Melting barriers to faunal exchange across ocean basins

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Abstract

Accelerated loss of sea ice in the Arctic is opening routes connecting the Atlantic and Pacific oceans for longer periods each year. These changes will increase the ease and frequency with which marine birds and mammals are able to move between the Pacific and Atlantic ocean basins. Indeed, recent observations of birds and mammals suggest these movements are already occurring. Reconnection of the Pacific and Atlantic Ocean basins will present both challenges to marine ecosystem conservation and an unprecedented opportunity to examine the ecological and evolutionary consequences of

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faunal exchange in real time. To understand these changes and implement effective conservation of marine ecosystems, we need to further develop modeling efforts to predict the rate of dispersal and consequences of faunal exchange. These predictions can be tested by closely monitoring wildlife dispersal through the Arctic Ocean and using modern methods to explore the ecological and evolutionary consequences of these movements.

INTRODUCTION

The marine fauna of the Arctic has a dynamic history of connectivity. Glacial cycles during the Pleistocene periodically obstructed interchange between the marine biota of the Pacific and Atlantic oceans (Marincovich and Gladenkov 2001), due to both sea ice and the intermittent presence of the Bering land bridge. During this time, distinctive assemblages of polar, subpolar, and temperate taxa populated each ocean basin (Marincovich et al. 1990, Vermeij 1991). Potential exchange between these communities could have occurred episodically during interglacial periods when sea ice was reduced (Polyak et al. 2010). For much of the Pleistocene, however, glacial periods were marked by thick layers of perennial sea ice that isolated the ocean basins (Polyak et al. 2010). Cooling in the Holocene resulted in persistent ice plugs in the Canadian Arctic Archipelago, which famously impeded mariners from making the fabled crossing through the "Northwest Passage" of the Arctic Ocean. It has also created an impassible physical boundary for most marine tetrapods, including Arctic and sub-Arctic species of marine mammals and seabirds (Haley 1984, Dyke et al. 1996). Low temperature and productivity in these ice-covered waters are also thought to create a dispersal boundary for smaller species with pelagically dispersing larvae (Vermeij 1991, Reid et al. 2007).

As a result of this geological and climactic history, faunal exchange between the Atlantic and Pacific basins has been infrequent over the last 3 million years for many species. The barrier formed by sea ice, cold water, and relatively low levels of productivity compared with temperate ecosystems produced a number of evolutionary distinct lineages and sister taxa with ranges limited to either the Pacific or the Atlantic Oceans (Friesen et al. 1996).

Today, warmer temperatures are reducing sea ice extent and thickness, resulting in more open ocean in the spring and summer than ever before (Stroeve et al. 2012). Current models suggest that by 2050 the Arctic ocean could be ice-free during September (Liu et al. 2013). The retreat of Arctic ice is recognized as the source of new challenges for Arctic ecosystem conservation (reviewed in Grebmeier 2012). Specifically, the increased rates of faunal exchange between the Atlantic and Pacific Ocean basins predicted by Vermeij and Roopnarine (2008), and observed by Reid et al. (2007) will raise new conservation questions.

To address the variety of conservation concerns and research opportunities arising from increasingly ice-free Northwest Passages we 1) review the evidence that the rates of tetrapod faunal exchange between basins are increasing, 2) identify some of the challenges this may pose for marine conservation, and 3) make preliminary recommendations for monitoring and research in an era of increasing connectivity between ocean basins.

EVIDENCE FROM TETRAPODS OF INCREASING FAUNAL EXCHANGE BETWEEN THE ATLANTIC AND PACIFIC OCEAN BASINS

The reduction of Arctic sea ice has already had ecological consequences for marine mammals and seabirds (see a review in Kovacs et al. 2011). Here, we focus on recent observations that provide evidence for novel inter-basin movements.

Satellite tracking of bowhead whales (*Balaena mysticetus*) provides the most direct evidence that the retreat of Arctic ice is increasing exchange between basins. Currently, separate populations of bowhead whales exist on either side of the Northwest Passages. While genetic evidence indicates both ancient and recent gene flow between these populations (Alter et al. 2012), the lack of bowhead fossils from interior locations in the Canadian Arctic Archipelago suggests that sea ice created a barrier to exchange during parts of the mid- and late Holocene (Dyke et al. 1996). In the summer of 2010, the Northwest Passages were sufficiently free of ice to allow individuals from two different populations to feed in the same region at the same time (Heide-Jorgensen et al. 2012). Although these two particular individuals retreated to their respective oceans after ten days, their occupation of common territory demonstrated the potential for increased ease of inter-population exchange (Heide-Jorgensen et al. 2012).

In light of the bowhead whale observations, recent sightings of gray whales (*Eschrichtius robustus*) in the Atlantic are intriguing. The gray whale currently occupies coastal margins of the North Pacific. Historically the range of the Pacific population extended from Japan to Mexico along the continental margin, and an extinct North Atlantic sister population is inferred from subfossil remains in both the western and eastern North Atlantic (Mead and Mitchell 1984, Bryant 1995). Gray whales occupy the edge of sea ice (Figure 1), but unlike bowhead whales, are unable to transit areas of thick consolidated ice (Rice and Wolman 1971). In the spring of 2010, a single gray whale was observed off the coast of Israel, marking the first record of the genus in the Atlantic for 200+ years (Scheinin et al. 2011). Subsequently, one or more individuals were sighted off the coast of Namibia in May and June of 2013 (Paterson 2013). The most likely route for a (re)-colonization of the Atlantic by gray whales is subject to debate. Although it seems unlikely that the first colonists would choose the Northwest Passages due to the frequent presence of dense pack ice in narrow inlets and danger of entrapment, a long transit through tropical pelagic regions seems even less likely, as gray whales are a primarily coastal species that feed in temperate or polar waters. However, recent satellite tag data has demonstrated that gray whales are capable of unexpected movements and migrations (Weller et al. 2012), indicating that our understanding of this species' ecology and biogeography may change with additional data from new technologies.

The potential ecological impact of cetacean range expansion is highlighted in work documenting the feeding of killer whales (*Orcinus orca*) in Hudson Bay (Ferguson et al. 2010). Killer whales were previously restricted in the Arctic by consolidated ice (Dyke et al. 1996). Recently they expanded into ice-free areas of Hudson Bay where they have been documented preying upon arctic marine mammals of the region including beluga (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), and bowhead (Ferguson et al. 2010). The arrival of a novel top predator could have cascading effects on the ecosystem as predators and prey respond to changes in the structure of the food web.

Recent seabird records also suggest movements through the Northwest Passages, as predicted by habitat models (Huettmann et al. 2011). The northern gannet (*Morus bassanus*, Sulidae) has a distribution limited to the North Atlantic Ocean. Sea ice presents an effective barrier because this species feeds on fish and needs access to open water when flying long distances. However, one was observed twice in Alaska in 2011 (Heinl 2011). In April 2012, a northern gannet reached the Farallon islands off Northern California (Webb 2012). These records are the only Pacific Ocean sightings in recorded history, indicating that previous dispersal events across tropical oceans were extremely unlikely. Its mode of feeding means it is unlikely to have reached the Pacific by flying over land or extensive areas of ice. Thus, the most plausible route to explain its arrival in the Pacific is via the Northwest Passages or Arctic Ocean now that mid-transit fishing is possible during the summer season. Such movements should become even easier as open water becomes more widely available in the Arctic Ocean.

The Manx shearwater (*Puffinus puffinus*, Procellaridae) is another seabird with a known breeding range limited to the North Atlantic. It has been increasingly observed in the North Pacific over the last several decades, with breeding suspected in the North Pacific (Force et al. 2006). Pacific sightings for a second species, the great shearwater (*Ardenna gravis*), have also increased over the last few years (Figure 2). Most sightings occurred in the boreal summer, including two records from off of California in the summer of 2013 (Hamilton et al. 2007, Shearwater 2013). Unidentified large, dark shearwaters have also been recorded from James Bay, Ontario (Holden 2010), out of range for sooty shearwater (*Ardenna griseus*) or short-tailed shearwater (*Ardenna tenuirostris*). While shearwaters are long-range migrants that may be capable of a southerly passage, the increasing frequency of out of range observations, and the fact that they occur during the summer when sea ice is at a minimum, suggest movement across the Northwest Passages and Arctic Ocean.

Auks (Alcidae), a lineage of diving birds currently restricted to the Northern Hemisphere, also provide evidence for movement through the Northwest Passages. Sea ice may impact the feeding of these birds, restricting the ranges of some alcid species to the Pacific. Two Pacific species of auk have recently been observed in the Atlantic. Sightings of long-billed murrelet (*Brachyramphus perdix*) have increased (Vinicombe 2007), and the tufted puffin (*Fratercula cirrhata*) was recently recorded in European waters (Magpie 2009) and Maine (Brunswick 2014). Additionally, the bridled morph of the common murre (*Uria aalge*), which makes up 50% of individuals at some North Atlantic colonies, was first recorded in the Pacific in 2008 (Schmidt and Warzybok 2011).

Although current evidence for novel faunal exchange between the Atlantic and Pacific basins through the Northwest Passages is still circumstantial in tetrapods, there is a clear need to consider how these movements will impact marine ecosystems. We propose the term "inter-basin taxa" to describe species that move between basins as a result of availability of open water in the Northwest Passages and Arctic Ocean. As the Arctic sea ice melts, inter-basin taxa will become increasingly common and will need to be explicitly considered in conservation and research efforts.

IMPLICATIONS FOR MARINE ECOSYSTEM CONSERVATION AND RESEARCH

Arctic ice retreat is already recognized as the source of new challenges for marine ecosystem conservation. Even in the absence of faunal exchange, increased ship traffic, fishing and oil exploration are already creating potential environmental problems as the Arctic becomes more accessible to humans (Huntington 2009, Alter et al. 2010, Moore et al. 2012). While these impacts are of most immediate importance, faunal exchange may have ecological effects that should be considered in long-term conservation planning.

New habitats will be colonized and distinct populations and species will mix as the reduced sea ice allows increased exchange across the Arctic. Range changes can have ecological impacts as expanding species compete with native fauna for prey, breeding sites, and other resources. Hybridization between previously diverged lineages can impact demographic and evolutionary trajectories for both populations. However, identifying which species will be most likely to be affected remains a challenge.

We identified marine mammal and bird species for which inter-basin movements appear to be limited by sea ice (Table 1). As sea ice in the Arctic is reduced, these species are most likely to become inter-basin taxa. These taxa can be divided into two groups: 1) Polar Species (PS), which currently inhabit available open water above the Arctic Circle (66.5622°), although individual populations may not yet be connected because of sea ice barriers, and 2) Ice Edge Species (IES), which traditionally inhabit the area south of the edges of the arctic sea ice, and take advantage of both subpolar and north temperate environments. Species in which only one sex occupies a polar range (i.e. sperm whale) were considered IES, while marine birds with transcontinental migration routes (some ducks and gulls) were excluded. The inter-basin taxa observed to date have been Ice Edge Species.

We expect that inter-basin movements will become increasingly common as Arctic sea ice recedes, but detecting such movements will be easier in some cases than others. Detecting the presence of a new species in the Atlantic or Pacific requires only a single observation, whereas detection of newly overlapping ranges of previously separate populations requires detailed movement records for individuals, such as were obtained for bowhead whales via satellite tagging, or population genetic evidence of recent inter-basin gene flow. Furthermore, ice edge species may be easier to detect than polar species, as these taxa will move across the Arctic and then seek more temperate environments, where there are higher densities of human observers.

CONSEQUENCES OF FAUNAL EXCHANGE FOR SPECIES AND ECOSYSTEMS

Paleontological and historical evidence demonstrates that faunal exchange between previously isolated communities can have profound impacts. For example, the rise of the Isthmus of Panama facilitated the Great American Biotic Interchange between North and South America. Placental mammals, particularly rodents, invaded South America, where they contributed to high extinction rates in local fauna as they competed for resources (Webb 2006). More recently, the opening of the Suez Canal in 1869 increased exchange of marine organisms between the Red Sea and the Mediterranean Sea. Many immigrants were at an advantage as they expanded into the Mediterranean due to the greater

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environmental variability of the Red Sea. The resulting ecological advantages allowed some of these taxa to outcompete natives (Mooney 2001). We expect similar patterns to emerge as the sea ice melts and rates of faunal exchange increase in the Arctic.

As with introduced or invasive species in other environments, inter-basin movements by marine birds and mammals may dramatically impact their habitats. Gray whales for example have been described as ecosystem engineers, transforming soft-sediment environments through excavation and bioturbation (Berke 2010). Seabirds play critical roles as epipelagic predators, scavengers, and in the transfer of marine nutrients to terrestrial environments (Wainright et al. 1998). The introduction of novel predators may alter food web dynamics and prey abundances resulting in substantial changes in community structure and ecosystem services (Grebmeier 2012). These impacts will be felt most strongly in systems without ecologically analogous species, or where geminal taxa have been lost. For example, the extirpation of gray whales from the North Atlantic and the disappearance of the genus *Morus* (gannets) from the North Pacific in the late Pleistocene left open niches after local extinctions (Bryant 1995, Nelson 2010).

Disease transmission may also play a significant role in restructuring newly joined marine tetrapod communities. Infections from *Toxoplasma gondii* are on the rise in Arctic marine mammals with transmission linked to interspecific predation (Jensen et al. 2010). Changes in the transmission patterns have caused phocine distemper virus, which historically affected Arctic dwelling seals, to infect more temperate populations. Patterns of communicability will change as previously isolated populations come into more frequent contact with related species (de Swart et al. 1995). Cetacean morbilliviruses affect small odontocete species across a wide geographic range (Rowles et al. 2011) and may reach even farther if separated populations come into contact. Transmissibility of avian influenza, and even *Borrelia garinii* (a causative agent of Lyme Disease), may increase in seabirds and waterfowl if populations renew contact along arctic passages (Staszewski et al. 2008). The potential for pathogens to jump vectors may also exacerbate disease transmission as previously isolated taxa suddenly exist in close proximity.

A PATH FORWARD

With the accelerating disappearance of Arctic sea ice, documenting shifting patterns in wildlife movements is increasingly urgent. In the Pacific, a Distributed Biological Observatory has been created by NOAA to establish baseline biogeographic boundaries and abundances (Grebmeier 2012). These data can be used to develop an understanding that will facilitate conservation of Arctic birds and mammals. We propose the following areas of emphasis:

Monitoring animal movements and the ecological and evolutionary consequences of their range shifts. With mounting evidence of increasing faunal exchange, it will be important to augment monitoring programs designed to document these movements:

- Increased satellite tagging and tracking of individuals from populations/species that are likely to make the crossing to ensure real time records.
- Employing citizen science programs to increase recorded observations of focal taxa, and accumulate records of migration events. Volunteer and hobbyist

programs are already the most active source of species level data for birds and mammals (e.g., eBird; Sullivan et al. 2009). The additional data points they offer provide more accurate time stamps for inter-basin transits.

- Collecting tissue samples and using genetic data to verify species (and where possible, population of origin).

Investigating ecological and evolutionary consequences of faunal exchange. As populations of organisms divide or become reconnected, a variety of evolutionary outcomes are possible:

- Inter-basin migrants could expand into territory occupied by genetically distinct populations creating competition for resources within a species, or with more distantly related taxa.
- Previously isolated populations could connect and interbreed resulting in homogenization of genetic diversity and slowing of local adaptation.
- Post-transit, founder populations could rapidly diverge from parent lineages under selection pressures driven by exposure to novel habitats and conditions, or simply as a result of genetic drift.

Gathering baseline data for PS and IES before they become inter-basin taxa will inform estimates of genetic diversity, drift and gene flow in populations that are currently isolated. This opportunity will permit more accurate prediction of the evolutionary consequences of novel migration. As colonizers move into new habitats and mate with new partners, follow-up time series data will allow us to interpret these changes as they occur and project into the future. In a comparative framework, genomic and transcriptomic data will help illuminate how these organisms respond physiologically to changing conditions and new habitats. The dramatic changes occurring in the Arctic present an opportunity to better understand the evolutionary processes that occur during colonization of new habitat in a comparative framework.

Projecting habitat suitability for dispersing organisms. Species distribution models are a common tool used to predict future distributions as climatic conditions change (Elith and Leathwick 2009). To date, the vast majority of these efforts have focused on terrestrial ecosystems where barriers to dispersal are much less dramatic than Arctic sea ice. Species distribution models have immediate applications to projecting the movements of marine mammals and birds as they colonize new ranges in the Pacific and Atlantic basins (Huettmann et al. 2011, Kaschner et al. 2011). Recent work estimating the suitable habitat range of gray whales projects highly suitable habitat for this species across the northeastern US and Canada (Kaschner et al. 2011, www.aquamaps.org 2013). Incorporating predictions about future feeding grounds, breeding locations, nesting sites and population densities will strengthen existing conservation efforts.

Policy and Management Implications. The ecological consequences of melting sea ice, including invasions by novel species, disease, habitat alteration, colonization of new habitats, and changing wildlife communities, all have policy and management implications. The proposed research to document shifting patterns, monitor movements and ecological/evolutionary consequences in real time, and project habitat suitability for dispersing organisms should inform policy design and management action in a number of ways.

Environmental protection of the Northwest Passages may need updating. The isolation and harsh climate of the biologically rich and ecologically sensitive Canadian Arctic Archipelago have effectively protected the area from resource exploitation, development, tourism, and commercial shipping. The opening, and the right of transit, could fundamentally change the economic calculus for exploitation, development, and shipping, posing numerous environmental and social risks (Kovacs et al. 2011). Moreover, the seasonal opening of the Northwest Passages could alter the legal status of the waters. Canada currently considers the passage as internal waters, but other nations dispute this and consider it an international strait, which comes transit rights per UNCLOS (King 2008). The change in legal status calls into question the environmental protections (national, international, customary) that apply (King 2008), and the emerging threats pose new challenges for any planned protection.

Conservation and management plans may also need amending. Information on changing species distributions and habitats are relevant to widespread calls to move towards ecosystem-based management, now mandated by US National Ocean Policy and called for by international agencies such as the United Nations Environmental Program. A key challenge with ecosystem based management is ensuring overlap of ecosystem and governance scales (Ruckelshaus et al. 2008), so changing movements and habitats will need to be considered in ecosystem based management plans. Another example where new information could be pertinent to management relates to marine mammal conservation and management plans required by the International Whaling Commission, as well as whaling permits (Simmonds and Isaac 2007).

Finally, novel movements across disappearing barriers will change our definitions and management of invasive species. Climate change impacts will need to be incorporated into analyses of pest risks, required by current laws such as the International Plant Protection Convention, and invasion-pathways assessments, mandated by the National Aquatic Invasive Species Act of 2007 (Pyke et al. 2008). Efforts to control invasive species will require a systematic, coordinated approach that targets key vectors and anticipates climate impacts (Bax et al. 2003). Current international and national policy and research on marine invasive species are insufficient to address the problem, especially under changing environmental conditions (Simberloff et al. 2005). The proposed research could support concrete actions, such as an early warning system for disease and invasive species that would (i) identify and eliminate threats as they appear; (ii) predict where outbreaks may occur and undertake risk assessments; and (iii) identify invasion pathways

CONCLUSIONS

Climate change, sea-level rise, and ocean acidification pose unprecedented changes to our marine environment. In the Arctic, one major change will be the increased potential for faunal exchange between ocean basins. By anticipating faunal exchange associated with the opening of Northwest Passages, we will be able to take advantage of an ecological experiment of grand proportions. Augmenting monitoring programs that track inter-basin movements and the exchange of genetic material and diseases will be critical to documenting these changes. These data will inform our inferences about some of the past episodes of global change on biogeography, evolution, and ecological interaction, as well as help predict consequences for the accelerating changes happening in the world today. We can further use these data to inform modern conservation and management policy. Effective policy requires careful consideration of changing conditions. Ongoing faunal exchange in the arctic offers managers the opportunity to lead by example as climate change threatens to rewrite ecosystems around the world.

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LITERATURE CITED

Alter, S. E., H. C. Rosenbaum, L. D. Postma, P. Whitridge, C. Gaines, D. Weber, M. G. Egan, M. Lindsay, G. Amato, L. Dueck, R. L. Brownell, M. P. Heide-Jorgensen, K. L. Laidre, G. Caccone, and B. L. Hancock. 2012. Gene flow on ice: the role of sea ice and whaling in shaping Holarctic genetic diversity and population differentiation in bowhead whales (*Balaena mysticetus*). Ecology and Evolution 2:2895-2911.

Alter, S. E., M. P. Simmonds, and J. R. Brandon. 2010. Forecasting the consequences of climate-driven shifts in human behavior on cetaceans. Marine Policy 34:943-954.

Bax, N., A. Williamson, M. Aguero, E. Gonzalez, and W. Geeves. 2003. Marine Invasive Alien Species: a Threat to Global Biodiversity. Marine Policy 27:313-323.

Berke, S. K. 2010. Functional Groups of Ecosystem Engineers: A Proposed Classification with Comments on Current Issues. Integrative and Comparative Biology 50:147-157.

Brunswick, C. N. 2014. Tufted Puffin seen on Atlantic coast for 1st time since 1830s.

Bryant, P. J. 1995. Dating Remains of Gray Whales from the Eastern North-Atlantic. Journal of Mammalogy 76:857-861.

de Swart, R., T. Harder, P. Ross, H. Vos, and A. Osterhaus. 1995. Morbilliviruses and Morbillivirus Diseases of Marine Mammals. Infectious Agents and Disease 4:125-130.

Dyke, A. S., J. Hooper, and J. M. Savelle. 1996. A History of Sea Ice in the Canadian Arctic Archipelago based on postglacial remains of the Bowhead Whale (*Balaena mysticetus*). Arctic 49:235-255.

Elith, J. and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677-697.

Ferguson, S., J. Higdon, and E. Chmelnitsky. 2010. The Rise of Killer Whales as a Major Acrtic Predator. Pages 117-136 *in* S. Ferguson, L. Lisetto, and M. Mallory, editors. A little less Arctic: changes to top predators in the world's largest nordic inland sea, Hudson Bay. Springer Netherlands.

Force, M., K. Morgan, and J. Jantunen. 2006. Manx Shearwater in British Columbia: comments on a pioneering seabird. Wildlife Afield 3:5-11.

Friesen, V., A. Baker, and J. Piatt. 1996. Phylogenetic Relationships Within the Alcidae (Charadriiformes: Aves) Inferred from Total Molecular Evidence. Molecular Biology and Evolution 13:359-367.

Grebmeier, J. M. 2012. Shifting patterns of life in the Pacific Arctic and Sub-Arctic Seas. Annual Review of Marine Science 4:63-78.

Haley, D. 1984. Introduction: Seabirds of Eastern North Pacific and Arctic Waters. Pacific Search Press.

Hamilton, R., M. Patten, and R. Erickson. 2007. Rare Birds of California. Western Field Ornithologists, Camarillo, California.

Heide-Jorgensen, M. P., K. L. Laidre, L. T. Quakenbush, and J. J. Citta. 2012. The Northwest Passage opens for bowhead whales. Biology Letters 8:270-273.

Heinl, S. 2011. Northern Gannet in Alaska.

Holden, B. 2010. Sooty/Short-tailed Shearwater. http://peregrineprints.com/zzzz_Article_2010_SOSH.htm.
Huettmann, F., Y. Artukhin, O. Gilg, and G. Humphries. 2011. Predictions of 27 Arctic pelagic seabird distributions using public environmental variables, assessed with colony data: a first digital IPY and GBIF open access synthesis platform. Marine Biodiversity 41:141-179.
Huntington, H. 2009. A preliminary assessment of threats to arctic marine mammals and their conservation in the coming decades. Marine Policy 33:77-82.
Jensen, S., C. Lydersen, K. Kovacs, K. Åsbakk, and J. Aars. 2010. The prevalence of *Toxoplasma gondii* in polar bears and its marine mammalian prey; evidence for a marine transmission pathway? Polar Biology 33:599-606.
Kaschner, K., D. Tittensor, J. Ready, T. Gerrodette, and B. Worm. 2011. Current and Future Patterns of Global Marine Mammal Biodiversity. PLoS ONE 6:e19653.
King, H. E. 2008. Protecting the Northwest Passage: Assessing the Threat of Year-Round Shipping to the Marine Ecosystem and the Adequacy of the Current Environmental Regulatory Regimes. Ocean and Coastal Law Journal 14:269.
Kovacs, K., C. Lydersen, J. Overland, and S. Moore. 2011. Impacts of changing sea-ice conditions on Arctic marine mammals. Marine Biodiversity 41:181-194.
Liu, J. P., M. R. Song, R. M. Horton, and Y. Y. Hu. 2013. Reducing spread in climate model projections of a September ice-free Arctic. Proceedings of the National Academy of Sciences of the United States of America 110:12571-12576.
Magpie. 2009. The Tufted Puffin visits the UK. http://www.puffinpalooza.com/tag/tufted-puffin-and-europe/
Marincovich, L., E. Brouwers, D. Hopkins, and M. McKeonna. 1990. Late Mesozoic and Cenozoic paleogeographic and paleoclimatic history of the Arctic Ocean Basin, based on shallow-water faunas and terrestrial vertebrates. Pages 403-426 *in* A. Grantz, L. Johnson, and J. Sweeney, editors. The Arctic Ocean Region. Geological Society of America.
Marincovich, L. and A. Y. Gladenkov. 2001. New evidence for the age of Bering Strait. Quaternary Science Reviews 20:329-335.
Mead, J. and E. Mitchell. 1984. Atlantic gray whales. Pages 33-53 *in* M. Jones, S. Swartz, and S. Leatherwood, editors. The gray whale *Eschrichtius robustus*. Academic Press, Orlando.
Mooney, H. A. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences - PNAS 98:5446-5451.
Moore, S. E., R. R. Reeves, B. L. Southall, T. J. Ragen, R. S. Suydam, and C. W. Clark. 2012. A New Framework for Assessing the Effects of Anthropogenic Sound on Marine Mammals in a Rapidly Changing Arctic. Bioscience 62:289-295.
Nelson, B. 2010. The gannet. Poyser, London.
Paterson, J. 2013. A rare and mysterious visitor in Walvis Bay. http://namibiandolphinproject.blogspot.com/2013/05/a-rare-and-mysterious-visitor-in-walvis.html.
Polyak, L., R. B. Alley, J. T. Andrews, J. Brigham-Grette, T. M. Cronin, D. A. Darby, A. S. Dyke, J. J. Fitzpatrick, S. Funder, M. Holland, A. E. Jennings, G. H. Miller, M. O'Regan, J. Savelle, M. Serreze, K. St John, J. W. C. White, and E. Wolff. 2010. History of sea ice in the Arctic. Quaternary Science Reviews 29:1757-1778.

Pyke, C. R., R. Thomas, R. Porter, J. Hellman, J. S. Dukes, D. M. Lodge, and G. Chavarria. 2008. Current Practices and Future Opportunities for Policy on Climate Change and Invasive Species. Conservation Biology 22:585-592.

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

Rice, D. and A. Wolman. 1971. The life history and ecology of the gray whale. American Society of Mammalogists.

Rowles, T. K., L. S. Schwacke, R. S. Wells, J. T. Saliki, L. Hansen, A. Hohn, F. Townsend, R. A. Sayre, and A. J. Hall. 2011. Evidence of susceptibility to morbillivirus infection in cetaceans from the United States. Marine Mammal Science 27:1-19.

Ruckelshaus, M. H., T. Klinger, N. Knowlton, and D. P. DeMaster. 2008. Marine Ecosystem-Based Management in Practice: Scientific and Governance Challenges. Bioscience 58:53.

Scheinin, A., D. Kerem, C. MacLeod, M. Gazo, C. Chicote, and M. Castellote. 2011. Gray whale (Eschrichtius robustus) in the Mediterranean Sea: anomalous event or early sign of climate-driven distribution change? . Marine Biodiversity Records 4:1-5.

Schmidt, A. and P. Warzybok. 2011. First record of the bridled morph of the Common Murre in the Pacific. Western Birds 42:45-48.

Shearwater, D. 2013. Shearwater Journeys. http://shearwaterjourneys.blogspot.com.

Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced Species Policy, Management, and Future Research Needs. *Dx.Doi.org.Eres.Library.Manoa.Hawaii.Edu*.

Simmonds, M. P. and S. J. Isaac. 2007. The Impacts of Climate Change on Marine Mammals: Early Signs of Significant Problems. Oryx 41:19.

Staszewski, V., K. D. McCoy, and T. Boulinier. 2008. Variable exposure and immunological response to Lyme disease Borrelia among North Atlantic seabird species. Proceedings of the Royal Society B-Biological Sciences 275:2101-2109.

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

Vermeij, G. J. 1991. Anatomy of an Invasion- The Trans-Arctic Interchange. Paleobiology 17:281-307.

Vermeij, G. J. and P. D. Roopnarine. 2008. The coming Arctic invasion. Science 321:780-781.

Vinicombe, K. 2007. Vagrancy and melting ice. Birdwatch 177:42-42.

Wainright, S., J. Haney, C. Kerr, A. Golovkin, and M. Flint. 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. Marine Biology 131:63-71.

Webb, S. 2012. Northern Gannet at SEFI - Evidence of Climate Change? http://losfarallones.blogspot.com/2012/04/northern-gannet-at-sefi-evidence-of.html.
Webb, S. D. 2006. The Great American Biotic Interchange: Patterns and Processes. Annals of the Missouri Botanical Garden 93:245-257.
Weller, D., A. Klimek, A. Bradford, J. Calambokidis, A. Lang, B. Gisborne, and R. Brownell. 2012. Movements of gray whales between the western and eastern North Pacific. Endangered Species Research 18:193-199.
http://www.aquamaps.org. 2013. Computer Generated Native Distribution Map for Eschrichtius robustus (gray whale). http://www.aquamaps.org.

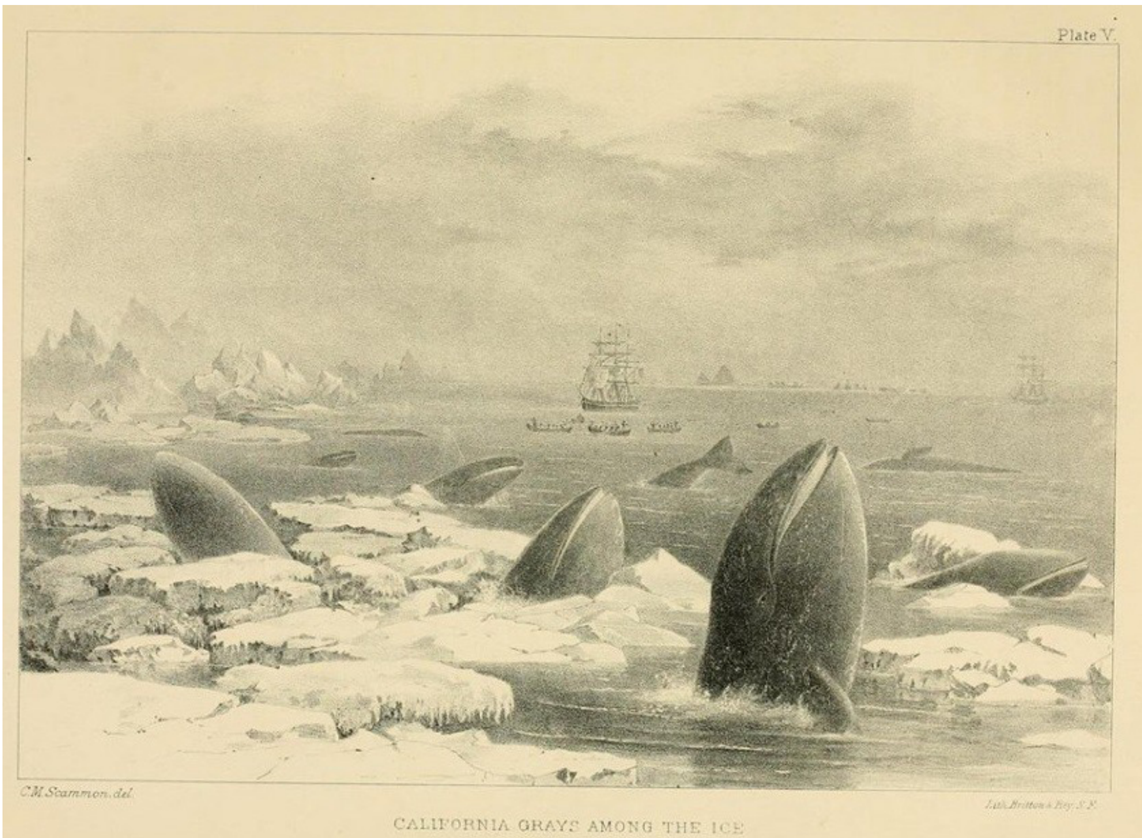

Figure 1: Plate V from Scammon 1874 "California grays among the ice"

Figure 2: Great Shearwater (lowest bird, with white collar) flying among Buller's Shearwaters and Pink-footed Shearwaters off of Central California. Photo by Steve Rottenborn.

Table 1: Bird and Mammal species likely to make inter-basin movements based on current range.

POLAR SPECIES (PS)	
Birds	
Artic Tern	*Sterna paradisaea*
Black Guillemot	*Cepphus grylle*
Black-legged Kittiwake	*Rissa tridactyla*
Brant Goose	*Branta bernicla*
Common Eider	*Somateria mollissima*
Common Murre	*Uria aalge*
Glaucous Gull	*Larus hyperboreas*
Harlequin Duck	*Histrionicus histrionicus*
Ivory Gull	*Pagophila eburnea*
King Eider	*Somateria spectabilis*
Leach's Storm Petrel	*Oceanodroma leucorhoa*
Little Auk (Dovekie)	*Alle alle*
Long-tailed Duck	*Clangula hyemalis*
Long-tailed Jaeger	*Stercorarius longicaudus*
Northern Fulmar	*Fularus glacialis*
Parasitic Jaeger	*Stercorarius parasiticus*

Pomarine Jaeger	*Stercorarius parmarinus*
Red-breasted Merganser	*Mergus serrator*
Red-throated Loon	*Gavia stellata*
Ross's Gull	*Rhodostethia rosea*
Sabine's Gull	*Xema sabini*
Sooty Shearwater	*Puffinus gravis*
Thick-Billed Murre	*Uria lomvia*
Mammals	
Bearded Seal	*Erignathus barbatus*
Beluga Whale	*Delphinapterus leucas*
bowhead Whale	*Balaena mysticetus*
Fin Whale	*Balaenoptera physalus*
Harbor Porpoise	*Phocoena phocoena*
Harbor Seal	*Phoca vitulina*
Harp Seal	*Pagophilus groenlandicus*
Minke Whale	*Balaenoptera acutorostrata*
Narwhal	*Monodon monoceros*
Orca	*Orcinus orca*
Ringed Seal	*Pusa hispida*
Walrus	*Odobenus rosmarus*

ICE EDGE SPECIES (IES)

Birds	
Atlantic Puffin	*Fratercula arctica*
Crested Auklet	*Aethia cristatella*
Fork-tailed Storm Petrel	*Oceanodroma furcata*
Great Shearwater	*Ardenna gravis*
Horned Puffin	*Fratercula corniculata*
Kittlitz's Murrelet	*Brachyramphus brevirostris*
Laysan Albatross	*Phoebastria immutabilis*
Least Auklet	*Aethia pusilla*
Long-billed Murrelet	*Brachyramphus perdix*
Manx Shearwater	*Puffinus puffinus*
Northern Gannet	*Morus bassanus*
Parakeet Auklet	*Aethia psittacula*
Pelagic Cormorant	*Phalacrocorax pelagicus*
Razorbill	*Alca torda*
Short-tailed Shearwater	*Puffinus tenuirostris*
Spectacled Eider	*Somateria fischeri*
Spectacled Guillemot	*Cepphus carbo*
Steller's Eider	*Polysticta stelleri*
Tufted Puffin	*Fratercula cirrhata*

Wilson's Storm Petrel	*Ocenites oceanicus*
Mammals	
Atlantic White-sided Dolphin	*Lagenorhynchus acutus*
Blue Whale	*Balaenoptera musculus*
Dall's Porpoise	*Phocoenoides dalli*
gray Seal	*Halichoerus grypus*
gray Whale	*Eshrichtius robustus*
Hooded Seal	*Cystophora cristata*
Humpback Whale	*Megaptera novaeangliae*
Long-finned Pilot Whale	*Globicephala melas*
North Atlantic Right Whale	*Eubalaena glacialis*
North Pacific Right Whale	*Eubalaena japonica*
Northern Bottlenose Whale	*Hyperoodon ampullatus*
Northern Elephant Seal	*Mirounga angustirostris*
Northern Fur Seal	*Callorhinus ursinus*
Ribbon Seal	*Histriophoca fasciata*
Sei Whale	*Balaenoptera borealis*
Spotted Seal	*Phoca largha*
Sperm Whale	*Physeter macrocephalus*
White-beaked Dolphin	*Lagenorhynchus albirostris*

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