





Climate change opens new frontiers for marine species in the Arctic: Current trends and future invasion risks

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Abstract

Climate change and increased anthropogenic activities are expected to elevate the potential of introducing nonindigenous species (NIS) into the Arctic. Yet, the knowledge base needed to identify gaps and priorities for NIS research and management is limited. Here, we reviewed primary introduction events to each ecoregion of the marine Arctic realm to identify temporal and spatial patterns, likely source regions of NIS, and the putative introduction pathways. We included 54 introduction events representing 34 unique NIS. The rate of NIS discovery ranged from zero to four species per year between 1960 and 2015. The Iceland Shelf had the greatest number of introduction events ($n = 14$), followed by the Barents Sea ($n = 11$), and the Norwegian Sea ($n = 11$). Sixteen of the 54 introduction records had no known origins. The majority of those with known source regions were attributed to the Northeast Atlantic and the Northwest Pacific, 19 and 14 records, respectively. Some introduction events were attributed to multiple possible pathways. For these introductions, vessels transferred the greatest number of aquatic NIS (39%) to the Arctic, followed by natural spread (30%) and aquaculture activities (25%). Similar trends were found for introductions attributed to a single pathway. The phyla Arthropoda and Ochrophyta had the highest number of recorded introduction events, with 19 and 12 records, respectively. Recommendations including vector management, horizon scanning, early detection, rapid response, and a pan-Arctic biodiversity inventory are considered in this paper. Our study provides a comprehensive record of primary introductions of NIS for marine environments in the circumpolar Arctic and identifies knowledge gaps and opportunities for NIS research and management. Ecosystems worldwide will face dramatic changes in the coming decades due to global change. Our findings contribute to the knowledge base needed to address two aspects of global change—invasive species and climate change.

KEYWORDS

alien species, aquaculture, climate warming, fisheries, invasion pathways, invasive species, knowledge gap, nonindigenous species, shipping, vessels

1 | INTRODUCTION

Human activities, such as shipping, aquaculture, stocking, and the building of canals, have facilitated the global movement of nonindigenous species (NIS) to places they would have not been able to reach unaided and at greater rates than what could occur naturally (Molnar, Gamboa, Revenga, & Spalding, 2008). To date, more than thousands of NIS have been recorded in marine, brackish, and freshwater ecosystems worldwide (AquaNIS Editorial Board, 2015; Molnar et al., 2008; U.S. Geological Survey, 2017). For example, more than 166 NIS are reported from the Laurentian Great Lakes Basin (U.S. Geological Survey, 2017), and 67 NIS are known to be established in the Baltic Sea (Ojaveer et al., 2017). Although not all NIS are harmful, some of them have led to changes within recipient ecosystems, causing substantial impacts on ecology (Bax, Williamson, Aguero, Gonzalez, & Geeves, 2003; Dvoretzky, 2012, 2013a; Salvaterra, Green, Crowe, & O'Gorman, 2013), economies (Dvoretzky, 2014; Dvoretzky & Dvoretzky, 2015, 2018; Lodge et al., 2006; Streftaris & Zenetos, 2006), and/or animal health (Burek, Gulland, & O'Hara, 2008; Dvoretzky, 2013b; Ruiz et al., 2000). For example, the carpet sea squirt, *Didemnum vexillum*, presently occurs in many temperate regions (Lambert, 2009), has spread rapidly across Georges Bank in the Northwest Atlantic and along the European coasts, competing with native benthic species, altering community structure, and potentially negatively impacting fisheries (Lengyel, Collie, & Valentine, 2009; McKenzie et al., 2017; Valentine et al., 2007). Additionally, a list of 100 NIS with recognized impacts on native biodiversity was compiled for the Mediterranean Sea (Streftaris & Zenetos, 2006). Indeed, biological invasions are considered a major threat to global biodiversity (Bax et al., 2003; CBD, 2002; Cook, Brown, Payne, & Macleod, 2016).

Climate change may further enhance the rate and extent of biological invasions (Hellmann, Byers, Bierwagen, & Dukes, 2008). The effects of climate change are already affecting native communities by decreasing productivity, altering food web dynamics, and modifying habitat complexity (Cheung et al., 2009; Hoegh-Guldberg & Bruno, 2010). Alterations to temperature regimes, surface currents, sea ice cover, and other key processes are expected to modify both natural and human-mediated species dispersal, enhance survival and establishment of NIS in previously unsuitable localities, and amplify impacts of existing NIS in invaded habitats (Hellmann et al., 2008; Occhipinti-Ambrogi, 2007; Stachowicz, Terwin, Whitlatch, & Osman, 2002).

The Arctic has historically been presumed a lower risk region for biological invasions due to limited access, harsh environmental conditions, and inadequate food resources that hinder dispersal, survival, growth, and/or reproduction for many species (Ruiz & Hewitt, 2009; Vermeij & Roopnarine, 2008). However, the region is now under unprecedented threat of biological invasions due to climate warming and increased human activity (Matishov, Makarevich, & Ishkulov, 2011; Miller & Ruiz, 2014; Ricciardi et al., 2017). For instance, the Arctic has had notable reductions in seasonal sea ice. Retreating sea ice is opening up the region for a range of human activities such as

shipping, resource exploration, and tourism, thereby increasing the potential of human-mediated introductions of NIS. One model predicts a scenario of ice-free summers in the Arctic by 2037 (Wang & Overland, 2008). Such a reduction in sea ice extent will have negative consequences for some native biota, while providing suitable conditions for more southern species. Mollusks and fishes, for example, may spread from the Pacific across the Arctic to the Atlantic Ocean under warmer climate as happened in the mid-Pliocene (Vermeij & Roopnarine, 2008; Wisz et al., 2015). Currently, conditions in some high-latitude systems are already suitable for temperate species, thus successful establishment may be possible once there is sufficient propagule supply (de Rivera, Steves, Fofonoff, Hines, & Ruiz, 2011). Additional warming may further enhance the suitability of Arctic coastal regions for temperate species (Goldsmith et al., 2018; Ware et al., 2014).

While biological invasions in the Arctic have begun to receive more attention recently, the knowledge base needed to identify research gaps and priorities for NIS research and management is limited (CAFF & PAME, 2017; Ricciardi et al., 2017). Here, we examined reports of primary introduction events (i.e., initial introductions and excluding subsequent spread within the region) in ecoregions of the marine Arctic realm to characterize temporal and spatial patterns of NIS introductions. More specifically, we identified Arctic regions that had the greatest number of introductions and their likely source region(s). In addition, we studied the pathway(s) likely responsible for these introductions and the taxa involved.

2 | NIS RECORDS IN THE MARINE ARCTIC

We used the Large Marine Ecosystems of the Arctic (Arctic LMEs; PAME, 2013) to delineate the Arctic boundary (Figure 1). The Arctic region is comprised of 18 Arctic LMEs, which are distinct ecological areas based on differences in bathymetry, hydrography, productivity, and trophic linkages (PAME, 2013). We defined NIS as those that have been introduced to any Arctic LME, having arrived from other world regions. We consulted the primary literature, white papers, reports, and online databases including AquaNIS (www.corpi.ku.lt/databases/aquanis), EMODnet-Arctic (<https://www.emodnet-arctic.eu/alien-species>), the National Exotic Marine and Estuarine Species Information System (NEMESIS; <https://invasions.si.edu/nemesis/>), the European Network on Invasive Species (NOBANIS; <https://www.NOBANIS.org>), Delivering Alien Invasive Species Inventories for Europe (DAISIE; <https://www.europe-aliens.org/>), and the Invasive Species Compendium (<https://www.cabi.org/isc/>) to compile records for each NIS and its corresponding introduction event(s). We verified records from online databases, when possible, with the original cited literature. Nomenclature is consistent with the World Register of Marine Species (WoRMS; <https://www.marinespecies.org/>) and AlgaeBase (<https://www.algaebase.org/>). We excluded introduction events that occurred before 1960 from our analysis because of the lack of baseline information on Arctic biodiversity when large areas of the region were unexplored at the time. This dataset provides NIS information to the year 2015. This avoids false

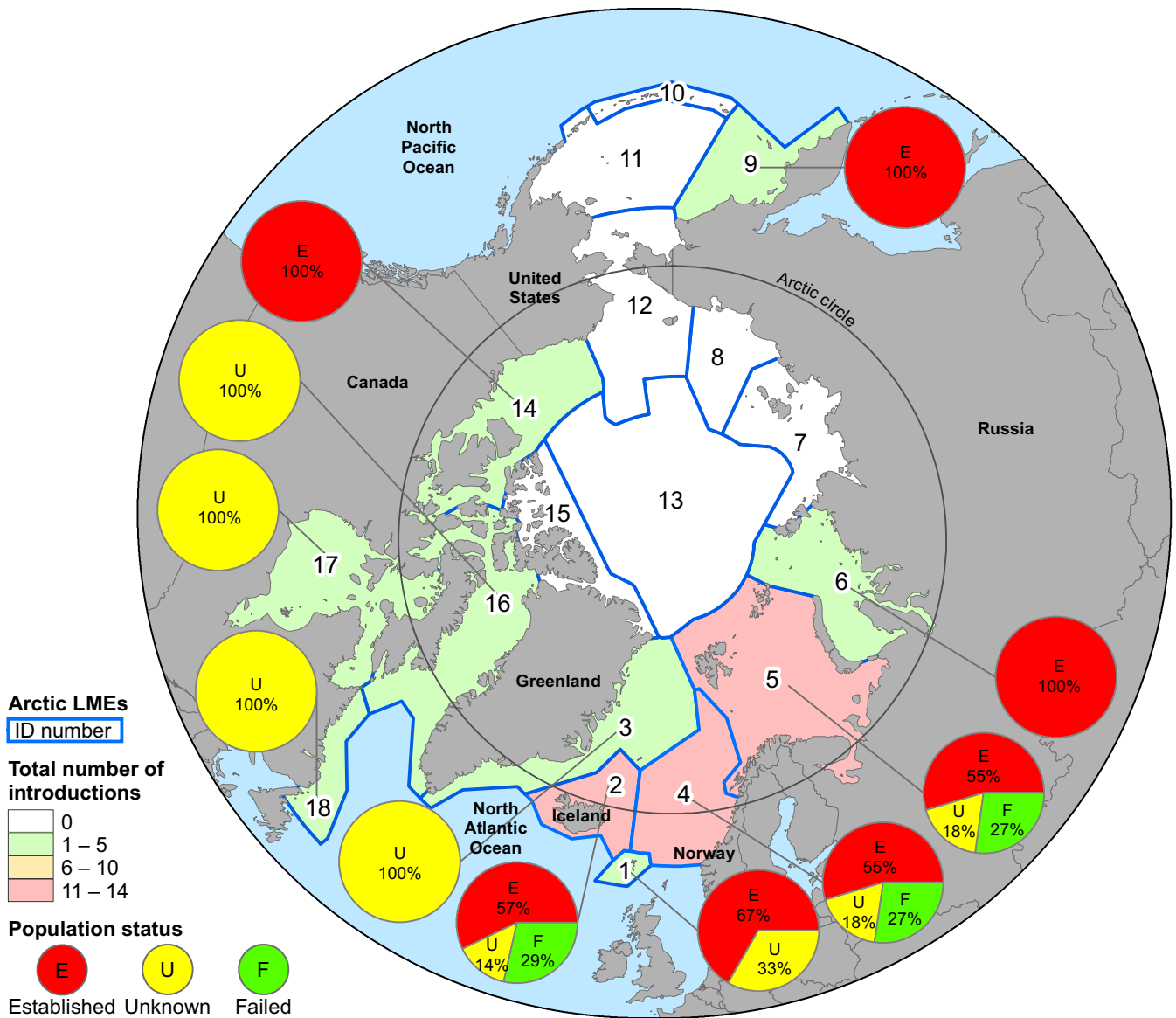


FIGURE 1 Map illustrating the Large Marine Ecosystems of the Arctic (Arctic LMEs) as defined by the Arctic Council's Protection of the Arctic Marine Environment Working Group (PAME, 2013). ID numbers 1 = Faroe Islands, 2 = Iceland Shelf, 3 = Greenland Sea East-Greenland, 4 = Norwegian Sea, 5 = Barents Sea, 6 = Kara Sea, 7 = Laptev Sea, 8 = East Siberian Sea, 9 = East Bering Sea, 10 = Aleutian Islands, 11 = West Bering Sea, 12 = Northern Bering Chukchi Sea, 13 = Central Arctic Ocean, 14 = Beaufort Sea, 15 = Canadian High Arctic-North Greenland, 16 = Canadian East Arctic-West Greenland, 17 = Hudson Bay, and 18 = Labrador-Newfoundland. Also shown are the total number of introduction events ($n = 54$) and the population status of NIS in each introduced region

negatives due to a lag time between first observation and reporting of NIS. Cryptogenic species (*sensu* Carlton, 1996) were excluded from our analysis due to missing information about the source region(s) and/or the mechanism(s) of introduction. Our database contains a comprehensive set of records of NIS introductions for marine environments in the Arctic, though we recognize that many NIS may remain undetected and/or undocumented. We recorded 54 introduction events, representing 34 unique aquatic NIS (Supporting Information Table S1).

We grouped the introduction events into separate Arctic LMEs to identify spatial patterns (Figure 1). Source regions were ascribed according to the 19 Food and Agriculture Organization of the United

Nations (FAO) major fishing areas (FAO, 2018; Figure 2) because it was otherwise difficult to describe source regions, which are generally broadly defined. These source regions may be the native range of NIS or an established nonindigenous population. For each introduction event, we assigned a population status following the definitions described by NEMESIS (Fononoff, Ruiz, Steves, Hines, & Carlton, 2003). "Established" populations are those that have been repeatedly detected, at minimum either at two separate locations or in two different years at the same location, with evidence of successful reproduction. An "unknown" status refers to an NIS found only once in the area or where the reproductive capability of the recorded population is uncertain. Finally, "failed" indicates an

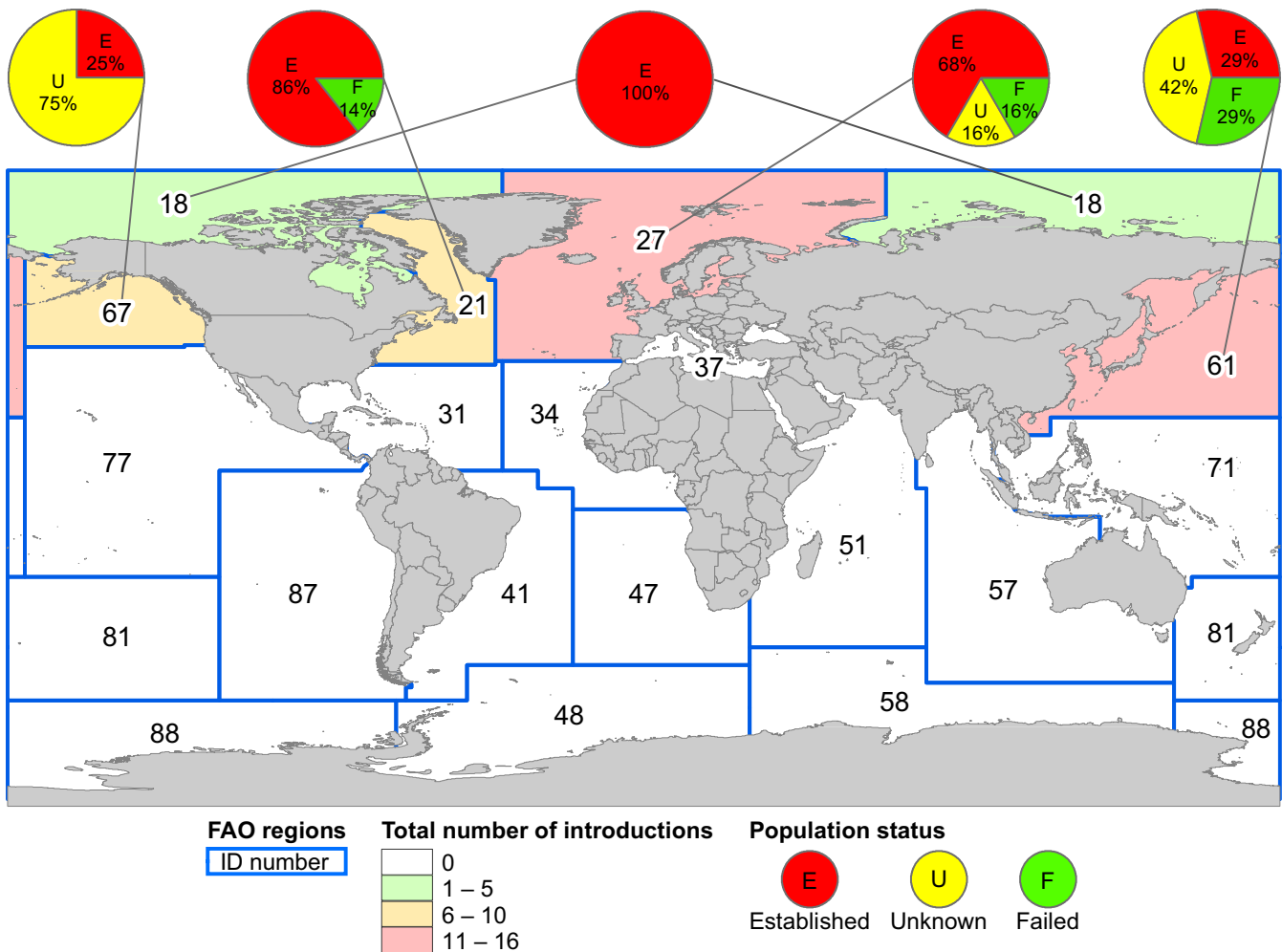


FIGURE 2 Map depicting the Food and Agriculture Organization of the United Nations (FAO) fishing regions (FAO, 2018) used to describe the source(s) of NIS introduced in the marine Arctic. ID numbers 18 = Arctic Sea, 21 = Northwest Atlantic, 27 = Northeast Atlantic, 31 = West Central Atlantic, 34 = East Central Atlantic, 37 = Mediterranean and Black Sea, 41 = Southwest Atlantic, 47 = Southeast Atlantic, 48 = Antarctic Atlantic, 51 = Western Indian Ocean, 57 = Eastern Indian Ocean, 58 = Antarctic and Southern Indian Ocean, 61 = Northwest Pacific, 67 = Northeast Pacific, 71 = Western Central Pacific, 77 = Eastern Central Pacific, 81 Southwest Pacific, 87 = Southeast Pacific, and 88 = Antarctic Pacific. Also shown are the total number of introductions originated from each FAO area ($n = 49$, excluding introduction events with no known source regions) and the population status of the corresponding NIS in the introduced regions

NIS that did not persist or was unlikely to establish a sustaining population.

We also examined the introduction pathway(s), the processes that result in the arrival of NIS from the source region into the recipient location (Hulme et al., 2008), associated with each introduction event. These included canals, aquaculture activities, live food trade, natural spread, vessels, wild fisheries, and unknown, as described by AquaNIS (AquaNIS Editorial Board, 2015). “Canals” involves NIS transfers between previously geographically isolated regions via man-made waterways. “Aquaculture activities” (labeled as culture activities in AquaNIS and renamed here to prevent confusion with sociological pathways like organism releases for religious reasons) relate to NIS introductions by aquaculture, stock movement, accidental releases and escapes, and associated water and packaging material. The pathway “live food trade” includes intentional release of live organisms imported for consumption and unintentional

introduction of associated pests and contaminants. “Natural spread” refers to the movement of NIS from an adjacent LME by means of water currents or other natural dispersal vectors, either as one of multiple possible pathways attributed to an introduction or as subsequent spread following initial arrival into the Arctic by human activities. As an exception, we also included long-distance movements of species between Arctic LMEs (i.e., trans-Arctic migration) by natural dispersal mechanisms. However, we excluded natural range expansion of a species from a neighboring Arctic LME that was native to that area. The pathway “vessels” includes transport of NIS in and on commercial ships, recreational crafts, and floating structures (e.g., anchor and anchor chains, ballast water, biofouling, sea chest, and tank sediments). “Wild fisheries” are associated with stocking, discard of by-catch, live bait release, and accidental introductions via fishing gear, live packaging material, processed live material, and transported water. Finally, “unknown” refers to NIS for which there is no

recognized pathway for an arrival in an Arctic LME but has almost certainly been spread anthropogenically. The assignment of pathways was performed based on direct evidence, deductions, or expert judgment (AquaNIS Editorial Board, 2015). Documented evidence of an introduction, such as the release of NIS into the wild and the observation of organisms in ships' ballast water samples, was not always available. Thus, introduction events were often ascribed to one or more pathways based on deductions, where a pathway(s) is known to operate in a locality and there is no other explanation for the presence of the NIS, or expert judgment, where the NIS is known to be introduced by the possible pathway(s) elsewhere (AquaNIS Editorial Board, 2015).

3 | TEMPORAL TRENDS OF NEW NIS

We used the year of first report for each NIS in the marine Arctic to identify temporal trends in their arrival ($n = 34$). The rate of reported NIS discovery varied annually from zero to four species (Figure 3a). The discovery rate of NIS in Arctic waters generally increased over time (Figure 3b), likely coinciding with increased human activities in the Arctic. Recent increases in NIS detection may also be attributed to expanded research effort in the Arctic, yet there are very few standardized or ongoing NIS detection and monitoring programs established in the region.

4 | SPATIAL PATTERNS OF INTRODUCTIONS

The Iceland Shelf has had the greatest number of NIS introductions (26% of all introductions), followed by the Barents Sea (20%) and the Norwegian Sea (20%; Figure 1). Not only do these regions have many NIS introductions, but also have many established populations of NIS. This pattern suggests that these regions may be particularly

vulnerable to biological invasions due to great diversity and abundance of species introduced (i.e., colonization pressure and propagule pressure, respectively), thus increased probability of successful establishment. In addition, these regions are becoming most hospitable for temperate NIS, as the area is transitioning from a cold Arctic to a warm Atlantic-dominated climate regime (Lind, Ingvaldsen, & Furevik, 2018). There were three introduction events in the Faroe Islands (6%), with two NIS established at known release sites (Figure 1). Although the Kara Sea, the East Bering Sea, and the Beaufort Sea each had a single introduction event, all of the introductions resulted in successful NIS establishment (Figure 1). All remaining Arctic LMEs had few introduction events, and none led to established populations. The observed pattern could be explained by a greater research effort in the Iceland Shelf, the Barents Sea, and the Norwegian Sea, as reflected by the number of NIS databases (e.g., AquaNIS, CABI, DAISIE, EMODnet-Arctic, and NOBANIS) covering these regions. The size of the Arctic LMEs could also confound the pattern, although the number of introduction events recorded for each region does not appear to be related to LME size (Figure 1).

We were unable to determine a source region for 16 of the 54 introduction events. In contrast, there were multiple possible sources for nine introduction events due to the spatial extent of the putative source regions. The majority of the introduction events with known source regions were attributed to the Northeast Atlantic (39%) and the Northwest Pacific (29%), followed by the Northeast Pacific (16%), the Northwest Atlantic (14%), and the Arctic Sea (2%; Figure 2). Data availability prevented us from exploring the extent of species movements within the Arctic versus those from lower latitudes into the Arctic. However, we were able to determine that six introduction events originated from within the Arctic, based on genetic data, stock movement records, and known distribution of the NIS (Supporting Information Table S1). Molecular approaches including phylogeographic surveys and population genetics or genomics studies will be required to further pinpoint the source(s) and reconstruct the routes of introduction for the remaining introduction events.

A large proportion of the introduction events (66%) originating from the Northeast Atlantic have led to established populations at release sites in Arctic waters. In contrast, only 29% of the introductions from Northeast Pacific resulted in successful establishment. There were six established NIS populations in the Arctic originating from the Northwest Atlantic and four from the Northeast Pacific, even though the Northeast Pacific contributed a greater number of introduction events (Figure 2).

5 | PATHWAYS OF INTRODUCTION

The majority (68%) of the introduction events were attributed to a single pathway, whereas 32% were attributed to multiple pathways. Vessels (48%) were the dominant pathway for single-pathway introductions, followed by natural spread (19%), aquaculture activities (14%), wild fisheries (14%), and live food trade (5%; Figure 4a). For multipathway introductions, we examined records using unweighted

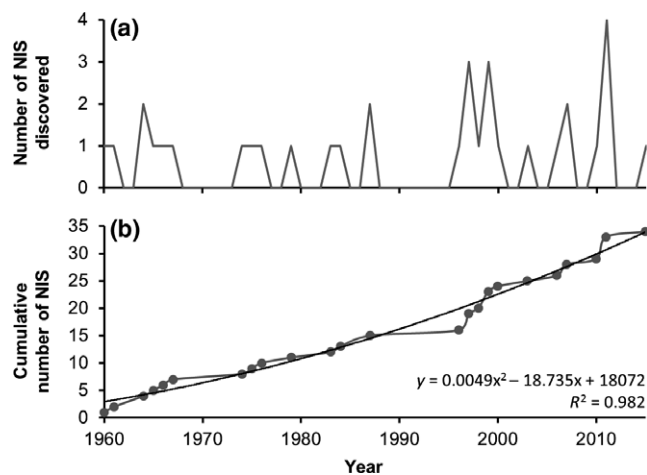


FIGURE 3 Number of new NIS discovered annually (a) and cumulative number of NIS detected with the best-fitted curve (b) in the marine Arctic from 1960 to 2015. Data shown represent the earliest reliable date of first report in the Arctic for 34 NIS

and weighted approaches (sensu Williams et al., 2013). The unweighted method identifies the maximum number of introduction events attributed to each possible pathway, whereas the weighted measurement gives an estimate of the relative contribution of each possible pathway to a single introduction event (Williams et al., 2013). As both approaches produced qualitatively similar results, only those obtained using the unweighted method are presented. The maximum number of pathways attributed to any introduction event was three; all of these introduction events ($n = 6$) were partially attributed to both vessels and natural spread. Vessels (39%) were the most important pathway, followed by natural spread (30%) and aquaculture activities (25%; Figure 4b). A small proportion of the multipathway introductions were attributed to canals (White Sea–Baltic Canal), live food trade, and wild fisheries (3% each). In general, introduction events associated with vessels were the most likely to result in NIS establishment at the release sites in the Arctic (25% of all introduction events), followed by aquaculture activities (13%), natural spread (12%), wild fisheries (4%), and canals (1%). No NIS introduced via the live food trade were successfully established in Arctic waters.

Not surprisingly, vessels are the leading pathway for both single and multipathway introductions. Maritime transport has played an important role in expeditions and exploration, community supply/re-supply, natural resource extraction and exportation, fisheries, and tourism in Arctic waters (Arctic Council, 2009). More recently, the commercial use of northern shipping routes is increasingly viable due to drastic reductions in Arctic sea ice cover (Melia, Haines, & Hawkins, 2016). Commercial ships can save weeks and thousands of nautical miles by sailing via the Northeast Passage (north of Eurasia) or the Northwest Passage (north of North America) rather than through the Panama or Suez Canals, resulting in significant cost savings from reduced fuel consumption and faster voyage turnover (Melia et al., 2016). Therefore, vessels have, and will likely continue to provide ample opportunities for the transfer of aquatic NIS to the Arctic.

Ballast water of commercial ships is an important transfer mechanism for aquatic NIS in the Arctic (Chan, MacIsaac, & Bailey, 2015; Sokolov, Strelkova, Manushin, & Sennikov, 2016; Ware et al., 2016). The risk of ballast-mediated introductions, however, is expected to be mitigated by the implementation of ballast water management

systems (BWMS). The *International Convention for the Control and Management of Ships' Ballast Water and Sediments*, adopted in 2004 and entered into force in 2017, requires management of ballast water with the aim to reduce the transfer of harmful aquatic organisms and pathogens, including harmful NIS (IMO, 2017a). Currently, there are 73 BWMS that have received Type Approval Certification, meaning they have demonstrated their abilities to meet ballast water discharge standards described in Regulation D-2 of this convention under specified conditions, such as different salinity and temperature regimes, turbidity, and organism concentrations (IMO, 2017b). There have been concerns regarding the effectiveness of BWMS in cold environments (Drillet et al., 2013; van den Brink, Kaag, & Sneekes, 2013), but a recent study found filtration combined with UV-C treatment effective at low temperature (2°C) with few viable organisms ≥ 10 to ≤ 50 μm in the treated water (Casas-Monroy et al., 2018).

Biofouling on commercial ships, on the other hand, may pose greater invasion risk than ballast water by transporting greater diversity and abundance of NIS in Arctic waters (Chan et al., 2015). While biofouling organisms on ships generally have poor survivorship during Arctic voyages, some NIS are capable of surviving transits from temperate to Arctic ports (Chan, MacIsaac, & Bailey, 2016). Furthermore, temperature differences between shallow ports and the open sea may induce spawning of biofouling biota, releasing zygotes that may form established populations in the port environment (Minchin & Gollasch, 2003). Biofouling on other vessel types, including leisure crafts, fishing vessels, floating platforms, and other artificial structures, may become increasingly important as transfer mechanisms for aquatic NIS due to the recent growth in tourism, fisheries, and oil and gas development in the Arctic. While no studies have examined the magnitude of biofouling on these vessel types in polar waters, they are recognized transfer mechanisms of fouling NIS globally (Minchin, Floerl, Savini, & Occhipinti-Ambrogi, 2006; Mineur et al., 2012). For example, the discovery of an intact subtropical reef community associated with an oil rig highlights the invasion potential of towing biofouled structures across biogeographic regions (Wanless et al., 2010). Furthermore, drift flotsam and jetsam, including plastics, may transport biota into Arctic waters (Barnes & Milner, 2005). Currently, antifouling paints are used to prevent biofouling organisms from accumulating on wetted surface areas of vessels;

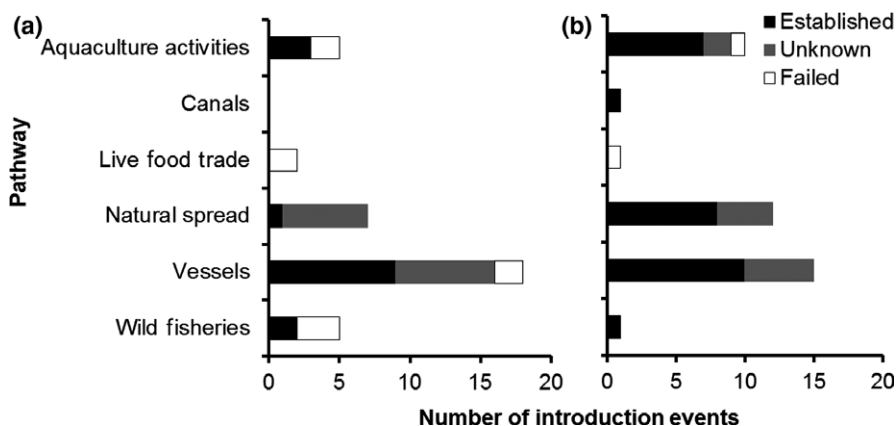


FIGURE 4 Analysis of primary introduction events attributed to a single pathway (a) and multiple pathways (b). Also shown is the population status of NIS at introduced sites in the marine Arctic

however, their effectiveness varies depending on the age and type (e.g., self-polishing copolymer with biocides vs. biocide-free foul-release) of coatings (Dafforn, Lewis, & Johnston, 2011; Sylvester et al., 2011). In polar waters, ice scouring can damage vessels' coatings, further comprising the effectiveness of antifouling paints, though biofouling organisms may be negatively impacted at the same time (Lee & Chown, 2009; Lewis, Riddle, & Hewitt, 2004). Therefore, topographically complex and protected areas on vessels may be of particular importance for the transfer of aquatic NIS into the Arctic, as in the case for the Antarctic (Hughes & Ashton, 2016; Lee & Chown, 2007).

Natural spread appears to be an important mechanism for multipathway introductions, as it is often cited as one of many possible pathways contributing to introductions. However, it is impossible to determine the relative importance of natural spread and other human-mediated pathways due to the uncertainty often associated with pathway assignment. For single-pathway introductions, natural spread has contributed to the secondary spread of the Snow Crab (*Chionoecetes opilio*) from the original release site in the Barents Sea to the Kara Sea (Sokolov et al., 2016; Zimina, 2015). Transfer of NIS is concerning when it occurs across biogeographic barriers, but also when it happens as secondary spread at regional scales, contributing to stepping-stone invasions (Apte, Holland, Godwin, & Gardner, 2000; David, Gollasch, & Pavliha, 2013). Natural spread also included the long-distance dispersal of the Pacific diatom (*Neodenticula seminiae*) from the North Pacific to the North Atlantic, as a result of reduced ice cover and increased inflow of Pacific water into the North Atlantic through the Canadian High Arctic (Miettinen, Koç, & Husum, 2013; Poulin, Lundholm, Berard-Therriault, Starr, & Gagnon, 2010; Reid et al., 2007). Such trans-Arctic invasion is expected to be more common under warmer climate as in the case of marine mollusks during the Pliocene (Reid, Edwards, & Johns, 2008; Vermeij & Roopnarine, 2008). Northward range expansion of temperate and tropical species into the Arctic, though beyond the scope of our study, will become increasingly common under climate warming. For example, the Snake Pipefish (*Entelurus aequoreus*), with a previously restricted northern range south of Iceland, has expanded its range northward to Svalbard (Fleischer, Schaber, & Piepenburg, 2007). Tropical disseminules, though unlikely to germinate, have frequently drifted to Nordic waters (Alm, 2003). Determining natural versus human-mediated dispersal of species will become increasingly difficult due to the effects of climate change that may promote species range expansion.

Aquaculture activities, wild fisheries, and the live food trade are also active pathways for delivering aquatic NIS to the Arctic. For example, the Rainbow Trout (*Oncorhynchus mykiss*), native to the North Pacific, are being farmed in sea cages in Arctic waters (Berger & Naumov, 2002). Trout escapes from farms are common in the Faroe Islands, the Iceland Shelf, the Norwegian Sea, and the Barents Sea, though self-reproducing populations in nature are rare (Berger & Naumov, 2002; Lysenko & Berestovsky, 1999; NOBANIS, 2018; Thorarindottir, Gunnarsson, & Gíslason, 2014). Cultivation in confinement at high densities often promotes the spread of pests,

parasites, and diseases (Minchin, 2007). Indeed, the transfer of the Atlantic Salmon (*Salmo salar*) from Swedish hatcheries to Norway resulted in the introduction and establishment of the Salmon Fluke (*Gyrodactylus salaris*) in the Norwegian Sea (Johnsen & Jensen, 1991) and in the White Sea (Ieshko, Shulman, Shchurov, & Barskaya, 2008). Several nonindigenous algal species, such as the Japanese Red Seaweed (*Bonnemaisonia hamifera*) and Japanese Wireweed (*Sargassum muticum*), have been unintentionally introduced into the Norwegian Sea and Iceland Shelf via the transport of aquaculture equipment and movement of live shellfish (Fofonoff et al., 2003; NOBANIS, 2018). Furthermore, the stocking of the Red King Crab (*Paralithodes camtschaticus*) in the Barents Sea might have indirectly increased the prevalence of trypanosome infection in cod by supporting an expanded population of the transmission vector, the circumpolar piscine leech *Johanssonia arctica* (Hemmingsen, Jansen, & MacKenzie, 2005). Arctic waters are predicted to be warmer in the near future, providing opportunities for expanded aquaculture and fishing activities (Barange et al., 2014) and increasing the risk of NIS introductions associated with these pathways.

6 | TAXONOMIC TRENDS OF ARCTIC NIS

Arthropoda contributed to the greatest number of introduction events (35%) in the marine Arctic, followed by Ochrophyta (22%), Chordata (17%), Mollusca (11%), Rhodophyta (7%), Platyhelminthes (4%), Chlorophyta (2%), and Myzozoa (2%; Figure 5). Over half of the introductions involving arthropods, such as the Snow Crab, Chinese Mitten Crab (*Eriocheir sinensis*), and Red King Crab, resulted in established populations in Arctic waters. The dominant pathway for arthropods was vessels (54%), followed by natural spread (18%), aquaculture activities (11%), live food trade (7%), wild fisheries (7%), and canals (3%). Ochrophyta detected in the Arctic included the orders Bacillariales, Chattonellales, Fucales, and Melosirales; however, only one third of these introductions led to establishment, though difficulties in confirming establishment of microalgae might have obscured the pattern. Ochrophytes were transferred to the Arctic by three pathways including natural spread (54%), vessels (38%), and aquaculture activities (8%). Chordates included the

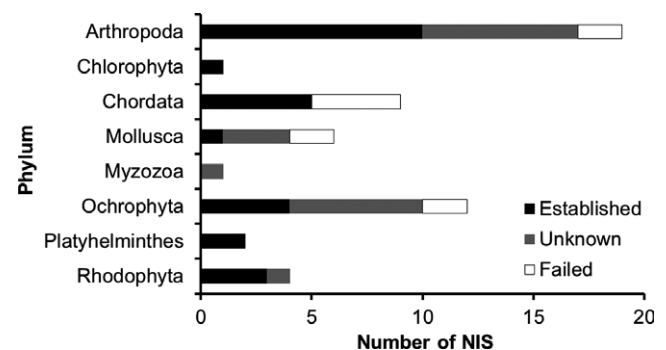


FIGURE 5 Number of NIS detected in Arctic waters by phylum and population status. Data shown represent 54 introduction events involving 34 NIS

Rainbow Trout and several other salmonid species, European Flounder (*Platichthys flesus*), and tunicates; over half of these introductions now have established populations in Arctic waters. A large proportion of the chordates were released into Arctic waters via wild fisheries (40%), followed by vessels (30%), aquaculture activities (20%), and natural spread (10%).

Introduced mollusks including the Pacific Oyster (*Magallana gigas*), Manila Clam (*Ruditapes philippinarum*), and the Mediterranean Mussel (*Mytilus galloprovincialis*) had limited success in Arctic waters; only one introduction (*M. galloprovincialis* in Barents Sea) led to establishment. The main pathways for mollusks into the Arctic were vessels (36%) and natural spread (36%), followed by aquaculture activities (19%) and live food trade (9%). In contrast, all but one introduction events involving rhodophytes, such as *Bonnemaisonia hamifera*, *Dasysiphonia japonica*, and *Dumontia contorta*, in Arctic waters resulted in establishment. Common pathways for rhodophytes in Arctic waters were aquaculture activities (44%) and vessels (44%), followed by natural spread (11%). *G. salaris* was the only introduced platyhelminthes reported in Arctic waters; both introduction events led to establishment and were related to aquaculture activities. There was only one introduced chlorophyte, Green Sea Fingers (*Codium fragile* subsp. *fragile*), in Arctic waters. The introduction of *C. fragile* subsp. *fragile* was successful and was related to

vessels. Finally, the only introduced myzozoon in Arctic waters was *Karenia mikimotoi*. It is unclear whether the species has established at the release site. Possible pathways responsible for the introduction include aquaculture activities, natural spread, and vessels.

7 | INFLUENCE OF CLIMATE CHANGE

Climate warming in the Arctic is expected to facilitate human activities at progressively higher latitudes including expanded transportation to and through the region, fishing and aquaculture, mining, recreational activities, and tourism (Ricciardi et al., 2017). There will be more human-mediated movements of NIS between temperate regions and northern seas, in addition to natural spread of introduced species and climate-induced northward range extensions. Figure 6 shows the water temperature at 5 m depth along the shipping lane through the Suez Canal (left panels) and the Northern Sea Route (right panels) from Rotterdam to Yokohama. There are small increases in temperature along both shipping routes since 1960 based on the global ocean water temperatures from the multiyear Simple Ocean Data Assimilation (SODA) archive (Carton & Giese, 2008). The transfer of NIS via the northern route, with the greatest increase in temperature (~1.8°C) observed at Barents Sea, is more likely to be tolerated by cool-temperate and cold-temperate species,

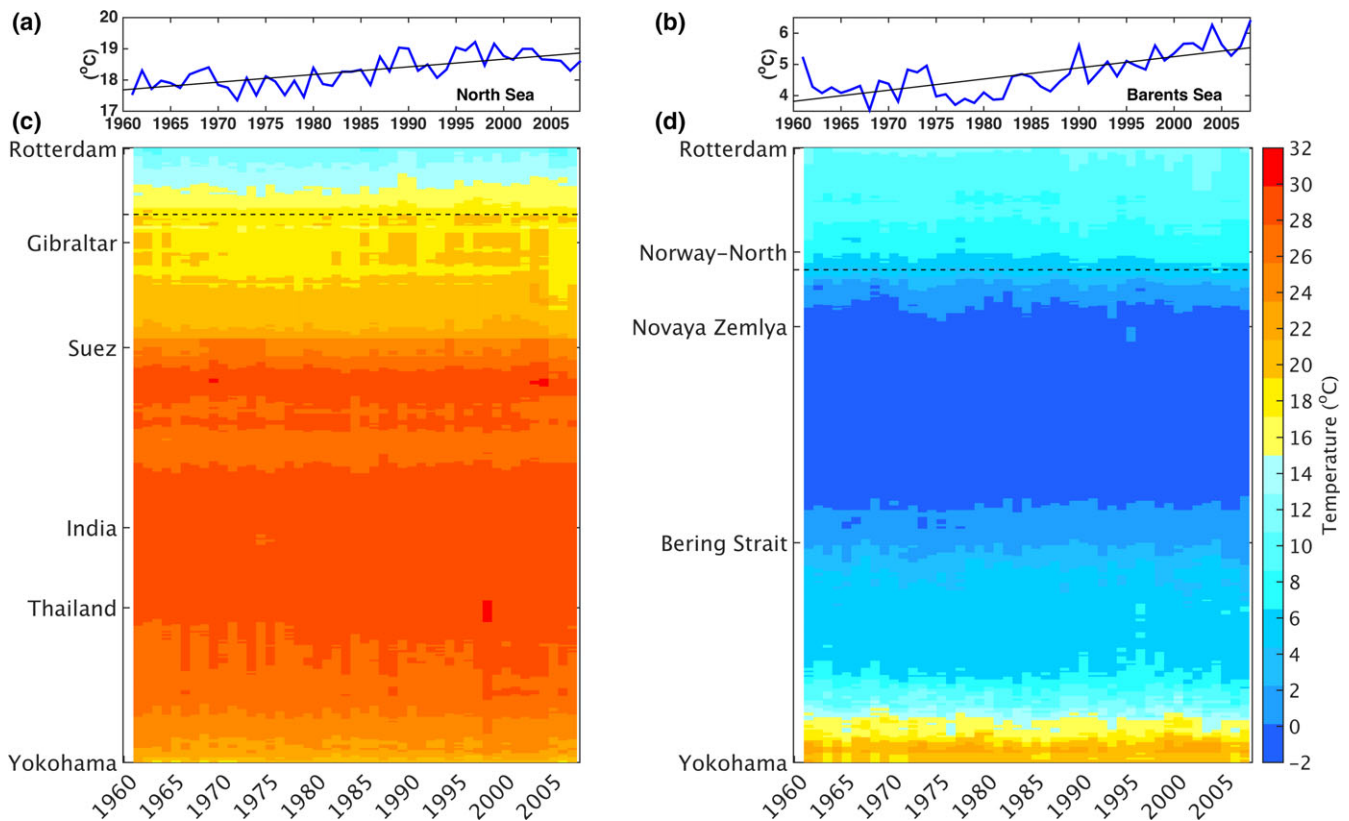


FIGURE 6 Annual mean water temperature at 5 m depth along the current route from Rotterdam to Yokohama using the Suez canal (~11,200 nautical miles; left panels) and when using the Northern Sea Route (~6,500 nautical miles; right panels). The y-axes in these panels are not to scale. Panels a and b show the temperature trends at the North Sea and the Barents Sea, which are the locations with the greatest increase in water temperature over time (dashed lines in panels c and d) along the current and the northern routes, respectively. For panels a and b, blue line = extracted temperature values along the dashed lines in panels c and d, and black line = temperature trend

as such species are usually adapted to low temperatures during winter and may survive Arctic waters. Larvae of cold-temperate species carried in ballast water, should they survive a polar route passage, are likely to prolong their pelagic phase under cold water conditions (Peck, 2005). A recent study detected NIS barnacles native to temperate habitats surviving transit to the Canadian Arctic on ships' hulls (Chan et al., 2016). Climate change in combination with the shorter journey of trans-Arctic voyages may foster greater-than-expected survival rates of NIS. Furthermore, the transfer process through the Arctic route may select for populations that are preadapted to the cold environment, thereby increasing the potential for successful establishment once released into the Arctic (Briski et al., 2018).

Native polar marine organisms generally live within a narrow and low-temperature range (Moore & Huntington, 2008; Peck, 2005; Pörtner, 2002). It is unlikely that many will have the ability to adapt to large temperature changes, except for those that are naturally exposed to great temperature fluctuations in areas where there are shallows or intertidal areas. Studies on Antarctic invertebrates, for example, have shown that these biota are unable to manage normal activities at temperatures much above 3°C (Peck, 2005). Such temperatures are likely to remain in deeper Arctic waters, but current temperature ranges in nearshore areas will almost certainly be exceeded during future summers. Polar species may become confined to a thermal biogeography on account of their requirement for high levels of dissolved oxygen, which declines with increases in temperature (Pörtner, 2001). Such cold-living species generally have poor physiological adaptability and prolonged generations. Therefore, native polar species may be out-competed by temperate NIS that arrive in the Arctic as a result of regional warming (de Rivera et al., 2011).

At the same time, changing environmental conditions may allow introduced NIS to survive and reproduce in areas where they previously could not do so and increase the magnitude of impact and/or the rate of spread (Hellmann et al., 2008). For example, the European Brown Shrimp (*Crangon crangon*) was accidentally introduced to the Iceland Shelf, likely via ships' ballast water (Gunnarsson, Ásgeirsson, & Ingólfsson, 2007; Thorarinsdottir et al., 2014). The establishment success of the species might be attributed to a lack of native species to provide biological resistance (Koberstein, 2013). The species has spread rapidly along the west and south coasts of Iceland since the initial detection of the species in 2003 (Gunnarsson et al., 2007) and may continue to spread as climate change is expected to expand the extent of suitable habitat for this NIS in Arctic waters (Ware et al., 2016).

8 | CONCLUSIONS AND RECOMMENDATIONS

We compiled 54 reports of 34 aquatic NIS that have been introduced into the Arctic region between 1960 and 2015. This number is relatively low when compared to other regions of the world. However, the potential of introducing NIS to Arctic seas is increasing

owing to a combination of climate change, natural resource development (e.g., oil, gas, and fish stocks), and expanded Arctic shipping. Elevated human activities in the Arctic will increase the propagule pressure and colonization pressure of potential NIS being transferred, thereby increasing invasion risk. At the same time, many native polar species may not be able to tolerate warming, opening up empty niches for NIS arriving in the Arctic. Therefore, management efforts that address the observed patterns and processes of biological invasions in the marine Arctic are needed to prevent new introductions and establishment of NIS, especially those with known negative impacts.

Vector management, aiming to reduce propagule pressure and colonization pressure associated with high-risk pathways, is recommended as the most cost-effective strategy to reduce invasion risk in the marine Arctic. Preventing undesired NIS from entering a pathway and/or from being released or escaping alive is regarded as the cornerstone of NIS management (Leung et al., 2002; Lodge et al., 2006; Ruiz & Carlton, 2003). Our analysis highlights the prominence of vessels as a pathway for the accidental transfer of aquatic NIS into the Arctic, and therefore, we propose that vessels should be prioritized for targeted management. While the risk of ballast-mediated introductions may be reduced via the implementation of BWMS, the potential of transferring NIS to Arctic waters via biofouling on commercial ships, leisure crafts, fishing vessels, floating platforms, and other artificial structures is expected to become increasingly important due to expansion in Arctic shipping, tourism, and natural resource development. Additional research should be conducted to identify antifouling systems that are effective in Arctic conditions. Natural spread also appears to play a significant role in the movement of NIS to and through Arctic waters. It is not practical to control the spread of NIS via natural dispersal mechanisms; however, recognizing oceanographic features and habitat suitability that affect NIS dispersal or establishment can direct management efforts of other simultaneous human-mediated pathways (Forrest, Gardner, & Taylor, 2009). For example, the focus of the national *Undaria pinnatifida* strategy in New Zealand is to prevent human-mediated transfer of the kelp to offshore islands of high conservation value that are suitable for establishment but beyond its natural dispersal capacity (Forrest et al., 2009). Other active pathways of aquatic NIS include aquaculture activities, wild fisheries, and the live food trade. Best management practices, such as the International Council for the Exploration of the Sea Code of Practice on the Introductions and Transfer of Marine Organisms (ICES, 2015), are needed for these activities to reduce the potential of transferring unwanted NIS into Arctic waters (Minchin, 2007). The rapid spread of the invasive *D. vexillum* on Georges Bank via fouled fishing gear and scallop discards serves as an example highlighting the importance of adopting better aquaculture and fishing practices to prevent new invasions (Lengyel et al., 2009).

Horizon scanning exercises, at the circumpolar scale involving multiple nations, may be performed to develop a list of unwanted NIS, or "door-knocker" species, that have not yet established in the Arctic for a species-specific management approach. In general,

horizon scanning is conducted to systematically evaluate potential threats and opportunities in order to guide research, policy, and management responses (Ricciardi et al., 2017; Sutherland & Woodroof, 2009). This process may involve literature review, interviews, expert workshops, Delphi questionnaires, expert consultation, trend analysis, and/or risk assessment (Ricciardi et al., 2017; Roy, et al., 2014; Sutherland & Woodroof, 2009). Horizon scanning has been used in Great Britain and the Netherlands, for example, to identify potential NIS which may have significant ecological impacts on the recipient environments for prioritizing management efforts (Matthews et al., 2017; Roy et al., 2014). While horizon scanning may be applied to all taxa groups, special attention should be given to Arthropoda, Ochrophyta, and Chordata as they are the taxa with the greatest number of NIS in the Arctic. Horizon scanning may also be used as a tool to screen NIS currently absent in certain Arctic LMEs, but present in neighboring regions or other regions that are connected via established pathways including shipping, aquaculture activities, live food trade, and wild fisheries. For instance, the potential impact of aquaculture or fishery species should be carefully examined prior to introduction into Arctic seas. The Red King Crab was introduced into the Barents Sea in the 1960s to establish a commercial fishery (Dvoretzky & Dvoretzky, 2015). While the introduction of the crab has brought economic benefits to Russia and Norway, there are concerns regarding its impacts on native communities, especially in Norwegian waters (Dvoretzky & Dvoretzky, 2015; Falk-Petersen, Renaud, & Anisimova, 2011; Oug, Cochrane, Sundet, Norling, & Nilsson 2011). To balance the economic benefits and ecological concerns, the Norwegian government implements two management regimes—a quota-regulated zone to sustain the crab population for exploitation and a free-fishing zone to reduce the rate of spread southward along the Norwegian coast (Jørgensen & Nilsen, 2011; Lorentzen et al., 2018). This example also highlights the need to coordinate NIS management strategies among Arctic nations, as introduced species may unintentionally spread to neighboring countries.

Early detection of undesired NIS at potential high-risk regions, such as the Iceland Shelf, the Norwegian Sea, and the Barents Sea, is essential for protecting the Arctic region from new invasions. However, NIS may be overlooked if they are rare or morphologically cryptic, and sampling methods can result in false negatives (i.e., failure to detect the occurrence of NIS in a given environment) at the initial stage of an invasion (Delaney & Leung, 2010; Stanislawczyk, Johansson, & Maclsaac, 2018). We recommend the use of molecular techniques to aid in early detection of NIS (Chown et al., 2015; Darling & Frederick, 2018; Ricciardi et al., 2017). A range of nucleic acid-based detection methods has been developed and applied to determine presence/absence, and even the abundance, of NIS in a given community (Darling & Frederick, 2018). For example, Zhan et al. (2013) demonstrated the ability of 454 pyrosequencing to detect rare NIS in spiked plankton samples. Metabarcoding has been effective for detecting NIS at a number of ports in the Canadian Arctic (Brown, Chain, Zhan, Maclsaac, & Cristescu, 2016). Additionally, the use of environmental DNA (eDNA) can assist in the

detection of NIS in aquatic environments, particularly when populations are difficult to detect by other means (Jerde, Mahon, Chadderton, & Lodge, 2011; Lacoursière-Roussel et al., 2018). A recent study has characterized the spatial and temporal patterns of biodiversity of aquatic communities in Arctic coastal environments using optimized eDNA metabarcoding methods (Lacoursière-Roussel et al., 2018).

Once harmful NIS are detected at new locations in the Arctic, rapid response strategies to prevent or manage their establishment in a timely manner may be implemented (Lodge et al., 2006; Ricciardi, Palmer & Yan, 2011). In general, complete eradication from aquatic environments is possible only if management action is taken before the NIS has established and spread from its initial introduction site (Beric & Maclsaac, 2015). These programs are often costly, though they are far less expensive than post-establishment control when NIS populations are large and geographically widespread (Forest et al., 2009; Mack et al., 2000). Lack of funding is a common reason for delayed action after first detection of NIS; therefore, allocation of contingency funds would facilitate a rapid response when required (Lodge et al., 2006). Rapid response strategies must be tailored to the local situation and the target species, as their effectiveness varies by taxonomic group, method type (e.g., chemical vs. mechanical), and spatial area, and thus require careful consideration and planning (Beric & Maclsaac, 2015). For instance, a meta-analysis of rapid response case studies in temperate aquatic environments revealed that plants are more likely to be eradicated than animals and that control of NIS is most successful when using chemical methods and in a small area of habitat (Beric & Maclsaac, 2015).

A comprehensive pan-Arctic inventory of biota would be useful in evaluating future changes to Arctic shelf regions (Lacoursière-Roussel et al., 2018; Matishov et al., 2011; Piepenburg et al., 2011). Currently, Arctic inventories are limited by relatively low search effort due to logistical challenges, high cost, and inhospitable environmental conditions (Piepenburg et al., 2011). Such an inventory should be an open access and up-to-date database with records verified by taxonomic experts (e.g., AquaNIS). A decline in the number of taxonomists and systematists to provide species identifications for biodiversity and monitoring studies impede additions to such an inventory (Archambault et al., 2010; CAFF, 2013). Wassmann, Duarte, Agustí, and Sejr (2011) remarked upon the difficulty of studying biodiversity changes that accompany climate change due to a lack of baseline data from which to evaluate changes to benthic and planktonic communities. The first pan-Arctic inventory of macro- and mega-benthic shelf species estimated that only about 70% of the mollusk, arthropod, and echinoderm species are observed (Piepenburg et al., 2011). Furthermore, recent surveys of benthic invertebrates in Canadian Arctic ports revealed that about 15% of identified invertebrates were new records for the region but could not clearly be assigned native or NIS status (Goldsmith, Howland, & Archambault, 2014). This prevalence of cryptogenic species emphasizes the need for more biodiversity studies within the Arctic region.

Human-mediated introduction of NIS, in addition to climate-induced range expansion, will change the biodiversity within the Arctic

region. Although currently there are comparatively few NIS known to the region, this number is expected to increase in the future due to the expected growth in human activities that accompany continuing climate change. Indeed, climate change may create more hospitable conditions fostering establishment of temperate NIS in the future.

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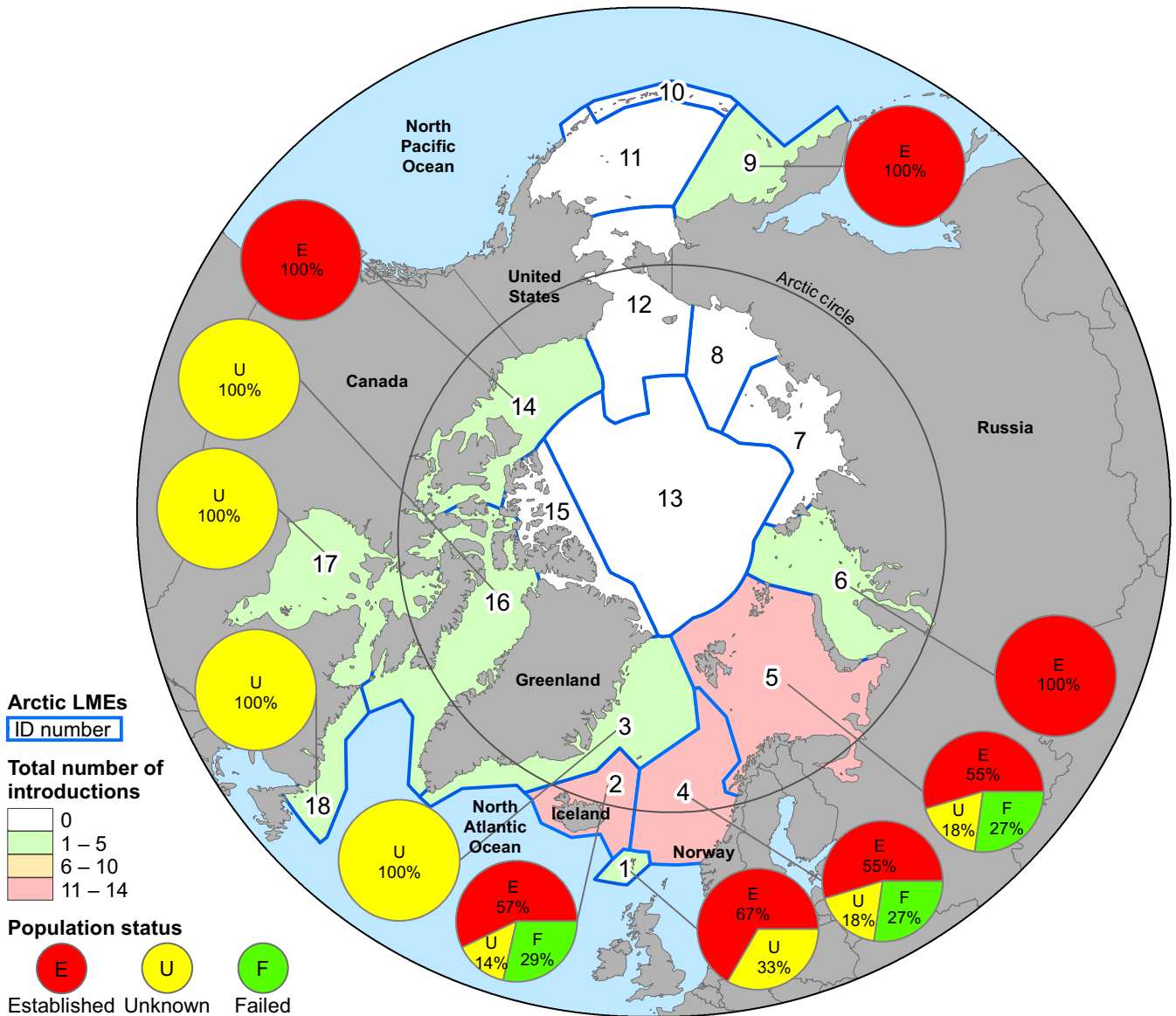
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Graphical Abstract

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This paper examines the current status and future risks of biological invasions in the marine environments of the Arctic, within the context of climate change, natural resource development, and expanded Arctic shipping. The number of nonindigenous species introductions varied across the region with the greatest number of introductions recorded in the Iceland Shelf, followed by the Barents Sea and the Norwegian Sea. Most introductions were attributed to vessels, natural spread, and aquaculture activities. Vector management, horizon scanning, early detection, rapid response, and a pan-Arctic biodiversity inventory are recommended to address future invasion risks.