# Title: What limits bioinvasions in the Arctic? Using predictive habitat models to investigate the role of cold water temperature on survival and reproduction … in the Bering Sea Investigating vessel traffic and the role of cold water temperatures on the survival and reproduction of non-native taxa in the Bering Sea

**Authors:** A. Droghini1, A. Fischbach2, J. Watson3, J.P. Reimer1

**Affiliations:** 1. Alaska Center for Conservation Science, University of Alaska Anchorage, 2400 W Campus Drive, Anchorage, AK 99508. 2. U.S. Geological Service, Alaska Science Center, Walrus Research Program, 4210 University Drive, Anchorage, AK 99508. 3. NOAA Alaska Fisheries Science Center, Auke Bay Laboratories, Ted Stevens Marine Research Institute, 17109 Pt. Lena Loop Rd., Juneau, AK 99801

**Corresponding author:** A. Droghini, adroghini@alaska.edu

# 

# 

# Abstract

Cold water temperatures and minimal shipping traffic are expected to limit biological introductions to polar ecosystems. However, these expectations have rarely been evaluated across multiple taxa and life stages. We examined the role of water temperature and salinity on the potential survival and reproductive habitat of 42 non-indigenous species (NIS) in the Bering Sea, a marine ecosystem characterized by a strong, subarctic-arctic latitudinal gradient. We built predictive habitat suitability models by comparing species-specific temperature and salinity thresholds to conditions in the Bering Sea as projected by three regional ocean models. We investigated the effects of climate change on suitability by generating and comparing models from two time periods: current (2003-2012) and mid-century (2030-2039). Lastly, we describe traffic and ballast water discharge from commercial and fishing vessels entering U.S. Bering Sea ports. Our models suggest that cold water may explain the lack of invasive species in areas where sea ice is seasonally present (i.e. north of 58°N). However, the southeastern Bering Sea was predicted to be highly suitable for the year-round survival of 83% of the taxa assessed (*n*=42). Suitable reproductive habitat also exist for many of the taxa considered, though the short summer season may limit species that require temperatures above 10ºC for development. Predicted warming of water temperatures is expected to lead to a major northward expansion of suitable habitat, largely favoring taxa that already have the ability to survive year-round. Analysis of vessel traffic and ballast water discharge reveal a network of continental and international traffic centered around the port of Dutch Harbor. Dutch Harbor also serves as a regional hub to local ports throughout the Bering Sea. These findings are particularly important given that areas predicted to support the highest number of NIS are also the most likely points of introduction. The southeastern Bering Sea, and the port of Dutch Harbor in particular, are high-risk areas for biological introductions and should be monitored.

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

# Introduction

In today’s warming, hyper-connected oceans, non-indigenous species (NIS) are expanding their range at an exhilarating pace (Seebens et al. 2017). Ships are the main vectors by which NIS are transported to new regions (Ruiz et al. 1997, Molnar et al. 2008); as a result, ports with high vessel traffic often have more NIS than ports that receive little traffic (Seebens et al. 2013, Lord et al. 2015). Although this relationship is not without its complexities (Verling et al. 2005), high rates of introductions, either in terms of introduction events or organism numbers, increase the probability of NIS arriving and establishing in new regions (Verling et al. 2005, Colautti et al. 2006, Floerl et al. 2009). The survival and establishment of NIS are also strongly determined by their ability to tolerate the water temperatures and salinity they encounter, both during the voyage and at the port of arrival. Water temperatures and salinities above or below optimal thresholds negatively affect behavioral, metabolic, and cellular processes, and when temperatures exceed a critical threshold, mortality ensues (Pörtner 2001, Kassahn et al. 2009). Even those species that can survive may not be able to establish a self-sustaining population, as reproduction, development, and growth often have narrower optimal ranges than survival (Woodin et al. 2013). The importance of these factors in dictating NIS establishment is expected to be greatest when there is a large difference between environmental conditions at the port of arrival and at the port of origin, such as marine NIS being transported to freshwater ports, or warm-temperate species making their way to the Arctic (Herborg et al. 2007, Iacarella et al. 2015).

Arctic oceans are very different from most other marine ecoregions because they receive very little vessel traffic and have cold water temperatures nearly year-round. Low vessel traffic and cold temperatures have been proposed to explain the low rates of introductions known from the Arctic, but few studies have explored whether these factors actually are severe enough to limit the transport, survival, and establishment of NIS. While the Arctic does have relatively low levels of vessel traffic, studies have shown that NIS are being transported from temperate regions to Arctic ports in ballast water and on wetted surfaces (“biofouling”), and are surviving the voyage (Chan et al. 2014, 2016, Ware et al. 2016). Most studies have focused on the potential for introductions from ballast water, which is transported by large vessels such as those involved with commercial, military, tourism, or research activities (but see Chan et al. 2016), However, the risk posed by biofouling, which, as opposed to ballast water, is present for both small and large vessels, may exceed the risk posed by ballast water (Chan et al. 2015). It is unclear whether NIS can establish self-sustaining populations in Arctic waters once (or assuming) they have been successfully transported. Because most NIS originate from temperate regions (cite), they may lack the ability to survive or reproduce in cold temperatures. Studies have typically focused on a very small subset of the total species that may be introduced to Arctic regions (de Rivera et al. 2011, Ware et al. 2016, Goldsmit et al. 2018). These studies have concluded that potentially suitable habitat exists for at least some NIS, but have come to different conclusions about whether suitable habitat is extensive (de Rivera et al. 2011) or limited (Ware et al. 2016, Goldsmit et al. 2018). Only one study (Ware et al. 2016) has modeled whether habitat was suitable for reproduction, which is essential to determine whether species can establish self-sustaining populations.

Understanding the factors that limit invasions in the Arctic is becoming increasingly urgent given the rapid oceanographic and socioeconomic changes that these polar systems are experiencing. Shipping traffic to the Arctic has increased exponentially since the beginning of the 21st century, spurred in part by declining sea ice extent and lengthening of ice-free season (Miller and Ruiz 2014, Eguíluz et al. 2016). This expansion of shipping activity is expected to increase the number and diversity of organisms that are being transported to Arctic regions. In addition, the climate itself is becoming warmer, and perhaps more hospitable for species originating in temperate and tropical systems. The Arctic is experiencing record-setting declines in sea ice thickness and extent, and surface air temperatures are increasing 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 northern range expansions and introductions (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).

Given the potential for impacts to fisheries, local livelihoods, and native ecosystems, risk assessments that reveal which areas are most at risk of invasion, and which NIS pose the biggest threat, are becoming essential components of aquatic ecosystem management (Mandrak and Cudmore 2015). In this paper, we explore whether cold water temperatures have the potential to limit introductions in the Arctic by examining whether the physiological thresholds of NIS would allow them to establish in the Bering Sea, a high-latitude marine ecosystem characterized by a strong, latitudinal gradient. We characterize whether suitable habitat existed for year-round survival, weekly survival, and reproduction of NIS under current and mid-century conditions. We also quantify vessel traffic and ballast water discharge for U.S. ports in the Bering Sea to identify potential entry points of NIS, and to consider the intersection between areas of high 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 water temperatures are expected to increase, we predicted that habitat would become more suitable for NIS in the future. We hope that our evaluation of the spatial and temporal components of invasion risk can be used to inform future research and management efforts in this and other polar ecosystems.

# Methods

## Study area

The Bering Sea lies between the temperate North Pacific Ocean and the arctic waters of the Chukchi Sea. This large, dynamic ecosystem spans 14 degrees of latitude and extends more than 1,500 kilometers from Alaska (USA) to Russia (Figure 1). It is comprised of a deep-water basin, an extensive eastern continental shelf, and a narrow western shelf (Figure 1). The Bering Sea’s eastern shelf boasts some of the highest level of marine productivity in the world, supporting a US $1 billion commercial fishery that provides the U.S. with 50% of its wild-caught seafood. The Bering Sea is also a hub for international and regional shipping traffic (McGee et al. 2006). To date, only four NIS 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).

## Defining taxa-specific tolerances

As part of a larger risk assessment project (Reimer et al. 2017), we compiled temperature (T) and salinity (S) thresholds for NIS that currently occur in the Bering Sea or 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 (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 euhaline or euryhaline species with a minimum survival salinity tolerance ≥30 parts per trillion (ppt). 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. 2017).

We found taxa-specific T-S survival tolerances for 42 NIS (Appendix A) and T-S reproductive tolerances for 29 NIS (Appendix B). We prioritized T-S thresholds from experimental or field-based studies, but used data inferred from geographic distribution 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. Survival thresholds were therefore defined as the absolute minimum and maximum values reported for that taxon, irrespective of life stage and geography. In contrast, reproductive 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

We compared taxa’s T-S thresholds to T-S values of the Bering Sea, which 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, which were chosen for their ability to accurately predict observed conditions in the Bering Sea and the northeastern Pacific (Wang et al. 2010, Hermann et al. 2016). 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 depths up to 40 m, and summarized the depth dimension for each pixel into a single value by taking the maximum T-S values.

Projections 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. Projections 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).

## Modeling habitat suitability

Our habitat suitability analyses evaluated each taxon and sought to answer three questions: 1) can the taxon survive in the Bering Sea year-round? (“Year-round Survival”); 2) if not, for how many weeks of the year can it survive? (“Weekly Survival”); and 3) how many weeks of the year have conditions that are suitable for reproduction and development? (“Reproduction Suitability”). We developed specific 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. We restricted our analyses to the continental shelves (depths < 200 meters) because most NIS invade near-shore habitats (Ruiz et al. 2015). Habitat suitability was analyzed separately for each ROMS and study period. Results for each study period were summarized across taxa and averaged across all three ROMS. All analyses were conducted in R version 3.3.2 (R Core Team 2015) 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 change in suitable habitat by subtracting our mid-century raster from our current raster. All numbers greater than zero were reclassified as +1, while all numbers less than zero were reclassified as -1. Increase in suitable area was calculated by dividing the number of positive (+1) pixels by the total number of pixels in our study area. Decrease in suitable area was similarly calculated.

### 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 × 42 taxa).

### Reproduction 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 2015).

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 (33 CFR §§ 151). Because regulations have changed in the last decade, especially with respect to mandatory reporting by crude oil tankers (Verna and Harris 2016), we only considered the three most recent, complete years (2014-2016). We queried Ship Arrival Records and Ballast Tank Records from the NBIC data portal for any vessel arriving in Alaska from 01 January 2014 to 31 December 2016. 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”. Records without a port name were removed (*n*=13).

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. 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

When averaged across the three ROMS, minimum (winter) water temperatures ranged from -2.6°C to +4.2°C for the 2003-2012 time period, and maximum (summer) temperatures ranged from +3.77°C to +16.27°C. Mid-century (2030-2039) models predicted minimum water temperatures between -2.5°C and +4.8°C, and maximum temperatures between 5.42°C and 18.62°C (see also Hermann et al. 2016). Meanwhile, minimum survival temperatures of NIS ranged from -10°C to +10°C (Appendix A). Nineteen of the 42 taxa we assessed (45%) had estimated minimum survival thresholds below 0°C, and 13 had minimum survival thresholds ≥1°C (Appendix A).

## Year-round Survival

Of the 42 taxa we assessed, 34 were predicted to have suitable year-round conditions in at least one pixel in the Bering Sea (Figure 2). Our models predict that the southeastern Bering Sea, including the coastlines of the Aleutian Islands and most of the Alaska Peninsula, can support the highest number of NIS (Figure 2). The northern Bering Sea (above 58°N) is unsuitable for most NIS (Figure 2). By 2039, one additional NIS is expected to be able to survive year-round, and 76.6% of the Bering Sea shelf is predicted to switch from unsuitable to suitable for at least one NIS. In general, suitable habitat is expected to expand northward from the southeastern Bering Sea, as well as eastward into Bristol Bay (Figure 2). Only 7.5% of the modeled pixels are expected to switch from suitable to unsuitable habitat.

## Weekly Survival

\*\*Need to flesh out weekly results\*\* 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 3). 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 3).

## Reproduction

Reproductive tolerances were available for 29 NIS. Under current conditions, the Bering Sea continental shelf is predicted to support anywhere from 0 to 20 taxa (median=7.33 taxa per pixel). Most areas of high NIS richness are in the southern Bering Sea, and include the Aleutian Islands, the Alaska Peninsula, the Commander Islands, and the Kamchatka Peninsula. Maximum NIS richness is also predicted along the southern Seward Peninsula and in Norton Sound (64°N; Supplementary Figure 1). Taxa that can reproduce in marine salinities (≥31 ppt) at 4°C had nearly year-round suitable reproductive habitat (Figure 4). However, number of consecutive weeks of suitable habitat declined exponentially with temperature thresholds (Figure 4). Marine taxa that required minimum temperatures of 12°C had fewer than six consecutive weeks, and species requiring minimum temperatures >14°C had less than one week (when averaged across models; Figure 4). Five taxa had no suitable habitat anywhere on the Bering Sea shelf (Figure 4); this includes three species that require fresh or brackish water for reproduction.

By 2039, the maximum number of taxa that can reproduce in the Bering Sea is expected to increase by one, and suitable habitat is expected to increase across taxa (median=8.33 taxa per pixel). The number of weeks suitable for reproduction is also expected to increase (Figure 4), though taxa with minimum reproductive thresholds ≥14°C are still predicted to have less than 2.5 weeks of suitable temperatures (Figure 4).

## Vessel traffic

From 2014 to 2016, the NBIC data reported a total of 816 arrival records and 15,837 ballast water discharge reports in U.S. Bering Sea ports[[1]](#footnote-1) from trips originating outside of the Bering Sea. 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 (Figure 5). 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 (Supplementary Figure 2).

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). While ports in the eastern Pacific Ocean accounted for more trips, most ballast water released in the Bering Sea originated from Asian ports (Supplementary Figure 2). 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 Arctic has few reported non-indigenous species (NIS), our results indicate that (1) potential NIS habitat currently exists in the Bering Sea; (2) this habitat is projected to expand by mid-century due to warming ocean conditions; and (3) mechanisms for NIS transport into and throughout the Bering Sea exist. Suitable temperature and salinity conditions exist for a large number of taxa we considered and for both survival and reproduction life stages. We found some evidence to suggest that cold water temperatures may limit introductions in arctic regions that are seasonally covered by ice. However, our results challenge the expectation that high-latitude marine ecosystems have low risk due to temperature limitations, as subarctic regions were suitable for a large number of temperate taxa. Warming ocean temperatures as a result of climate change will likely increase the area of suitable habitat northward. Importantly, our analyses revealed that areas of high habitat suitability were also areas that received the highest number of commercial and fishing vessels, and therefore areas where organisms are most likely to be introduced.

## The role of cold water temperature on survival

Of the 42 taxa we considered, most (*n*=34) had suitable habitat for year-round survival in at least parts of the Bering Sea. Our findings are similar to those of de Rivera et al. (2011), who found that he Bering Sea was highly suitable for survival of four NIS. However, by considering a much larger pool of NIS, we revealed some interesting, community-level patterns. Potential NIS richness followed a latitudinal gradient, with high richness in the southern Bering Sea shelf, and a sharp decrease above 58ºN (Figure 2). Our results suggest that the lack of suitable habitat in arctic regions may be driven by species’ inability to tolerate cold temperatures. For one, all taxa were predicted to have suitable survival habitat from early July to mid-August, when water temperatures were warmest, but taxa without year-round survival habitat were unable to survive from December to April, when water temperatures are coldest. The northward decline in potential NIS richness is also coincident with the limit of seasonal sea ice extent in the Bering Sea (Grebmeier et al. 2006b, Stabeno et al. 2012). The southeastern Bering Sea is largely ice-free, though sea ice can form along the northern Alaska Peninsula during very cold winters (Stabeno et al. 2012). Meanwhile, the northern Bering Sea is strongly influenced by the presence of sea ice; consequently, its hydrology and biodiversity are more akin to the Arctic Ocean than they are to the southern Bering Sea (Grebmeier et al. 2006a, Mueter and Litzow 2008).

## Reproduction: Is there enough time?

Very few studies have modeled whether reproductive habitat for NIS exists in Arctic regions, even though in many cases successful sexual reproduction is a key component of NIS establishment. Of the taxa we evaluated, most had at least one week of suitable reproductive habitat. In contrast to our year-round survival models, Norton Sound (~64°C) was predicted to support the greatest number of NIS during the summer months (Supplementary Figure 1). Waters in Norton Sound are very shallow, creating a thermal hotspot in the Bering Sea (Ladd and Overland 2009, Hermann et al. 2016). It is difficult to determine whether taxa would have enough time to brood their eggs or develop into juveniles within the Bering Sea’s short summer season, especially when considering that cold temperatures may increase time to development (e.g. de Rivera et al. 2007). Interestingly, the two NIS that are currently established in the Bering Sea (*Caprella mutica* and *Mya arenaria*), required the lowest minimum reproductive temperatures (4°C) of all the species we assessed, and were the two outliers in our dataset that had nearly year-round reproductive habitat (>51 consecutive weeks). In contrast, taxa that require salinities ≤30 ppt or temperatures ≥14°C for reproduction or development are predicted to have very few weeks of suitable reproductive habitat (Figure 4). However, to fully understand the reproduction capacity of NIS in new regions or under climate change conditions, more experimental studies are needed to determine development rates of NIS under different temperature conditions, and examine the various facets of reproduction, as asexual reproduction, fertilization, brooding, and development stages may all require different temperature thresholds (Westerman et al. 2009).

Multi-species risk assessments inevitably entail a trade-off between ecological realism and the number of taxa considered, and successfully surmounting the stages of invasion (i.e. transport, introduction, and establishment) is more nuanced than the metrics we included. While we recognize that an organism’s survival and establishment is influenced by a suite of biotic factors and abiotic factors, our intention was not to determine whether a species could invade, but rather if water temperature would cause failure – for, while many factors work together to determine whether a species can survive and reproduce in an area, only one factor is needed to cause failure (Blackburn et al. 2011). 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, especially with regards to phenotypic plasticity (Sorte et al. 2011, Huang et al. 2017), and the potential for interactions and non-linear responses, all of which may be especially important at the tail-end of species’ thermal response curves (Monaco and Helmuth 2011, Sorte 2014, Miller 2016). Given the resolution of the climate models we used, our habitat models may underestimate summer water temperatures near the coastlines and in shallow waters < 10 m deep. In addition, the ROMS we used do not account for the influence of local dynamics such as ice scour and freshwater warming, which may affect species’ distribution and persistence (Fetzer and Arntz 2008, Miller 2016). While the ROMS do include a coarse estimate of freshwater runoff, it does not account for the warming of shallow, coastal waters caused by river discharge. The influence of rivers is significant in our study area given the many large rivers that drain into the Bering Sea (e.g. the Yukon, Kuskokwim, and Nushagak rivers), and measurements from finer scale models have recorded temperatures as high as 19°C near the Yukon River (from MODIS; <https://neo.sci.gsfc.nasa.gov/>), whereas our models never predicted temperatures above 16.3°C. However, the warming effects of these rivers, while not fully captured by the ROMS, do not last for more than a few weeks, and do negate our results for year-round survival.

## Effects of climate change on invasion risk

Increased water temperatures are predicted to allow between 1-2 species to survive in the Bering Sea by 2039, however for the most part the expansion of suitable habitat we observed would largely favor taxa that already have the capacity to survive in the southern Bering Sea. Our models agree with other Arctic studies (de Rivera et al. 2011, Ware et al. 2016, Goldsmit et al. 2018) that predict a northward expansion in suitable habitat (Supplementary Figure 1). Northward range shifts have already been documented in the Pacific Arctic 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).

According to our models, an average increase of 1°C or less in minimum winter temperatures was associated with a 76% increase in suitable area. Changes in summer temperatures are expected to be even more pronounced than increases in winter temperatures, with increases as high +5.0°C predicted in Bristol Bay. Studies from temperate systems have found that warmer water temperatures have a positive influence on growth rates (de Rivera et al. 2007), local abundance (Saunders and Metaxas 2007, Witte et al. 2010), fecundity (Valdizan et al. 2011, Dijkstra et al. 2017), and onset of recruitment (Stachowicz et al. 2002, Valdizan et al. 2011). Given the interplay between water temperatures and reproductive success, the Bering Sea is likely to become increasingly suitable for NIS in the near future. From our analyses, it appears that prominent invaders such as *Botrylloides violaceus* and *Carcinus maenas* either do not have suitable temperatures or do not have enough time to complete development, despite having the capacity to live year-round across moderately large areas of the shelf (de Rivera et al. 2007, Westerman et al. 2009). The European green crab in particular is an interesting example, as knowledge of its developmental requirements suggest that temperatures in the southern Bering Sea are at the limit of its thermal tolerances (de Rivera et al. 2007). Climate change is likely to shift habitat in the Bering Sea from marginal to moderately suitable, and lessen the role of temperature on preventing or greatly limiting establishment .

## Vessel traffic

Commercial and fishing vessel traffic, as well as ballast water discharge, point to the port of Dutch Harbor as being by far the most visited port in the Bering Sea. Traffic to Dutch Harbor was up to two orders of magnitude more than traffic to other ports, and trips ending in Dutch Harbor originated from more than ten countries from around the world. Compared to ballast water data, fishing vessel traffic was highly regional, connecting the port of Dutch Harbor to ports of the Pribilof Islands, Bristol Bay, and Akutan. Dutch Harbor has long been recognized as a potentially important point of entry for non-native species (McGee et al. 2006, Verna et al. 2016), and is the largest fisheries port in the U.S. However, traffic from smaller fishing vessels, which may not take up ballast water but may still transport fouling organisms, has not been considered previously, even though fouling may be a larger contributor of propagules than ballast water (Chan et al. 2015). The high traffic and high connectivity of the port of Dutch Harbor emphasize its importance as a regional transport hub, with the potential to transport fouling NIS to remote communities across the Bering Sea (Floerl et al. 2009, Ashton et al. 2014).

We assumed that high-traffic ports are more susceptible to receiving NIS than low-traffic ports, and that shipping traffic and ballast water discharge are adequate proxies of propagule pressure. 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 such as its physiological condition, the voyage duration, a the type and speed of the ship, and environmental differences between donor and recipient ports (Ruiz et al. 2000, Verling et al. 2005, Chan et al. 2014). Studies from the Canadian Arctic suggest that both planktonic and fouling organisms have low survivorship during transport (Chan et al. 2014, 2016), and that survivorship was inversely related to the length of the voyage (Chan et al. 2014). Thus, while Dutch Harbor is considered to be at “medium risk” of invasion in terms of discharged water volumes, the relatively long residence time of the ballast water discharged in Dutch Harbor is likely to reduce invasion risk (Verna et al. 2016). 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. As well, there is a need to consider the projected increase of Arctic shipping traffic. 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.

# Conclusion

Our work significantly extends previous research by providing a comprehensive assessment of the role of temperature on high-latitude invasions based on an understanding of NIS physiological tolerances and modeled ocean conditions. It also addresses an important knowledge gap in Pacific Arctic research, a region of high productivity and high economic importance. Our findings suggest that cold water temperatures currently limit the establishment of NIS in the northern Bering Sea, but emphasize the susceptibility of the southeastern Bering Sea, whose relatively warmer water temperatures are suitable for the year-round survival and reproduction for a large number of taxa. The suitable temperature conditions of the southern Bering Sea are especially concerning given the high vessel traffic in the region, notably to and from the port of Dutch Harbor. Considering the speed at which the oceanographic and socioeconomic context is changing in the Bering Sea, there is a need to fund a continuous monitoring program in the region. The Bering Sea is an excellent candidate for prevention and early detection given the very low numbers of biological introductions that have been reported in the region.

# Acknowledgements

Funding for this project was made available by the North Pacific Research Board (project #1532) and the Aleutian and Bering Sea Islands Landscape Conservation Cooperative. Tracey Gotthardt and Aaron Poe were involved with spearheading the project. Casey Greenstein, Lindsey Flagstad, Bonnie Bernard, Jaime Weltfelt, and Curtis Whisman contributed to the development of the ranking system and the species status reports. J.W. thanks Jen Karnak of Marine Exchange of Alaska, who assisted with vessel identification. A.F. thanks Rob Bochenek and Dr. William Koeppen of Axiom Data Science for assistance extracting the ROMS data. A.D. thanks Marcus Geist for his GIS wizarding, and Dr. Al Hermann for insightful conversations about the ROMS. Additional thanks goes to Dr. Matt Carlson for initial feedback on this manuscript.

**References**

Ashton, G., I. Davidson, and G. M. Ruiz. 2014. Transient small boats as a long-distance coastal vector for dispersal of biofouling organisms. Estuaries and Coasts 37:1572–1581.

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.

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.

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.

Dijkstra, J. A., E. L. Westerman, and L. G. Harris. 2017. Elevated seasonal temperatures eliminate thermal barriers of reproduction of a dominant invasive species: A community state change for northern communities? Diversity and Distributions 23:1182–1192.

Eguíluz, V. M., J. Fernández-Gracia, X. Irigoien, and C. M. Duarte. 2016. A quantitative assessment of Arctic shipping in 2010-2014. Scientific Reports 6:3–8.

Fetzer, I., and W. 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.

Floerl, O., G. J. Inglis, K. Dey, and A. Smith. 2009. The importance of transport hubs in stepping-stone invasions. Journal of Applied Ecology 46:37–45.

Fofonoff, P. W., G. M. Ruiz, B. Steves, C. Simkanin, and J. T. Carlton. 2003. National Exotic Marine and Estuarine Species Information System (NEMESIS).

Fuller, P. F., and A. J. Benson. 2013. Nonindigenous Aquatic Species Database (NAS).

Goldsmit, J., P. Archambault, G. Chust, E. Villarino, G. Liu, J. V. Lukovich, D. G. Barber, and K. L. Howland. 2018. Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic. Biological Invasions 20:501–517.

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.

Herborg, L.-M., C. L. Jerde, D. M. Lodge, G. M. Ruiz, and H. J. MacIsaac. 2007. Predicting Invasion Risk Using Measures of Introduction Effort and Environmental Niche Models 17:663–674.

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.

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.

Iacarella, J. C., J. T. A. Dick, M. E. Alexander, and A. Ricciardi. 2015. Ecological impacts of invasive alien species along temperature gradients : testing the role of environmental matching. Ecological Applications 25:706–716.

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.

Ladd, C., and J. E. Overland. 2009. Retrospective analysis of sea surface temperature in the northern Bering and Chukchi seas. NOAA Technical Memorandum OAR PMEL-145. Seattle, WA.

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., 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.

Mandrak, N. E., and B. Cudmore. 2015. Risk assessment: Cornerstone of an aquatic invasive species program. Aquatic Ecosystem Health and Management 18:312–320.

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.

McGee, S., R. Piorkowski, and G. Ruiz. 2006. Analysis of recent vessel arrivals and ballast water discharge in Alaska: Toward assessing ship-mediated invasion risk. Marine Pollution Bulletin 52:1634–1645.

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. O. 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.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

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.

Reimer, J. P., A. Droghini, A. Fischbach, J. T. Watson, B. Bernard, and A. Poe. 2017. Assessing the risk of non-native marine species in the Bering Sea. Anchorage, AK.

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., P. W. Fofonoff, J. T. Carlton, M. J. Wonham, and A. H. Hines. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics 31:481–531.

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.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. Winter, M. Arianoutsou, S. Bacher, B. Blasius, G. Brundu, C. Capinha, L. Celesti-Grapow, W. Dawson, S. Dullinger, N. Fuentes, H. Jäger, J. Kartesz, M. Kenis, H. Kreft, I. Kühn, B. Lenzner, A. Liebhold, A. Mosena, D. Moser, M. Nishino, D. Pearman, J. Pergl, W. Rabitsch, J. Rojas-Sandoval, A. Roques, S. Rorke, S. Rossinelli, H. E. Roy, R. Scalera, S. Schindler, K. Štajerová, B. Tokarska-Guzik, M. van Kleunen, K. Walker, P. Weigelt, T. Yamanaka, and F. Essl. 2017. No saturation in the accumulation of alien species worldwide. Nature Communications 8:14435.

Seebens, H., M. T. Gastner, and B. Blasius. 2013. The risk of marine bioinvasion caused by global shipping. Ecology Letters 16:782–790.

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. 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.

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. E., and B. P. Harris. 2016. Review of ballast water management policy and associated implications for Alaska. Marine Policy 70:13–21.

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.

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.

Westerman, E. L., R. Whitlatch, J. A. Dijkstra, and L. G. Harris. 2009. Variation in brooding period masks similarities in response to changing temperatures. Marine Ecology Progress Series 391:13–19.

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.

Woodin, S. A., T. J. Hilbish, B. Helmuth, S. J. Jones, and D. S. Wethey. 2013. Climate change, species distribution models, and physiological performance metrics: Predicting when biogeographic models are likely to fail. Ecology and Evolution 3:3334–3346.

# extra References

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.

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

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

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 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**

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 5. Commercial (a) + fishing vessel chord diagrams (b).

Supplementary Figure 1: same as figure 2 but for reproduction

Supplementary Figure 2: ballast water discharge



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)