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*Igor Krupnik, Michael A. Lang,
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Latitudinal Patterns of Biological Invasions in Marine Ecosystems: A Polar Perspective

Gregory M. Ruiz and Chad L. Hewitt

ABSTRACT. Biological invasions in coastal ecosystems have occurred throughout Earth's history, but the scale and tempo have increased greatly in recent time due to human-mediated dispersal. Available data suggest that a strong latitudinal pattern exists for such human introductions in coastal systems. The documented number of introduced species (with established, self-sustaining populations) is greatest in temperate regions and declines sharply at higher latitudes. This observed invasion pattern across latitudes may result from differences in (1) historical baseline knowledge, (2) propagule supply, (3) resistance to invasion, and (4) disturbance regime. To date, the relative importance of these mechanisms across geographic regions has not been evaluated, and each may be expected to change over time. Of particular interest and concern are the interactive effects of climate change and human activities on marine invasions at high latitudes. Shifts in invasion dynamics may be especially pronounced in the Northern Hemisphere, where current models predict not only an increase in sea surface temperatures but also a rapid reduction in sea ice in the Arctic. These environmental changes may greatly increase invasion opportunity at high northern latitudes due to shipping, mineral exploration, shoreline development, and other human responses.

INTRODUCTION

The extent and significance of biological invasions in coastal marine ecosystems has become increasingly evident in recent years. On multiple continents, studies have described invasions by nonnative marine species, occurring primarily in shallow waters of bays and estuaries (e.g., Cohen and Carlton, 1995; Cranfield et al., 1998; Orensanz et al., 2002; Hewitt et al., 2004; Kerckhof et al., 2007; Fofonoff et al., in press). Although the ecological effects of most invasions have not been explored, it is evident that some nonnative species exert strong effects on the structure and function of invaded coastal ecosystems (Ruiz et al., 1999; Carlton, 2001; Grosholz, 2002).

Marine invasions have occurred throughout Earth's history, occurring sometimes as punctuated events in geologic time that correspond to changes in climate and dispersal barriers (e.g., Vermeij, 1991a, 1991b). However, invasions in modern time differ from those of the past, especially with respect to spatial and temporal scale. Most invasions are now driven primarily by the human-mediated transfer of organisms, instead of natural dispersal processes. As one consequence,

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the potential range of dispersal is arguably less constrained than in the past, without the need for geographic adjacency. Marine organisms are now often moved quickly by humans across great distances and dispersal barriers (e.g., ocean basins, hemispheres, and continents), which were previously insurmountable in ecological timescales for most coastal species.

Human transport of organisms also has increased the rate of invasions in recent time. It is clear that the documented rate of marine invasions from human causes has increased dramatically, especially in the past 100–200 years, in many global regions (e.g., Cohen and Carlton, 1998; Hewitt et al., 1999, 2004; Wonham and Carlton, 2005). The current tempo of invasions may, in fact, be unprecedented, resulting from the massive and growing scope of global trade, but it remains challenging to estimate actual rates of invasion that adequately control for potential biases (Ruiz et al., 2000). Nonetheless, a broad consensus exists that the pace of invasions has increased sharply in many well-studied regions.

Despite considerable literature on patterns and processes of marine invasion, there is surprisingly little analysis of latitudinal patterns of invasion. In this paper, we review the current state of knowledge about human-mediated invasions (hereafter invasions or introductions) along a gradient from temperate to polar marine ecosystems, and we consider possible effects of climate change on invasions at high-latitudes. An extension of this comparison to tropical latitudes is the focus of future analyses.

TEMPERATE-POLAR PATTERN OF INVASIONS

For marine systems, most introductions (established, self-sustaining populations of nonnative species) are documented from temperate latitudes, including North America, Australia, Europe, New Zealand, and South America (see Cranfield et al., 1998; Hewitt et al., 1999, 2004; Reise et al., 1999; Ruiz et al., 2000; Hewitt, 2002; Orensanz et al., 2002; Castilla et al., 2005; Kerckhof et al., 2007; CIESM, 2007). While scores to hundreds of nonnative species are known from single bays and estuaries in temperate regions, few invasions are known from similar high-latitude sites, especially in polar regions.

This pattern is illustrated by the sharp decline in documented introductions with increasing latitude along western North America (Figure 1). In an analysis of available literature and collection records, Ruiz et al. (2006a) examined the number of nonnative marine invertebrate species reported from 12 large bays and estuaries (each including

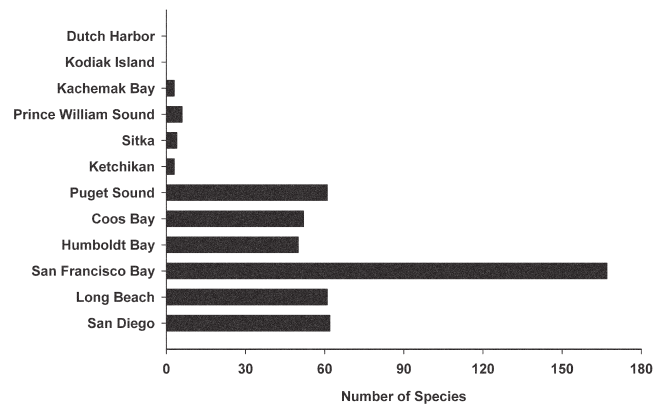


FIGURE 1. Total number of nonnative marine invertebrate species with established populations in bays along western North America. Data are summarized from species reported in the literature and collections in each of 12 sites from California to Alaska (from Ruiz et al., 2006a).

commercial ports) between 32° and 61°N latitude. For the six southernmost sites, from California to Washington, the number of documented introductions ranged from 50 to 170 species, with the largest number reported for San Francisco Bay (often the initial site for reported introductions that spread to other bays; see Cohen and Carlton, 1995, for further discussion). In contrast, the six northern sites in Alaska were at least one order of magnitude lower in the number of known introductions, ranging from 0 to 5 species.

For the entire Arctic ($\geq 66^\circ\text{N}$), we are aware of only one nonnative marine species that is known to have an established population. The Alaskan king crab, *Paralithodes camtschaticus*, was intentionally introduced to the White Sea in the 1960s to establish a fishery and now occurs abundantly from Russia to Norway (Jorgensen, 2005). While other nonnative species have been reported for Arctic bioregions (e.g., Streftaris et al., 2005), it appears that such occurrences either have not been documented above 66°N or are not known to exist as established populations.

For the Antarctic ($>60^\circ\text{S}$), two nonnative species have been reported recently, both on the Antarctic Peninsula, but neither are known to have established populations. Two specimens of the North Atlantic spider crab *Hyas araneus* were found in collections from 1986, including one male and one female (Tavares and De Melo, 2004). In addition, the European green alga *Ulva intestinalis* was also reported (Clayton, 1997); however, the morphological identification may be suspect. While these two species,

and perhaps others, may have invaded the Antarctic, this has not been confirmed to date (Lewis et al., 2003, 2004; Clarke et al., 2005).

To some extent, the observed differences in nonnative species richness across latitudes may reflect bias in search effort and taxonomic knowledge, which undoubtedly declines from temperate regions to the poles. It is virtually certain that other nonnative species are present at high latitudes and have not been recognized because of either lack of sampling or insufficient taxonomic and biogeographic resolution. However, such differences in historical baseline are unlikely to account for the overall latitudinal pattern, especially when considering the larger, conspicuous organisms (e.g., decapods, shelled molluscs, and ascidians). This is further supported by recent surveys in Alaskan waters that found a paucity of nonnative sessile invertebrates relative to other sites in the continental United States (Ruiz et al., 2006a, unpublished data).

The poleward decline in invasions apparently results from latitudinal differences in propagule supply of nonnative species, resistance (or susceptibility) to invasion, or disturbance regimes. These may operate alone or in combination to produce the observed pattern of nonnative species richness. There exists theoretical and empirical support for the role of each factor in invasion dynamics (see Ruiz et al., 2000, and references therein), although these have not been evaluated for latitudinal patterns of marine invasions. Below, we consider each of these potential mechanisms and how they may contribute to observed patterns in further detail, focusing particular attention on western North America.

DIFFERENCES IN INVASION MECHANISMS ACROSS LATITUDES

PROPAGULE SUPPLY

The delivery pattern of organisms (propagules) greatly affects the likelihood of established populations. Propagule supply can be further divided into multiple components, including total number of propagules and the frequency (rate) and magnitude of inocula. Assuming suitable environmental conditions exist for a species to persist (including survival, growth, and successful reproduction), the likelihood of establishment is generally expected to increase with an increase in each component (Ruiz and Carlton, 2003; Lockwood et al., 2005; Johnston et al., in press).

Most marine introductions are thought to result from species transfers by vessels and live trade. For North America, at least 50% of introduced marine species have

been attributed to commercial ships, which move species associated with their underwater surfaces and also in ballasted materials (Ruiz et al., 2000; Fofonoff et al., 2003; see Carlton, 1985, for description of the history and use of solid ballast and ballast water). After shipping, live trade is the second largest mechanism (vector) of marine introductions to North America, resulting from species transfers for aquaculture, fisheries, bait, and aquaria (e.g., Cohen and Carlton, 1995; Carlton, 2001; Fofonoff et al., in press); invasions from live trade include both the target species of interest as well as many associated species, such as epibionts, parasites, and pathogens. These two vectors are active and often dominant throughout the world, although their relative importance certainly varies in space and time (e.g., Cranfield et al., 1998; Hewitt et al., 1999; 2004; Orensanz et al., 2002; Wasson et al., 2001; Castilla et al., 2005; see also Ribera and Boudouresque, 1995; Ribera Siguan, 2003; Hewitt et al., 2007).

Once established, nonnative species often spread along the coast from the initial site of introduction. Some introduced marine species can expand their range in a new territory to encompass hundreds of kilometers (e.g., Grosholz, 1996; Thresher et al., 2005). This spread may occur by a combination of natural dispersal and anthropogenic means, depending upon the circumstances. Thus, invasion to a particular location can result by an initial introduction from distant sources or spread from an adjacent population. In general, proximity to potential source populations may often increase the chances of colonization, especially for the latter.

The current level of human activity, and especially shipping and live trade, is relatively low in polar regions, limiting opportunity for human-mediated transfers (e.g., Lewis et al., 2003, 2004). Moreover, the arrival of nonnative organisms from adjacent regions by natural dispersal is also likely to be low, resulting from a combination of low prevalence of nonnative species in adjacent regions and also the considerable distances or barriers that exist between potential sources for invasion of polar habitats.

It is informative to compare the magnitude of commercial shipping to various regions of the United States (Figure 2). For 2004–2005, far fewer ship arrivals occurred in Alaska compared to other regions at lower latitudes. Unlike the latter regions, most ship arrivals to Alaska were from domestic sources, originating from other U.S. ports (particularly those on the west coast) instead of foreign ports.

Importantly, even the current level of shipping to Alaska is only a very recent development, increasing substantially over just the past few decades. Although these temporal changes in shipping have not been fully quantified, an

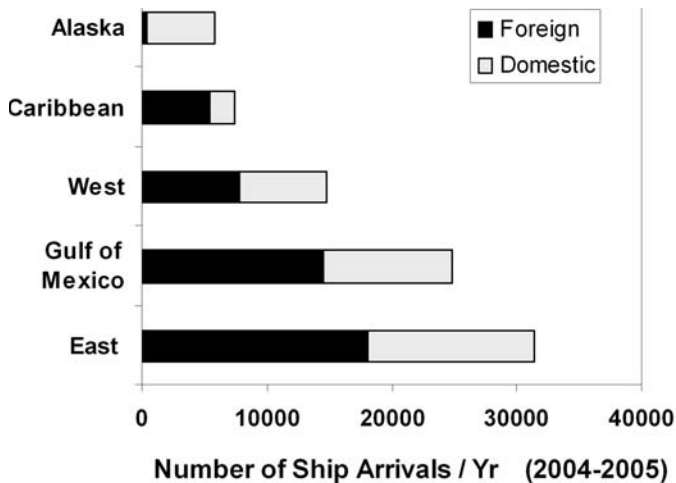


FIGURE 2. Estimated number of commercial ship arrivals per year (2004–2005) to regions of the United States. (Data are from Miller et al., 2007.)

obvious increase has occurred. This is best exemplified for oil tankers. Recent studies show a large number of marine organisms are delivered to Alaska in the ballast water of oil tankers. In 1998, it was estimated that oil tankers discharged a mean volume of 32,715 m³ of ballast water per arrival to Port Valdez (61°N), containing an average density of 12,637 plankton per m³ (as sampled by 80- μ m mesh net, $n = 169$ vessels, chain-forming diatoms excluded; Hines and Ruiz, 2000). Most of these ships came from ports in California and Washington that are a potential source for many nonnative species (Figure 1). Over 17,000 oil tankers have arrived to Port Valdez since 1977, when the Alyeska pipeline was completed (Alyeska Pipeline Service Company, 2008). Prior to this date, tanker trade to Port Valdez simply did not exist.

While we can consider the number of arrivals to be a coarse proxy for ship-mediated propagule supply to a region, especially for a specific trade route and ship type (as above), this approach has clear limitations. Considerable variation exists among ships, voyage routes, and seasons in both the density and diversity of associated organisms (Smith et al., 1999; Coutts, 1999; Verling et al., 2005). In addition, the changing patterns of ship movements and trade present radically different invasion opportunities that are not captured in assessing the number of arrivals at one point in time (Hewitt et al., 1999, 2004; Minchin, 2006). As a result, the extent of species transfers by ships to locations is poorly resolved for any time period. Similar limitations exist for most other transfer mechanisms in coastal ecosystems, making it challenging to estimate the

actual propagule supply of nonnative species and provide direct comparisons across latitudes.

Despite existing information gaps, the magnitude of nonnative propagule supply (both historically and presently) has undoubtedly been low in polar regions. Historically, whaling and sealing activities, particularly in the Southern Ocean (Murphy, 1995), provided some opportunity for ship-mediated species transfer. Today, modern shipping continues to provide a transfer mechanism to high latitudes in both hemispheres (Hines and Ruiz, 2000; Lewis, 2003, 2004). However, compared to temperate latitudes, the number of ship arrivals and the diversity of routes (source ports) for the Arctic Ocean and Southern Ocean have been extremely limited. Rafting of marine species to the poles also appears to be low relative to lower latitudes (Barnes, 2002). Finally, natural dispersal of nonnative species is likely to be uncommon to both poles, perhaps especially in the Southern Hemisphere where distance and the Antarctic Circumpolar Circulation appear to create a significant dispersal barrier (see reviews by Clarke et al., 2005, and Barnes et al., 2006).

RESISTANCE TO INVASIONS

Independent of propagule supply, high latitudes may be more resistant (less susceptible) to invasions. This can result from environmental resistance, whereby physical or chemical conditions in the recipient environment are not conducive to survivorship, reproduction, and population growth. Alternatively, biotic resistance can result from predators, competitors, food resources or other biological interactions that limit colonization success.

There is support for environmental resistance to polar invasions due to the current temperature regime. In the Antarctic, low temperature is considered to be responsible through geologic time for the low diversity of decapod crustaceans, sharks, and other taxonomic groups and is also thought to operate today as a potential barrier to colonization (Thatje et al., 2005a, 2005b; Barnes et al., 2006; but see Lewis et al., 2003). This is, perhaps, best illustrated by research on lithodid crabs, which are physiologically unable to perform at the current polar temperatures (Aronson et al., 2007).

In the Northern Hemisphere, using environmental niche models, deRivera et al. (2007) found that the northern ranges of some introduced species (the crab *Carcinus maenas*, the periwinkle *Littorina saxatilis*, the ascidian *Styela clava*, and the barnacle *Amphibalanus improvisus*) along western North America are not limited by temperature. While none of these species appeared capable of

colonizing the Arctic Ocean under current climatic conditions, their estimated ranges all included Alaskan waters (where they do not presently occur). Thus, available analyses indicate both Antarctic and Arctic waters are currently beyond the thermal tolerance for some species, but the extent to which invasions can occur in these polar regions is not known.

Temperature may often serve as a barrier to polar invasions by directly limiting larval development rate, which is highly temperature dependent (Thatje et al., 2003, 2005a, 2005b; deRivera et al., 2007). Many species are able to persist and grow at cold temperatures as juveniles or adults, compared to larvae that require warmer water for successful development to metamorphosis. High latitudes can also have short seasons when sufficient food exists to sustain larval development. These direct and indirect effects of temperature are thought to have greatly favored nonplanktotrophic larvae at high latitudes (see Thatje et al., 2005a, and references therein).

Aside from food limitation, the potential importance of biotic resistance for high-latitude marine invasions is largely unexplored. Specifically, it is not clear whether competition or predation would greatly affect invasion establishment at high latitudes, especially in comparison to more temperate regions. As discussed by deRivera et al. (2007), it is conceivable that biotic interactions operate to reduce the likelihood of invasions to Alaska, despite suitable environmental conditions, but this hypothesis has not been tested empirically. More broadly, understanding biotic resistance to invasion is a critical gap in marine systems.

DISTURBANCE REGIME

Disturbance can play an important role in invasion dynamics through a variety of mechanisms. In general, the role of disturbance in invasion ecology has focused on changes in biotic interactions, thereby reducing biotic resistance to invasion. This can result from changes in competition that affect availability of resources, such as open space for colonization, food, or nutrients. Alternatively, changes in predation pressure can increase invasion opportunities. While disturbance agents may operate directly to affect competition or predation, they can also have an indirect effect of these interactions. For example, changes in sediment or nutrient loading may cause a change in resident community structure (including species composition or abundance) that affects the strength of biotic interactions for newly arriving species.

In marine systems, literature on the role of disturbance in invasions has focused primarily on anthropo-

genic sources of disturbance (e.g., Ruiz et al., 1999; Piola and Johnston, 2006). Past studies have especially considered effects of fisheries exploitation, changes to habitat structure (whether physical or biological in nature), and chemical pollution. Invasions themselves have also been considered an important source of disturbance in cases where invasions either have (1) negative effects on resident biota by reducing biotic resistance (Grosholz, 2005) or (2) positive effects on newly arriving species by providing habitat, hosts, or food resources that were previously limiting (Simberloff and Von Holle, 1999).

Anthropogenic disturbance can clearly play an important role in invasion dynamics, in terms of both establishment and abundance of nonnative species, for which there is strong theoretical and empirical underpinning. While considered likely to be a key factor in the high diversity of nonnative species in some estuaries, such as San Francisco Bay (Cohen and Carlton, 1998), the relative contribution of disturbance to observed invasion histories is not well understood, as there are many confounding variables that vary among sites (Ruiz et al., 1999).

The magnitude of local and regional sources of anthropogenic disturbance has been low in high-latitude and polar marine systems to date, compared to lower latitudes, reflecting the low level of human activities. In contrast, climate change represents a global-scale and human-mediated disturbance, with pronounced effects expected for high latitudes (Arctic Climate Impact Assessment, 2005; Intergovernmental Panel on Climate Change (IPCC), 2007). While several researchers have begun to explore the potential effects of climate change to marine invasions (Stachowicz et al., 2002; Occhipinti-Ambrogi, 2007), they have focused primarily on effects of temperature at mid-latitudes. Below, we expand this scope to examine potential direct and indirect effects of projected temperature changes at high latitudes, considering especially the response of human activities and implications for changes in propagule supply, invasion resistance, and local/regional disturbance.

EFFECTS OF CLIMATE CHANGE ON INVASIONS

Climate change is expected to affect many dimensions of coastal ecosystems, including temperature regimes, sea level, upwelling, ocean currents, storm frequency and magnitude, and precipitation patterns, which will influence land-sourced runoff, leading to changes in nutrients and turbidity (IPCC, 2007). Shifts in these key physical processes

are expected to cause myriad and complex changes to the structure, dynamics, and function of biological communities. The magnitude and rate of climate change are the focus of ongoing research, as are the expected changes to coastal ecosystems.

One of the clear effects of climate change is elevated sea surface temperature, which is expected to be greatest at high latitudes and includes the complete loss of Arctic sea ice in the summer (IPCC, 2007). While models estimate the seasonal disappearance of Arctic sea ice in the next 50–100 years, empirical measures suggest ice loss is occurring at a more rapid rate (Serreze et al., 2007; Stroeve et al., 2007, 2008). In contrast, no trend in sea ice change has been detected in the Antarctic (Cavalieri et al., 2003; but see Levevre and Goosse, 2008). In Table 1, we consider some consequences of climate change in polar ecosystems for invasions, comparing potential responses in the Arctic and Antarctic. Our goal is to explore how the direct effects of climate and indirect effects on human activities (in response to climatic shifts and associated opportunities) may affect invasion dynamics at high latitudes.

Temperature is expected to have a direct effect on environmental resistance to invasion. It is clear that thermal regime sets range limits of many species, and these species are expected to shift in response to changing temperatures (Stachowicz et al., 2002; Occhipinti-Ambrogi, 2007). The projected changes for the Arctic and Antarctic waters

should allow species invasions (both natural and human-mediated) to occur that are not possible now due to constraints in thermal tolerance and possibly food availability (e.g., Thatje et al., 2005a; deRivera et al., 2007; Aronson et al., 2007). Thus, we hypothesize increased invasions at both poles (Table 1), caused by natural dispersal and human-aided transport. However, the rate of new invasions may differ greatly between Arctic and Antarctic ecosystems, depending upon the interaction of temperature, propagule supply, and invasion resistance.

Currents are expected to shift as a component of climate change and will no doubt affect propagule supply. While considerable uncertainty exists about changes in ocean currents, we hypothesize (Table 1) that especially strong effects of currents on propagule supply may occur across the Arctic Ocean due to (1) loss of sea ice, potentially allowing greater water movement, and (2) the continuous nature of the shoreline, providing adjacent source communities for transport. It appears likely that these adjacent communities will increase in species richness with rising temperature as many native and nonnative species expand their northern range limits in response. We posit that currents would therefore operate with temperature to facilitate species transport and coastwise spread across the Arctic. While currents can also supply larvae to the Antarctic (Barnes et al., 2006), we do not expect an analogous and increasing role with temperature rise there (Table 1),

TABLE 1. Hypothesized effects of climate change on invasion dynamics in Arctic and Antarctic ecosystems. A plus (+) indicates projected increase in invasion resulting from specified independent variables and response variables (mechanisms that affect invasion dynamics); a dash (—) indicates no expected effect or ambiguous outcome.

Agent	Independent variable(s)	Response variable(s)	Projected changes for invasions	
			Arctic	Antarctic
Climate	Temperature	Environmental resistance	+	+
	Currents	Dispersal	+	—
Commercial shipping	Number of ship transits	Dispersal, disturbance	+	—
	Shift in trade routes	Dispersal	+	—
Shoreline development	Port development	Dispersal, disturbance, new habitat	+	—
	Shoreline development	Disturbance, new habitat	+	—
	Mineral extraction	Dispersal, disturbance, new habitat	+	—
Fisheries	Natural stocks	Dispersal, disturbance	+	—
	Aquaculture	Dispersal, disturbance, new habitat	+	—
Tourism	Number of visits	Dispersal, disturbance	+	+
Debris	Quantity of debris	Dispersal, disturbance	+	—

due in part to the great distances from other coastal habitats and adjacent populations as well as the nature of the continuous Antarctic Circumpolar Circulation that creates a significant dispersal barrier.

There is considerable historical precedent for trans-Arctic exchange of biota between the Pacific and the Atlantic. Vermeij (1991a) documented 295 species of molluscs that crossed the Arctic Ocean from the Pacific to the Atlantic (261 species) or in the reverse direction (34 species) after the opening of the Bering Strait in the early Pliocene. This analysis included both species that took part in the interchange and species that were descended from those that did. While the faunal exchange occurred in geologic time, it may have been punctuated and also underscores the potential for such current-mediated transport in the future. We are now exploring further the environmental conditions under which this interchange occurred to better understand its implication for expected climate change in the Arctic. It is also noteworthy that a diatom species of Pacific origin, *Neodenticula seminae*, was recently discovered in the North Atlantic, where it now appears to be well established (Reid et al., 2007). The species, detected from collections in 1998, is thought to be a recent trans-Arctic exchange, although the possibility of ship-mediated introduction via ballast water cannot be excluded.

In response to projected temperature changes in polar regions, we expect major shifts in the level of many human activities that will affect marine invasion dynamics at high latitudes and elsewhere. Moreover, we hypothesize that the human responses and effects on invasions will be asymmetrical, with the greatest changes in the Northern Hemisphere (Table 1). The greatest effects (and greatest asymmetries) are likely to result from increases in commercial shipping and shoreline development, followed by fisheries and tourism.

As sea ice disappears in the Arctic, the opportunities for shipping and mineral (especially oil) exploitation increase dramatically. If the Arctic becomes safe for navigation, its use for commercial shipping would have strong economic incentive, reducing transit times and fuel costs. For example, the Northwest Passage between Europe and Asia is estimated to be approximately 9,000 km shorter than transiting the Panama Canal (Wilson et al., 2004). In addition, there is added expense (use fees) and often delays associated with the Panama Canal. Currently, 13,000–14,000 vessels transit the Panama Canal per year (Ruiz et al., 2006b), and approximately 75% of these vessels are on routes in the Northern Hemisphere. Thus, a large number of vessels could benefit from using an Arctic trade route, especially when considering additional ships

now transiting the Suez Canal that may also save time and expense on this new route.

A deflection of shipping routes into the Arctic has several likely consequences from an invasion perspective. First, this would greatly increase the number of ships transiting the polar waters and thereby increase the delivery of nonnative propagules associated with hulls and ballast tanks to high latitudes. The per-ship magnitude of this supply is not immediately clear as it depends upon source. Second, the source ports for transiting vessels would increase the diversity of organisms being delivered. Because few ships now visit Arctic water, they certainly do not include the full selection of geographic source ports (and associated biotic assemblages) of ships now transiting the Panama and Suez canals. Third, ships also have chemical discharges, whether intended or accidental (such as oil spills and leaching of active antifouling compounds), which represent a form of disturbance that may affect invasion resistance.

On a broader geographic scale, we expect the decrease in transit time may greatly improve survivorship of organisms associated with ballast water because survivorship in transit is time-dependent (Verling et al., 2005). The same is likely to be true for organisms on ships' hulls. Improved survivorship for either or both would result in increased propagule supply to subsequent ports of call, including major ports in Asia, Europe, and North America. While survivorship of shipborne organisms is time-dependent, the relative effects of transiting warm (Panama Canal) versus cold (Arctic) water will also affect the magnitude of change in mass flux of organisms among existing temperate ports. A cold temperature may serve to lower metabolic requirements, extending competency and survivorship of associated organisms. However, the overall effects of ambient temperature are likely to be complex, varying with species and source regions, and remain to be explored.

With warming temperatures and retreating sea ice, we expect a potentially large increase in shore-based activities in the Arctic, especially due to increase in mineral extraction and export. We consider three different but related activities that can result in increased invasion opportunity.

1. Commercial port development will occur on some scale to support oil extraction offshore, where large reserves exist. This will result in some increase in (1) propagule supply by ships, (2) local disturbance from chemical discharges from ship and port operations, and (3) local disturbance in the creation of novel habitat (rip rap, piers, etc.) associated with shoreline modifications. The latter is especially relevant given that many nonnative species are

found on such artificial substrates (Cohen and Carlton, 1995; Hewitt et al., 2004; Glasby et al., 2007), which may be especially important focal areas for colonization. If local export of oil occurs by shipping, this could greatly increase the scale of port development as well as propagule supply, as exemplified by oil export from Port Valdez (see above).

2. The scope of shoreline development, and especially associated habitat alteration and disturbance (as outlined above), is likely to exceed that for commercial shipping alone. Specifically, we expect some level of development to support oversight of territorial jurisdiction among Arctic countries, shore-based mineral extraction, tourism, and fisheries. It is difficult to gauge the potential scale of such development, although it is noteworthy that several countries have recently increased their presence in the Arctic (including military and surveying activities) in support of claims to Arctic territory and underlying mineral resources.

3. Offshore mineral extraction itself will also create opportunities for increased dispersal of propagules as well as some disturbance. It is not uncommon to use mobile drilling platforms for oil exploration, where the platforms are towed among sites at slow speeds. Although little studied, this movement can occur over great distances (i.e., across ocean basins) and may result in the transport of organisms at much greater densities than found on operating ships because (1) the platforms sometimes reside at previous sites for long periods, accumulating dense assemblages of organisms, and (2) the speed of transport is relatively slow, increasing the chance that organisms will remain associated. To our knowledge, strategies to assess or to reduce the associated risk of species transfers have not been explored for mobile drilling platforms. As with port development, offshore oil platforms, when fixed, create artificial (novel) habitats and have some risk of chemical discharge, and both types of disturbance may affect susceptibility to invasion.

For the Antarctic, we do not expect commercial shipping or shoreline development to occur to any great extent, simply because the same economic drivers do not exist there at this point in time. There are not major shipping routes that would benefit from transiting near Antarctica, and access to mineral and other resources is restricted under the Antarctic Treaty System.

The potential exists for fisheries to expand much more rapidly in the Arctic than in the Antarctic. This difference results in large part from access. The Arctic is in relatively close proximity to current centers of population and human activity, and a considerable history of fisheries at northern

high latitudes already exists in the Arctic. In contrast, access to fisheries resources in Southern Ocean waters $>60^{\circ}\text{S}$ is managed under the Antarctic Treaty System, specifically the Convention on the Conservation of Antarctic Marine Living Resources. It is difficult to say whether aquaculture would occur to any extent in high-latitude systems; however, current aquaculture trends indicate that it is highly likely. As discussed for commercial shipping, fisheries activities can increase the levels of propagule supply and disturbance, with the latter resulting from operation of ships (and discharges), removing predators and competitors, and creating physical disturbance with fishing gear (especially bottom trawls; Thrush et al., 1995).

Tourism is already a growing industry to both the Arctic and Antarctic, and we expect this trend to continue. As with fishing, the scope for growth appears greater in the Arctic, simply because of distance and access (including cost). As most tourism occurs by ships, the potential consequences for invasions are as outlined previously.

Finally, we predict an increase in the quantity of human-derived floating debris to occur in the Arctic and surrounding high latitudes in the Northern Hemisphere, coincident with increased levels of shipping, shoreline development, fisheries, and tourism, as these are all potential sources for floating debris. While Barnes (2002) reported relatively few organisms colonizing floating debris at high latitudes, the number may also increase under warmer temperatures. Further, in the absence of sea ice in the summer, the potential for longer-distance transport of floating material across the Arctic exists. Thus, we surmise that floating debris may play an important future role in the inoculation and, especially, regional spread of species in the Arctic, in contrast to much smaller changes expected in the Antarctic.

CONCLUSIONS

At the present time, very few introduced species are known from marine ecosystems at high latitudes in either hemisphere, especially for polar regions. This low number most likely results from a combination of low propagule supply of nonnative species and environmental resistance to invasion due to cold water temperatures and seasonal fluctuations in resources. The relative lack of anthropogenic disturbance may also serve to limit invasion opportunity.

With projected increases in temperature and the disappearance of Arctic sea ice in summer, we should expect invasions to increase as (1) temperatures fall within the thermal tolerance limits of organisms that are arriving

and (2) human-mediated responses to climate change increase the propagule supply and decrease the resistance to invasion (to the extent it exists) through disturbance. The change in invasion risk at high latitudes is expected to increase most in the Northern Hemisphere, driven by potentially large scale increases in the level of commercial shipping and shoreline development (especially associated with extraction of mineral resources). Fisheries, tourism, and floating debris also are likely to increase the opportunity for invasions, but to a much smaller degree.

The consequences of climate change for invasions at high latitudes deserve serious attention from a conservation and management perspective. While global shifts in climate (especially temperature) are underway and serve to increase chances of polar invasions, it appears that human responses to climate change will largely determine the number of invasions that occur. Although nonnative species can arrive to polar ecosystems by natural dispersal (Barnes et al., 2006), these regions are relatively isolated geographically, and the scope for human transport is far greater. Significant efforts should now focus on understanding and reducing the transfer of nonnative species to the poles, aiming to avoid the high number and significant impacts of introductions experienced in temperate waters.

Efforts to minimize invasion risk at lower latitudes have employed several approaches that are applicable and should be adopted in polar regions. These are conceptually simple, focusing especially on (1) prevention or reduction of species transport by human activities and (2) detection of invasions by nonnative species. In many nations, regulations exist to greatly reduce the delivery of organisms that pose some risk of invasions (Ruiz and Carlton, 2003). While these sometimes focus on specific species that are known to survive or cause significant impacts in a region, many strategies are now aimed at reducing transfers of all organisms associated with a known vector, especially because the number of potential species is vast and the risks of colonization and impacts are simply not known (i.e., have not been examined) for most species. As an example, this approach of vector management is now being applied to commercial ships in many countries, where ships are required to treat their ballast water before discharging in coastal areas, reducing the concentrations of all coastal organisms (e.g., Minton et al., 2005).

A comprehensive effort to reduce species transfers should include an assessment of potential human-mediated vectors as the basis for developing and implementing vector management (Ruiz and Carlton, 2003). For polar systems, policies could be adopted immediately to reduce

transfers by commercial ships, extending efforts developed in temperate latitudes, since ships' ballast water and hulls are known to carry a risk of invasions (Ruiz et al., 2000; Fofonoff et al., 2003; Hewitt et al., 2004). Analyses of additional present and future vectors, such as oil drilling platforms and fisheries activities, would be obvious next steps to estimate the potential magnitude of species transfers and to consider options for vector management.

In addition to vector management, efforts to detect invasions and to measure temporal changes in invasions should be established in polar regions. Ideally, this would include an initial baseline survey and repeated surveys through time designed explicitly to test hypotheses about invasions (e.g., Ruiz and Hewitt, 2002) and address several management needs. First, these data would provide a measure of whether invasions are occurring and help identify specific vector(s) for management, providing feedback on how well management strategies are working to limit invasions (Ruiz and Carlton, 2003). Second, resulting detections of new invasions would also enable efforts to eradicate or control invasions, as deemed desirable.

These strategies for prevention and detection are easily understood, but implementation is not so easy to achieve. Often, there are issues related to resources (time and funding), limiting the desired scope of effort. In addition, there can be issues related to jurisdiction that further complicate implementation, resulting from political (geographic) boundaries and institutional (legal) authorities. Unfortunately, in temperate marine systems, these impediments to effective management strategies are often not overcome until a threshold of significant ecological or economic impacts is reached.

Since few invasions are known for polar systems to date, the opportunity now exists to implement management and policy that would greatly limit invasions and their unwanted impacts in these unique communities. Given the transboundary aspects of polar systems, there is a clear need for international cooperation and agreements in this area. We hope this article stimulates actions to evaluate and reduce invasion risks at high latitudes, applying the principals, methods, and experiences from temperate marine systems around the globe.

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