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Melting Barriers to Faunal Exchange Across Ocean Basins

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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 may increase the ease and frequency with which marine birds and mammals move between the Pacific and Atlantic ocean basins. Indeed, recent observations of birds and mammals suggest these movements have intensified in recent decades. 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 inter-oceanic 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 & 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 populations of many taxa within each ocean basin (Polyak *et al.*, 2010). Likewise, cooling in the Holocene resulted in persistent ice barriers 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 many Arctic and sub-Arctic species of marine mammals and seabirds (Dyke *et al.*, 1996, Haley, 1984). Low temperature and productivity in these ice-covered waters are also thought to create a dispersal boundary for smaller species with pelagically dispersing larvae (Reid, 1990, Reid *et al.*, 2007, Vermeij, 1991).

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, Reid, 1990, Wares & Cunningham, 2001).

Today, warmer temperatures are reducing sea ice extent and thickness, resulting in more open ocean in the summer and fall 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 now 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 several authors (Bluhm *et al.*, 2011, Kovacs *et al.*, 2011, Reid *et al.*, 2007) raise new conservation questions.

To address the variety of conservation concerns and research opportunities arising from increasingly ice-free Arctic Ocean basin we 1) review a recent flurry of observations of marine tetrapods and other Arctic and Subarctic marine taxa observed beyond their known ranges, probably as a result of thawing Arctic ice barriers, 2) identify some of the challenges that an increase in such out-of-range movements may pose for marine conservation, and 3) highlight current efforts at biodiversity monitoring and research and make recommendations for further study in this era of increasing connectivity between ocean basins. The goal of this opinion article is not to exhaustively review extralimital records of Arctic tetrapods, but rather to illustrate the conservation challenges and research opportunities provided by increased tetrapod faunal exchange among ocean basins.

EVIDENCE FROM TETRAPODS: RECENT FAUNAL EXCHANGE BETWEEN THE ATLANTIC AND PACIFIC OCEAN BASINS

The reduction of Arctic sea ice has already had ecological consequences for many Arctic taxa, including marine mammals and seabirds (Bluhm *et al.*, 2011, CAFF, 2013, Kovacs *et al.*, 2011). Here, we focus on recent observations that provide evidence for novel and potentially increasing inter-basin movements.

Currently, separate management stocks of bowhead whales exist on either side of the Northwest Passages. New 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). Satellite tracking of bowhead whales (*Balaena mysticetus*) provides direct evidence that the retreat of Arctic ice is allowing movement between ocean basins. 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 known from subfossil remains in both the western and eastern North Atlantic (Alter *et al.*, 2015, Bryant, 1995, Mead & Mitchell, 1984). Gray whales occupy the edge of sea ice (Figure 1), but unlike bowhead whales, are unable to transit areas of thick consolidated ice (Rice & Wolman, 1971). Alter *et al.* (2015) used ancient DNA and predictive habitat modeling to show that gray whales transited between the Pacific and Atlantic several times over the Pleistocene and Holocene, corresponding to periods when climatic conditions would have permitted passage through the Arctic. 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 but is likely to be a coastal route through the Arctic Ocean. As summer feeding grounds in the Beaufort and Chukchi Seas expand northward with the recession of seasonal sea-ice, possibilities for more whales to transit the Arctic and enter the Atlantic will increase. A long transit through tropical pelagic regions seems less likely, as gray whales are a primarily coastal species that feed in temperate and sub-polar waters. However, recent satellite tag data has demonstrated that gray whales are capable of unexpected movements and migrations (Weller *et al.*, 2012). Our understanding of this species' ecology and biogeography may change with additional data from new technologies. Both predictive habitat modeling and inferences from past movements indicate that gray whales are likely to find suitable habitat in the Atlantic and that additional migrants are likely as Arctic routes become more accessible (Alter *et al.*, 2015).

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 were documented preying upon Arctic marine mammals including beluga (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), bowhead (Ferguson *et al.*, 2010) and at least four species of seal (Higdon *et al.*, 2012). While diet specialization is common among killer whales, comparatively little is known about the ecology of populations that use Arctic waters (Higdon *et al.*, 2012). Thus, while marine mammal-eating ecotypes have been definitively observed, this does not preclude the possible presence of fish-eating ecotypes in the Arctic as well. Regardless of ecotypes present, the arrival of even small numbers of a novel top predator such as killer whale could have cascading effects on the ecosystem as predators and prey respond to changes in the structure of the food web (Springer *et al.*, 2003).

Recent seabird records also suggest movements through the Arctic Ocean. 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*), and demonstrating the use of newly ice-free passages by shearwaters. 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 Northern Passages and Arctic Ocean.

Auks (Alcidae), a lineage of diving birds currently restricted to the Northern Hemisphere, also provide evidence for movement through arctic marine Passages. Sea ice may impact the feeding of these birds, restricting the ranges of some alcid species to the Pacific. Several Pacific species of auk have recently been observed in the Atlantic. Sightings of Long-billed Murrelet (*Brachyramphus perdix*), a species known for vagrancy, have increased (Vinicombe, 2007) along with those of Ancient Murrelet (*Synthliboramphus antiquus*). Tufted Puffin (*Fratercula cirrhata*) was recently recorded in European waters (http://www.puffinpalooza.com/tag/tufted-puffin-and-europe/)(Magpie, 2009) and Maine (http://www.cbc.ca/news/canada/new-brunswick/tufted-puffin-seen-on-atlantic-coast-for-1st-time-since-1830s-1.2680540)(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 & Warzybok, 2011).

Evidence for novel movements of subspecies of seaducks also exists. In 2011, an Atlantic subspecies of Common Eider (*Somateria mollissima dresseri*) was observed in Del Norte County California (Able *et al.*, 2014). In 2005, the Pacific subspecies of Common Eider (*Somateria mollissima v-nigra*), was observed in Newfoundland (http://brucemactavish1.blogspot.co.uk/2014/02/the-ice-is-coming.html), with a second bird found in Norway in 2014 (http://birdingfrontiers.com/2014/02/19/pacific-eider-in-norway-a-new-western-palearctic-bird/).

Current evidence for novel faunal exchange between the Atlantic and Pacific basins through the Northwest Passages is still somewhat circumstantial in tetrapods. It is difficult to tease apart the probability of a true increase in faunal exchange from a similar recent increase in observer effort and experience. Efforts to establish biodiversity baselines for the Arctic are ongoing (CAFF, 2013, Gill *et al.*, 2011), but there is now 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 IN ECOLOGY AND EVOLUTION

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 (Alter *et al.*, 2010, Huntington, 2009, Moore *et al.*, 2012). While these impacts are immediately important, 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. Genomes previously adapted to the rigors of one ocean basin will be confronted with novel adaptive challenges from distinct environmental and community assemblage differences in the other. Moreover, hybridization between previously diverged lineages can impact demographic and evolutionary trajectories for both populations (Allendorf *et al.*, 2010, Cook *et al.*, 2013). However, identifying which species will be most likely 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, gulls, and loons) were excluded. The inter-basin taxa observed to date have been Ice Edge Species. Understanding which species are most likely to become inter-basin taxa will require extensive review of the natural history of the listed species. The relative numbers of IES bird species found in the Pacific basin in comparison to the Atlantic (15 Pacific / 4 Atlantic IES birds), suggests that West to East will be the dominant direction of travel. Mammal distribution appears more equitable (7 Pacific/ 6 Atlantic IES mammals).

We expect that inter-basin movements will become increasingly common as Arctic sea ice recedes, but detecting true migration events 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, or population genetic evidence of recent inter-basin gene flow (Alter *et al.*, 2012). 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 (Woodburne, 2010). 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 are at an advantage as they expand into the

Mediterranean because the Red Sea is saltier and more environmentally variable. The resulting ecological advantages as well as increasing temperatures in the Mediterranean allowed some of these invasive taxa to outcompete natives (Edelist *et al.*, 2012, Galil *et al.*, 2015, Mooney, 2001, Yahia *et al.*, 2013). 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). Likewise, 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.

NEW CHALLENGES AND OPPORTUNITIES

With the accelerating disappearance of Arctic sea ice, documenting shifting patterns in wildlife movements is increasingly urgent. New monitoring programs, including the Circumpolar Biodiversity Monitoring Program (CBMP; Gill *et al.* (2011)) and NOAA's Distributed Biological Observatory (Grebmeier, 2012), and the North Pacific Pelagic Seabird Database (http://alaska.usgs.gov/science/biology/nppsd/index.php) will help establish a baseline for environmental and biogeographic data. These data will inform not only conservation efforts for Arctic birds and mammals, but also efforts to learn from what may become the largest faunal exchange event to occur during the historical era. To take full advantage of this opportunity 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 tagging and satellite tracking of individuals from populations/species that are likely to make the crossing to ensure real time records.
- Collecting tissue samples from populations in both basins. Compiling genetic data to verify species and population of origin via parentage-based tagging methodology.
- Employing citizen science programs to increase recorded observations of focal taxa, and accumulate records of migration events as well as augmenting both methods above. 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.

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. See Cook *et al.* (2013) for a thorough discussion of the uses of genetic methods in Arctic biodiversity research.

Projecting habitat suitability for dispersing organisms. Species distribution models are a common tool used to predict future distributions as climatic conditions change (Elith & 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. In the Arctic, there are relatively few examples of species distribution modeling (Huettman et al., 2011, Kaschner et al. 2011). 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 estimated the suitable habitat range of gray whales and projected highly suitable habitat for this species across the northeastern US and Canada (Kaschner et al. 2011, http://www.aquamaps.org. 2013. Computer Generated Native Distribution Map for *Eschrichtius robustus* (gray whale)). 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 can inform policy design and management action in a number of ways.

The current environmental laws governing the Northwest Passage have relied upon premises that are challenged by melting sea ice and associated increased faunal exchange, and as such may need updating. The first premise is the lack of access, which diminished the need to institute environmental protections of fauna. The isolation and harsh climate of the biologically rich and ecologically sensitive Canadian Arctic Archipelago have served to protect 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). The second premise relates to the lack of significant faunal movement through the passage. Because of the historical rarity of significant faunal exchange through the strait, environmental protection for fauna has received relatively little international or national policy attention. The third premise is based on the legal nature of the ocean. The seasonal opening of the Northwest Passages could alter the legal status of the waters. Canada currently considers the passage as internal waters, using national environmental policy to protect resources, including fauna. Other nations dispute Canada's claim and consider it an international strait, with all transit rights per UNCLOS (King, 2008). The change in legal status calls into question the environmental protections (national, international, customary) that currently 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 & 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 surveillance system for diseases 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.

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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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)

Basin	Birds	
Atlantic	Atlantic Puffin	*Fratercula arctica*
Pacific	Crested Auklet	*Aethia cristatella*
Pacific	Fork-tailed Storm Petrel	*Oceanodroma furcata*
Atlantic	Great Shearwater	*Ardenna gravis*
Pacific	Horned Puffin	*Fratercula corniculata*
Pacific	Kittlitz's Murrelet	*Brachyramphus brevirostris*
Pacific	Laysan Albatross	*Phoebastria immutabilis*
Pacific	Least Auklet	*Aethia pusilla*
Pacific	Long-billed Murrelet	*Brachyramphus perdix*
Atlantic?	Manx Shearwater	*Puffinus puffinus*
Atlantic	Northern Gannet	*Morus bassanus*
Pacific	Parakeet Auklet	*Aethia psittacula*
Pacific	Pelagic Cormorant	*Phalacrocorax pelagicus*
Pacific	Razorbill	*Alca torda*
Pacific	Short-tailed Shearwater	*Puffinus tenuirostris*
Pacific	Spectacled Eider	*Somateria fischeri*
Pacific	Spectacled Guillemot	*Cepphus carbo*
Pacific	Steller's Eider	*Polysticta stelleri*
Pacific	Tufted Puffin	*Fratercula cirrhata*
Both	Wilson's Storm Petrel	*Ocenites oceanicus*
	Mammals	
Atlantic	Atlantic White-sided Dolphin	*Lagenorhynchus acutus*
Both	Blue Whale	*Balaenoptera musculus*
Pacific	Dall's Porpoise	*Phocoenoides dalli*
Atlantic	Gray Seal	*Halichoerus grypus*
Pacific	Gray Whale	*Eshrichtius robustus*
Atlantic	Hooded Seal	*Cystophora cristata*
Both	Humpback Whale	*Megaptera novaeangliae*
Both	Long-finned Pilot Whale	*Globicephala melas*
Atlantic	North Atlantic Right Whale	*Eubalaena glacialis*
Pacific	North Pacific Right Whale	*Eubalaena japonica*
Atlantic	Northern Bottlenose Whale	*Hyperoodon ampullatus*
Pacific	Northern Elephant Seal	*Mirounga angustirostris*
Pacific	Northern Fur Seal	*Callorhinus ursinus*
Pacific	Ribbon Seal	*Histriophoca fasciata*
Both	Sei Whale	*Balaenoptera borealis*
Pacific	Spotted Seal	*Phoca largha*
Both	Sperm Whale	*Physeter macrocephalus*
Atlantic	White-beaked Dolphin	*Lagenorhynchus albirostris*

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.