, A. J., Malamud, B. D., & Francis, R. A. (2017). Mapping the global state of invasive alien species: patterns of invasion and policy responses. *Global Ecology and Biogeography, 26*(1), 78-92.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography, 21*(2), 272-281.

Valle, M., Chust, G., del Campo, A., Wisz, M. S., Olsen, S. M., Garmendia, J. M., & Borja, Á. (2014). Projecting future distribution of the seagrass *Zostera noltii* under global warming and sea level rise. *Biological Conservation, 170*, 74-85.

Verbruggen, H., Tyberghein, L., Belton, G. S., Mineur, F., Jueterbock, A., Hoarau, G., . . . De Clerck, O. (2013). Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. *PLoS ONE, 8*(6), e68337.

Verlaque, M. (2001). Checklist of the macroalgae of Thau Lagoon (Hérault, France), a hot spot of marine species introduction in Europe. *Oceanologica Acta, 24*(1), 29-49.

Villarino, E., Chust G., Licandro P., Butenschön M., Ibaibarriaga L., Larrañaga A., & X., I. (2015). Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change. *Marine Ecology Progress Series, 531*, 121-142.

Wagner, F. J. E. (1977). Recent mollusc distribution patterns and palaeobathymetry, southeastern Beaufort Sea. *Canadian Journal of Earth Sciences, 14*(9), 2013-2028.

Ware, C., Berge, J., Jelmert, A., Olsen, S. M., Pellissier, L., Wisz, M. S., . . . Alsos, I. G. (2016). Biological introduction risks from shipping in a warming Arctic. *Journal of Applied Ecology, 53*, 340-349.

Wassmann, P., Duarte, C. M., Agusti, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology, 17*(2), 1235-1249.

Weinert, M., Mathis, M., Kröncke, I., Neumann, H., Pohlmann, T., & Reiss, H. (2016). Modelling climate change effects on benthos: Distributional shifts in the North Sea from 2001 to 2099. *Estuarine, Coastal and Shelf Science, 175*, 157-168.

Wells, M. L., Mayer, L. M., & Guillard, R. R. L. (1991). Evaluation of iron as a triggering factor for red tide blooms. *Marine Ecology Progress Series*, 93-102.

Wisz, M. S., Broennimann, O., Grønkjær, P., Møller, P. R., Olsen, S. M., Swingedouw, D., . . . Pellissier, L. (2015). Arctic warming will promote Atlantic-Pacific fish interchange. *Nature Climate Change, 5*(3), 261-265.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., . . . Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews of the Cambridge Philosophical Society, 88*(1), 15-30. doi:10.1111/j.1469-185X.2012.00235.x

Xu, J., Wickramarathne, T. L., Chawla, N. V., Grey, E. K., Steinhaeuser, K., Keller, R. P., ... & Lodge, D. M. (2014). Improving management of aquatic invasions by integrating shipping network, ecological, and environmental data: data mining for social good. In *Proceedings of the 20th ACM SIGKDD International Conference on Knowledge Discovery and Data Mining,* USA, 1699-1708. doi: 10.1145/2623330.2623364

Young, R. (2016). *Molecular species delimitation and biogeography of Canadian marine planktonic crustaceans* (Doctoral disertation). Retrieved from: https://atrium.lib.uoguelph.ca/xmlui/handle/10214/9753

Zimina, O. L. (2014). Finding the snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda: Majidae) in the Kara Sea. *Russian Journal of Marine Biology, 40*(6), 490-492.