# Title: Limits to bioinvasions in the Bering Sea: Predicting suitable conditions from regional ocean models

**Running title:** Limits to bioinvasions in the Bering Sea

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# Abstract

Cold water temperatures and minimal vessel traffic are expected to limit biological introductions to polar ecosystems; however, to date, these expectations have not been comprehensively evaluated for a large marine ecosystem. We evaluated whether suitable conditions exist in the Bering Sea for the survival and reproduction of 42 non-indigenous species (NIS). To do so, we compared species-specific temperature and salinity thresholds to conditions projected by three regional ocean models during two study periods: recent (2003-2012) and mid-century (2030-2039). In addition, we explored patterns of vessel traffic and connectivity among Bering Sea ports and international and regional ports from which NIS may be transported. We found that the southeastern Bering Sea was highly suitable for the year-round survival of 81% NIS assessed, but that cold water may limit NIS in areas with seasonal sea ice (i.e. north of 58°N). Although we found suitable reproductive conditions for many taxa, short summers may limit those that require temperatures above 10ºC for reproduction. Predicted ocean warming is expected to expand suitable conditions northward, largely favoring taxa that already have the ability to survive year-round within the study area. Traffic patterns apparent from ballast water discharge data and fishing vessel records reveal a network of coastwise and transoceanic traffic centered on Dutch Harbor, with connectivity throughout the Bering Sea. Areas predicted to support the highest number of NIS were also the most likely points of human-mediated introductions. Our findings provide an important foundation for risk assessments of NIS in a commercially important Arctic system and can inform research on climate change and bioinvasions in other high-latitude marine systems.

**Key words:** Arctic, climate change, physiological thresholds, habitat suitability, biological invasion, non-native species, North Pacific, Alaska, risk assessment

**Paper type:** Primary research

# Introduction

Marine non-indigenous species (NIS) are a global concern because of their potential to become invasive and to impact native ecosystems and commercial fisheries. This concern is increasing as warming ocean temperatures and marine transport fuel rapid range expansions of NIS around the world (Seebens et al. 2017). NIS are transported to new regions primarily through vessels (Ruiz et al. 1997, Molnar et al. 2008); as a result, ports that receive high levels of vessel traffic are more at-risk of biological introductions (Seebens et al. 2013, Lord et al. 2015). This relationship, though not without its nuances (e.g. Verling et al. 2005), is especially true for mid-latitude, saline ports, whose mild water temperatures and salinity levels are well within the thresholds of most marine species. Temperature and salinity become increasingly limiting for NIS as the difference between environmental conditions at the port of origin and port of arrival increase (Herborg et al. 2007, Iacarella et al. 2015), and may result in some geographic regions (e.g. Arctic waters) being relatively ‘safe’ from the establishment of NIS. Suitable temperature and salinity are crucial to the survival and establishment of aquatic species. Values above or below an organism’s physiological threshold can adversely affect behavioral, metabolic, and cellular processes, and values that exceed an organism’s critical thresholds are fatal (Portner 2001, Kassahn et al. 2009). Moreover, because optimal temperature and salinity ranges are typically narrower for reproduction, development, and growth, not all organisms that survive in a new region may not be able to establish self-sustaining populations (Woodin et al. 2013).

Compared to most marine ecosystems, Arctic marine ecosystems receive relatively little vessel traffic and have cold water temperatures nearly year-round. These factors have been proposed to explain the low rates of NIS introductions to the Arctic (Ruiz and Hewitt 2009, de Rivera et al. 2011), yet studies have shown that NIS are being transported on vessels from temperate to Arctic regions and are surviving the voyage (Chan et al. 2014, 2016, Ware et al. 2016). Few studies, however, have examined whether ocean temperatures are low enough to limit the survival of NIS and the establishment of self-sustaining populations. Previous studies looking at a small subset of potential NIS found that suitable habitat for survival exists for at least some, but these studies have disagreed as to whether suitable habitat is extensive (de Rivera et al. 2011) or limited (Ware et al. 2016, Goldsmith et al. 2018). Only one study evaluated suitable reproductive habitat for NIS in Arctic systems, and only for a limited number of species (n = 8; Ware et al. 2016).

Understanding the factors that limit invasions in the Arctic is increasingly important given the rapid oceanographic and socioeconomic changes that Arctic systems are experiencing. Warming sea temperatures and reductions in sea ice have already facilitated range expansions and introductions to Arctic systems (Reid et al. 2007, Renaud et al. 2015), and 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). Moreover, reductions in sea ice extent and lengthening of the ice-free season have contributed to an increase in vessel traffic (Miller and Ruiz 2014, Eguíluz et al. 2016), which is expected to increase the number and diversity of organisms transported to Arctic regions.

In this paper, we explore whether suitable conditions (temperature and salinity) currently exist for the survival and establishment of NIS in the Bering Sea, and whether predicted ocean warming will facilitate NIS survival and/or establishment. To do so, we compare physiological thresholds of NIS with modeled temperature and salinity values for the Bering Sea under recent (2003-2012) and mid-century (2030-2039) conditions. We also quantify vessel traffic and ballast water discharge for U.S. ports in the Bering Sea to explore the intersection between areas of high traffic and NIS suitability. The Bering Sea is a high-latitude marine ecosystem characterized by a strong latitudinal gradient in water temperature and sea ice formation (Stabeno et al. 1999). Since relatively few NIS have been documented in the Bering Sea (Reimer et al. 2017), we predicted that survival and establishment of NIS would be limited under current conditions. Given projections for increased sea temperatures and receding sea ice, we predicted that ocean conditions would become more suitable by mid-century, which would be reflected in an increase in the overall number of NIS capable of surviving and reproducing in the Bering Sea. For NIS already capable of surviving or establishing in the Bering Sea, we predicted increased survival and reproductive duration.

# Materials and methods

## Study area and taxa

The Bering Sea lies between the temperate North Pacific Ocean and the Arctic waters of the Chukchi Sea. It spans 14 degrees of latitude and extends more than 1,500 kilometers from Alaska (U.S.) to Russia (Figure 1). The Bering Sea marks a transition zone between arctic and subarctic marine systems. Sea ice forms seasonally in the north, reaching its maximum extent in April, though the location of the ice boundary shifts from year to year (Grebmeier et al. 2006a). It is comprised of a deep-water basin in the southwest, an extensive eastern continental shelf, and a narrow western shelf. The Bering Sea’s eastern shelf has some of the highest levels of marine productivity in the world, supporting a USD $1 billion commercial fishing industry (NMFS 2017). The Bering Sea is also a hub for international and regional vessel traffic (McGee et al. 2006). To date, only four NIS have been reported in the Bering Sea (Fofonoff et al. 2018): the American shad (*Alosa sapidissima* Wilson, 1811), the Japanese skeleton shrimp (*Caprella mutica* Schurin, 1935), the soft-shell clam (*Mya arenaria* Linnaeus, 1758; see Powers et al. (2006) for a discussion on the history of *M. arenaria* in the Bering Sea), and the Atlantic salmon (*Salmo salar* Linnaeus, 1758). Of these, only the Japanese skeleton shrimpand the soft-shell clamhave established self-sustaining populations (Ashton et al. 2008).

We selected NIS to include in our analysis based on occurrence records from two national databases: the National Exotic Marine and Estuarine Species Information System (NEMESIS; Fofonoff et al. 2018) and the Nonindigenous Aquatic Species Database (Fuller and Benson 2013). We included NIS that had occurrence records either within the Bering Sea or that have been reported within three marine ecoregions away i.e. up to the Washington-Oregon border in the east Pacific and up to the Sea of Japan to the west. We considered only euhaline taxa that can tolerate salinities ≥30 parts per trillion (ppt) (as per the Venice system of classification, Anonymous 1958). Of the NIS we included, the most common taxonomic groups were Crustacea (*n*=15), Mollusca (*n*=11), and Tunicata (*n*=8). All taxa included have been documented to spread via at least one anthropogenic vector (e.g. ballast water, biofouling, intentional introductions; see Reimer et al. 2017).

## Modeling suitable conditions

We considered the potential for NIS to: a) survive year-round; b) survive for at least one week of the year; and c) reproduce for at least one week of the year. We defined “suitable conditions” as a function of temperature, salinity, and water depth. While detailed habitat requirements are unknown for many of the taxa we considered, temperature and salinity thresholds for survival and reproduction were available for many of the taxa we considered. Furthermore, most NIS inhabit nearshore or otherwise shallow waters (Ruiz et al. 2015) and models specific to the Bering Sea have been built to define ocean temperatures and salinity for both recent timeframes and future predictions (Hermann et al. 2013, 2016).

## Defining taxa-specific thresholds

We obtained taxa-specific temperature (T) and salinity (S) survival thresholds for 42 NIS and T-S reproductive thresholds for 29 NIS reported in peer-reviewed publications, reports, and electronic databases (Appendix A). We prioritized T-S thresholds from experimental or field-based studies, but used thresholds inferred from geographic distributions in the absence of published thresholds. We defined survival thresholds as the broadest range of temperatures and salinities a given taxon can tolerate. Survival thresholds were therefore identified 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 were developed to require information on minimum and maximum thresholds for both temperature and salinity. For taxa that have been observed in temperatures that exceeded the Bering Sea maximum (~17°C), but for which no maximum temperature threshold was reported, we assigned an arbitrary maximum temperature value of +999 to ensure its inclusion in our model analyses. For taxa that had been reported from marine ecoregions whose salinities were comparable to those of the Bering Sea, but for which no salinity thresholds were reported, we set a 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 derived T-S values of the Bering Sea 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 models (GCMs): 1) CGCM3-t47, 2) ECHO-G, and 3) MIROC3.2, which were chosen for their ability to satisfactorily 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 with a 6-nautical mile (NM) spatial resolution and for 16 vertical depth levels (Hermann et al. 2016). T-S values are available for the entire Bering Sea; however, given the coastal affinities of most NIS, we restricted our analyses to the continental shelves i.e. waters with total depths < 200 meters (m). Because temperature and salinity change with depth, T-S values are available for several water depth intervals (roughly every 10 m up to 300 m; Hermann et al. 2016). We restricted our analyses to the upper stratum of the water column (depths up to 40 m) and collapsed the depth dimension for each pixel into a single value by taking the maximum T-S values.

We considered two 10-year study periods: recent (2003-2012) and mid-century (2030-2039) to evaluate changes in environmental suitability over time. Opting for a decadal study period (rather than a single year) allows us to incorporate system uncertainty inherent from annual fluctuations in Bering Sea conditions. 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 near-term, results from A1B GCMs do not differ substantially from other emission scenarios over the length of our study period (2003-2039; Nakićenović et al. 2000).

## Analyzing potential for survival and reproduction

We analyzed whether suitable conditions were available for each of the following categories:

1. Year-round survival: for each taxon, we defined a 6 NM pixel as ‘suitable’ if the pixel’s T-S values remained within the taxon’s T-S survival range for all weeks of a given year. Within each 10-year study period, we classified the pixel as ‘suitable year-round’ if it was suitable for at least seven of the 10 years. Across-taxa suitability was determined for each pixel by summing the number of taxa with suitable year-round conditions in that pixel. We examined change in suitable conditions by subtracting the mid-century suitability raster from the recent suitability raster. For a given pixel, a positive value indicates that more taxa are predicted to have suitable conditions by mid-century compared to the recent time period.
2. Weekly survival: for each week, a taxon was considered to have suitable survival conditions if at least one pixel had T-S values that were within the taxon’s T-S survival range. Weekly survival was then calculated as the number of weeks per year with suitable survival conditions, averaged across each 10-year study period. Unlike our year-round survival analysis, where the same pixel had to remain suitable year-round, in this analysis we allowed suitable conditions to shift in pixel-space from one week to the next. We summarized results across taxa by summing mean weekly survival values for each pixel and study period. Pixel values can therefore range from zero to 2,184 (52 weeks × 42 taxa).
3. Weekly reproduction: for each taxon, we defined a pixel as ‘suitable’ if the pixel’s T-S values were within the taxon’s T-S reproduction range for at least one week of a given year. For each year within our 10-year study periods, we calculated the number of consecutive weeks of suitable reproductive conditions, 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.

Suitability categories were analyzed separately for each ROMS, but final results were 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: doSNOW, dplyr, ggplot2, ncdf4, maptools, plyr, rgdal, raster, rasterVis, rgeos, sp, viridis.

## 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 NOAA Fisheries Vessel Monitoring Systems (VMS) for Alaska commercial fishing vessels. These data allowed us to quantify the magnitude and spatial patterns of traffic arriving at U.S. ports in the Bering Sea from fishing vessels and from other 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 U.S. (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 - 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 reported trips 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, which includes many fishing vessels. We therefore relied on VMS data (not publicly available) from Alaska to examine patterns of fishing vessel traffic. Current regulations by the National Marine Fisheries Service (NMFS) require VMS on 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 temporal 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 4,133 trips by 566 vessels during this time. Port connections with fewer than three different vessels were omitted according to confidentiality rules, and discharge reports that did not include valid source locations were omitted from the analyses.

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 for the recent (2003-2012) study period, minimum water temperatures ranged from -2.6°C to +4.2°C, and maximum water temperatures ranged from +3.8°C to +16.3°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 +18.6°C (see also Hermann et al. 2016; note that reference acknowledges a ‘cold-bias’ in model results). Minimum survival temperatures for the 42 NIS assessed ranged from -2°C to +10°C (Appendix A). Nineteen taxa had estimated minimum survival thresholds below 0°C, while 13 taxa had minimum survival thresholds ≥1°C (Appendix A).

## Year-round Survival

For the recent (2003-2012) study period, all models predicted that suitable conditions existed for a median of 10 NIS per pixel. The maximum number of taxa with suitable conditions varied by model (Supplementary Figure ###). The CGCM3-t47 model predicted suitable conditions for a maximum of 35 taxa, the ECHO-G model predicted suitable conditions for a maximum of 33 taxa, and MIROC3.2 predicted suitable conditions for a maximum of 34 taxa. Across all models, areas that were predicted to support the highest number of NIS were the coastlines of the Aleutian Islands and western Bristol Bay (Figure 2). The minimum number of taxa with suitable conditions predicted by all models was zero. Areas that were inhospitable for all taxa included northern Norton Sound (≥63.7°N) and the northern Gulf of Anadyr (≥65.0°N). The ECHO-G and CGCM3-t47 also predicted a continuous area without any suitable conditions along the coastline of the Yukon-Kuskokwim Delta from Norton Sound south to Kuskokwim Bay (Supplementary Figure ##).

Under mid-century (2030-2039) conditions, the CGCM3-t47 and the MIROC3.2 models predicted that the Bering Sea would become more suitable for NIS survival, both in terms of NIS richness and in terms of spatial area. The median number of taxa per pixel increased from 10 taxa per pixel to 11 taxa/pixel for the MIROC3.2 model and 12 taxa/pixel for the CGCM3-t47 model. Moreover, the maximum number of taxa with suitable conditions increased by one for both the MIROC3.2 and the CGCM3-t47 models to a maximum of 35 and 36 NIS, respectively. The ECHO-G model did not predict any change in these values compared to recent predictions. With respect to area, the CGCM3-t47 model predicted 694 pixels would be suitable for fewer taxa by mid-century, 6,199 would be suitable for more taxa, and 3,331 would be suitable for the same number of taxa. The MIROC3.2 model predicted a similar overall increase in suitable area: 378 pixels were predicted to become suitable for fewer taxa, 5,437 would be suitable for more taxa, and 4,409 would be suitable for the same number of taxa. The ECHO-G model predicted that most pixels (5,777) would be suitable for the same number of taxa under both study periods. Nevertheless, it predicted that 3,808 pixels would be suitable for more taxa, whereas only 639 pixels would be suitable for fewer taxa under mid-century conditions. Averaged across the three models, 5,148 out of 10,224 pixels in our Bering Sea study area are predicted to become suitable for the year-round survival of additional NIS by 2039, whereas less than 6% of our study area (570.3 pixels) is predicted to be suitable for fewer NIS compared to recent conditions. Given that each pixel has an area of 36 NM, these values represent an additional area of ~635,600 sq. km. (185,328 NM) shifting from unsuitable to suitable conditions by 2039, while only ~70,400 sq. km. (20,523 NM) would shift to becoming less suitable over the same time period. Regions between 57°N and 59°N are expected to experience the greatest increases in NIS suitability (Supplementary Figure ###). When averaged across the three models, an additional 16 taxa are expected to find suitable conditions by 2039 (Supplementary Figure ###).

## Weekly Survival

We found a seasonal pattern of survival suitability that was consistent across latitudes and study periods. In the first third of the year (weeks 1 to 17), survival conditions were present only for NIS whose survival thresholds allowed year-round survival (Figure 3). In the second third of the year (weeks 17 to 34), conditions rapidly became suitable for all or nearly all NIS. The number of NIS that could survive gradually declined in the last third of the year (Figure 3).

This pattern was similar under both recent and mid-century study periods, though mid-century conditions predict a lengthening of the highly suitable, species-rich summer season. The number of consecutive weeks that can support additional taxa increased from a minimum of 11 to 14 weeks. This period of increasing suitability began at the end of April (week 17) and continued until either the beginning of July (week 27; recent study period) or early August (week 30; mid-century). Mid-century models also predicted that conditions in mid- to late winter would be suitable for a larger number of taxa than recent conditions (Figure 3).

The latitudinal gradient we observed in year-round survival was also evident when considering survival on a weekly basis. In general, southern latitudes had conditions to support a greater number of taxa and, for taxa without year-round survival, conditions were suitable for a greater number of weeks than northern latitudes (Figure 3). Pixels between 52°N and 53°N supported the most taxa year-round, equivalent to the minimum number of taxa with year-round survival in the previous section. Pixels between 58°N and 59°N supported slightly fewer taxa year-round but were suitable for all 42 taxa for the longest length of time. This high summertime suitability at these latitudes was consistently predicted for all models and study periods. For the recent study period, the ECHO-G model predicted that conditions would be suitable for all taxa at these latitudes from mid-July to early September (weeks 29 to 36). The CGCM3-t47 and MIROC3.2 models predicted constant survival until week 36 beginning as early as late June (week 26) and early July (week 27), respectively. Under mid-century conditions, the length of time where conditions were suitable for all taxa increased. The MIROC3.2 model predicted that conditions would become suitable one week earlier and persist until the last week of September (week 39), for a total of 14 weeks. In the case of the ECHO-G model, this period of time began two weeks earlier (week 27) but ended at the same time (week 36), and consequently increased in length from eight to 10 weeks. Lastly, the CGCM3-t47 model predicted that suitable conditions would begin at the same time (week 26) but end later in the season (week 39), representing an increase from 11 to 14 weeks.

## Reproduction and establishment

Through our literature search, we identified reproductive temperature and salinity thresholds for 29 NIS. Areas that were highly suitable for NIS reproduction were in the southern Bering Sea, as well as further north along coastlines of the southern Seward Peninsula and in Norton Sound (64°N; Supplementary Figure ###).

Models varied with respect to the median and maximum number of taxa per pixel that were predicted to have at least one week of suitable reproductive conditions. For the recent study period, when averaged across the 10 years, the CGCM3-t47 model predicted a median of 5.2 taxa per pixel and a maximum of 13.1. The ECHO-G model predicted a median of 3.8 taxa per pixel and a maximum of 13.7. Finally, MIROC3.2 predicted a median of 2.8 taxa per pixel and a maximum of 13.3. For the mid-century study period, the CGCM3-t47 and MIROC3.2 models predicted an increase in both the median and maximum number of taxa with suitable reproductive conditions. The CGCM3-t47 model predicted that the median would increase to 6.7 taxa per pixel and the maximum would increase to 13.8, while the MIROC3.2 model predicted the median would increase to 3.7 taxa per pixel and the maximum to 16.2. The ECHO-G model also predicted the median would increase to 3.8 taxa per pixel. However, the maximum number of taxa decreased to 12.5.

Suitable conditions were completely absent for five NIS under the recent study period. Two of these NIS, the American shadandthe Atlantic salmon, required fresh or brackish water for reproduction (i.e. salinities <30 ppt). The remaining three NIS, the Pacific oyster (*Crassostrea gigas* Thunberg, 1793), *Hediste diadroma* (Sato and Nakashima 2003), and the Japanese littleneck (*Venerupis philippinarum* A. Adams and Reeve, 1850), required minimum temperatures of ≥16°C for reproduction or development, which was outside the range of temperatures predicted for any model-year combination. In contrast, taxa with minimum reproductive temperatures of 4°C and salinity requirements >30ppt were predicted to have nearly year-round suitable conditions every year. For the mid-century study period, all models predicted that the American shad, the Atlantic salmon, and *H. diadroma* would remain without suitable reproductive conditions. The CGCM3-t47 and MIROC3.2 models predicted that the Pacific oysterwould have very limited reproductive conditions, averaging less than one week per year over the 10-year study period. The MIROC3.2 also predicted very limited suitability for the Japanese littleneck, with reproduction predicted for only one week and for only one year out of ten.

## 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 from trips originating outside of the Bering Sea. Records were distributed across 9 vessel types: Bulker (*N* = 2,755), 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* = 9,935), and Fishing (*N* = 1,140), with Tankers accounting for more than 90% of the total ballast water volume discharged. 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).

Arrivals originating from outside of Alaska accounted for 83.3% of NBIC records (Figure 5a). 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 NBIC, 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 (7,183 mt), Canada (6,912 mt), and Washington (3,852 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). Among these non-port source locations, 75.5% of the coordinates occurred in water depths greater than 200m (i.e., off the continental shelf), where the risk of NIS is likely less.

# Discussion

## Current model predictions

Although the Bering Sea has few reports of NIS to date, our results indicate that recent oceanographic conditions offer potentially suitable conditions for a large number of taxa, both for their survival and reproduction. Of the 42 taxa assessed, 34 had year-round suitable survival conditions, and the remaining had suitable conditions for at least six weeks during summer (early July to mid-August). In addition, conditions in the Bering Sea were predicted to be suitable for the reproduction and growth of 24 of 29 taxa (69%). The southern Bering Sea, which includes the Aleutian Islands chain, the Pribilof Islands, and the northwestern Alaska Peninsula, was highly suitable for both survival and establishment of NIS. Since the taxa we assessed have all been observed in marine ecoregions close to the Bering Sea, it is conceivable that these species may frequently be transported to the Bering Sea, and given enough opportunity, may survive and establish populations under current Bering Sea conditions.

We considered potential NIS richness by summing results across all NIS, and found a latitudinal gradient in potential NIS richness that was high in the southern Bering Sea and decreased sharply above 58ºN. The 58ºN “threshold boundary” predicted by our models is coincident with the current limit of seasonal sea ice extent in the Bering Sea (Grebmeier et al. 2006b, Stabeno et al. 2012). Above this “boundary”, all taxa were predicted to have suitable survival conditions in summer. However, year-round survival was limited to those taxa that could tolerate sub-zero water temperatures. While tolerance to sub-zero temperatures was not uncommon, most taxa we considered had minimum temperature thresholds ≥0°C. At least for the time being, biological invasions in Arctic waters may tbe limited to taxa that are adapted to polar environments or that are tolerant of low temperatures (de Rivera et al. 2011).

Although most taxa we evaluated had at least one week of suitable reproductive conditions, the presence of suitable habitat was more restricted in both space and time. As with our survival analysis, the southern Bering Sea was highly suitable for NIS establishment. In addition, suitable conditions were predicted for several taxa in Norton Sound (~64°N) (Supplementary Figure 1). Although Norton Sound freezes annually, its shallow waters create a high-latitude thermal hotspot in the summer (Ladd and Overland 2009, Hermann et al. 2016). The presence of such hotspots could create a window of opportunity for NIS to establish in arctic waters. Because the Bering Sea experiences such short summers, the time available for reproduction and development may be limiting for several NIS. Although we did not collect data on the time needed to complete development, taxa requiring temperatures ≥ 14°C had less than three weeks of suitable reproductive conditions. NIS such as *Botrylloides violaceus* (Oka, 1927) and the European green crab (*Carcinus maenas* Linnaeus, 1758), which are of high concern elsewhere along the eastern Pacific coast (Fofonoff et al. 2018; Fuller and Benson 2013), either did not have suitable temperatures or did not have enough time to complete development (de Rivera et al. 2007, Westerman et al. 2009), despite having the capacity to live year-round across moderately large areas of the shelf. Interestingly, the two NIS that are currently known to be established in the Bering Sea (the Japanese skeleton shrimp and the softshell clam) required the lowest minimum reproductive temperatures (4°C) of all NIS assessed and were the only ones that had suitable reproductive conditions nearly year-round (> 51 consecutive weeks).

## Future model predictions

The Bering Sea is already experiencing significant effects from 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 and surface water temperatures have increased by 0.23°C per decade since then (Mueter and Litzow 2008). Recent years have experienced several of the lowest sea ice extents on record, which has caused the location of the ice boundary to shift further north (Onarheim et al. 2018). In addition, there have been substantial decreases in the length of the ice-covered season (Onarheim et al. 2018). Furthermore, surveys of commercial fish species in this area have already illustrated northward shifts under steadily changing conditions (Kotwicki and Lauth 2013; Barbeaux and Hollowed 2018), so it is not surprising that potential NIS habitat expansions would follow similar patterns. Our models suggest that warming water temperatures will increase the amount of suitable area for taxa that can already survive in parts of the Bering Sea. This increased area is predicted to present itself as a northward expansion and is in agreement with other NIS modeling studies for Alaska (de Rivera et al. 2011) and elsewhere in the Arctic (Ware et al. 2016, Goldsmith et al. 2018). Our models also predict increases in the length of the reproductive season as a result of warming summer temperatures, potentially allowing NIS to establish sustainable populations in the Bering Sea. Studies in temperate systems have shown that NIS typically respond favorably to warmer spring and summer water temperatures by increasing their growth rates (de Rivera et al. 2007), abundance (Saunders and Metaxas 2007, Witte et al. 2010), fecundity (Valdizan et al. 2011, Dijkstra et al. 2017), or onset of recruitment (Stachowicz et al. 2002, Valdizan et al. 2011).

Given that cold water temperatures currently seem to limit survival and reproduction in the Bering Sea, warming temperatures might have the greatest implication for taxa that are at the limit of their temperature thresholds (e.g. Miller 2016). For example, laboratory experiments and modeling efforts on the European green crab suggest that recent temperatures in the southern Bering Sea are at the limit of its thermal tolerances for larval development (de Rivera et al. 2007). Our mid-century models suggest that warming temperatures will cause the southern Bering Sea to shift from marginal to moderately suitable conditions for the green crab’s growth and reproduction, which would allow this species to move from merely surviving under recent Bering Sea conditions to being able to reproduce and establish a population under mid-century projections (model results for specific species, including the European green crab, can be found at http://beringinvaders.org/).

## Model limitations

The ROMS we used to predict suitable conditions underestimate summer water temperatures near the coast and in shallow waters < 10 m deep. The models’ spatial resolution does not extend to the edge of the coastline and computational limitations required water depths to be set to a minimum of 10 m depth (A. Hermann, pers. comm.). Moreover, while the ROMS include a coarse estimate of freshwater runoff, they do not account for the warming of shallow, coastal waters caused by river discharge. The influence of rivers is likely significant in our study area given the many large rivers that drain into the Bering Sea, notably the Yukon, Kuskokwim, and Nushagak rivers. 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/>), and field measurements at the mouth of the Yukon have been as high as 21°C (T. Jorgenson, pers. comm.). In contrast, maximum temperatures predicted by the ROMS never exceeded 16.3°C. However, while the warming effects of these rivers are not fully captured by the ROMS, they do not last for more than a few weeks. Thus, while we may be underestimating the number of weeks of suitable reproductive conditions, model limitations should not affect the results of our year-round survival analysis.

Our approach, which uses physiological thresholds 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). However, we found that there were limited data on physiological thresholds, especially with respect to cold water tolerances and to reproductive and developmental processes. Estimating tolerances for reproduction and development is particularly complex given that organisms have different temperature and time requirements for spawning, brooding, and metamorphosis. Moreover, exposure to temperatures at the tail-end of an organism’s tolerance threshold can increase the time required for development (e.g. de Rivera et al. 2007). Additional research is needed to understand taxa’s thermal response curves (Westerman et al. 2009, Monaco and Helmuth 2011, Sorte 2014, Miller 2016) and the potential for rapid evolution (Huang et al. 2017, Ricciardi et al. 2017), which could enable taxa to increase their tolerances to cold water. More comprehensive models can be built for a subset of high-interest NIS that take into account additional habitat requirements such as substrate type, wave exposure, and prey availability.

## Interactions between vessel traffic and predicted NIS habitat

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. Data from commercial and fishing vessel traffic, and from ballast water discharge, point to the port of Dutch Harbor as 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 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. While many of these vessels may not discharge ballast water, they can still transport fouling organisms, which may be a larger contributor of propagules than ballast water (Chan et al. 2015).

Dutch Harbor is one of the largest fisheries port in the U.S. (NMFS 2017) and has long been recognized as a potentially important point of entry for non-native species based on patterns of vessel traffic (McGee et al. 2006, Verna et al. 2016). Given Dutch Harbor’s connectivity to other ports, it may also act as a “transport hub” (Floerl et al. 2009) introducing NIS to remote communities across the Bering Sea. The vulnerability of Dutch Harbor to biological introductions is particularly salient because of its location in the southern Bering Sea (Figure 1). The southern Bering Sea and the Aleutian Islands chain is predicted to have the most favorable conditions for year-round survival and establishment of NIS (Figure XX). Although the northern Bering Sea may be less at-risk because of low traffic and cold water temperatures, it is experiencing rapid and dramatic changes in ocean climate, which may increase its vulnerability to NIS. Certain areas in the northern Bering Sea, such as the coastlines of Norton Sound, are already predicted to be warm enough to support reproduction and survival of certain NIS (Figure XX). The socioeconomic realities of Arctic waters are also changing. Shipping and oil and gas exploration may lead to the continued development of plans for industrial-scale facilities in northern ports such as Nome, which currently receives little traffic. Northern ports may experience increases in fishing vessel traffic as range shifts of commercial fish species move northward and fishing fleets follow suit (Pinsky and Fogarty 2012, Fossheim et al. 2015).

It is currently unknown whether vessels arriving to Bering Sea ports are transporting viable non-native organisms, and several factors affect an organism’s survivorship during the voyage from one port to another. Introductions to the Bering Sea may be relatively low due to the long transit times between Bering Sea ports and other regional or international ports. Indeed, a study from the Canadian Arctic found that NIS richness and abundance was inversely related to the length of the voyage, and that ballast water age was the most important predictor of richness and abundance (Chan et al. 2014). Thus, although Dutch Harbor receives high volumes of ballast water, the relatively long residence time of the ballast water discharged in Dutch Harbor may reduce its invasion risk (Verna et al. 2016). In the absence of data on propagule pressure, future analyses of vessel traffic in the context of invasive species transport may benefit from using Automatic Identification System (AIS) data, which are available for a greater portion of vessels traveling through Alaskan waters.

While it has recently been believed that NIS introductions and establishment have been restricted in the Arctic due to cold water temperatures which yield inhospitable environments for many introduced taxa, our results indicate that (1) recent Bering Sea conditions offer potential habitat for a large number of NIS, and for both survival and reproduction life stages; (2) suitable conditions for NIS are projected to expand by mid-century due to warming ocean temperatures; and (3) mechanisms for NIS transport into and throughout the Bering Sea exist and overlap with conditions suitable for NIS survival and reproduction. 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. As declining sea ice cover makes the Arctic an increasingly popular shortcut between the Pacific and Atlantic, we expect the risk of NIS introductions in the region to increase. Given the low number of NIS that currently exist in the region, the Bering Sea can benefit from ongoing monitoring and programs aimed at prevention and early detection.

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