# 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 the intersection between vessel traffic and suitable environmental conditions among Bering Sea ports. We found that the southeastern Bering Sea was highly suitable for the year-round survival of 80% 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 and fishing vessel records reveal a network of coast-wise 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. Results from this study can provide support for invasive species management by identifying high-risk areas and NIS of concern in a commercially important Arctic system.

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

# Introduction

Marine non-indigenous species (NIS) are a global concern because of their potential to become invasive and to impact aquatic systems, commercial fisheries, and native biodiversity. 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 arrival and 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 have negative impacts on 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, even 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 oceans 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 becoming 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, a high-latitude marine ecosystem characterized by a strong latitudinal gradient in water temperature and sea ice formation (Stabeno et al. 1999). We also examined whether predicted ocean warming will facilitate NIS survival and/or establishment. To do so, we compared physiological thresholds of NIS with modeled temperature and salinity values for the Bering Sea under recent (2003 – 2012) and mid-century (2030-2039) conditions. Lastly, we quantified 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. Since relatively few NIS have been documented in the Bering Sea (see 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 there would be an increase in suitable conditions by mid-century, which would be reflected in increased suitability for a larger number of NIS and for a longer annual-period of time.

# 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 ocean 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: *Alosa sapidissima*, *Caprella mutica*, *Mya arenaria*, and *Salmo salar* (Fofonoff et al. 2018; 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 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 only NIS that had occurrence records either within the Bering Sea, or that have been reported no farther than the Washington-Oregon border in the east Pacific and 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

Few environmental covariates are available for the Bering Sea and detailed habitat requirements are unknown for many of the taxa we considered. However, models have been built to define ocean temperatures and salinity for both recent timeframes and future predictions, and temperature and salinity thresholds are available for many taxa. Moreover, most NIS inhabit nearshore or otherwise shallow waters (Ruiz et al. 2015). We therefore define “suitable conditions” as a function of temperature, salinity, and water depth, and 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.

## 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 define 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 10 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-nautical mile 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. Changes in suitable area were calculated as the percent of positive (i.e. increase) or negative (i.e. decrease) pixels in the study area.
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 2184 (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. 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 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 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 4133 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). 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 taxa per pixel. The maximum number of taxa varied by model (Supplementary Figure XX). The CGCM3-t47 model predicted a maximum of 35, the ECHO-G model predicted a maximum of 33 taxa, and MIROC3.2 predicted 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 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 XX).

With respect to mid-century (2030-2039) conditions, both the CGCM3-t47 and the MIROC3.2 models predicted an increase in both the median and maximum number of taxa. The CGCM3-t47 model predicted a median of 12 taxa per pixel, with a maximum of 36 taxa. The MIROC3.2 model predicted a median of 11 taxa per pixel, with a maximum of 35 taxa. The ECHO-G model did not predict any change in these values. All models predicted that pixels were more likely to support additional number of NIS, when compared to recent conditions. The CGCM3-t47 model predicted 694 pixels supporting fewer taxa, 6,199 supporting more taxa, and 3,331 supporting the same number of taxa. The ECHO-G model predicted 639 pixels would be suitable for fewer taxa under mid-century conditions than under recent conditions, whereas 3,808 pixels would support more taxa. 5,777 pixels supported the same number of taxa under both study periods. The MIROC3.2 model predicted that 378 pixels would be suitable for fewer taxa, 5,437 would be suitable for more taxa, and 4,409 would support the same number of taxa. On average, then, models predict that 570.3 pixels will become suitable for fewer taxa by 2039 and 5148 pixels would become suitable for more taxa. Because each pixel has an area of 36 NM, these values are equivalent to 20,523 NM (~70,392 sq. km.) becoming less suitable by 2039, compared to 185,328 NM (~635,657 sq. km.) becoming more suitable. The area that is predicted to experience the largest change lies between 57°N and 59°N (Supplementary Figure XX). Averaged across all model, this area is expected to become suitable for an additional 16 taxa by 2039 (Supplementary Figure XX).

## Weekly Survival

\*\*Need to flesh out weekly results\*\* Of the taxa that could not survive year-round during recent conditions (n = 8), all had suitable conditions for at least six weeks during early July to mid-August (weeks 28 to 33; Figure 3). Across these taxa, survival conditions were unsuitable from December to early May (weeks 49 to 19), when temperatures in the upper water column fall below 1°C (Figure 3). [SUMMARIZE weekly survival in mid-century study period: make analogous statements; then summarize distribution of expansion of n weekly survial; ...]

## Reproduction and establishment

Reproductive thresholds were identified for 29 NIS. For the recent study period, the maximum number of taxa that a single pixel could support was 20 taxa, with a median of 7.3 taxa per pixel. Under mid-century conditions, the maximum number of taxa that a single pixel could support ranged from 0 to 21 taxa, with a median of 8.3 taxa per pixel. Five taxa had no suitable reproductive conditions anywhere on the Bering Sea shelf, including three species that require fresh or brackish water for reproduction (*Alosa sapidissima*, *Salmo salar*) and two species with min. repro. Temps > XX.

Most areas of high NIS reproductive richness were in the southern Bering Sea. maximum NIS reproductive richness along the southern Seward Peninsula and in Norton Sound (64°N; Supplementary Figure 1).

For the recent study period, marine taxa requiring at least 12°C for reproduction or growth had fewer than six consecutive weeks, while taxa requiring >14°C had less than one week (Figure 4). Taxa that can reproduce at 4°C in marine salinities (≥ 31 ppt) had nearly year-round suitable reproductive conditions (Figure 4). During the mid-century study period, models predict an increase in the number of consecutive weeks that are suitable for reproduction. Taxa with thresholds ≥14°C are predicted to have less than three weeks of suitable conditions (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 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 (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

## Current model predictions

Although the Bering Sea has few reports of non-indigenous species (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 for their reproduction. Of the 42 taxa assessed, 80% 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 20 of 29 taxa (69%). Since the taxa we assessed have all been observed within three marine ecoregions of the Bering Sea, it is conceivable that these species may frequently be transported to the region, and given enough opportunity, may survive and establish populations under current Bering Sea conditions.

When we summed our models across all taxa, potential NIS richness followed a latitudinal gradient 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, but taxa without year-round survival conditions failed to survive from December to April, when water temperatures fell below 0°C. In contrast, taxa that could tolerate sub-zero freezing temperatures had suitable conditions year-round throughout most of the Bering Sea. These findings are similar to those of de Rivera et al. (2011), who built habitat suitability models in Alaskan waters for four cold-tolerant, non-native species. Within the subset of taxa we considered, tolerance to sub-zero temperatures was somewhat common, but most taxa had minimum temperature thresholds ≥0°C. Biological invasions in Arctic waters may therefore be limited to taxa that are adapted to polar environments or that are tolerant of a wide range of temperatures (such as the European green crab, *Carcinus maenas*). In contrast, the southern Bering Sea, which includes the Aleutian Islands chain, the Pribilof Islands, and the northwestern Alaska Peninsula, had suitable year-round survival conditions for ((almost all) NIS we considered.

Our analysis of suitable reproductive conditions has more uncertainties given our limited knowledge of physiological thresholds and the complexity of the reproductive and developmental processes. Organisms have different temperature requirements for spawning, brooding, and undergoing metamorphosis, and each of these stages takes a certain amount of time to complete. In some cases, 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). It is therefore difficult to determine whether organisms have enough time to reproduce and develop in the Bering Sea’s short summer season. Most taxa we evaluated had at least one week of suitable reproductive conditions. The two NIS that are currently known to be established in the Bering Sea (*Caprella mutica* and *Mya arenaria*) 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). In contrast, taxa requiring temperatures ≥ 14°C had less than three weeks of suitable reproductive conditions. NIS such as *Botrylloides violaceus* and *Carcinus maenas*, which are of high concern elsewhere along the eastern Pacific coast (Fofofnoff et al. 2003), 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. However, our model projections suggest that these restrictions may loosen as season length and water temperatures increase. As with our survival analysis, areas of high suitability included the southern Bering Sea. We were also surprised to see suitable conditions for several taxa in Norton Sound (~64°N) (Supplementary Figure 1). Norton Sound freezes annually, but in the summer its shallow waters create a thermal hotspot in an otherwise chilly sea (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. Some marine organisms have specialized lifeforms that allow them to persist even if temperatures fall below their adult survival thresholds. In other cases, a yearly influx of eggs or mature adults could lead to the establishment of a seasonal population that persists year-round in mild winter years and disappears in other years. Our model projections suggest that temperature restrictions on year-round survival and reproduction may loosen as water temperatures and season length increase.

## Future model predictions

The Bering Sea is experiencing significant changes as a result of climate change (e.g. Grebmeier et al. 2006b, Stabeno et al. 2007, Mueter and Litzow 2008). Sea ice cover has decreased substantially since the 1950s, 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 extent on record, shifting the location of the ice boundary further north (Onarheim et al. 2018). In addition, there has been substantial decreases in the length of the ice-covered season (Onarheim et al. 2018).

These observed and ongoing changes are predicted to increase the amount of suitable conditions, both in terms of area and number of NIS. Warming winter temperatures and decreases in sea ice extent will allow NIS to survive year-round in previously inhospitable areas, whereas warming summer temperatures will increase the length of the reproductive season. Indeed, Of the 42 taxa assessed, XX% had year-round suitable ?conditions?, and the remaining X% had suitable conditions for at least six weeks during early July to mid-August. In addition, conditions in the Bering Sea were predicted to be suitable for the reproduction and growth of XX% of the subset of taxa assessed. These results suggest…

Our models agree with other NIS risk assessments in the Arctic (de Rivera et al. 2011, Ware et al. 2016, Goldsmith et al. 2018) that predict a northward expansion in suitable survival conditions as the result of predicted increases in winter water temperatures (Supplementary Figure 1). The number of NIS that a single ‘pixel’ can support is expected to increase In addition, our models predict that warming summer temperatures will increase the length of time that is suitable for growth and development. Few studies have modeled the reproductive capacity of NIS in Arctic regions, but studies in temperate systems have shown that NIS typically respond favorably to warmer spring and summer water temperatures. Taxa respond in a variety of ways including by increasing their 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). For taxa that are at the limit of its temperature thresholds in the Bering Sea, warming temperatures could allow species to considerably expand suitable conditions. For example, when we consider *C. maenas*, a NIS of great concern (Fofonoff et al. 2018; Fuller and Benson 2013), our mid-century models suggest that warming temperatures will cause the southern Bering Sea to shift from marginal to moderately suitable conditions for *C. maenas* growth and reproduction, which would allow this taxon to move from merely surviving under recent Bering Sea conditions, to being able to reproduce and establish a population under mid-century projections. Given that cold water temperatures currently seem to be limiting survival and reproduction in the Bering Sea, projected increases in water temperatures will likely open up habitat for NIS and may allow for future growth, establishment and spread of NIS. This may be exacerbated by the potential for rapid evolution (Huang et al. 2017, Ricciardi et al. 2017), which would enable taxa to increase their tolerances to cold waters. However, very little is known about what happens at the tail-end of taxa’s thermal response curves (Monaco and Helmuth 2011, Sorte 2014, Miller 2016) and experimental studies are needed to determine stress responses and development rates under cold-water temperature regimes (Westerman et al. 2009).

## Model limitations

The ROMS used to estimate ocean conditions either do not predict, or underestimate summer water temperatures near the coast and in shallow waters < 10 m deep. These limitations are due to the models’ spatial resolution, and of computational limitations that require water depths to be set to at least 10 m. 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, the warming effects of these rivers, while not fully captured by the ROMS, do not last for more than a few weeks. Thus, we may be underestimating the number of weeks of suitable reproductive conditions, but these limitations should not affect the results of our year-round survival analysis.

## Interactions between vessel traffic and predicted NIS habitat

Commercial and fishing vessel traffic and 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 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 one of the largest fisheries port in the U.S. (NMFS 2017). 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 connectivity 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). 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. 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 declining sea ice cover makes the Arctic an increasingly popular shortcut between the Pacific and Atlantic, we expect the risk of NIS introductions to 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. Furthermore, as range shifts of commercial fish species have moved northward, shifts in fishing locations have followed (Pinsky and Fogarty 2012), leading to potentially increased fishing vessel connections among more northern Bering Sea ports like Nome.

[Need paragraph describing the overlap between active ports and suitable habitat during recent and mid-century study periods. Just generalize the overlap, maybe a map, discuss the implications.]

Despite high traffic levels, NIS introductions may be relatively low due to the long transit times between Bering Sea ports and other regional or international ports. Studies from the Canadian Arctic suggest that survivorship is inversely related to the length of the voyage (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 be reducing its invasion risk (Verna et al. 2016). Other factors that can affect survivorship during the voyage include: an organism’s physiological condition, the type and speed of the ship, and the conditions encountered at sea (Ruiz et al. 2000, Verling et al. 2005, Chan et al. 2014). Additional data are needed to quantify propagule pressure and environmental conditions before and after a vessel docks in a Bering Sea port.

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 NIS habitat for a large number of taxa, and for both survival and reproduction life stages; (2) suitable conditions 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 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, [Insert statement about NIS evolution and the need for additional habitat things like substrate and prey]. 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 low numbers of biological introductions that have been reported in the region.

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