Biological introduction risks from shipping in a warming Arctic

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Summary

1. Several decades of research on invasive marine species have yielded a broad understanding of the nature of species invasion mechanisms and associated threats globally. However, this is not true of the Arctic, a region where ongoing climatic changes may promote species invasion. Here, we evaluated risks associated with non-indigenous propagule loads discharged with ships' ballast water to the high-Arctic archipelago, Svalbard, as a case study for the wider Arctic.

2. We sampled and identified transferred propagules using traditional and DNA barcoding techniques. We then assessed the suitability of the Svalbard coast for non-indigenous species under contemporary and future climate scenarios using ecophysiological models based on critical temperature and salinity reproductive thresholds.

3. Ships discharging ballast water in Svalbard carried high densities of zooplankton (mean 1522 ± 335 SE individuals m^{-3}), predominately comprised of indigenous species. Ballast water exchange did not prevent non-indigenous species introduction. Non-indigenous coastal species were present in all except one of 16 ballast water samples (mean 144 ± 67 SE individuals m^{-3}), despite five of the eight ships exchanging ballast water *en route*.

4. Of a total of 73 taxa, 36 species including 23 non-indigenous species were identified. Of those 23, sufficient data permitted evaluation of the current and future colonization potential for eight widely known invaders. With the exception of one of these species, modelled suitability indicated that the coast of Svalbard is unsuitable presently; under the 2100 Representative Concentration Pathway (RCP) 8·5 climate scenario, however, modelled suitability will favour colonization for six species.

5. *Synthesis and applications.* We show that current ballast water management practices do not prevent non-indigenous species from being transferred to the Arctic. Consequences of these shortcomings will be shipping-route dependent, but will likely magnify over time: our models indicate future conditions will favour the colonization of non-indigenous species Arctic-wide. Invasion threats will be greatest where shipping transfers organisms across biogeo-

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graphic realms, and for these shipping routes ballast water treatment technologies may be required to prevent impacts. Our results also highlight critical gaps in our understanding of ballast water management efficacy and prioritization. Thereby, our study provides an agenda for research and policy development.

Introduction

Globally, few marine ecosystems remain immune from the potential impacts of non-indigenous species introduction (Catford *et al.* 2012). With the exception of some commercially harvested seaweeds, molluscs and arthropods (Pickering, Skelton & Sulu 2007), most invasive marine species have been introduced to their invasive habitats unintentionally, largely as a result of shipping activity (Molnar *et al.* 2008). Shipping connects distant global regions (Keller *et al.* 2011), and even remote Antarctic and Arctic port-regions are vulnerable to species introduction through active shipping networks (Chan *et al.* 2012; Ware *et al.* 2014). Ports worldwide have become heavily invaded by non-indigenous species and now serve as sources for the further spread of invasive species (Keller *et al.* 2011). As a result, a major challenge for biosecurity managers is to develop an understanding of marine species invasion threats, and to implement measures to manage them appropriately.

Ships may transfer organisms to new environments through ballast water uptake and subsequent discharge. To reduce the transfer of non-indigenous species in ballast water, international and domestic efforts have been made to regulate this vector (IMO 2004). These management frameworks are currently in transition around the world (Frazier, Miller & Ruiz 2013). Presently, ballast water is managed to reduce invasion threats using a practice known as ballast water exchange or saltwater flushing (IMO 2004; Frazier, Miller & Ruiz 2013). In theory, this practice should reduce the abundance and richness of species contaminating ballast water by either purging the water (releasing the organisms into a lethal habitat), or killing the organisms through osmotic shock (Wonham, Lewis & MacIsaac 2005). In practice, ballast water exchange can effectively reduce invasion risk between freshwater ecosystems using a marine (saline) exchange *en route*. However, efficacy is less apparent when shipping connects marine ecosystems (Wonham, Lewis & MacIsaac 2005; Bailey *et al.* 2011).

Requirements to install ballast water treatment systems in ships to limit (or even eliminate) non-indigenous species transfer should be realized in coming years under the International Convention for the Control and Management of Ships' Ballast Water and Sediments (IMO 2004; Norwegian Ministry of the Environment 2009; Frazier, Miller & Ruiz 2013). However, technological and logistical hurdles are expected to delay the immediate impact of this requirement (Balaji, Yaakob & Kho 2014), and until such time some level of regional species introduction threat from this source will likely remain.

Marine biological invasion threats to the Arctic are poorly understood. While the number of documented established marine non-indigenous species, including invasive species, is low in the region (Streftaris, Zenetos & Papathanassiou 2005; Molnar *et al.* 2008; Ruiz & Hewitt 2009), detection effort is also substantially lower compared to other global regions (Streftaris, Zenetos & Papathanassiou 2005; Ruiz & Hewitt 2009). Potentially rapid changes in climate for the coming century in combination with the pronounced effect of changes in the Arctic region (Koenigk *et al.* 2012) are expected to promote the establishment of non-indigenous species (Hoegh-Guldberg & Bruno 2010). Increasing surface temperatures and changing salinity levels are forecast for Arctic waters (see for example Bopp *et al.* 2013; Wisz *et al.* 2015). These changes will likely reduce environmental barriers currently preventing the colonization of more temperate species. This applies to species that may be introduced through human agency, but also to lower-latitude species able to expand their ranges into Arctic waters (Vermeij & Roopnarine 2008; Sorte, Williams & Carlton 2010). Few data are available to compare the rates of introduction mediated by either mechanism. However, the capacity of ships to repeatedly transfer communities of organisms across biogeographic boundaries, and the synergistic interactions among invasive species that can lead to accelerated ecosystem impacts ('invasional meltdown,' Simberloff & Von Holle 1999; Ricciardi & MacIsaac 2000), suggests that human-mediated introductions may need managing. Recent efforts quantifying the vulnerability of Arctic ecosystems to ship-mediated marine species introduction and invasion (Chan *et al.* 2012; Ware *et al.* 2014) indicate some level of threat exists presently and is set to increase as climate change progresses; however, conclusions have been drawn largely in the absence of biological samples.

Vector sampling provides a powerful means of gaining data from which risk at the transport stage of species introduction can be evaluated (e.g. David & Perkovič 2004; Chan, MacIsaac & Bailey 2015a; Chan *et al.* 2015b). From sample data, direct measures of biotic composition and propagule pressure can be obtained providing information directly related to establishment and invasion processes (Lockwood, Cassey & Blackburn 2005). While such information may provide qualitative

assessments of risk, more refined assessments can be achieved when these are combined with models of recipient habitat suitability for candidate species (Herborg *et al.* 2007; Floerl *et al.* 2013).

Temperature and salinity are two physical factors fundamental to population persistence for marine zooplankton (Krause *et al.* 2003; Sunday, Bates & Dulvy 2012), as both influence survival and successful development. Zooplankton have been shown to occupy large portions of their fundamental thermal tolerance limits (Sunday, Bates & Dulvy 2012), suggesting that these are a useful indicator of habitat suitability. Experimentally derived data characterizing marine species' threshold tolerances to both temperature and salinity are often available. Mapping these ecophysiological parameters presents a biologically meaningful way of spatially estimating a species' fundamental climatic niche (Hutchinson 1957; Monahan 2009). More accurate estimates of colonization potential can be further obtained by mapping the typically narrower range of tolerances that are required for successful reproduction (i.e. the regeneration niche – Jackson *et al.* 2009).

In this study, we investigated zooplankton density and taxonomic composition in the ballast water tanks of ships travelling to the Arctic. We use the bulk shipping network to the Norwegian archipelago, Svalbard, as a case study for this assessment. We evaluated the potential for ballast-transported non-indigenous species to establish around Svalbard by mapping reproduction thresholds for candidate species onto projections of current and future ocean climates. Macroinvertebrates constitute a large proportion of all marine organisms demonstrated to cause negative impacts on natural systems (Molnar *et al.* 2008). As such, our overall aim was to evaluate the vulnerability of Svalbard to zooplankton non-indigenous species introduction and establishment. We did so based on an assessment of the following three factors: (i) the identification of non-indigenous coastal species present in the unexchanged ballast water of ships travelling to Svalbard from European ports; (ii) the effectiveness of ballast water exchange by determining whether non-indigenous coastal species were present in the exchanged ballast water of ships and (iii) the suitability of recipient habitats for population establishment of transported non-indigenous species, under present and future projected climatic conditions. By doing so, we provide the first sample-based assessment of present and future ship-mediated species introduction threats to an Arctic region.

Materials and methods

SVALBARD AND THE BULK SHIPPING NETWORK

Svalbard is a Norwegian archipelago extending from 74° to 81° N and 10° to 35° E (Fig. 1). The port marine environments of Svalbard are characterized by a mean annual sea surface temperature of 3 °C (range: −2 to 8 °C) reflecting warm inflow of Atlantic water towards the Arctic and, thus, salinities approaching 35 practical salinity units (psu) (Ware *et al.* 2014). To the north of the islands, temperatures are lower and salinity is affected by the fresher polar mixed layer. Using the ocean-atmosphere global climate model EC-Earth (Hazeleger *et al.* 2012) under the high-end Representative Concentration Pathway (RCP) 8·5 scenario, Svalbard port mean sea surface temperatures are projected to increase by as much as 1·7 and 5·2 °C by 2050 and 2100, respectively (e.g. Koenigk *et al.* 2012; Wisz *et al.* 2015). Evidence of sea surface warming is already apparent around the archipelago (Berge *et al.* 2005; Bjørklund, Kruglikova & Anderson 2012).

Of the range of vessel classes visiting Svalbard, bulk carriers receiving coal are the only class to discharge large quantities of ballast water (C. Ware, unpublished data). Ships travelling to Norway carrying ballast water sourced from an area outside of the Norwegian Exclusive Economic Zone, or Norwegian territorial waters including Svalbard, are required to manage ballast water under the Norwegian Ballast Water Regulation (Norwegian Ministry of the Environment, 2009, Ware *et al.* 2014). Bulk carriers visiting Svalbard typically visit from non-Norwegian European ports where they take on ballast (Ware *et al.* 2014), and are thus required to manage ballast water (Fig. 1).

SHIP OPERATIONS AND SAMPLING

Vessels arriving to Svalbard were sampled between July and October 2011, the period encompassing the majority of coal shipments from Svalbard. All vessels travelled from non-Norwegian ports and were therefore subject to the requirements of the Norwegian Ballast Water Regulation. Five vessels complied with the Regulation, while the remaining three did not perform any form of ballast water management. Thus, ballast water discharged in Svalbard was mostly sourced from marine waters (92%), with the remainder sourced from brackish ports (14–19 psu) (Ware *et al.* 2014). Total ballast water discharged by all eight vessels was 148 000 m³; total ballast water estimated to have been discharged by the entire 2011 fleet of 31 ships travelling to Svalbard was 653 000 m³ (Ware *et al.* 2014). Exchange locations varied greatly (Fig. 1) as did the age of exchanged ballast water upon discharge (range: <1–12 days). The age of ballast water aboard the three vessels that did not perform any ballast water exchange was 7, 12 and 14 days-old upon discharge. Voyage length ranged from 7 to 22 days (mean 10·2, SE ± 1·7) (Ware *et al.* 2014).

Seventeen ballast water samples were collected from eight ships (two samples per ship plus one control sample: see Appendix S1, Supporting information) (Fig. 1). Samples were collected using a plankton net deployed through ballast water tank access hatches or, where there were no access hatches, using a hand pump to draw samples through a sounding pipe. Sampling methods are further described in Appendix S1.

ZOOPLANKTON IDENTIFICATION

Organisms were identified based on morphological characters and/or analysed using molecular methods. Larvae commonly form a large proportion of zooplankton present in ballast water tanks, and are challenging to identify based on their morphology. Typically, studies of organisms collected from ballast water tanks fail to identify a large proportion of meroplanktonic larval forms (e.g. David & Perkovič 2004; Chan, MacIsaac & Bailey 2015a) compromising subsequent assessments of risk. Therefore, we used DNA
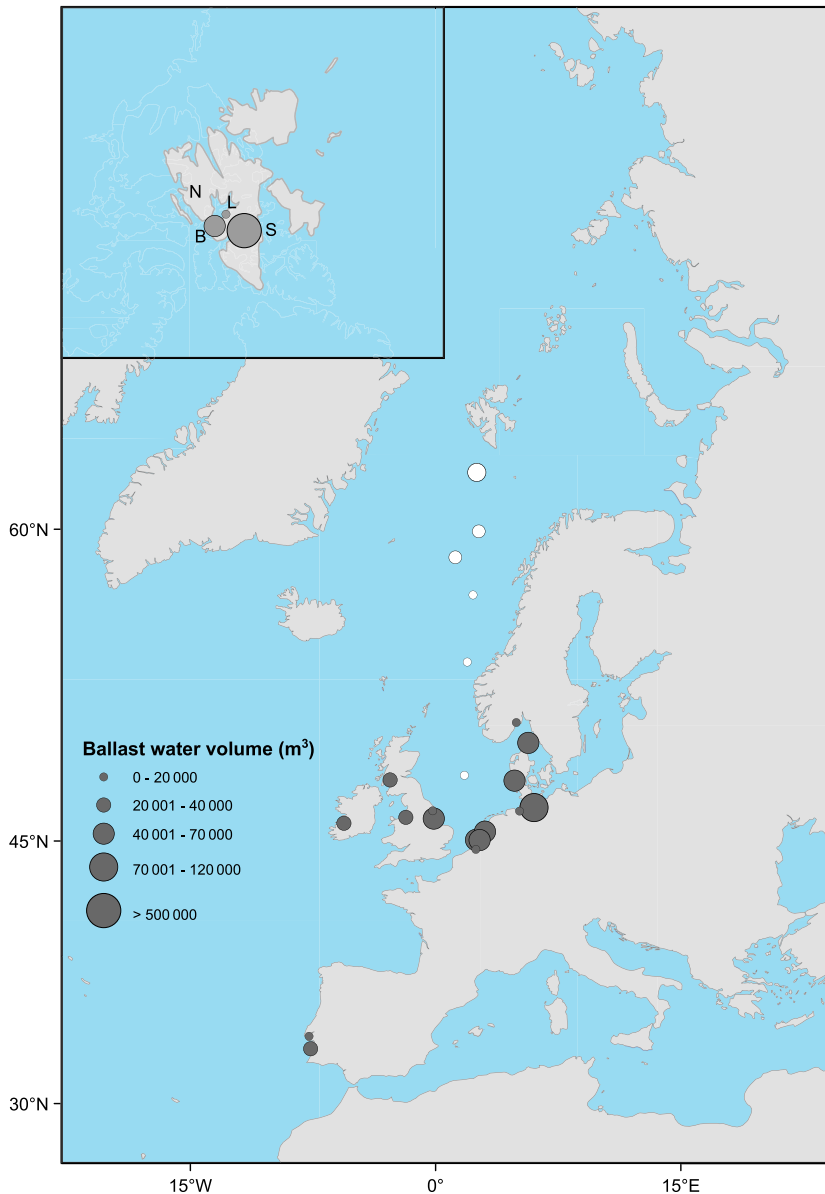
Fig. 1. Regions from which ballast water was sourced by vessels prior to discharge in Svalbard in 2011: grey circles – original ballast water source estimated for all vessels; open circles – mid-ocean exchanged ballast water reported by eight vessels. Inset: ballast water discharged in Svalbard. S – Svea; B – Barentsburg; L – Longyearbyen; N – Ny Ålesund: no ballast water was discharged in Ny Ålesund (reproduced from Ware *et al.* 2014 with permission).

barcoding to resolve species identity primarily in larval organisms, and also to refine identifications based on morphological characteristics. Morphological species identifications were performed under a dissecting microscope by the authors and several taxonomic experts (see Acknowledgements). DNA barcoding methods used for species identification are described further in Appendix S2 and Table S2. The biogeographical status of species (either indigenous or non-indigenous to Svalbard) was assigned based on published distributional data and expert knowledge. We considered species which had been recorded in Svalbard waters, but for which no knowledge of reproducing populations exists, to be non-indigenous. Several species which we classified as non-indigenous (see Results) under this criterion have been previously recorded around Svalbard (e.g. *Metridia lucens* and *Evadne nordmanni*: Weydmann *et al.* 2014); however, their occurrence is best considered ephemeral and a result of advection from the Norwegian Sea with favourable West Spitsbergen Current conditions (S. Kwasniewski, unpublished data). Zooplankton density estimates are reported as numbers of individuals per cubic metre of water sampled.

HABITAT SUITABILITY

From the list of non-indigenous species identified in ballast water samples, Svalbard habitat suitability was modelled for those which we could identify appropriate experimentally derived ecophysiological data for. To evaluate changing habitat suitability for species colonization, we collected data on the period of time required at critical minimum thermal and salinity thresholds for reproduction. Values were obtained for the number of threshold days required to complete all juvenile life stages (including egg hatching where available) for each selected species (Table S3). We acknowledge that numerous other factors may affect whether a non-indigenous species colonizes a novel habitat (both abiotic and biotic). However, we restrict our analysis to these fundamental temperature and salinity reproductive thresholds as they provide a framework for understanding how species may respond to changing climatic gradients.

Regions climatically suitable for reproduction were then mapped using a series of 'if-then-else' statements for each point

in climatic space (i.e. each grid cell) to determine whether threshold criteria were met for each species. If the two conditions (requisite number of days at temperature x and salinity x; i.e. degree days – see Table S3) were met for a cell, the cell was classified as suitable for reproduction; if either condition was not met, the cell was classified as unsuitable. This procedure was then repeated for conditions projected under future climates. We used modelled environmental data for 2011 and model forecasts for the years 2050 and 2100 (RCP 8·5 emissions scenario) regridded to a regular 0·5° resolution (approximately 55 km^2 at the equator) (see Ware *et al*. 2014 Appendix S1, and Wisz *et al*. 2015, for a description of the environmental data and climate scenario projections). Mean monthly data for sea surface temperature and salinity (upper 10 m) were used, which were interpolated to daily values using splines so that degree days could be calculated. The resulting maps indicated areas climatically suitable for reproduction and areas that were outside of these fundamental thresholds.

We focus on a single emissions scenario for two reasons. First, the trajectory of emissions recorded over the last decade, and that which is predicted for the near future, is most comparable to the high-end business-as-usual (RCP 8·5) emissions scenario (Friedlingstein *et al*. 2014; Wisz *et al*. 2015). Second, we do not try to predict the future state of the Svalbard marine ecosystem; instead our aim is to determine how, under a plausible future scenario, conditions required for population establishment for introduced non-indigenous species may change. Our analysis is therefore an assessment of the sensitivity of the biophysical system, rather than a prediction.

For all species, occurrence data were downloaded from the GBIF data base (http://gbif.org/). These were mapped onto current threshold ranges to inspect the present level of regeneration climatic niche filling. All spatial analyses were performed in R (version 3.0.1, libraries [raster, ncdf]; http://www.r-project.org).

Results

ZOOPLANKTON COMPOSITION

Our set of ballast water samples represented 26% of the total shipping fleet discharging ballast water in Svalbard during 2011 (*n* ships = 31), or 23% of the total ballast water discharged. Of the total shipping fleet discharging ballast water, ships travelled to Svalbard from 16 different European ports. We obtained samples from ships that had sourced ballast water from seven of these ports (44·4% of all ports). The seven ports represented in our samples span the range of ecoregions (Spalding *et al*. 2007) connected to Svalbard via ballast water transfer. In total, we identified 73 unique zooplankton taxa among all samples including 36 different genera and 36 different species (see Table S1). Of the total specimens identified to species, barcoding contributed 10 identifications from morphologically cryptic specimens, and confirmed the identity of 11 identifications made based on microscopy (Table S1).Twenty-three species were considered non-indigenous to Svalbard. The copepod, *Calanus finmarchicus*, dominated samples in terms of density (mean = 147·1 ± 69·2 SE individuals m^{-3}) and presence among samples (62% of samples, 62% of ships).

Copepoda dominated samples overall (31% of all taxa). The most abundant non-indigenous species present was the copepod *Centropages typicus* (mean = 19·7 ± 31·9 SE individuals m^{-3}, present in 44% of samples, 37·5% of ships), followed by another copepod, *Temora longicornis* (mean = 4·1 ± 2·6 SE individuals m^{-3}, present in 25% of samples, 20% of ships). Non-indigenous species were present in all but two samples (88% of samples; mean 144·4 ± 66·9 SE individuals m^{-3} per sample), and were found in at least one sample from all ships.

Samples collected by pump contained lower density and richness estimates compared with those collected by net; samples collected by pump, however, were of smaller volume. Mean richness across all samples was 12·2 taxa (±2·2 SE). Zooplankton density per sample ranged from 10 to 4500 m^{-3} (mean 1522 ± 335 SE individuals m^{-3}) with pump samples accounting for the three smallest sampled densities. The mean number of non-indigenous species across all samples of unexchanged ballast water was 2 (±0·8 SE) per sample, while mean non-indigenous species richness of exchanged ballast water samples was 7·6 (±1·8 SE). There was a possible positive effect of ballast water exchange on the richness of non-indigenous species identified in samples (see Appendix S3). However, we note that we have too few sample replicates to formally test this association, or the effects of voyage duration and sampling technique.

HABITAT SUITABILITY

Reproductive thresholds were available to explore Svalbard habitat suitability under present and future environmental scenarios for eight non-indigenous species (Copepoda – *Acartia tonsa, Eurytemora affinis*; Decapoda – *Carcinus maenas, Hemigrapsus takanoi, Cranagon crangon*; Cladocera – *Podon leuckartii*; Balanidae – *Amphibalanus improvisus*; Austrobalanidae, *Austrominius modestus*).

The known distributions of all species were within their respective ecophysiological reproductive limits, with the exception of one occurrence location for *C. crangon* that lies north of the threshold margin (Fig. 2, and global distribution show in Fig. S1). Suitable habitat was also estimated to be unoccupied for all species, suggesting partial underfilling of the fundamental climatic niche (Fig. 2; Fig. S1). *P. leuckartii* was the only one of the eight species apparently ecophysiologically suited to present Svalbard port conditions (Fig. 2 bottom row). The scenario comparisons indicate that conditions permitting successful reproduction may shift poleward for all species over the coming century. Under the 2050 scenario, suitable conditions were estimated to be present as far north as Svalbard port environments for both *A. modestus* and *P. leuckartii*. Locations around the tip of southern Svalbard were projected to provide suitable conditions for *A. improvisus, A. tonsa* and *E. affinis*. Under the 2100 scenario, modelled reproduction thresholds of all study species overlap Svalbard port environments, with the
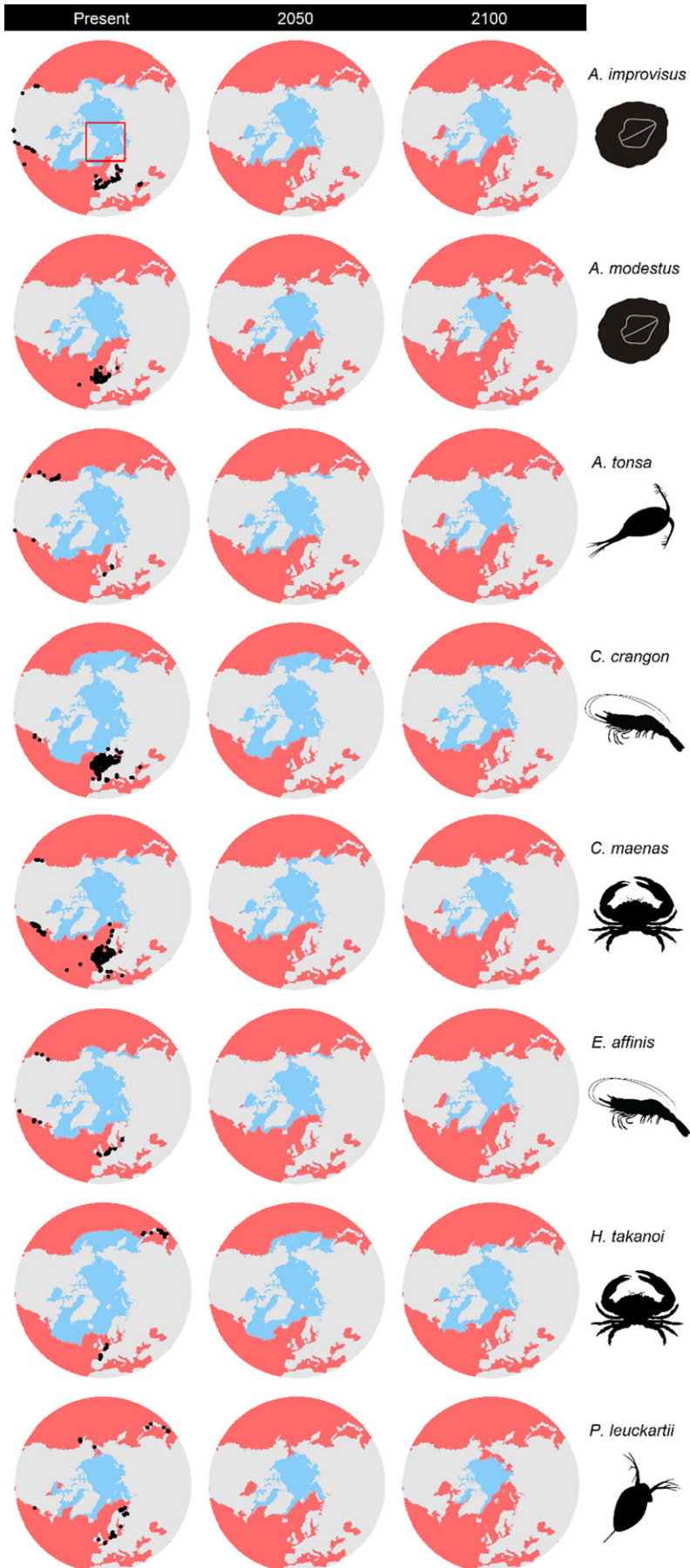
Fig. 2. Projected ecophysiological thresholds for the eight assessed non-indigenous species. Thresholds were based on the number of days required at critical minimum temperature and salinity values for successful reproduction. Thresholds were projected into the future based on ocean climates forecast under the Representative Concentration Pathway (RCP) 8·5 emissions scenario. Red indicates suitable habitat (i.e. critical values above the minimum thresholds), while blue indicates unsuitable habitat (i.e. critical values below the critical thresholds). Black points indicate known occurrences of the species (http://www.gbif.org/). Maps are North Pole Lambert Azimuthal Equal Area Projected and show latitudes above 30°. The location of Svalbard is highlighted in the first panel.

exception of those for *C. crangon* and *H. takanoi* (Fig. 2). Suitable conditions extending just beyond Svalbard and the Russian archipelagos of Franz Joseph Land and Severnaya Zemyla represented the most northerly extensions for any of the eight study species under the 2100 scenario, but substantial northerly extensions were also evident around Southern Greenland, in Hudson Bay, and in the Sea of Okhotsk.

Discussion

Our sampling demonstrated that high densities of zooplankton, including many non-indigenous species, are discharged through ballast water to Svalbard. Notably several well-known marine invaders (e.g. the barnacles *A. improvisus, A. modestus,* and the crab *C. maenas*) are introduced to Svalbard in this way. While Svalbard hydrographic conditions currently are suitable for only one of the assessed non-indigenous species, future sea surface conditions may permit the successful establishment of more non-indigenous species; under the 2100 scenario, six of the eight species modelled could potentially establish in Svalbard port environments. The assessed species have caused wide-ranging impacts elsewhere including fouling (*A. modestus*; Molnar *et al.* 2008), parasite introduction (*C. crangon*; Stentiford *et al.* 2012), reducing indigenous diversity and abundance (*C. maeans*, Grosholz *et al.* 2000; *A. modestus*, Bracewell *et al.* 2012), and trophic cascades (*C. maeans*, Trussell *et al.* 2004; *A. improvisus*, Kotta *et al.* 2006). Our results indicate an increasing vulnerability of Svalbard to marine species invasion under the climate change scenario we explored here. Our scenario projections also identified suitable habitat for the modelled non-indigenous species in other Arctic waters. While not coupled to measures of propagule pressure in other regions, our projections demonstrate the potential for Arctic-wide increases in the availability of habitat for potential invaders from lower latitudes.

BALLAST WATER DYNAMICS AND HABITAT SUITABILITY

Zooplankton densities found in this study were within the ranges of samples collected from ships arriving at other high latitude regions (Hines *et al.* 2000; Chan *et al.* 2014). Our samples were comprised mostly of species considered indigenous to Svalbard. These were predominately calanoid copepod species, the ranges of which extend much further south, though not to ports of origin (http://www.gbif.org/). Therefore, these species were most likely collected from oceanic locations during ballast water exchange. This likely accounts for the higher densities of organisms found in samples from ballast water tanks that had been exchanged compared to unexchanged. We found lower zooplankton densities in samples from ships with older ballast water, but note that any inferred association is confounded by our requirement to use different sampling methods on different ships and the low number of

independent samples (see also Appendix S3). Nevertheless, survivorship studies carried out over the duration of voyages elsewhere (Simard *et al.* 2011; Chan *et al.* 2015b), and statistical associations (Chan *et al.* 2014), have previously demonstrated that increasing voyage durations tend to reduce zooplankton density and richness.

We also observed higher numbers of non-indigenous species in samples of exchanged ballast water compared to unexchanged ballast water, and identified a possible positive effect of ballast water exchange on non-indigenous species richness (Appendix S3). Non-indigenous species were comprised of marine species likely sourced during mid-ocean exchange, but also of coastal species unlikely to be present at the location of exchange. As with the finding of lower densities of organisms in samples taken from older ballast water, this observation requires further sampling to determine whether it is indicative of a more general trend. However, the suggestion is that the effect of ballast water exchange is a poorer mechanism of reducing non-indigenous species densities than the effect of longer voyages alone for the studied shipping routes. It is plausible that non-indigenous species that do not get flushed from ballast water tanks during exchange benefit from the addition of oxygen and nutrients introduced (Carver & Mallet 2004; Briski *et al.* 2012; Chan *et al.* 2015b).

Organisms most likely to survive ballast water exchange are those that originated from coastal or marine ports rather than freshwater ports, and are thus tolerant of oceanic salinities. The sampling of seven *C. maenas* megalopae from one ship that initially took on ballast water from the coastal port of Esbjerg, and subsequently performed ballast water exchange, exemplifies this. This finding is also mirrored in other studies. Briski *et al.* (2012) found several adult *C. maenas* individuals in recently exchanged ballast water, highlighting the potential for ballast water exchange to promote survivorship. Chan *et al.* (2015b) also reported increases in species richness and abundance following ballast water exchange during transoceanic voyages.

Sub-optimal performance of ballast water exchange may mean non-indigenous species transfer occurs elsewhere in the Arctic. Increasingly, trans-Arctic shipping routes (i.e. the Northern Sea Routes and the North East Passage) are becoming viable alternatives to established Asian-European routes via either the Suez or Panama canals (Miller & Ruiz 2014). The associated potential for the introduction of largely novel species assemblages to Asian or European ports with this change in shipping pattern warrants greater attention (Miller & Ruiz 2014).

Our analyses showed that ranges of suitable habitat for all eight study species are estimated to increase into the Sea of Okhotsk and parts of Hudson Bay. Data exist elsewhere with which to compare the Svalbard shipping network to other Arctic shipping networks. Chan *et al.* (2012) reported that vessels transporting ballast water to Canadian Arctic ports did so from several of the same

European ports as those from which ships in this study travelled. Moreover, several copepod species present in our samples were also present in ballast water samples taken from ships arriving to the Canadian Arctic port of Churchill (Chan, MacIsaac & Bailey 2015a), though these did not include species for which we modelled habitat suitability. Ballast water exchange is a requirement for ships travelling from European ports to Canadian waters, and it seems likely that the copepod species identified were sourced during mid-ocean exchange. No coastal species indicating ineffective ballast water exchange were identified in the Canadian study, although higher resolution taxonomic data than reported would be required to fully resolve this. Reported voyage times to the Canadian Arctic were typically longer than in the current study (range 8–30 days) (Chan *et al.* 2012). Of note, Chan, MacIsaac & Bailey (2015a) also collected biofouling samples from ships arriving to the port of Churchill. Species identified again included non-indigenous species present in the ballast water samples we collected, including both *A. improvisus* and *A. modestus* for which suitable habitat is projected to exist at Churchill by the end of the century (Fig. 2). Elsewhere in the Arctic, ships discharging ballast water into Alaskan ports also travel from European (though mainly Asian) ports (McGee, Piorkowski & Ruiz 2006). Our methods could be extended to assess whether suitable habitat may be available for additional species elsewhere under scenarios of future change.

IMPLICATIONS FOR RESEARCH AND POLICY

We should be mindful when interpreting our results that the future climate is inherently uncertain, and we have applied the results of a single model of a single carbon emissions pathway. The robust feature of the analysis is the direction of the changes. More species from lower latitudes will likely be able to establish in Arctic waters given ongoing transport. While we have focussed on the potential for species colonization mediated by shipping, species will naturally expand their ranges poleward as climates continue to warm (Sorte, Williams & Carlton 2010). It is unrealistic, and probably undesirable to preclude species expanding their ranges poleward naturally in the face of warming conditions. The ecological impacts of range-shifting species may be as great as those from introduced non-indigenous species (Sorte, Williams & Carlton 2010), though can be reduced by the presence of natural enemies with overlapping ranges. The greatest threat of impacts from range-expanding species most likely lies where new species arrivals occur at such a rapid rate that ecosystem processes are overwhelmed (Lockwood, Cassey & Blackburn 2005). In such a scenario, ship-mediated introductions may have limited consequences. Continued introduction of species by shipping in the face of warming conditions, however, is likely to enable species to track their climatic envelopes more accurately and result in greater propagule pressure. While this suggests effective management interventions should be beneficial, the interface between global change biology and invasion ecology has not been sufficiently explored in the context of marine invasions.

In the case study addressed here, shipping bridges distinct biogeographic marine provinces ('Arctic' and 'Temperate North Atlantic' provinces; Spalding *et al.* 2007). Biotic interchange across these provinces occurs (e.g. Berge *et al.* 2005; Bjørklund, Kruglikova & Anderson 2012), but whether the natural arrival of more southerly non-indigenous species is inevitable under favourable climate scenarios is yet to be considered. Threats of ship-mediated biological invasion are more clearly identifiable on Arctic shipping routes that span considerable longitude, across which natural dispersal is unlikely, but join regions experiencing more similar temperature regimes. Such movements are more likely to result in successful establishment of biological invaders under present climates. Arctic destination shipping (Miller & Ruiz 2014) such as that which occurs on the Northern Sea Routes or shipping connecting European and Canadian Arctic ports, represent such high-risk routes. These shipping routes may be leading candidates for the adoption of ballast water treatment technologies. Implementing this will require transitioning the regulatory framework appropriately, and improving levels of compliance beyond those reported in this study. The International Ballast Water Convention performance standard ('D2,' IMO 2004) sets upper limits for the allowable number of viable organisms of several specified size-classes released in ballast water discharge. However, the ballast water management technologies approval regime specified in the Convention (G8 guidelines) does not currently require testing under cold water conditions (IMO 2004; see also Drillet *et al.* 2013). Consequently, trials evaluating ballast water treatment efficacy under polar conditions will be required. One additional management avenue identified here is the potential that not exchanging ballast water confers improved outcomes over performing an exchange. We expect the conditions under which this may be the case to be limited to certain voyage durations and ports of departure, and may therefore only be relevant to particular routes. Further sampling or experimental work would be worthwhile to evaluate this possibility given the potential benefits.

Managing the emerging invasion risks in the face of uncertainty suggests an adaptive management framework with appropriately defined objectives. Where an objective of preventing ecosystem impacts from natural range-expanding species is unrealistic, investment in modified ballast water management should reflect this. Our work identifies a need for alternative ballast water management practices to those currently used in order to prevent the introduction of non-indigenous species. Whether this is an appropriate policy shift for all Arctic shipping routes requires careful consideration of risk-return trade-offs. Appropriate decision aid tools such as multi-criteria decision analysis (Liu *et al.* 2015) and new research on the

role of marine species translocations under climate change will be required to adequately assess risk and derive appropriate regional policies.

CONCLUSIONS

By evaluating species introduction and establishment risks associated with a major vector of marine species transfer, our study offers an effective basis for developing more informed measures to manage species translocations in Arctic waters. It highlights that non-indigenous species are routinely introduced into Svalbard waters through ballast water discharge, most of which are presently inconsequential. Bulk carrying ships travelling to other Arctic destinations do so from the same geographic port regions as did ships in this study; therefore, we expect species assemblages similar to those sampled from ships in this study to be transferred more widely across the Arctic, with greater potential for negative impacts from biological invasions. The risk of a number of known invasive species will increase rapidly over the coming decades. Appropriately managing these emerging risks will require flexible, adaptive management frameworks under which options can be prioritized and targeted appropriately to routes deemed sufficiently risky. This will require improving our understanding of the potential consequences of different patterns of species translocations.

Data accessibility

DNA sequences are available from GenBank: GenBank accession numbers KT952463–KT952516. Climate data used to map habitat suitability are available from Dryad Digital Repository doi:10.5061/dryad.k18nk (Ware *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Sampling methods.

Appendix S2. DNA barcoding methods.

Appendix S3. Ordination of ballast water data.

Table S1. Zooplankton identified from ballast water samples.

Table S2. Primers used to barcode sampled organisms.

Table S3. Critical reproductive thresholds for the studied non-indigenous species.

Figure S1. Known distributions of each of the eight studied non-indigenous species.

Figure S2. CCA ordination summarizing the non-indigenous species composition in samples of ships ballast water as a function of considered variables.