**Potential journals for publication?**

* Biological Invasions (8000 word limit)
* Global Change Biology (8000 words)
* Journal of Biogeography (approx. 7000 words)
* ICES Journal of Marine Science (3000-7000 words)
* Diversity & Distribution (6000 words)
* Hydrobiologia
* Marine Biology (cannot find word limit?)
* Marine Ecology Progress Series (4000-12000 words)
* Aquatic Invasions (quarterly, 9000 words incl. references)

General:

* Ecological Applications (60 pages double-spaced)
* PLoS One (if it doesn’t fit in a more specific journal)
* Scientific Reports
* Ecosphere
* Journal of Applied Ecology (7000 word limit)
* Ecology (20 page double-spaced limit, unless we argue why it should be longer)

Geography-based:

* Polar research
* Polar biology
* Polar science
* Arctic
* Arctic, Antarctic, and alpine research
* Polar Biology

# Title: What limits invasions in arctic marine systems? Investigating the role of water temperature on survival and reproduction in the Bering Sea

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# Abstract

Cold water temperatures and minimal shipping traffic are expected to limit biological introductions in polar ecosystems, but evaluations of this expectation across multiple taxa and life stages are lacking. We evaluated these expectations in the Bering Sea, a marine ecosystem characterized by a strong, subarctic-arctic latitudinal gradient, by (1) examining how water temperatures affect potential survival and reproductive habitat of invasive species; and (2) quantifying vessel traffic and ballast water discharge into U.S. Bering Sea ports. We built taxa-specific, habitat suitability models by comparing species’ temperature and salinity thresholds to conditions in the Bering Sea projected by three regional ocean models. We investigated climate-driven changes in habitat suitability by considering two time periods: current (2003-2012) and mid-century (2030-2039). Under current conditions, 83% of the taxa assessed (*n*=42) have temperature tolerances that would allow them to survive year-round in the southern Bering Sea. Areas north of 58°N, which have been annually covered by sea ice and have had winter water temperatures below 0°C, were largely inhospitable. Future models predict a northward expansion of suitable habitat, largely favoring taxa that already have the ability to survive year-round. While suitable reproductive temperatures exist for many of the taxa considered, the short summer season may limit those that require more than six weeks to complete development. We found substantial trans-oceanic cargo and fishing vessel traffic and ballast water discharge, with the greatest amount occurring in Dutch Harbor, which serves as a hub connected to local ports throughout the Bering Sea. Our analyses indicate that there currently exists suitable habitat and transport mechanisms for non-native taxa in the Bering Sea, and environmental barriers are expected to decrease in the near future. The southeastern Bering Sea, and the port of Dutch Harbor in particular, are high-risk areas for biological introductions and should be monitored.

by developing species-specific habitat suitability models and quantifying vessel traffic we were able to determine spatial risk

**Key words:** Arctic, climate change, physiological thresholds, habitat suitability, biological invasion, marine, non-native species, shipping, Bering Sea, Alaska, risk assessment

# Introduction

Shipping, temperature, and salinity are strong, predictive factors of the distribution and invasion potential of aquatic, non-indigenous species (NIS) (Hewitt and Hayes 2002, Barry et al. 2008, Lord et al. 2015). Shipping is a primary pathway by which species are introduced to new regions (Ruiz et al. 1997, Molnar et al. 2008), as organisms are unintentionally transported in ballast water and on the wetted surfaces of ships (“biofouling”). Patterns of vessel traffic – including the port of origin, the route taken, the duration of the voyage, the type of ship, and the difference in environmental conditions between origin and recipient ports – collectively influence the diversity, number, and frequency of these introductions (Verling et al. 2005, Colautti et al. 2006, Miller and Ruiz 2014). Because higher rates of introductions increases the probability of successful invasion, areas with little shipping traffic, like polar regions, are predicted to be less at risk than high-traffic regions. Following successful transport, water temperatures are thought to be particularly influential in determining survival and establishment, especially in cold regions (Ruiz and Hewitt 2009). When temperatures are below optimal thresholds, behavioural, metabolic, and cellular processes are negatively affected; if these temperatures drop below a critical threshold, mortality ensues (Pörtner 2001, Kassahn et al. 2009). NIS originating from more temperate regions may lack adaptations to cold water temperatures, and their optimal thermal ranges may be skewed towards temperatures that may be several degrees warmer than the minimum temperature of Arctic systems (Lord et al. 2015). Even species that can survive in cold waters may not be able to establish a self-sustaining population, as reproduction and ontogenetic development often have narrower thermal ranges than survival (de Rivera et al. 2007). Some organisms may not have sufficient time to develop, especially considered that there is often a strong link between temperature and time to development: in general, the colder the temperature, the longer it takes for larvae to develop and metamorphose into adults (de Rivera et al. 2007). Other organisms simply do not spawn when water temperature falls below a certain threshold, or they can produce viable gametes, but larvae do not develop properly or do not transition through all the ontogenetic stages (Hines et al. 2004, Byrne et al. 2016).

Vessel traffic and water temperature is likely critical for predicting invasions in Arctic systems, where water temperatures can fall below freezing, and summers are cold and short. However, studies have come to different conclusions about whether NIS can survive Arctic voyages and the conditions they encounter upon arrival. In Arctic systems, seasonal sea ice has limited vessel traffic, with the assumption of low propagule pressure. NIS are already being transported to Arctic ports, both in ballast water and on wetted surfaces (“biofouling”) (Chan et al. 2014, 2016, Ware et al. 2016). Survivorship of NIS during voyages to the Arctic appears to be low compared to temperate, marine systems (Chan et al. 2014); low water temperatures and the length of the journey may be important factors in reducing survivorship (Chan et al. 2014, 2016). However, these factors do not completely prevent introductions, as some organisms are surviving the voyage (Chan et al. 2015, 2016, Ware et al. 2016), and high-profile introductions in northern waters (e.g. the snow crab in Barents Sea) have been linked to anthropogenic transport mechanisms (Alvsvåg et al. 2009). Some studies have explored the potential for NIS to survive in Arctic regions were they to be successfully transported there. Habitat modeling studies in coastal Alaska found that of the four species considered, all were able to survive in the north Pacific and the Bering Sea, far beyond their current range, and three had tolerances which allowed for survival above 65N (de Rivera et al. 2011). In contrast, Ware et al. (2016) examined the potential distribution of eight NIS in the Norwegian Arctic, and found that current temperature and salinity conditions were unsuitable for all but one of the species studied. These studies have focused on suitability of only a few potential species; however, the actual number of taxa that are being transported on voyages to the Arctic is likely higher. Without prior knowledge of which organisms are being transported on ships, focusing on a suite of species – with consideration of both survival and reproductive suitability - would provide greater insight for risk assessments, as well as extend the generality of the findings.

Because both Arctic sea temperatures and trans-oceanic vessel traffic are expected to increase in the near-future, exploring the role of temperature in limiting biological introductions is necessary. In recent decades, the Arctic has experienced record-setting declines in sea ice thickness and extent, and surface air temperatures have increased at a rate that is twice that of the global average (Lemke et al. 2007, Stroeve et al. 2012). Warming sea temperatures and sea ice reductions have facilitated range expansions and introductions into previously inhospitable or inaccessible waters elsewhere (Reid et al. 2007, Renaud et al. 2015), and distribution models predict that Arctic waters will become even more suitable to invasions over the next century (de Rivera et al. 2011, Ware et al. 2014, 2016). Warming climatic conditions have also favoured expansions in global shipping and other human activities. Since the beginning of the 21st century, there has been an exponential increase in Arctic shipping, both through the Northwest Passage and the Northern Sea Route, spurred in part by declining sea ice extent and lengthening of ice-free season (Miller and Ruiz 2014). ((add stats)). In addition to commercial vessel traffic, the Arctic is also expected to see different types of ships and activities, such as natural resource exploration and extraction, and Arctic tourism. Changes in traffic volume and patterns are expected to increase the number and diversity of organisms that are being transported to Arctic regions.

In this paper, we explore whether cold water temperatures have the potential to limit introductions in the Arctic by examining whether non-native taxa had thresholds that would allow them to survive and reproduce in the Bering Sea, a high-latitude marine ecosystem characterized by a strong, latitudinal gradient. We also quantify vessel traffic and ballast water discharge for U.S. ports in the Bering Sea to identify potential entry points of non-native species, and to consider the interplay of traffic and habitat suitability. We hypothesized that survival would depend on species’ tolerance to cold water temperatures, and predicted that potential NIS richness would be higher in the southern Bering Sea, and decline in the north. Because climate change is expected to increase water temperatures in the Bering Sea, we predicted that habitat would become more suitable for non-native taxa in the future. To address this hypothesis, we examine current and mid-century marine temperature regimes across the Bering Sea and characterize survival and reproductive habitat for potential NIS. Our work extends previous research by providing a comprehensive assessment of the role of temperature on high-latitude invasions based on a understanding of NIS physiological tolerances, modeled ocean conditions and available data on vessel and ballast water movements.

# Methods

## Study area

The Bering Sea lies between the temperate North Pacific Ocean and the arctic waters of the Chukchi Sea. It spans 13 degrees of latitude and extends more than 1,500 kilometers from Alaska (USA) to Russia (Fig. 1). This large, dynamic ecosystem boasts some of the highest level of marine productivity in the world, supporting a US $1 billion commercial fishery and providing the U.S. with 50% of its wild-caught seafood (XXX). The Bering Sea is comprised of a deep-water basin, an extensive and highly productive eastern continental shelf, and a narrow western shelf (Fig. 1) (Stabeno et al. 1999). While our analyses encompass the entire latitudinal breadth of the Bering Sea, we restricted ourselves to the two continental shelves i.e. depths < 200 meters (m) because most non-native taxa invade near-shore habitats (Ruiz et al. 2015). Only four non-native species have been reported in the Bering Sea: *Alosa sapidissima*, *Caprella mutica*, *Mya arenaria*, and *Salmo salar* (Fofonoff et al. 2003; see Powers et al. (2006) for a discussion on the history of *M. arenaria* in Alaska). Of these, only *C. mutica* and *M. arenaria* have established populations (Ashton et al. 2008). ((characterize vessel – the bering sea is the only waterbody that is included in both NSR and northwest passage, few recreational vessels))

## Defining taxa-specific tolerances

We compared temperature (T) and salinity (S) thresholds of non-native, animal taxa to the T-S values of the Bering Sea for two, 10-year time periods: current (2003-2012) and mid-century (2030-2039). We based our models on taxa-specific, physiological T-S thresholds required for two stages on invasion: survival and establishment, which we define here to include both growth and reproduction (Blackburn et al. 2011). These thresholds were compiled using a targeted literature review as part of a larger research project by Reimer et al. (2018). Reimer et al. (2018) developed a ranking system for the Bering Sea and assessed the risk of 46 non-native, marine taxa that are considered invasive in other systems, and that have been reported in nearby marine ecoregions (sensu Spalding et al. 2007). The taxa list was developed by downloading and digitizing occurrence records from the National Exotic Marine and Estuarine Species Information System (NEMESIS; Fofonoff et al. 2003) and the Nonindigenous Aquatic Species Database (NAS; Fuller and Benson 2013). Given the time required for ranking, the list was subset to include only taxa that had been reported no further away than Washington-Oregon border in the east Pacific and the Sea of Japan to the west. Taxa were restricted to marine or euryhaline species capable of tolerating salinities of at least 30 parts per trillion (ppt) for part or all of their life cycle (Appendix A). The most common taxonomic groups were Crustacea (N=15), Mollusca (N=11), and Tunicata (N=8). Included in this list were two anadromous fish (*Alosa sapidissima* and *Salmo salar*), and one catadromous crab (*Eriocheir sinensis*). All taxa used at least one anthropogenic vector (e.g. ballast water, biofouling, intentional introductions) for transport (Reimer et al. 2018).

Of the 46 taxa included in the ranking system, taxa-specific T-S survival tolerances were available for 42 taxa (Appendix A) and T-S reproductive tolerances for 29 taxa (Appendix B). We prioritized T-S thresholds from experimental or field-based studies, rather than data that were inferred from geographic distribution, which may be biased or incomplete (cite??). Nevertheless, we did use the latter when necessary because we considered this source of data to be superior to no data. Survival thresholds were intended to represent the broadest range of temperatures and salinities that a given taxon could tolerate. Therefore, for each taxon, we defined survival thresholds as the absolute minimum and maximum values reported for that taxon, irrespective of life stage and geography. In contrast, establishment thresholds represent the narrowest T-S range required for growth or reproduction. If multiple thresholds were available (e.g. spawning versus larval development), we chose the thresholds associated with the least tolerant life stage.

Our models required information on minimum and maximum thresholds for both temperature and salinity. To maximize the number of taxa we could include in our models, we developed two additional criteria:

1. If the maximum temperature threshold was unknown, but survival had been observed in temperatures that exceeded the Bering Sea maximum (~17°C), we assigned an arbitrary maximum temperature value of +999 to ensure its inclusion in our analyses.
2. If salinity thresholds were unknown, but the taxon was a marine taxon that had been reported from ecoregions whose salinities were comparable to those of the Bering Sea, we set its salinity range to average seawater values (31 to 35 ppt), which would confer salinity survival to 98.8% of the Bering Sea shelf.

## Defining temperature and salinity of the Bering Sea

Values for the Bering Sea’s T-S regimes were obtained from three Regional Ocean Modeling Systems (ROMS) developed by NOAA's Pacific Marine Environmental Laboratory (PMEL) (Hermann et al. 2013, 2016). Each ROMS was generated by downscaling one of three general circulation model (GCM): 1) CGCM3-t47, 2) ECHO-G, and 3) MIROC3.2 (Hermann et al. 2016). These GCMs were chosen for their ability to correctly? predict observed conditions in the Bering Sea and the northeastern Pacific (Wang et al. 2010, Hermann et al. 2016), and were based on the A1B emissions scenario from the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (Nakićenović et al. 2000). Compared to other scenarios, the A1B scenario implies moderate greenhouse forcing mitigation. However, because all scenarios generally track each other in the short-term, results from A1B GCMs do not differ substantially from other emission scenarios over the study period we considered (2003-2039; Nakićenović et al. 2000).

ROMS outputs provide weekly values of temperature and salinity across the Bering Sea with a 6-nautical mile spatial resolution and for 10 vertical depth levels (Hermann et al. 2016). We restricted our analyses to the Bering Sea continental shelf (i.e. water depths less than 200 m), and to the top seven ocean layers (surface and 5, 10, 15, 20, 30, 40 m depths). For each pixel, we summarized the depth dimension into a single value by taking the maximum T-S values. Projections from ROMS for the Bering Sea were available for 37 years (from 2003 to 2039). We considered two 10-year study periods: current (2003-2012) and future (2030-2039) to explore potential changes in habitat suitability over time.

## Modeling habitat suitability

Our habitat suitability analyses consisted of three components: 1) year-round survival, 2) weekly survival, and 3) weekly reproduction. We developed suitability criteria for each of these components, but at its simplest, a taxon was considered to have suitable habitat if at least one pixel in our study area had T-S values that were within the taxon’s T-S thresholds. Habitat suitability was analyzed separately for each taxon, ROMS, and study period, and results were summarized across taxa. All analyses were conducted in R version 3.3.2 (R Core Team 2016) with support from the following packages: ddply, doSNOW, dplyr, ggplot2, ncdf4, maptools, plyr, rgdal, raster, rasterVis, rgeos, sp, viridis.

### Year-Round Survival

For each taxon, we defined a 6-nautical mile pixel as ‘suitable’ if the pixel’s T-S values remained within the taxon’s survival range for all weeks of a given year. We classified the pixel as ‘suitable year-round’ if it remained suitable for at least 7 years out of the 10-year study period. Cumulative suitability was then determined for each pixel by summing the number of taxa that had suitable year-round habitat in that pixel. We expressed the change in number of taxa predicted to have year-round habitat by calculating the difference in number of taxa from current to mid-century projections. Positive change values indicate that more taxa are predicted to have year-round survival in the future, compared to current predictions, while the inverse is true for negative values. A value of zero indicates that the predicted number of taxa with year-round survival remains the same across both study periods. Lastly, we calculated the percent increase in suitable area by dividing the sum of pixels with positive change by the total number of pixels in our study area, and multiplying by 100. Percent decrease in suitable area was similarly calculated using the number of pixels with negative change as the numerator.

### Weekly Survival

For each week, a taxon was considered to have suitable survival habitat if its T-S requirements were met in at least one pixel of the Bering Sea. Weekly survival was then calculated as the number of weeks per year identified as having suitable survival habitat, averaged across each 10-year study period. Unlike our year-round habitat analysis, where the same pixel had to remain suitable year-round, in this analysis we allowed suitable habitat to move in space from one week to the next. We summarized results across taxa by calculating the cumulative weekly averages for all 42 taxa; pixel values therefore represent 'average suitable week x number of taxa', with a theoretical maximum value of 2184 (52 weeks x 42 taxa).

### Reproductive Suitability

For each taxon, we defined a pixel as having suitable reproductive habitat if the T-S values for that pixel were within the taxon’s reproductive T-S thresholds for at least one week of a calendar year. For each year within our 10-year study periods, we calculated the number of consecutive weeks of suitable reproductive habitat, such that pixel values could range from 0 to 52. For our analysis, we used the maximum number of consecutive weeks within each 10-year study period as our metric; this value was calculated for each taxon and ROMS.

## Vessel traffic

We analyzed current vessel traffic and ballast water discharge in the Bering Sea using two datasets: the National Ballast Information Clearinghouse (NBIC) and Alaska’s Vessel Monitoring System (VMS). These data allowed us to quantify the magnitude and spatial pattern of traffic arriving at U.S. ports in the Bering Sea from fishing vessels and from large, commercial vessels (> 24 m). First-order port connections were examined using the circlize package (Gu 2014) in R Statistical Software version 3.3.2 (R Core Team 2016).

NBIC data are publicly available (https://invasions.si.edu/nbic/search.html) reports of vessel landings and their ballast water activities. Most large vessels (> 24 m) are required to report their ballast water exchanges when entering any port in the United States (USCG, 33 CFR Part 151). Because regulations have changed in the last decade, especially with respect to mandatory reporting by crude oil tankers (Verna et al. 2016), we only considered the three most recent, complete years (2014 – 2016). For vessel landings, we queried Ship Arrival Records from the NBIC data portal for any vessel arriving in Alaska from 01 January 2014 to 31 December 2016. Records without a port name were removed (*N*=13), and spellings for each port were standardized. Ports in Alaska were binned into one of the following regions: Arctic, Bering Sea / Aleutian Islands (BSAI), Gulf of Alaska (GOA), or Southeast Alaska (SEAK). Source ports with fewer than five trips reported were binned in a group labeled “Other”. For ballast water volumes and their sources, we queried Ballast Tank Records from the NBIC data portal with the same locale and date parameters as described above.

While the NBIC provides data on large, commercial vessels, it does not apply to smaller vessels ≤ 24 m long. Therefore, we relied on VMS data from Alaska to examine patterns of fishing vessel traffic. Current regulations by the National Marine Fisheries Service (NMFS) require VMS reporting by all fishing vessels that target walleye pollock, Pacific cod, Atka mackerel, and crab in the BSAI and the GOA (Spalding 2016). These locations are transmitted at 30-minute intervals. For consistency with the NBIC data, we examined all trips by vessels with VMS from 2014 – 2016, using methods from Watson and Haynie (2016). We analyzed a total of 4133 trips by 566 vessels during this time. Port connections with fewer than 3 different vessels were omitted according to confidentiality rules.

Some U.S. fishing vessels appeared in both the NBIC and the VMS databases, but are not easily queried because ‘Fishing’ is not a vessel type category in the NBIC database. To identify these records, we used their co-occurrence to create a ‘Fishing’ vessel type, thereby removing these vessels from the ‘Other’ category. These vessels were identified by linking NMFS fishing permit and U.S. Coast Guard numbers to the International Maritime Organization (IMO) vessel identifiers in the NBIC data via a NMFS vessel database (st.nmfs.noaa.gov/coast-guard-vessel-search/index).

# Results

Describe max/min water temperature threshold (minimum temperature thresholds ranged from -2C to …) talk about median? summer temps. . 1/3 of the taxa we considered had minimum temperature tolerances of 0C

## Survival

Under current conditions (2003-2012), our habitat models estimate that 33 to 35 (of the 42 taxa assessed) can survive year-round in the Bering Sea (Table 1). Of the taxa that cannot survive year-round, all have suitable habitat for at least six weeks during early July to mid-August (weeks 28 to 33; Figure 4). but for the most part habitat is unsuitable from December to early May (weeks 49 to 19), when temperatures in the upper water column fall below 1°C (Figure 4). Non-native species richness follows a strong latitudinal pattern. Our models predict that the southeastern Bering Sea, including the coastlines of the Aleutian Islands, the western Alaska Peninsula, and western Bristol Bay, can support the highest number of NIS (Figure 2). The northern Bering Sea (above 58°N) remains unsuitable for nearly all assessed NIS (Fig XX). Across all three models, the amount of suitable habitat is also expected to increase by mid-century. By 2039, between 37% and 60% of the Bering Sea shelf is predicted to become suitable for at least one NIS (Table 1). In contrast, only a small amount of habitat (less than 7%) is expected to switch from suitable to unsuitable (Table 1). In general, the ROMS project a northward expansion of suitable habitat in the southeastern Bering Sea, and eastward into Bristol Bay (Figure 3). Both CGCM3-t47 and MIROC3.2 models project mid-century (2030 – 2039) conditions that would enable one additional NIS to survive year-round (Table 1). Species with max salinity tolerances <=30ppt have little survival habitat.

## Reproduction

Suitable habitat for reproduction was identified for 20 to 24 species (out of 29) in the Bering Sea (Table E-1). Under current conditions, most species have suitable reproductive habitat for approximately six to nine consecutive weeks. Species that require temperatures >= 15°C, were not found to have suitable reproductive conditions. NIS that only required 12C for reproduction were found to have an average of 5.5 (SD=2.8) consecutive weeks of reprodutction within the study area. While NIS that required only 10C were found to have nearly three months of suitable reproductive temperatures within the study area (x=11.2, SD=3.5). Two species (*Caprella mutica* and *Mya arenaria*) had suitable habitat nearly year-round. In contrast, several species had less than one week of suitable habitat, and an average of six species had no suitable reproductive habitat (Table E-1). Three of these (*Alosa sapidissima, Hediste diadroma*, *Salmo salar*) were primarily limited by salt conditions, requiring either fresh or brackish water for at least part of their development. The other three require temperatures of at least 16°C for reproduction, and were shit out of luck. Current maximum water temperatures (projected by the ROMS) never exceed 17°C (Table 4). Mid-century water temperatures maximums are expected to increase by 0.2°C to 2.3°C, with maximum temperatures in the Bering Sea projected to exceed 18°C. By mid-century, the number of suitable weeks for NIS reproduction is expected to increase slightly (Table 1; Table E-1). CGCM3-t47 and MIROC 3.2 models estimate that by mid-century, habitat will become suitable for an additional two and four species (Table 1; Table E-1).

## Vessel traffic

The NBIC data reported a total of 816 arrival records and 15,837 ballast water discharge reports in Alaska[[1]](#footnote-1)for Bering Sea ports from 2014 to 2016. Records were distributed across 9 vessel types: Bulker (*N*=2755), Container (*N*=295), General Cargo (*N*=114), Other (*N*=396), Passenger (*N*=774), Refrigerated Cargo (*N* = 418), Roll-on/Roll-off Cargo (*N* = 10), Tanker (*N*=9935), and Fishing (*N*=1140). Dutch Harbor received the greatest amount of traffic for both NBIC and VMS reported boats. Nome received the second highest amount of traffic for NBIC reported vessels, and Akutan received the second highest amount of traffic for VMS reported vessels. With respect to ballast water discharge, the majority of reported discharge occurred in Dutch Harbor, with Nome having the second largest discharge volume (Figure 6).

82.7% of arrivals (of NBIC ships?) originated from outside Alaska (Figure 5a). According to the NBIC dataset, California (*N*=175), Washington (*N*=142), and South Korea (*N*=127) accounted for greater portions of vessel traffic into the Bering Sea than the more proximate Gulf of Alaska ports (*N*=120). However, from VMS data, which predominantly includes smaller fishing vessels that do not report to the USCG, an overwhelming majority of trips originated from Gulf of Alaska ports (*N*=657; Figure 5b). Ballast water exchange data revealed a different pattern than the ship arrival records: while ports in the eastern Pacific Ocean accounted for more trips, most ballast water released in the Bering Sea originated from Asian ports (Figure 6). South Korea and China each accounted for an order of magnitude more ballast water (18,728 and 17,453 mt, respectively) than the next greatest sources, Japan (7183 mt), Canada (6912 mt), and Washington (3852 mt). Approximately 20% of the 15,837 ballast water exchange records (representing 10.6% of the discharged volume) identified the source of their ballast water using coordinates (typically from offshore waters) instead of port names. Among these non-port ballast water sources, 25% of water originated from locations in the northeast Pacific Ocean (defined here as latitudes > 23.5° N, longitudes between 179.9° W and 110°W) and 15% originated from locations in the northwest Pacific Ocean (defined here as latitudes > 23.5° N, longitudes between 100° E and 180° E).

# Discussion

Although the Pacific Arctic has few reported non-indigenous species (NIS), our results indicate that (1) potential NIS habitat exists in the Bering Sea; (2) this potential NIS habitat is projected to expand by mid-century due to warming ocean conditions; and (3) mechanisms for NIS propagule transport into and throughout the Bering Sea exist and may well increase. These results challenge the expectation that high-latitude marine ecosystems have low risk due to temperature limitations on habitat and low propagule pressure. [..]

Across the 42 taxa we examined, survival suitability was predicted as high in the southern Bering Sea, but decreased drastically in the north. Temperatures suitable for growth and reproduction do exist, but taxa with long-lived larval or development stages may be limited by the Bering Sea’s short summer season. Areas of high habitat suitability were also areas that received the highest number of commercial and fishing vessels. Collectively these results suggest that…. Areas of high vessel traffic intersect with areas of high habitat suitability, which is cause for concern.

## The role of cold water temperature on survival

Because the species we considered are from more temperate regions, we expected that a lack of cold water tolerance would be the limiting factor. Two pieces of evidence from our research confirm these results. First, all taxa we considered could survive for at least six weeks of the year, when water temperatures were warmest (from early July to mid-August). However, taxa without year-round habitat were unable to survive during the coldest months of the year (from December to April), even under projected mid-century conditions (2030-2039). Second, we uncovered a strong, latitudinal gradient in non-native species richness, with high richness in the southern Bering Sea shelf, and a sharp decrease above 58ºN (Fig. XX). This gradient is coincident with the limit of seasonal sea ice extent (Grebmeier et al. 2006b, Stabeno et al. 2012) in the Bering Sea. Seasonal sea ice cover in the southern Bering Sea is either entirely absent (e.g. the Aleutian Islands), or strongly variable from one year to the next (Stabeno et al. 2012). Meanwhile, the northern Bering Sea is more similar to arctic ecosystems and its seasonal dynamics are driven, to a large extent, by the presence, timing, and extent of sea ice (Grebmeier et al. 2006a). Our findings suggests that winter water temperatures present an important obstacle to the invasion of arctic, but not subarctic systems. There already exists ecological differences between the subarctic and arctic regions of the Bering Sea, with native species in the northern Bering Sea being more akin to species in the Chukchi Sea and the Arctic Ocean than in the Pacific; this is especially true for demersal and benthic organisms that experience a “cold pool” (water temperatures below 2°C) in the summer, which is a direct result of melting winter sea ice (Wyllie-Echeverria and Wooster 1998, Mueter and Litzow 2008). de Rivera et al. (2011), who developed ecological niche models to predict the distribution of four potentially invasive species in Alaska, three of which we consider here. Our models support their main finding that current environmental conditions in high-latitude systems do not preclude survival (de Rivera et al. 2011), but by considering a larger number of taxa, we found that most species do not have the ability to live up to the Arctic… (Fig. XX). Our approach, which uses physiological tolerances rather than environmental matching, is especially meaningful in systems such as the Arctic, where environmental conditions fall outside the range of values to which taxa are exposed in their current range (Miller 2016). Nevertheless, there is a lack of knowledge on the physiological thresholds of most marine organisms. Even within a taxa, different populations can exhibit different tolerances, or exhibit impressive phenotypic plasticity (Sorte et al. 2011, Huang et al. 2017). The limitations of considering only one or a few variables (e.g. temperature, salinity) in isolation have been discussed elsewhere; beyond the need to consider additional factors such as availability of food resources and substrate, there is also the potential for interactions and for non-linear responses, both of which may be especially important at the tail-end of species’ thermal response curves (Monaco and Helmuth 2011, Sorte 2014, Miller 2016). We also recognize that sea temperatures do not tell us about the organism’s body temperature (the true limiting factor), which can also be affected by a multitude of environmental factors e.g. wind (Monaco and Helmuth 2011).

## Reproduction: Is there enough time?

Although most (21 of 29) of the evaluated species had at least one week of suitable reproductive habitat. Most species that were unable to reproduce required brackish or freshwater for reproduction; in theory, these species would have access to many estuaries and rivers. For axa that require temperatures above 10C, the Bering Sea’s short summer season may be insufficient for taxa to reproduce and develop. The role of cold temperature on either preventing development, or lengthening time required for development, has been well documented (e.g. de Rivera et al. 2007). Thus, several taxa of concern in nearby ecoregions (e.g. *Amphibalanus amphitrite*, *Botrylloides violaceus*, *Carcinus maenas*), may have limited opportunities for reproduction under current conditions in the Bering Sea, despite having the capacity to live year-round across moderately large areas of the shelf. However, our models may underestimate summer water temperatures near the coastlines, and especially near the mouth of major rivers, potentially underestimating the time and amount of suitable habitat available. The spatial resolution of the ROMS (6-nautical mile) is coarse in the context of habitat studies for marine invertebrates. Because of the resolution and numerical limitations, the ROMS lack resolution in shallow waters (< 10 m deep), and models do not reach the shoreline, often falling several kilometers short. In addition, the ROMS we used do not account for the influence of rivers of ocean temperatures (the effect on salinity is included, though estimates are coarse). The influence of rivers is significant in our study area given the many large rivers that drain into the Bering Sea (e.g. Yukon, Kuskokwim, Nushagak..). These rivers not only contribute to freshening the Bering Sea, but also increase near-shore water temperatures by several degrees in the summer. Measurements from finer scale models have have recorded temperatures as high as 19°C near the Yukon River. Local dynamics such as freshwater runoff influences salinity and temperature and is likely to affect species’ distribution and persistence (Fetzer and Arntz 2008, Miller 2016). Interestingly, the two non-native species that are thought to be established in the Bering Sea, not only had year-round survival ability, but were also the two outliers in our reproductive models that had nearly year-round reproductive habitat as well (between 49 and 52 consecutive weeks of suitable repro habitats). We did not consider the potential for asexual reproduction, and there are instances of some species establishing self-sustaining populations based on asexual reproduction alone (e.g. *Nematostella vectensis*; Hand 1994—need cit).

## Vessel traffic

Both commercial and fishing vessel traffic, and ballast water discharge point to the port of Dutch Harbor as being by far the most visited port in the Bering Sea region. Vessel traffic patterns also indicate a high degree of connectivity between Dutch Harbor and ports from both the eastern and western Pacific Ocean. Trips ending in Dutch Harbor originated from more than ten countries from around the world. Moreover, the connectivity of Dutch Harbor to other Bering Sea ports, like those of the Pribilof Islands, Bristol Bay, and Akutan, emphasizes the scale of connectivity among many Alaskan communities and further underscores the potential impacts of invasive species in Dutch Harbor. Without a road system to provide access to Alaska’s port communities, vessels of all types form a marine highway system that is traveled by ferries, tugs, barges, and as demonstrated here, fishing vessels. Many of these vessels are not required to report ballast water activities because of their size or because they remain within State waters. In Svalbard, Norway (XX degrees N), research vessels were found to pose one of the biggest risks to introductions in the near future (Ware et al. 2014), but these vessel types are not included in our anlaysis Given this, future analyses of vessel traffic in the context of invasive species transport may benefit from analysis of Automatic Identification System (AIS) data, which are available for a greater portion of vessels traveling through Alaskan waters.

We assumed that high-traffic ports are more susceptible to receiving non-native species than low-traffic ports, and that shipping traffic and ballast water discharge are adequate proxies of propagule pressure. previous studies indicate that shipping traffic is correlated to non-native species richness (e.g. Lord et al. 2015; Lacoursière-Roussel et al. 2016), and ballast water discharge volume has been shown to be ?? (see Verna et al. 2016..). While these simplifying assumptions were necessary considering the data that were available to us, we recognize that an organism’s survival during a sea voyage is influenced by several factors including its physiological condition, the voyage duration, and environmental differences between donor and recipient ports (Carlton 1996, Verling et al. 2005, Chan et al. 2014). Both planktonic and fouling organisms that are transported from temperate to Arctic regions appear to have low survivorship (Chan et al. 2014, 2016, Ware et al. 2016) Verna et al. (2016) quantified ballast water risk of Alaskan ports and found that while Dutch Harbor was at medium risk in terms of discharged water volumes, the relatively long residence time of the ballast water that was discharged there was likely to reduce the probability of establishment. In 2006, Ruiz et al. deployed fouling plates at several ports in Alaska, and found no non-native species on plates from Dutch Harbor (the only Bering Sea port considered in their study) – none were found

## Effects of climate change on invasion risk

The Bering Sea is experiencing significant oceanographic changes as a result of climate change (e.g. Grebmeier et al. 2006b, Stabeno et al. 2007, Mueter and Litzow 2008). Sea ice cover has decreased substantially since the 1950s, with a concomitant increase in surface water temperatures of 0.23°C per decade (Mueter and Litzow 2008). These changes are projected to continue (Wang et al. 2012, Hermann et al. 2016). In the next twenty years, our models predict a major northward expansion in suitable habitat (Fig. XX) that would largely favour non-native taxa that already have the capacity to survive in the southern Bering Sea (Table XX). Contextualize degree change in temp. with % change in suitable habitat. Northward range shifts in the Pacific Arctic have already been documented for native fish, zooplankton, and benthic invertebrates (e.g. Grebmeier et al. 2006b, Matsuno et al. 2011, Stabeno et al. 2012, Kotwicki and Lauth 2013). The role of temperature as a limiting factor in northern Europe was shown for Crepidula fornicata

Several studies have suggested that non-native species can persist at a low population size for years and suddenly undergo a boom when conditions become favourable (Witte et al. 2010). In temperate systems, warming ocean temperatures affect the survival (Groner?), growth rates, reproductive output, and phenology of non-native taxa (Stachowicz et al. 2002, Saunders and Metaxas 2007, Valdizan et al. 2011, Lord 2017). ((future climate change)) Warmer winter water temperatures have been linked to the earlier onset of recruitment and increased recruitment of non-native taxa We did not consider possible interactions between temperature, salinity, and water chemistry, and these might be especially important in the context of climate change as melting sea ice in the north is expected?? To lower salinities, and ocean acidification is lowering pH and causing problems for calcareous?? Organisms.

The suitable temperature conditions of the southern Bering Sea are especially concerning considering the high vessel traffic in the region. The Bering Sea receives nearly 50% of all traffic in the Arctic region, and an additional 600 to 900 vessels are expected to navigate the Bering Sea by 2025 (Ellis and Brigham 2009).

As the Arctic becomes an increasingly popular shortcut between the Pacific and Atlantic, the risk of non-native species introductions into the Bering Sea will likely increase. Future expansions of the Arctic for shipping and oil and gas exploration may lead to continued development of plans for establishing industrial scale port facilities in northern ports such as Nome, which currently receives little traffic. Our current models emphasize southeastern Alaska… home to largest U.S. fishery port….. and economic driver of Alaska… Situated at 53.9°N, this port is one of the most southerly ports in the Bering Sea, is ice-free year-round, and experiences relatively warm water temperatures compared to the rest of the Bering Sea.

A study in the contiguous U.S. found that temperature and cargo shipping traffic explained 53% of the variation in non-native species richness in marinas (Lord et al. 2015).

potential papers to cite:

The risk of nonindigenous species invasion in Prince William Sound associated with oil tanker traffic and ballast water management : pilot study / presented to Regional Citzens' Advisory Council of Prince William Sound ; presented by Gregory M. Ruiz and Anson H. Hines.

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**References**

Alvsvåg, J., A. L. Agnalt, and K. E. Jørstad. 2009. Evidence for a permanent establishment of the snow crab (Chionoecetes opilio) in the Barents Sea. Biological Invasions 11:587–595.

Ashton, G. V., E. I. Riedlecker, and G. M. Ruiz. 2008. First non-native crustacean established in coastal waters of Alaska. Aquatic Biology 3:133–137.

Barry, S. C., K. R. Hayes, C. L. Hewitt, H. L. Behrens, E. Dragsund, and S. M. Bakke. 2008. Ballast water risk assessment: principles, processes, and methods. ICES Journal of Marine Science 65:121–131.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26:333–339.

Byrne, M., M. Gall, K. Wolfe, and A. Agüera. 2016. From pole to pole: the potential for the Arctic seastar Asterias amurensis to invade a warming Southern Ocean. Global Change Biology 22:3874–3887.

Carlton, J. T. 1996. Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78:97–106.

Chan, F. T., E. Briski, S. A. Bailey, and H. J. MacIsaac. 2014. Richness–abundance relationships for zooplankton in ballast water: temperate versus Arctic comparisons. ICES Journal of Marine Science 71:1876–1884.

Chan, F. T., H. J. MacIsaac, and S. A. Bailey. 2016. Survival of ship biofouling assemblages during and after voyages to the Canadian Arctic. Marine Biology 163:250.

Chan, F. T., H. J. MacIsaac, S. A. Bailey, and M. Krkošek. 2015. Relative importance of vessel hull fouling and ballast water as transport vectors of nonindigenous species to the Canadian Arctic. Canadian Journal of Fisheries and Aquatic Sciences 72:1230–1242.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biological Invasions 8:1023–1037.

Fetzer, I., and W. E. Arntz. 2008. Reproductive strategies of benthic invertebrates in the Kara Sea (Russian Arctic): Adaptation of reproduction modes to cold water. Marine Ecology Progress Series 356:189–202.

Grebmeier, J. M., L. W. Cooper, H. M. Feder, and B. I. Sirenko. 2006a. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Progress in Oceanography 71:331–361.

Grebmeier, J. M., J. E. Overland, S. E. Moore, E. V Farley, E. C. Carmack, L. W. Cooper, K. E. Frey, J. H. Helle, F. A. McLaughlin, and S. L. McNutt. 2006b. A major ecosystem shift in the Northern Bering Sea. Science 311:1461–1464.

Hermann, A. J., G. A. Gibson, N. A. Bond, E. N. Curchitser, K. Hedstrom, W. Cheng, M. Wang, E. D. Cokelet, P. J. Stabeno, and K. Aydin. 2016. Projected future biophysical states of the Bering Sea. Deep-Sea Research Part II: Topical Studies in Oceanography 134:30–47.

Hermann, A. J., G. A. Gibson, N. A. Bond, E. N. Curchitser, K. Hedstrom, W. Cheng, M. Wang, P. J. Stabeno, L. Eisner, and K. D. Cieciel. 2013. A multivariate analysis of observed and modeled biophysical variability on the Bering Sea shelf: Multidecadal hindcasts (1970-2009) and forecasts (2010-2040). Deep-Sea Research Part II: Topical Studies in Oceanography 94:121–139.

Hewitt, C. L., and K. R. Hayes. 2002. Risk assessment of marine biological invasions. Pages 456–466*in* E. Leppäkoski, S. Gollasch, and S. Olenin, editors.Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Springer Netherlands.

Hines, A. H., G. M. Ruiz, N. G. Hitchcock, and C. E. de Rivera. 2004. Projecting range expansion of invasive European green crabs (Carcinus maenas) to Alaska: temperature and salinity tolerance of larvae. Edgewater, MD.

Huang, X., S. Li, P. Ni, Y. Gao, J. Bei, Z. Zhou, and A. Zhan. 2017. Rapid response to changing environments during biological invasions: DNA methylation perspectives. Molecular Ecology 12:3218–3221.

Kassahn, K. S., R. H. Crozier, H. O. Pörtner, and M. J. Caley. 2009. Animal performance and stress: Responses and tolerance limits at different levels of biological organisation. Biological Reviews 84:277–292.

Kotwicki, S., and R. R. Lauth. 2013. Detecting temporal trends and environmentally-driven changes in the spatial distribution of bottom fishes and crabs on the eastern Bering Sea shelf. Deep-Sea Research Part II: Topical Studies in Oceanography 94:231–243.

Lemke, P., J. Ren, R. B. Alley, I. Allison, J. Carrasco, G. Flato, Y. Fujii, G. Kaser, P. Mote, R. H. Thomas, and T. Zhang. 2007. Observations: Changes in snow, ice and frozen ground. Pages 337–383*in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors.Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Lord, J. P. 2017. Impact of seawater temperature on growth and recruitment of invasive fouling species at the global scale. Marine Ecology 38:1–10.

Lord, J. P., J. M. Calini, and R. B. Whitlatch. 2015. Influence of seawater temperature and shipping on the spread and establishment of marine fouling species. Marine Biology 162:2481–2492.

Matsuno, K., A. Yamaguchi, T. Hirawake, and I. Imai. 2011. Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. Polar Biology 34:1349–1360.

Miller, A. W., and G. M. Ruiz. 2014. Arctic shipping and marine invaders. Nature Climate Change 4:413–416.

Miller, K. B. 2016. Forecasting at the edge of the niche: Didemnum vexillum in Southeast Alaska. Marine Biology 163:1–12.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6:485–492.

Monaco, C. J., and B. Helmuth. 2011. Tipping Points, Thresholds and the Keystone Role of Physiology in Marine Climate Change Research. Page Advances in Marine Biology.

Mueter, F. J., and M. A. Litzow. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecological Applications 18:309–320.

Nakićenović, N., J. Alcamo, G. Davis, B. de Vries, J. Fenhann, S. Gaffin, and K. Gregory. 2000. IPCC Special Report on Emissions Scenarios: A special report of Working Group III of the Intergovernmental Panel on Climate Change. Page Emissions Scenarios. Cambridge University Press, Cambridge, UK.

Pörtner, H. 2001. Climate change and temperature-dependent biogeography: Oxygen limitation of thermal tolerance in animals. Naturwissenschaften 88:137–146.

Powers, S. P., M. A. Bishop, J. H. Grabowski, and C. H. Peterson. 2006. Distribution of the invasive bivalve Mya arenaria L. on intertidal flats of southcentral Alaska. Journal of Sea Research 55:207–216.

Reid, P. C., D. G. Johns, M. Edwards, M. Starr, M. Poulin, and P. Snoeijs. 2007. A biological consequence of reducing Arctic ice cover: Arrival of the Pacific diatom Neodenticula seminae in the North Atlantic for the first time in 800000 years. Global Change Biology 13:1910–1921.

Renaud, P. E., M. K. Sejr, B. A. Bluhm, B. Sirenko, and I. H. Ellingsen. 2015. The future of Arctic benthos: Expansion, invasion, and biodiversity. Progress in Oceanography 139:244–257.

de Rivera, C. E., N. G. Hitchcock, S. J. Teck, B. P. Steves, A. H. Hines, and G. M. Ruiz. 2007. Larval development rate predicts range expansion of an introduced crab. Marine Biology 150:1275–1288.

de Rivera, C. E., B. P. Steves, P. W. Fofonoff, A. H. Hines, and G. M. Ruiz. 2011. Potential for high-latitude marine invasions along western North America. Diversity and Distributions 17:1198–1209.

Ruiz, G. M., J. T. Carlton, E. D. Grosholz, and A. H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. American Zoologist 37:621–632.

Ruiz, G. M., P. W. Fofonoff, and J. T. Carlton. 2015. Invasion history and vector dynamics in coastal marine ecosystems: a North American perspective. Aquatic Ecosystem Health & Management 18:299–311.

Ruiz, G. M., and C. L. Hewitt. 2009. Latitudinal patterns of biological invasions in marine ecosystems: a polar perspective. Pages 347–358*in* I. Krupnik, M. A. Lang, and S. E. Miller, editors.Smithsonian at the Poles: Contributions to International Polar Year Science. Smithsonian Institution Scholarly Press, Washington, DC.

Saunders, M., and A. Metaxas. 2007. Temperature explains settlement patterns of the introduced bryozoan Membranipora membranacea in Nova Scotia, Canada. Marine Ecology Progress Series 344:95–106.

Sorte, C. J. B. 2014. Synergies between climate change and species invasions: Evidence from marine systems. Invasive Species and Global Climate Change:101–116.

Sorte, C. J. B., S. J. Jones, and L. P. Miller. 2011. Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. Journal of Experimental Marine Biology and Ecology 400:209–217.

Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57:573–583.

Stabeno, P. J., N. A. Bond, and S. A. Salo. 2007. On the recent warming of the southeastern Bering Sea shelf. Deep-Sea Research Part II: Topical Studies in Oceanography 54:2599–2618.

Stabeno, P. J., N. B. Kachel, S. E. Moore, J. M. Napp, M. Sigler, A. Yamaguchi, and A. N. Zerbini. 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep-Sea Research Part II: Topical Studies in Oceanography 65:31–45.

Stabeno, P. J., J. D. Schumacher, and K. Ohtani. 1999. The physical oceanography of the Bering Sea. Pages 1–28*in* T. R. Loughlin and K. Ohtani, editors.Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, AK.

Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the United States of America 99:15497–500.

Stroeve, J. C., M. C. Serreze, M. M. Holland, J. E. Kay, J. Malanik, and A. P. Barrett. 2012. The Arctic’s rapidly shrinking sea ice cover: A research synthesis. Climatic Change 110:1005–1027.

Valdizan, A., P. G. Beninger, P. Decottignies, M. Chantrel, and B. Cognie. 2011. Evidence that rising coastal seawater temperatures increase reproductive output of the invasive gastropod Crepidula fornicata. Marine Ecology Progress Series 438:153–165.

Verling, E., G. M. Ruiz, L. D. Smith, B. Galil, A. W. Miller, and K. R. Murphy. 2005. Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. Proceedings of the Royal Society B: Biological Sciences 272:1249–1257.

Verna, D., B. Harris, K. Holzer, and M. Minton. 2016. Ballast-borne marine invasive species: exploring the risk to coastal Alaska, USA. Management of Biological Invasions 7:199–211.

Wang, M., J. E. Overland, and N. A. Bond. 2010. Climate projections for selected large marine ecosystems. Journal of Marine Systems 79:258–266.

Wang, M., J. E. Overland, and P. Stabeno. 2012. Future climate of the Bering and Chukchi Seas projected by global climate models. Deep-Sea Research Part II: Topical Studies in Oceanography 65–70:46–57.

Ware, C., J. Berge, A. Jelmert, S. M. Olsen, L. Pellissier, M. Wisz, D. Kriticos, G. Semenov, S. Kwaśniewski, and I. G. Alsos. 2016. Biological introduction risks from shipping in a warming Arctic. Journal of Applied Ecology 53:340–349.

Ware, C., J. Berge, J. H. Sundet, J. B. Kirkpatrick, A. D. M. Coutts, A. Jelmert, S. M. Olsen, O. Floerl, M. S. Wisz, and I. G. Alsos. 2014. Climate change, non-indigenous species and shipping: assessing the risk of species introduction to a high-Arctic archipelago. Diversity and Distributions 20:10–19.

Watson, J. T., and A. C. Haynie. 2016. Using vessel monitoring system data to identify and characterize trips made by fishing vessels in the United States North Pacific. PLoS ONE 11:1–20.

Witte, S., C. Buschbaum, J. E. E. van Beusekom, and K. Reise. 2010. Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? Biological Invasions 12:3579–3589.

Wyllie-Echeverria, T., and W. S. Wooster. 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fisheries Oceanography 7:159–170.

# extra References

Ashton, G., Davidson, I., and Ruiz, G. [2014]. Transient small boats as a long-distance coastal vector for dispersal of biofouling organisms. Estuaries and Coasts 37(6): 1572–1581. https://doi.org/10.1007/s12237-014-9782-9

Floerl, O., Inglis, G.J., Dey, K., and Smith, A. [2009]. The importance of transport hubs in stepping-stone invasions. Journal of Applied Ecology 46(1): 37–45. https://doi.org/10.1111/j.1365-2664.2008.01540.x

Fofonoff, P.W., G.M. Ruiz, B. Steves, C. Simkanin, and J.T. Carlton. 2003. National Exotic Marine and Estuarine Species Information System (NEMESIS). Available online: http://invasions.si.edu/nemesis/

Fuller, P.F., and A.J. Benson. 2013. Nonindigenous Aquatic Species Database (NAS). Available online: https://nas.er.usgs.gov/

Gu, Z. (2014) circlize implements and enhances circular visualization in R. Bioinformatics. DOI: [10.1093/bioinformatics/btu393](https://doi.org/10.1093/bioinformatics/btu393)

National Ballast Information Clearinghouse 2017. NBIC Online Database. Electronic publication, Smithsonian Environmental Research Center & United States Coast Guard. Available from http://invasions.si.edu/nbic/search.html; searched 27 July 2017.

Pinsky, M. L., and Fogarty, M. (2012) Lagged social-ecological responses to climate and range shifts in fisheries. Climatic Change 115: 883–891.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Wasson, K., Zabin, C.J., Bedinger, L., Cristina Diaz, M., and Pearse, J.S. [2001]. Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biological Conservation 102(2): 143–153. https://doi.org/10.1016/S0006-3207(01)00098-2

Whitehouse, A., and S. Zador. (2016). Preliminary assessment of the Alaska Arctic. In: Zador, S., and Siddon, E, eds.. Ecosystem Considerations 2016: Status of the Eastern Bering Sea Marine Ecosystem, Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council, Anchorage, AK.

Table 1. Change in the number of species and percent area projected to have year-round suitable habitat for non-native marine species (42 assessed) between current (2003-2012) and mid-century (2030-2039).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Model** | **Current species count** | **Mid-century species count** | **Habitat gained** | **Habitat lost** |
| CGCM3-t47 | 35 | 36 | 59.88% | 6.70% |
| ECHO-G | 33 | 33 | 36.78% | 6.17% |
| MIROC3.2 | 34 | 35 | 52.52% | 3.65% |

Table 2. Average number of weeks of consecutive reproductive habitat for the three ROMS models and two study periods. We assessed suitable habitat for 29 species using species-specific, published temperature and salinity thresholds required for growth and reproduction. Prior to calculations, we excluded species that could not reproduce in our study area (number of weeks = 0) and two “outliers” that were able to reproduce nearly year-round (number of weeks ≥ 49). Maximum projected temperature values for the Bering Sea, up to 40m depth, are listed.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Study Period** | **Model** | **Consecutive weeks** (mean ± SD) | **Number of species** | **Maximum temperature** (°C) |
| Current  (2003-2013) | CGCM3-t47 | 9.19 ± 8.19 | 21 | 16.26 |
| ECHO-G | 5.60 ± 6.90 | 22 | 16.95 |
| MIROC3.2 | 6.72 ± 6.36 | 20 | 16.28 |
| Future  (2030-2039) | CGCM3-t47 | 9.40 ± 9.31 | 23 | 16.64 |
| ECHO-G | 6.21 ± 7.02 | 22 | 17.15 |
| MIROC3.2 | 8.53 ± 6.94 | 24 | 18.62 |

**Figures**

Note: Figures 1 and 2 should have all (or some?) Bering Sea ports on the maps to help readers place the network plot results from Jordan’s figure. If it’s too cluttered, we can create a simple reference map to go along with the network plots.

Figure 1: Study area map with all place names and U.S. ports.

Figure 2. **Ensemble mean for year-round survival.** Number of species with year-round habitat suitability under a) current (2003-2012) and b) future (2030-2039) climate conditions, averaged across the 3 ROMS we analysed (CGCM3-t47, ECHO-G, and MIROC 3.2).

Figure 3. **Number of taxa with survival as a function of latitude + weeks (heat map).**

Figure 4. **Average number of consecutive weeks of reproduction by temperature threshold**. Based on taxa tolerances, averaged across models or separate out? Current is probably most interesting & I don’t think things change drastically?? With future but should double-check. See below for an example.

Figure 6. Commercial + fishing vessel chord diagrams (2 figures).

Supplementary:

-ballast water discharge



Figure 5. **Average number of consecutive weeks of reproduction by temperature threshold**.



Figure newX2. Illustration of vessel transit origins (below dashed line) outside of the Bering Sea and their Bering Sea destination (bold text, above dashed line), 2014 - 2016. Numbers in parentheses indicate numbers of records for a given port. (Top) Data from arrival records in the National Ballast Information Clearinghouse. “Other” includes ports with ≤ 5 transits. (Bottom) Fishing vessel data from vessel monitoring systems. Connections with fewer than three vessels have been excluded to retain confidentiality.



Figure XXBallast. Amounts of ballast water (mt) transported to the Bering Sea (bolded ports, above dashed line) and their regions of origin (unbolded text, below dashed line). Numbers in parentheses show total volumes per region. Figure excludes ballast water exchanges not reported by a specific port / country (e.g., open ocean exchanges), totaling ~80% of reported ballast water exchange. Data from the National Ballast Information Clearinghouse.

1. Discharge reports that did not include valid source locations were omitted from the analyses. [↑](#footnote-ref-1)