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Impacts of climate change on marine species invasions in northern hemisphere high-latitude ecosystems

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Abstract. High-latitude marine ecosystems have experienced fewer species invasions than temperate marine ecosystems, a discrepancy that may be attributed to barriers such as low propagule pressure, extreme and seasonal abiotic conditions, and biotic resistance of relatively intact communities. Each of these barriers is being affected by climate change and increasing human activity in high-latitude (>55° N) areas. We reviewed the evidence for each of these barriers limiting species invasion in high-latitude areas in the northern hemisphere. Based on records from government documents of high-latitude countries, non-native species appear to be increasing in number (in Denmark and the United States) although there remains a paucity of data on invasive species establishment for high-latitude regions. Future study is needed to identify the drivers and impacts of invasions at high latitudes so that managers looking to prevent invasions can focus their efforts on bolstering barriers to invasion in these unique ecosystems.

Keywords: climate change, species invasions, marine ecosystems, dispersal barriers, propagule pressure, extreme climates, seasonality, biotic resistance, high-latitude, northern hemisphere

Introduction

Species invasions and climate change are two of the greatest threats to global biodiversity (Bellard et al., 2016a; Occhipinti-Ambrogi, 2007; Simberloff et al., 2013). Invasive species are defined, here, as species that have been introduced by humans to an area outside their native range and have successfully established and spread within their non-native range. Understanding the degree to which invasion and climate change interact, either synergistically or antagonistically, in different contexts is critical to anticipating and effectively mitigating impacts on biodiversity (Sorte et al., 2013).

One way that these two aspects of global change could interact is that climate change could increase species invasions by breaking down existing barriers to invasion. Species invasion proceeds along a known pathway: propagules are *transported* to a new area, individuals that survive the novel conditions are able to *colonize*, a population is *established* when individuals successfully reproduce, and this established population may then *expand* its range to adjacent locations within the non-native region (Theoharides and Dukes, 2007). Invasion may be obstructed by barriers along this pathway (Figure 1), including a lack of transportation vectors, lethal abiotic conditions that

prevent colonization, or interactions with native species that make establishment untenable (Hellmann et al., 2008; Ruiz and Hewitt, 2009). These barriers have historically been strongly represented (Willig et al., 2003) in northern high-latitude ecosystems (defined here as areas located at >55° N latitude), where far fewer introduced species have been documented than in temperate (30°-55° latitude) areas (Krug et al., 2009; Ruiz and Hewitt, 2009; Ware et al., 2014). However, climate change is acting on each of these barriers, reducing them to a degree that may allow an unprecedented wave of species invasions in these historically uninvaded high-latitude ecosystems (Fig. 1) (Stachowicz et al., 2002; Holland and Bitz, 2003; Ruiz and Hewitt, 2009; de Rivera et al., 2011; Thyrning et al., 2017).

Marine ecosystems may be vulnerable to the breakdown of invasion barriers due to rapid increases in human disturbance and propagule pressure, as well as a tendency for non-native marine species to outperform their native counterparts under climate change (Molnar et al., 2008; Sorte et al., 2013). We conducted a literature review to evaluate the factors limiting invasion in high-latitude marine ecosystems and the evidence that these barriers are changing. We focus on three types of barriers: low propagule pressure, harsh abiotic conditions, and

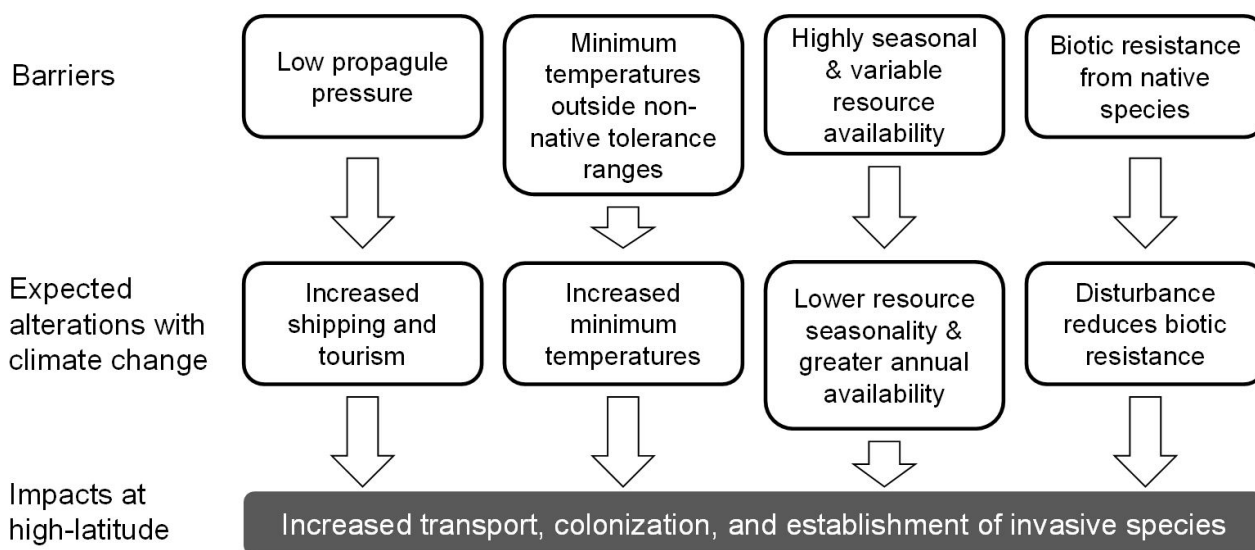


Figure 1. Climate change is likely to increase the invasion of high-latitude ecosystems by breaking down existing invasion barriers across the invasion pathway, from transport to colonization and establishment.

biotic resistance, all of which we expect to be affected by climate change. To determine whether changes in these barriers were reflected in the number of species invasions, we compiled a database of invasive marine species in high-latitude countries (from national government documents) and in Alaska, USA (from the peer-reviewed literature). Where available, we used dates of first record (i.e., the date of first collection or documentation of an invasive species in an area) to analyze changes in the number of invasive species present over time.

Propagule Pressure

The most significant sources of invasive propagule pressure in marine systems are shipping, aquaculture and the aquarium trade (Rueness, 1989; Padilla and Williams, 2004; Keller et al., 2011; Hughes and Ashton, 2017). Ship-mediated transport (e.g., hull biofouling or ballast water) accounts for much of the non-native marine species introduction in high-latitude ecosystems and globally (Ruiz et al., 1997; Seebens et al., 2013). Aquaculture has allowed the escape of cultivated organisms and the incidental introductions of hitchhiker species like the alga *Sargassum muticum* (Rueness, 1989; Josefsson and Jansson, 2011; Keller et al., 2011; Piccolo and Orlikowska, 2012), and the aquarium trade has been responsible for the release of lionfish *Pterois volitans* (Padilla and Williams, 2004) and the toxic alga *Caulerpa taxifolia* (Jousson et al., 1998).

High-latitude areas have historically experienced lower levels of human traffic and development than more temperate areas, limiting propagule pressure in these ecosystems; however, this longstanding barrier to invasion appears primed for change due to increases in shipping, accessible trade routes, and tourism (Miller et al., 2007; Ruiz and Hewitt, 2009; Ware et al., 2014). Over 50 million metric tons of ballast water were discharged along the coast of

Alaska during a three-year period from 2009–2012, which is a higher per-year rate of discharge than was documented from 1999–2003 (McGee et al., 2006; Verna et al., 2016). Most of this water can be traced back to ports on the west coast of North America, many of which are populated by species already identified as potential invaders in Alaska based on their climate tolerances (de Rivera et al., 2011). Arctic ice melt is also opening new trade routes and enabling oil extraction in previously inaccessible sites, increasing shipping traffic in these areas (Seebens et al., 2013; Eguíluz et al., 2016; Pizzolato et al., 2016; Verna et al., 2016). The possibility of introducing non-native species in ballast water is becoming increasingly recognized and regulated (Molnar et al., 2008). International treaties on the handling of ballast water are supplemented by individual government mandates on the removal of hull-fouling organisms and ballast water exchange (Williams et al., 2013). This wave of regulations, coupled with technological advances in ballast water treatment, has great potential to reduce species introduction through these vectors (Rivas-Hermann et al., 2015). However, it is unclear whether these changes will offset increases in shipping to prevent an increase in propagule introduction in high-latitude areas (Verna et al., 2016; Hughes and Ashton, 2017).

Propagule pressure is also likely to increase due to intentional and unintentional introductions associated with aquaculture and tourism. The increase in sea surface temperatures will lead to a poleward shift in the areas with optimal conditions for key aquaculture species, like the Atlantic salmon *Salmo salar* (Stenevik and Sundby, 2007). Commercially raised Atlantic salmon frequently escape into the wild and may compete with – and introduce pathogens to – populations of native salmon species (e.g., *Oncorhynchus* spp. in Alaska; Piccolo and Orlikowska, 2012). Tourism has also increased dramatically in high-latitude areas, and

this trend is expected to continue (Lasserre and Têtu, 2015). High-latitude tourism provides opportunities to view glaciers, observe whales in their natural habitat and experience pristine ecosystems, but may be endangering the species that they are traveling to observe (Hall et al., 2010). Cruise ship traffic in high-latitude areas of Canada has been increasing since 1984 (Stewart et al., 2007). More recently, the number of cruise ships operating in Greenland waters tripled over a five-year period and similar trends were observed in Iceland, Alaska, and other high-latitude areas (Hall et al., 2010; Ware et al., 2012).

Abiotic Resistance

Once non-native species are introduced to high-latitude ecosystems, their persistence is often precluded by abiotic conditions, including low seasonal temperatures and variable resource availability (Peck et al., 2006; Aronson et al., 2007; Krug et al., 2009). Temperature limits invasion in high-latitude marine ecosystems by increasing physiological stress or exceeding physiological tolerances of potentially invasive species (Thatje, 2005; Thatje et al., 2005; Aronson et al., 2007). Temperature dissimilarity between locations is so widely accepted as a barrier to invasion that it is frequently used as the sole parameter when modeling invasion potential (Seebens et al., 2013). For example, Thatje et al. (2005) argue that ocean temperature is the main factor limiting king crab (*Lithodes confundens*) incursion into Antarctic waters. Thyrring et al. (2017) identified air temperature as a factor limiting the abundance of high-latitude populations of *Mytilus* species along the coast of Greenland. With climate change, temperatures in polar areas will rise by 2–3 times the global average (Holland and Bitz, 2003), making non-native species from lower latitudes more likely to survive throughout the year (Holland and Bitz, 2003; de Rivera et al., 2011; Ware et al., 2014; Thyrring et al., 2017). de Rivera et al. (2011) compared the physiological tolerances of four invasive marine species inhabiting the contiguous USA to present and future conditions along the coast of Alaska. They found that current conditions in parts of Alaska were suitable for each of the four species, and the potential ranges of these species expanded dramatically when climate change projections were incorporated. The rapid environmental shifts in high-latitude ecosystems are particularly notable when considered alongside the latitudinal diversity gradient: biodiversity generally increases with decreasing latitude, meaning that a modest shift in environmental conditions in a high-latitude ecosystem could enable invasion by a significantly larger set of species (Valentine et al., 2008; Krug et al., 2009).

Rising temperatures are also driving changes in latitudinal patterns of seasonal resource variability (Thatje et al., 2005; IPCC, 2007). Resource availability across trophic levels exhibits extreme seasonal variation due to variation in temperature, light availability, and water mixing across the year (Clarke, 1982; Polovina et al., 1995; Valentine et al., 2008; Krug et al., 2009). Species native to high-latitude areas are better adapted to cope with temporal variation in resource

availability than those native to temperate areas via mechanisms including highly variable growth rates and intensive direct, as opposed to planktotrophic, larval development (Clarke, 1982; Conover and Present, 1990; Kendall et al., 1997; Valentine et al., 2008; Krug et al., 2009). Species native to temperate latitudes, conversely, are accustomed to less seasonal variation in primary producer growing season and shorter periods of relative resource scarcity, and they demonstrate increased resource specialization (Krug et al., 2009). The role of a short growing season, limited by temperature and photoperiod, as a barrier to invasion in high-latitude ecosystems has been extensively studied in trees (Saikkonen et al. 2012). However, the same principle likely applies to invasive marine primary producers and consumers, when there is a large discrepancy between the growing season in the native range and the invasive range of a species (Saikkonen et al. 2012).

Climate change is affecting spatial and temporal patterns of resource availability, including extending the length of the growing season in terrestrial ecosystems (Barichivich et al., 2013), and this extension may also occur in marine systems. Furthermore, rising CO₂ levels may have a fertilizing effect, increasing marine primary production by as much as 30% at the lower light intensities found in the winter at high-latitude areas (Hein and Sand-Jensen, 1997; Bopp et al., 2001; Gao et al., 2012). Climate change may also alter the competitive balance between invasive and native species (Cheung et al., 2009; Sorte et al., 2013). Studies in a temperate, epibenthic fouling community showed that higher temperatures increased the recruitment and establishment of invasive species whereas native species recruitment was reduced or unchanged under warmer conditions (Stachowicz et al., 2002; Sorte et al., 2010b). Given that space is the limiting resource in epibenthic systems, differential impacts of temperature on recruitment could significantly advantage invasive species if they are the first to colonize the substrata and priority effects perpetuate. Furthermore, results of a cross-ecosystem synthesis indicated that invasive species fared better than native species under changing climatic conditions, particularly when resources were increased and more so in aquatic than terrestrial systems (Sorte et al., 2013). If invasive species are favored over native species by changes in abiotic conditions, this could subsequently influence the ability of native communities to resist invasion.

Biotic Resistance

Biotic resistance is defined as the inhibition of invader establishment via interactions with the native community (Elton, 1958; Stachowicz et al., 1999; de Rivera et al., 2005) and is directly related to community diversity at local scales (Levine, 2000; Melbourne et al., 2007;). More diverse communities use resources more effectively (e.g., Byers and Noonburg, 2003), either due to complementarity (i.e., niche partitioning; Stachowicz et al., 1999; Stachowicz and Byrnes, 2006) or a sampling effect (i.e., greater probability of including a highly competitive species or group; Arenas et al., 2006). Establishment and spread of invasive species

can also be limited by native consumers, including consumers to which invasive prey are currently relatively naïve and undefended (Levine et al., 2004; de Rivera et al., 2005; Parker and Hay, 2005). Diversity itself is negatively associated with disturbance, which drives mortality, potentially opening up resources for non-native species and reducing biotic resistance (Kennedy et al., 2002; Britton-Simmons, 2006; Clark and Johnston, 2009).

Biotic resistance is the least studied barrier to invasion in high-latitude marine ecosystems (Ruiz and Hewitt, 2009; de Rivera et al., 2011), and the ways in which it may be affected by climate change are largely unresolved. However, we might expect that biotic resistance will decrease under increased disturbance due to direct human actions and rapid abiotic shifts (Byers, 2002; Britton-Simmons and Abbott, 2008; Clark and Johnston, 2009; Sorte et al., 2013). Increased human activity in high-latitude areas – such as through shipping and tourism as described above – will disturb native ecosystems by releasing pollutants (Cloern and Jassby, 2012) and clearing or altering substrate (Airoldi and Bulleri, 2011; Simkanin et al., 2012). These activities will increase mortality for existing populations while also potentially freeing up resources for establishment of new species (Stachowicz et al., 1999; Byers, 2002). Disturbance might also drive cascading extinctions when it leads to mortality of foundation species, who themselves increase diversity of associated native species (Reusch, 1998; Paulay et al., 2002; Williams, 2007; Simkanin et al., 2012).

Eutrophication, a frequent consequence of human activity, can reduce local species diversity (and, thus, biotic resistance) when one or a few species are best able to capitalize on pulses of increased resources (Smith et al., 1999), leading to algal blooms and downstream effects such as hypoxia-driven mortality across the community (Diaz and Rosenberg, 2008). One particularly impactful algal bloom, dubbed the “Silent Spring in the Sea”, occurred in high-latitude waters off the northern coast of Denmark in 1988 (Rosenberg et al., 1988). The bloom occurred during an unseasonably warm period that coincided with high levels of nitrogen and phosphorus in the surface water from unusually high runoff. The bloom caused widespread mass mortality across taxonomic groups, including habitat-forming kelp species *Saccharina latissima* and the predatory sea-star *Asterias rubens* (Rosenberg et al., 1988). The extirpation of habitat-forming and consumer species from high-latitude areas would likely reduce local biodiversity and, by extension, biotic resistance. Climate change may also increase the disturbance of native communities by increasing the frequency of extreme weather events, including severe storms and heat waves, which can cause widespread mortality and provide openings for invasive colonists (Valentine et al., 2008; Krug et al., 2009).

Although disturbance is a relatively non-selective force that could reduce biotic resistance by decreasing diversity, human activities might also reduce biotic resistance by selectively removing consumers from high-latitude ecosystems (de Rivera et al., 2005;

Simkanin et al., 2013). Predation pressure has been historically altered by humans through fishing, which is globally skewed toward large predatory fish (Pauly et al., 1998), and the fur trade, which extirpated sea otters in certain high-latitude areas (Doroff et al., 2004). The active removal of predators may rise with increasing human presence, reducing predation pressure on invasive species and weakening biotic resistance (de Rivera et al., 2005; Simkanin et al., 2013). Conversely, increased regulation of fishing practices and otter reintroduction programs may increase predation pressure in high-latitude areas. We also note that the magnitude and direction of the effect of predation pressure on biotic resistance varies by taxon. A predator which selectively preys on non-native species might increase biotic resistance whereas a generalist predator or one which prefers native prey might have a negligible or negative effect on biotic resistance (de Rivera et al., 2005).

Of the three barriers reviewed here (propagule pressure, abiotic conditions, and biotic resistance), biotic resistance is the least well supported as driving the historically low level of invasion in high-latitude ecosystems. In fact, biotic resistance may generally be weak in these ecosystems given that it increases with diversity and that the diversity of many groups decreases with increasing latitude (Kimbrow et al., 2013; Harper and Peck, 2016). There is even a possibility that biotic resistance in high-latitude ecosystems will increase with climate change as species from adjacent regions undergo poleward range shifts into high-latitude communities.

Baseline Data on High-Latitude Marine Invasions

A Global Perspective: There are currently no published studies reporting the changes in marine invasions over time in high-latitude ecosystems. Despite the limitations to empirical analysis, we used the following methods to compile a baseline data set of invasive marine species recorded in northern high-latitude ecosystems (>55° N) in documents published by or specifically for government agencies after an initial search yielded few peer-reviewed publications. We identified thirteen countries with high-latitude marine habitat in the northern hemisphere and searched their government websites or the sites of agencies responsible for natural resource management for lists of invasive species in these countries’ waters. We supplemented this with Google Scholar searches using the country’s name with terms to specify invasive species and high-latitude, marine ecosystems. We found ten government documents that reported the number or names of invasive species present in six of the thirteen high-latitude countries: Denmark, Estonia, Finland, Norway, the United Kingdom and the United States (Table 1). These documents included 188 established invaders and 65 species that were predicted to invade in the near future. Where provided, we collected the date of first record (i.e., the year in which an invasive species was first observed or collected in a given area;

Table 1. Summary of invasive species management documents prepared by 6 high-latitude countries.

Country	Agency	Title	Citation	# Invasive Species Present	# Invasive Species Predicted
Denmark	Danish Centre for Environment and Energy	Trends in records and contribution of non-indigenous species (NIS) to biotic communities in Danish marine waters	Stæhr <i>et al.</i> , 2016	83	
Estonia	Ministry of the Environment	CBD Thematic Report on Alien Species- Estonia	EEK, 2000	2	
Finland	Ministry of Agriculture and Forestry in Finland	Finland's National Strategy on Invasive Alien Species	Ministry of Agriculture and Forestry, 2012	14	5
Finland	Ministry of the Environment	Alien species in Finland	Nummi, 2001	2	
Norway	The Norwegian Biodiversity Information Centre	Ecological Risk Analysis of Alien Species	Gederaas <i>et al.</i> , 2007	42	
Norway	The Norwegian Biodiversity Information Centre	Alien Species in Norway	Gederaas <i>et al.</i> , 2012	13	55
United Kingdom	Department for Environment, Food and Rural Affairs	Invasive Identification Sheets	Sewell, 2011; Stebbing <i>et al.</i> , 2012; Wade <i>et al.</i> (undated)	3	
United Kingdom	Scottish Natural Heritage	Scottish Natural Heritage	Sweet, 2011; Sweet, 2012a; Sweet, 2012b; Sweet, 2012c; Bishop, 2012	7	
United States	Alaska Department of Fish and Game	Alaska Aquatic Nuisance Species Management Plan	Fay, 2002		5
United States	Prince William Sound Regional Citizens' Advisory Council & U.S. Fish & Wildlife Service	Biological Invasions in Alaska's Coastal Marine Ecosystems: Establishing a Baseline	Ruiz <i>et al.</i> , 2006	22	

Ruiz et al., 2000). These dates represent when a species was detected and, therefore, may lag behind the true date of establishment. When a period of time was given for the first record or detection, we used the midpoint of the time period (e.g., 1975 for a record of first detection that only specified the 1970s)."

The cumulative number of invasive species recorded in Denmark and the United States (the only documents that provided dates of first record) has increased over time (Fig. 2). Although these patterns suggest that Denmark was invaded earlier and by a greater number of species than the United States, which might make sense given the longer history of high-volume shipping around Denmark than in Alaskan waters, these data likely reflect significant biases in monitoring. These biases likely obscure patterns across space (as species in less accessible areas are less likely to be detected) and time (as sampling protocols change with interest and technology). More recent patterns are likely the most reliable. Denmark instituted a standardized monitoring protocol in 1989, after which the cumulative number of invasive species continued to increase. Continuing increases are also apparent in the United States data set, which was compiled in all years using standardized collection protocols for sessile species and supplemental surveys for mobile species, allowing comparison across all time points.

The government document data set included 144 unique species documented across six high-latitude countries, with 40 of these species documented in more than one country. 30 species were documented in two countries, eight were observed in three countries, and only two species (the Pacific oyster *Crassostrea gigas* and alga *Sargassum muticum*) were documented as invasive in four countries. The two marine invaders that have established in the most high-latitude countries are associated with transportation via aquaculture (Sjøtun et al., 2008; Williams et al., 2013). The Pacific oyster, *C. gigas*, was introduced in northern Europe for use in aquaculture and individuals escaped (Nehring,

2011). *C. gigas* has planktonic larvae and is especially reproductive in years following warm winters, giving the species a potential advantage over native competitors amid warming temperatures (Stachowicz et al., 2002; Nehring, 2011). *S. muticum* is believed to have been introduced incidentally with imported oysters (Josefsson and Jansson, 2011). *C. gigas* and *S. muticum* displace native competitors while also providing habitat and increasing water filtration (Josefsson and Jansson, 2011; Nehring, 2011).

Seven of the ten most prolific high-latitude invaders, those which have invaded three or four high-latitude countries, have native ranges primarily in temperate zones, mostly between 30° and 45° latitude. The trend of lower-latitude species invading high-latitude areas reflects poleward shifts in climate isoclines and may also be fueled by the larger pool of potential invaders in more biodiverse lower-latitude zones (Ware et al., 2014). This trend (of movement of species from temperate to high-latitude areas) may be intensified by movement from highly invaded temperate ports that serve as stepping stones, so that ship traffic from even a single temperate port may lead to the secondary introduction of a wide variety of species to high-latitude areas (de Rivera et al., 2011).

Alaska as a Case Study: To evaluate whether there is evidence that climate change is altering invasibility of Alaska, in particular, we searched all records in Web of Science through 29 May 2018 using "Alaska" as a search term along with search strings for marine invasive species published in Sorte et al. (2010a). After narrowing by categories, we reviewed 402 titles and 109 abstracts, finding a total of 15 relevant papers that reported eight established invasive species (four ascidians and one each of bryozoans, amphipods, bivalves, and algae; Table 2) and seven species likely to invade under current or future conditions. Interestingly, our review of government documents, described above, provided a more complete listing of established invaders in Alaska (22 species) than our literature search (eight species).

The most striking pattern among the species from the Alaska literature review is the prevalence of species inhabiting the marine epibenthic "fouling" community, which account for five of the eight invasive species reported and are also well-represented (16 established invasive species and nine predicted invaders) in the government document data set. It is important to note that the economic impact and high visibility of fouling species may have garnered them more attention than less conspicuous or economically relevant species. In addition, many of the scientists who contributed to the government documents and scientific literature are tunicate specialists which likely leads to a sampling bias towards fouling community habitats. Fouling community species have many of the traits of successful invaders (Kolar and Lodge, 2001): they can be transported either attached to the hulls of ships or to debris in the ballast water, display rapid growth, quickly achieve sexual maturity, and require relatively few individuals to establish a breeding population (Lambert and Lambert, 1998;

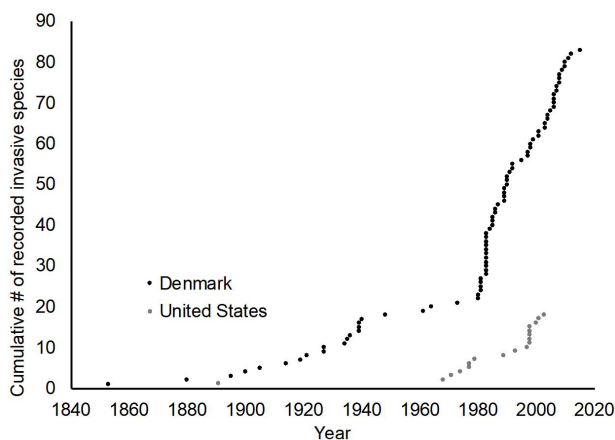


Figure 2. Cumulative number of invasive marine species reported in government documents in Denmark (black) and the United States (Alaska; gray). Standardized monitoring protocols were used in the United States (all years) and in Denmark after 1989.

Table 2. Invasive species established or predicted to colonize Alaska based on a structured literature review.

Species	Taxon	Established	Predicted	Reference
<i>Amphibalanus improvisus</i>	Crustacean		x	De Rivera <i>et al.</i> , 2011
<i>Botrylloides violaceus</i>	Ascidian	x		Lambert and Sanamyan, 2001
<i>Botryllus schlosseri</i>	Ascidian	x		Simkanin <i>et al.</i> , 2016
<i>Caprella mutica</i>	Crustacean	x		Ashton <i>et al.</i> , 2008
<i>Carcinus maenas</i>	Crustacean		x	De Rivera <i>et al.</i> , 2011
<i>Didemnum vexillum</i>	Ascidian	x		Cohen <i>et al.</i> , 2011
<i>Eriocheir sinensis</i>	Crustacean		x	Hanson and Sytsma, 2008
<i>Littorina saxatilis</i>	Mollusc		x	De Rivera <i>et al.</i> , 2011
<i>Molgula citrina</i>	Ascidian	x		Lambert <i>et al.</i> , 2010
<i>Mya arenaria</i>	Bivalve	x		Powers <i>et al.</i> , 2006
<i>Salmo salar</i>	Fish		x	Piccolo and Orlikowska, 2012
<i>Sargassum muticum</i>	Alga	x		Kerrison and Le, 2016
<i>Schizoporella japonica</i>	Bryozoan	x		Dick <i>et al.</i> , 2005
<i>Spartina</i> spp.	Plant		x	Morgan and Sytsma, 2013
<i>Styela clava</i>	Ascidian		x	De Rivera <i>et al.</i> , 2011

Sorte *et al.*, 2010b; Lord *et al.*, 2015). The native Alaskan fouling community has lower species diversity than temperate fouling communities and does not appear to be space-limited, suggesting that biotic resistance is comparatively low and invasive susceptibility may be high in these communities (Elton, 1958; Lord *et al.*, 2015).

Comparison with Temperate and Tropical Systems

The barriers to species invasion and the potential impacts of climate change on these barriers differ between high-latitude, temperate, and tropical systems. Temperate regions have historically been hotspots of invasion detection (Coles and Eldredge, 2002; Hewitt, 2002; Molnar *et al.*, 2008) and are also susceptible to shifts in invasion dynamics under climate change (Raitsos *et al.*, 2010; Bellard *et al.*, 2016b), although the relative impact given current high levels of invasion may be lower than that in high-latitude systems. An assessment of publicly available datasets by Molnar *et al.* (2008) identified the temperate northern Atlantic Ocean and the temperate northern Pacific Ocean as the most invaded open-water marine ecosystems globally. San Francisco Bay alone contains more invasive species than the 144 invasive species identified by our study across all high-latitude marine regions. The 234 invasive species identified in San Francisco Bay collectively account for as much as 99% of biomass in some locations (Cohen and Carlton, 1998). The same changes increasing invasion in high-latitude ecosystems may be affecting invasion in temperate areas. Shipping is a primary driver of propagule pressure in temperate areas (Bellard *et al.*, 2016b) as 16 of the 20 of the ports most central to the global shipping network are located in temperate zones (Kaluza *et al.*, 2010). Many of these shipping routes connect ports

with similar environmental conditions (Seebens *et al.*, 2013) which likely increases establishment success for species with propagules transported through ballast water or hull fouling. Increasingly, tropical species may be transported to temperate regions through widening of canals (Galil *et al.*, 2015; Muirhead *et al.*, 2015) and shipping, and rising water temperatures are making temperate areas more hospitable to tropical species (Raitsos *et al.*, 2010). Another key barrier to invasion, biotic resistance, is likely being affected by human disturbance through the reduction of abundance and diversity of native species (Early *et al.*, 2016). A land cover study of terrestrial human disturbance by Hannah *et al.* (1995) identified temperate areas to be the most impacted, followed by tropical areas, with high-latitude areas being least disturbed. The increases in propagule pressure, likelihood of tropical species establishment under warming conditions, and human disturbance effects on biotic resistance suggest that species invasion in temperate areas will increase in the coming years. On one hand, the relative effect of increasing invasion on temperate systems as a whole is likely to be lower than in high-latitude systems given that many temperate systems are already highly invaded. However, it is also possible that temperate systems will see more local extinctions due to increasingly precipitous declines in native populations (Wilcove *et al.*, 1998; Streftaris and Zenetos, 2006; Maggi *et al.*, 2015).

Comparatively few invasive species have been detected in tropical marine areas (Hewitt, 2002; Havel *et al.*, 2015; Tricarico *et al.*, 2016), but barriers to invasion in these systems also appear poised for change. Ports in the tropics experience lower shipping intensity than ports in other parts of the world (Seebens *et al.*, 2013), suggesting that tropical marine ecosystems experience lower propagule pressure than other regions. Although abiotic conditions tend to be relatively benign with low temperature variability (Mahlstein *et al.*, 2011; Barlow *et al.*, 2018), biotic resistance to invasion in

tropical ecosystems is high (Coles and Eldredge, 2002; Freestone et al., 2013) as a result of unparalleled species diversity and low human disturbance relative to temperate areas (Hannah et al., 1995; Fine, 2002). In the future, propagule pressure in tropical areas is likely to increase (Ducruet and Notteboom, 2012). In addition, climate change is expected to increase temperature variation and extremes in tropical ecosystems to globally unique levels (Barlow et al., 2018). This shift might increase physiological stress on native species that are adapted to less variable thermal conditions (Tewksbury et al., 2008), reducing biotic resistance, while also potentially favoring species adapted to more variable environmental conditions (including temperate species; Astudillo et al., 2016). Direct human-mediated disturbance is also on the rise in many tropical systems worldwide (Laurance and Useche, 2009; Peh, 2010; MacNeil et al., 2015). The impacts of increases in propagule pressure and decreases in biotic resistance could, therefore, lead to increases in the invasion of tropical ecosystems, many of which occur in countries that have lower capacity to detect and manage such increases (Early et al., 2016). We note that invasions in tropical ecosystems – particularly tropical marine ecosystems – have been less well studied than those in temperate zones (Drake and Lodge, 2004) and existing tropical studies have often focused on islands (Coles and Eldredge, 2002; Hutchings et al., 2002), which are more susceptible to invasion than mainland areas (Sax and Brown, 2000). Further studies are required to understand the implications of human disturbance and climate change on species invasion in tropical ecosystems.

Conclusions

High-latitude ecosystems have experienced few species invasions relative to many lower-latitude regions, likely due to limited propagule transport, low rates of human disturbance, low minimum annual temperatures, and high resource seasonality (Ruiz et al., 2006; Ruiz and Hewitt, 2009). These factors are changing with shifting human activity and climate change, potentially precipitating a breakdown of these same invasion barriers which could be contributing to the increasing number of documented species invasions in high-latitude regions. There are still few data identifying these drivers and impacts in northern high-latitude ecosystems (Ruiz and Hewitt, 2009; de Rivera et al., 2011), and future studies are needed to resolve the effect of shifting, interactive factors and expand our understanding of invasion resistance in high-latitude ecosystems. Data on the number and abundance of invasive species as a proportion of the total community, which would be integral to a more quantitative assessment of invasion, are particularly scarce. In addition, although our study focused on northern high-latitude systems (where propagule pressure is increasing rapidly unlike in the Antarctic; Ruiz and Hewitt, 2009), southern high-latitude ecosystems are also experiencing changes in abiotic conditions (Aronson et al., 2007; Turner et al., 2009), potentially increasing habitat suitability for non-native species

while increasing physiological stress on – and, therefore, reducing biotic resistance from – native species. Insight from increased study of high-latitude ecosystems globally could then be applied to management, identifying mechanisms most important for conferring invasion resistance and most susceptible to decline with climate change or direct human disturbance.

National and international efforts to prevent the spread of non-native species are ongoing. International organizations like the European Network on Invasive Alien Species (NOBANIS) compile data and disseminate information to the public with the goal of reducing invasive species dispersal (<https://www.nobanis.org>). The Ballast Water Management convention, an international agreement through the United Nations International Marine Organization which began enforcement in 2017, standardizes protocol for the dumping of ballast water to reduce the likelihood of species introduction (David et al., 2015; Yang et al., 2017). At the same time as regulations to prevent transport via ballast water and hull fouling are likely reducing propagule pressure, the effects of climate change on abiotic invasion resistance may make individual propagules more likely to establish. Furthermore, our study uncovered high variability by country in government documentation of invasive species, which may be biased across ecosystems and taxa by accessibility or the expertise of the surveyors. Improved, standardized monitoring programs will provide a more thorough picture of species invasion to inform further action.

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