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Arctic Marine Biodiversity

An Update of Species Richness and Examples of Biodiversity Change



Under-ice image from the Bering Sea. *Photo credit: Miller Freeman Divers (Shawn Cimilluca)*

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ABSTRACT. The societal need for—and urgency of obtaining—basic information on the distribution of Arctic marine species and biological communities has dramatically increased in recent decades as facets of the human footprint alter Arctic marine biodiversity. The primary goals of this article are to present updated species inventories based on focused biodiversity research over the last decade, to give examples of emerging recent changes in diversity as indicators of environmental change, and to recommend future diversity-related research areas. Species inventories across all eukaryotic taxonomic levels now total close to 8,000 species, with several thousand additional benthic species predicted to be recorded or discovered in the future. The currently known Arctic species richness estimate includes close to 2,000 phytoplankton taxa,

over 1,000 ice-associated protists, greater than 50 ice-associated metazoans, ~ 350 multicellular zooplankton species, over 4,500 benthic protozoans and invertebrates, at least 160 macroalgae, 243 fishes, 64 seabirds, and 16 marine mammals. Endemic and abundant species are present in all three environmental realms (sea ice, water column, and seafloor) and across phyla. The few published time series on Arctic marine biodiversity have detected interannual and interdecadal variability or change both in pelagic and benthic habitats, and at virtually all trophic levels. We identify knowledge gaps and stress the urgency to fill them. We recommend regular, strategic, and sustained monitoring of Arctic marine biodiversity in a public, open-access fashion in order to provide comprehensive data to inform management, conservation, and other decisions.

WHAT IS BIODIVERSITY AND WHY DO WE CARE ABOUT IT IN THE ARCTIC?

Biological diversity, contracted to the term biodiversity, is most commonly defined as the variety of life (Gaston, 2010). The definition by the Convention on Biological Diversity (CBD) reads: “the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the complexes of which they are part; this includes diversity within species, between species and of ecosystems” (<http://www.cbd.int/convention/text>).

In this article, we present an overview of organismal and ecological diversity, with some examples of genetic diversity of Arctic marine biota, from microbes to mammals. The primary goals are twofold: to present an updated review on species inventories, here defined as numbers of species occurring per realm and broad taxonomic group, and to give examples of emerging recent changes in diversity on species and community levels. While other recent publications present regional biodiversity inventories—including Arctic regions—in much more detail (e.g., Archambault et al., 2010; Carr, 2011, for Canadian waters), we focus on the pan-Arctic macroscale across all habitats. We also discuss observed changes in Arctic biodiversity to highlight the need for, and usefulness of, collecting data on the distribution over time of individual species and communities as indicators of Arctic environmental and ecosystem change. In the Arctic, major stressors include, for example, climate change, species invasions, fisheries effects, oil and gas exploration, shipping, ocean acidification,

pollutants, and tourism (ACIA, 2005; Johnsen et al., 2010). One of the most visible ongoing changes is the reduction of sea ice cover and thickness, in particular during the summer months, reducing the habitat for ice-related flora and fauna. Concurrently, increased subsurface light levels and water temperatures now occur in many regions previously covered continuously with ice (Perovich et al., 2007). The predicted total loss of summer ice by mid-century, and the anticipated increased human presence, will alter Arctic ecosystems’ functioning, with regional changes in, for example, primary production, species distributions (including those of disease-causing taxa), and indigenous subsistence use. To understand such change, biodiversity studies spanning regional species lists to functional linkages between indices of diversity and ecosystems are critical.

Various definitions exist for the marine Arctic and its boundaries, with most based on a combination of temperature, geopolitical boundaries, and sea ice cover. Here, we consider the Arctic primarily as those marine regions north of Bering Strait on the Pacific side and areas with consistent seasonal sea ice cover on the Atlantic side, recognizing, however, that the literature cited does not consistently use this definition.

RECENT AND ONGOING ARCTIC MARINE BIODIVERSITY INITIATIVES

Much of today’s marine biodiversity research builds on the tremendous (and ongoing) effort of dozens of taxonomists from the Russian Federation where substantial emphasis on Arctic species identification and description for over

a century has produced fundamental knowledge of marine life in the Arctic (e.g., Sirenko, 2001; Vassilenko and Petryashev, 2009; Buzhinskaja, 2011). In addition, the early explorers laid the foundation for many of the following research projects by describing their biotic findings in their diaries and expedition reports.

More recently, the Arctic Ocean Diversity project (ArcOD, 2004–2011), as part of the Census of Marine Life, was an international collaborative effort to inventory biodiversity in Arctic marine realms on a pan-Arctic scale. Led by authors of this article, the project compiled historic and new data in an online open-access database, improved taxonomic identification of existing samples, and made new collections focused on taxonomic, regional, and habitat gaps. Legacy products include, for example, the Arctic Register of Marine Species (ARMS; <http://www.marinespecies.org/arms>), which expands the previously most complete list by Sirenko (2001), both in terms of taxa and regional coverage. The majority of taxon distribution records (defined here as georeferenced location of an identified specimen), underlying both ARMS and related publications, are available through the Ocean Biogeographic Information System (OBIS: <http://www.iobis.org>; Figure 1) and ArcOD’s web portal (<http://www.arcodiv.org>) with microbial data housed within MICROBIS (<http://icomm.mbl.edu/microbis>). ArcOD also provided species pages to the Encyclopedia of Life (<http://www.eol.org>) and genetic sequences to the marine Barcode of Life Initiative (<http://www.marinebarcoding.org>). The scientific network developed through ArcOD

continues its activities—though with reduced financial support—beyond 2011.

Currently, international teams are engaged in the Arctic Biodiversity Assessment (ABA), an initiative aimed at synthesizing and assessing the status and trends of biological diversity in the Arctic (<http://www.caff.is/aba>). This initiative was created by the Arctic Council in response to the ambitious (though not attained) target set by the United Nations Environmental Programme (UNEP) and CBD to reduce the loss of biodiversity globally by 2010 (Mace et al., 2010). ABA chapters include terrestrial, aquatic, and marine biodiversity at organismic and ecosystem scales in addition to genetic diversity and ecosystem goods and services. ABA is intended to provide policymakers and conservation managers with a current synthesis to help guide future work and “help ensure sustainability of Arctic biodiversity and communities” (<http://www.caff.is/aba>). The ABA baseline information aims at identifying main stressors, key mechanisms driving change, and data gaps, and will produce recommendations by 2013; a shorter report on biodiversity trends has already

been published (CAFF, 2010). The hope is that synthesis efforts such as this will eventually lead to informed timely decision making for international policy, resource management, and conservation.

Also under the umbrella of the Arctic Council’s Conservation of Arctic Flora and Fauna (CAFF), the currently prepared Circumpolar Biodiversity Monitoring Plan (CBMP) is intended to enhance and harmonize biodiversity monitoring efforts (<http://www.caff.is>). The CBMP’s Marine Expert Monitoring Group, co-led by Norway and the United States, has developed biodiversity indicators along with approaches to survey them and a strategy for implementation (e.g., Gill et al., 2011). The goal of the implemented effort is to detect biodiversity trends in the Arctic and pinpoint sources of variability or change. Challenges ahead include funding the efforts on a pan-Arctic scale, implementing a common data structure, and agreeing on standard methodologies.

Various other international Arctic observation networks that include biodiversity components are in the planning process such as the Distributed Biological Observatory (DBO) in the

Pacific Arctic region, which could fulfill part of the CBMP goals. DBO is suggested to include a range of biological and environmental measurements, supplemented by satellite observations, at four key areas in the Bering, Chukchi, and Beaufort Seas with the goals of detecting and tracking the effects of changing oceanographic conditions, from microbes to mammals (Grebmeier et al., 2010).

Several large national Arctic initiatives—with international collaborators—include biodiversity components at some level, such as ArcticNet, a Canadian network of centers of excellence, and ARCTOS, an Arctic marine ecosystem research network of Norwegian institutions.

ENVIRONMENTAL SETTINGS

The oceanographic, bathymetric, and historic characteristics of the Arctic that collectively shape today’s Arctic biota with regard to its biogeographic, compositional, and regional patterns are presented in other articles in this special issue, and are, therefore, greatly abbreviated here. Briefly, the backdrop for the current Arctic biota is a central deep ocean that is divided into four abyssal basins by prominent ridges surrounded by shallow—and often broad—shelves comprising ~ 50% of the Arctic (Jakobsson et al., 2004; Figure 2). The only existing deepwater connection to the world’s ocean is through Fram Strait. Prominent abiotic forcing factors include the extreme seasonality of light, combined with the sea ice that historically covered a maximum of 14 million km² in winter and a minimum of 7 million km² in summer (Thomas and Dieckmann, 2010). The central Arctic

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Ocean is permanently stratified owing to seasonal ice melt and freshwater input from huge river systems that reduce the salinity of surface waters to < 32 , while deepwater salinities typically exceed 34. Inorganic nutrient concentrations exhibit strong regional gradients from high nutrient regimes (e.g., the Chukchi Sea shelf) to oligotrophic conditions (e.g., in the Beaufort Gyre; e.g., Gradinger, 2009). Abundant terrigenous sediments originate in riverine discharge and coastal erosion, or glacial erosion, while marine-derived organic content is greatest in areas of high nutrient concentration and productivity. Seafloor sediments, relevant for benthic communities and demersal fishes, are typically muddy on the outer shelves and in the central basins, and coarser with sand and gravel on the inner shelves or at locations with stronger ocean currents (Naidu, 1988). Local accumulations of boulders (Dunton et al., 1982) and rocky islands like Svalbard (Wesławski et al., 2010) can provide isolated hard substrates, although overall such habitat is spatially limited.

RICHNESS OF SPECIES IN THE THREE ARCTIC REALMS

The most recent estimates of species richness are presented in this section, organized by the three major realms of the Arctic: sea ice, pelagic (water column), and benthos (seafloor), with vertebrates in a fourth section that cuts across these realms. The degree of completeness of the species inventories varies greatly across realms, taxonomic groups, and geographic regions due to differing levels of sampling effort, ease of capture, and actual species numbers present. In most cases, the underlying species lists are based on standardized

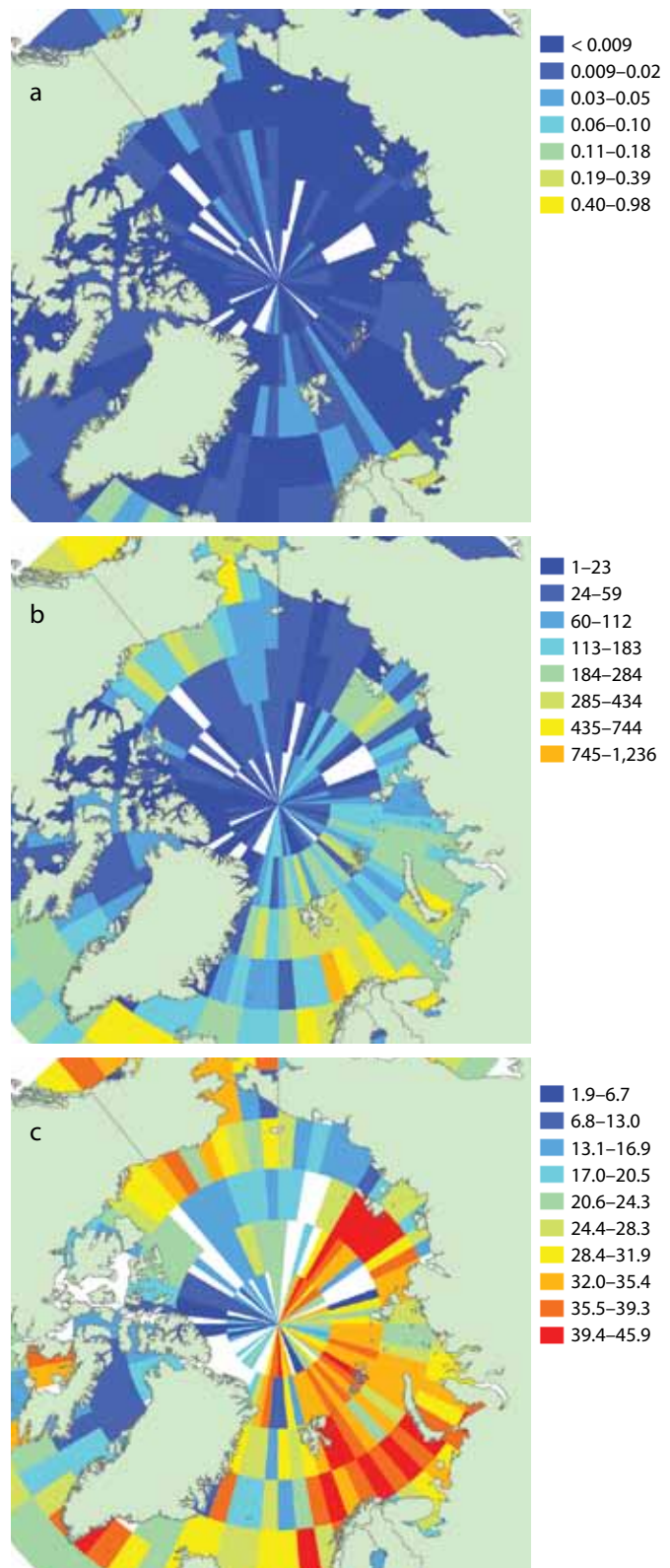


Figure 1. Taxonomic records in the Arctic per 5° cell and per km^2 as archived in the Ocean Biogeographic Information System (<http://www.iobis.org>) as of October 2010. (a) Density of records ($N \text{ km}^{-2}$), (b) observed number of taxa ($S \text{ km}^{-2}$), (c) estimated number of taxa in 50 randomly chosen individuals ($ES(50) \text{ km}^{-2}$). One record is one taxon occurrence at one location at a given time. S is a function of sampling effort reflected in N , while $ES(n)$ is a sample-size independent proxy for species richness (Magurran, 2004). An additional $\sim 50,000$ records are currently in preparation by the Arctic Ocean Diversity project.

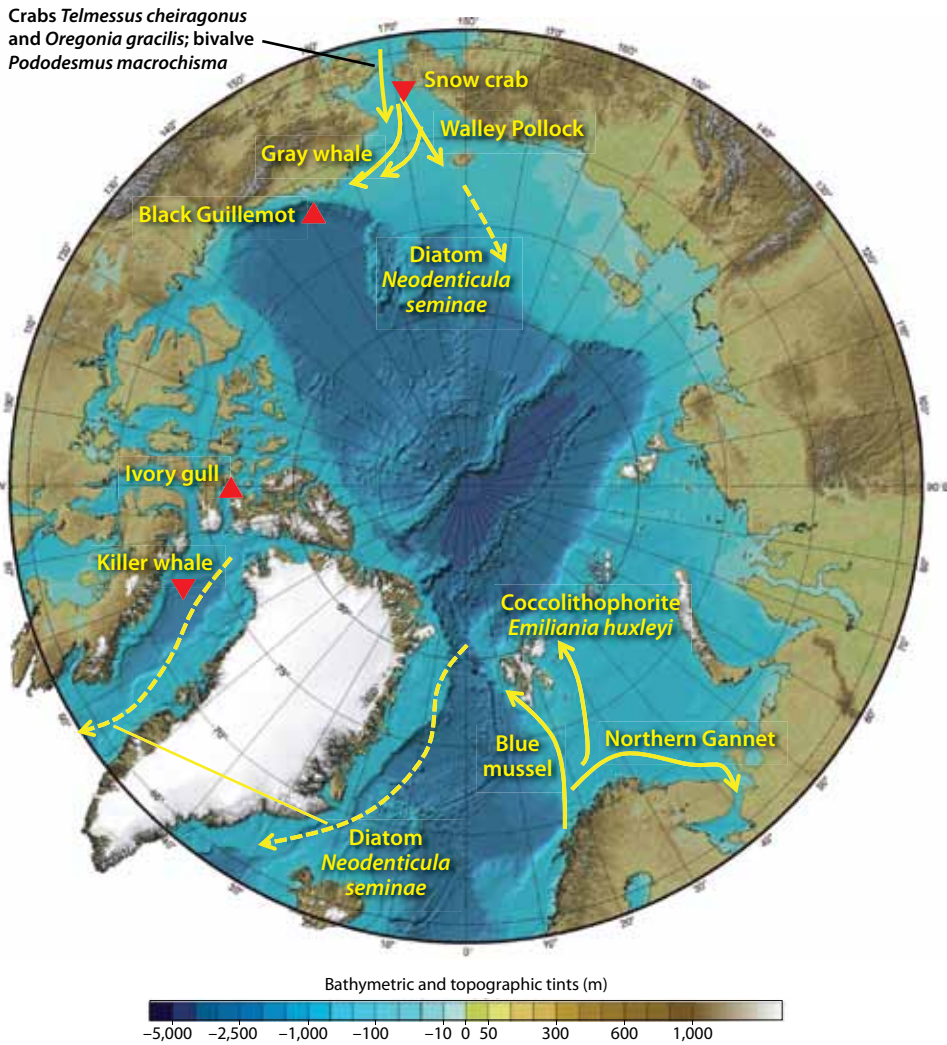


Figure 2. Schematic of examples of recent change in species distributions or population size or sightings that have been attributed to global climate change (details in text). The yellow arrows show the general direction of the species range change and end in the general area of the new occurrence, but are not meant to suggest exact pathways. For the diatom *Neodenticula seminae*, no arrow was drawn across the Arctic Ocean since the distribution pathway is unclear according to Reid et al. (2007). Red triangles indicate increases (▼) or decreases (▲) in population numbers or sightings. After data from: Krasnov and Barrett (1997), Berge et al. (2005), Feder et al. (2005), Gilchrist and Mallory (2005), Mecklenburg et al. (2007; 2011), Reid et al. (2007), Sirenko and Gagaev (2007), Bluhm et al. (2009), Moline et al. (2008), Ferguson (2009)

taxonomy as accepted in the World Register of Marine Species (<http://www.marinespecies.org>). Brief introductions outline relevant characteristics of each environment and its associated communities. Recent discoveries of new species in all realms and across taxa demonstrate that the inventory, here the number of species per realm, region, or higher taxon, is still incomplete despite the significant progress made in recent years.

Sea Ice Realm

A specialized, sympagic (ice-associated) community lives within a brine-filled network of pores and channels or at the ice-water interface. Observed taxa include viruses, archaea, bacteria, protists, and metazoans. Ice algal productivity exhibits strong regional gradients with maximum contributions of up to ~ 50% of total primary productivity in the central Arctic, and lower contributions in the

seasonally ice-covered seas (Gosselin et al., 1997; Gradinger, 2009). Typically, ice algal blooms start with the availability of sufficient light for photosynthesis about mid-March in the coastal sea ice zones, when meiofaunal ice algal grazers also start appearing in high abundances (e.g., Gradinger et al., 2009). The timing of the ice algal maximum is related to the local light climate and is latest in the central Arctic. Most of the algal and faunal biomass and production is present in the bottom few centimeters of the ice where temperatures and nutrient concentrations are highest and salinity is lowest (e.g., Gradinger et al., 2009). Bacteria, in contrast, can be abundant in interior ice sections and are active at more extreme salinities (> 100) and temperatures (< -10°C; Junge et al., 2004). Three-dimensional under-ice structure, including sea ice pressure ridges and crevasses, provides different microhabitats for under-ice fauna and flora (Ambrose et al., 2005; Gradinger et al., 2010a). The under-ice metazoan fauna, dominated by gammaridean amphipods and Arctic or polar cod, transfers particulate organic matter from the ice realm to the water column through the release of fecal pellets and as prey for fishes, seals, and whales. Most of the organic carbon produced in the sea ice system, however, is not grazed by these ice meiofaunal and under-ice grazers (e.g., Nozais et al., 2001) and therefore serves as an early and high-quality food pulse for the underlying fauna both in the water column and at the seafloor (e.g., Sun et al., 2009).

Pan-Arctic inventories of ice bacteria and archaea are lacking, but first studies conducted north of Svalbard and in the Greenland Sea catalogued over 30 bacterial phylotypes dominated by

proteobacteria and the Cystophaga-Flavobacterium group (Brinkmeyer et al., 2003). Recently, 22 sea ice bacterial phylotypes were described for seasonal ice from the Franklin Bay region (Collins et al., 2010). On the eukaryotic level, a total of 1,027 sympagic marine single-celled protist species were recently compiled for the Arctic, with separate inventories provided for the following marine regions: Alaska, Canada, Scandinavia including Greenland, and the Russian Arctic (Poulin et al., 2011). Diatom species (74% of all listed taxa) and dinoflagellate species (13% of all listed taxa) dominated the total protist inventory, excluding amoebae, ciliates, foraminiferans, and radiolarians. *Melosira arctica*, *Fragilariopsis cylindrus*, *F. oceanica*, and *Nitzschia frigida* are examples of sympagic diatoms that consistently colonize annually formed sea ice, with *N. frigida* being a characteristic ice-endemic species (Poulin et al., 2011). Inventories of ciliates and other protozoans from sea ice are incomplete. The description of four new ciliate species in a single study of an ice floe near Svalbard (Agatha et al., 1993) and the common occurrence of suctorian and peritrich ciliates on the sympagic amphipod *Gammarus wilkitzkii* (Arndt et al., 2005) suggest the potential for further discovery in these taxa.

In addition to these protists, at least 50 species of metazoans live within the sea ice brine channels or at the ice-water interface. For sea ice meiofauna, these species include at least eight of Rotifera, three Nematoda, 11 Copepoda, four Polychaeta (larvae and juveniles), and several unidentified Acoela (summarized in Bluhm et al., 2010a). A similar diversity of metazoan species occurs at the ice-water interface (e.g., 11 species

of Amphipoda; Table 1) with partial overlap with the pelagic biota. The inventory remains incomplete due to the need for live identification of several dominant sea ice taxa, such as rotifers and acoel flatworms, and the concurrent lack of taxonomists working on those groups in the Arctic. Recently described ice-endemic species include the first known sympagic hydroid, *Sympagohydra tuuli* (Piraino et al., 2008) and one of the few, but very abundant, sympagic nematode species, *Cryonema tenue* (Tchesunov and Riemann, 1995). Sea ice endemic species also include several prominent amphipods (Table 1).

Pelagic Realm

Typically, phytoplankton production begins with ice melt in April and ends in early September with a growth curve generally characterized by a single peak in primary production (Sakshaug, 2004). Enhanced plankton activity on the Arctic shelves is fueled by the seasonal retreat of sea ice, allowing for the formation of ice-edge algal blooms, with reduced surface salinity increasing vertical stability. During this period, the often large herbivorous zooplankton species accumulate substantial lipid reserves for winter survival and early reproduction the following spring (Pasternak et al., 2001). Predatory zooplankton species rely on continuous availability of their prey, and generalists and scavengers show broad flexible diets (Laakmann et al., 2009). Their low metabolic rates at cold temperatures allow low rates of annual primary production in the central Arctic to support relatively large stocks of metazoan zooplankton.

Most marine microbe groups are present in the Arctic plankton, based on the analysis of small subunit rRNA genes

(SS rRNA) used to delineate operational taxonomic units (OTUs) (Lovejoy et al., 2011). For pelagic picoplankton, Lovejoy et al. (2011) estimate ~ 500 OTUs of pico-Eucarya and ~ 500 OTUs of Archaea per water mass (of which ~ 300 of each are unique to that water mass) for a total of ~ 4,500 OTUs in each group, assuming 15 distinct water masses occur in the Arctic. The number of bacterial OTUs is estimated to be an order of magnitude higher (Table 1).

A total of 1,874 single-celled marine protist species have been compiled from Arctic phytoplankton studies (Poulin et al., 2011), again excluding amoebae, ciliates, foraminiferans, and radiolarians. Some of those 1,874 species also occur in sea ice (e.g., Table 1). Poulin et al. (2011) argue that this number is high compared to the most recent estimate of ~ 5,000 phytoplankton species globally by Tett and Barton (1995). Taxa from four of the six super-groups present in a widely accepted eukaryote classification system were recorded for the Arctic, and diatoms again dominated in all four regions (57%), followed by dinoflagellates (23%). Poulin et al. (2011) caution that the recorded highest species richness in the Canadian Arctic and lowest in the Alaskan Arctic may be biased by the numbers of studies conducted, and they point out that their inventory is primarily comprised of cells > 20 µm (e.g., Table 1). Examples of fairly recently described pelagic protist species include several prasinophytes from the Canadian Arctic (Daugbjerg and Moestrup, 1993). For protozoan groups not summarized by Poulin et al. (2011), the two most common pelagic foraminiferans are *Neogloboquadrina pachyderma* and *Globigerina quinqueloba* (Carstens and Wefer, 1992; Carstens et al., 1997), which

Table 1. Species richness estimates by realms or taxon group, and examples of Arctic endemic species and species that are very abundant and typically widespread in the Arctic, based on cited references and authors' knowledge

Taxon/realm	Number of species/taxa	Species endemic to the Arctic	Abundant and/or widespread species	Key reference(s)
Single-celled eukaryotes in phytoplankton and sea ice	2,106 (1,027 sympagic, 1,875 pelagic)	Diatoms <i>Melosira arctica</i> and <i>Nitzschia frigida</i>	Diatoms <i>Nitzschia frigida</i> , <i>Melosira arctica</i> , <i>Chaetoceros furcillatus</i> , <i>Thalassioria nordenskiöldii</i> , <i>Fragilariopsis oceanica</i> , <i>F. cylindrus</i> , and <i>Cylindrotheca closterium</i> , Dinoflagellate <i>Protoperidinium pellucidum</i>	Poulin et al., 2011
Sea ice fauna	At least 50	Hydroid <i>Sympagohydra tuuli</i> ; nematodes <i>Theristus melnikovii</i> , <i>Cryonema tenue</i> , and <i>C. crissum</i> ; amphipods <i>Gammarus wilkitzkii</i> , <i>Apherusa glacialis</i> , <i>Onisimus nansenii</i> , and <i>O. glacialis</i>	Unidentified Acoela; copepod nauplii; amphipods <i>Gammarus wilkitzkii</i> , <i>Apherusa glacialis</i> , <i>Onisimus nansenii</i> , and <i>O. glacialis</i>	Bluhm et al., 2010a
Zooplankton	354	Copepods <i>Spinocalanus elongatus</i> , <i>S. horridus</i> , <i>Paraeuchaeta polaris</i> , <i>Scaphocalanus polaris</i> , and <i>Lucicutia pseudopolaris</i> ; Cnidarians <i>Rhabdoon reesi</i> and <i>Rudjakovia plicata</i> ; larvacean <i>Fritillaria polaris</i>	Copepods <i>Calanus hyperboreus</i> , <i>C. glacialis</i> , <i>Metridia longa</i> , <i>Oithona similis</i> , <i>Oncaea borealis</i> , and <i>Paraeuchaeta glacialis</i> ; chaetognaths <i>Parasagitta elegans</i> , <i>Eukrohnia hamata</i> , and <i>Homoeonema platygonon</i> ; amphipod <i>Themisto libellula</i>	Kosobokova et al., 2011
Seaweeds	~ 160	<i>Platysiphon verticillatus</i> , <i>Jonssonia pulvinata</i> , <i>Chukchia pedicellata</i> , <i>C. endophytica</i> , <i>Kallymenia schmitzii</i> , and <i>Leptophytum arcticum</i>	<i>Agarum clathratum</i> , <i>Desmarestia aculeate</i> , <i>Ectocarpus siliculosus</i> , <i>Saccharina latissima</i> , <i>Polyshiponia arctica</i> , <i>Odonthalia dentate</i> , and <i>Ulva intestinalis</i>	Wilce, 1990, 2009, and recent work; Mathieson et al., 2010
Zoobenthos	~ 4,600	Amphipod <i>Onisimus caricus</i> , bryozoan <i>Alcyonidium disciforme</i> ; holothuroids <i>Elpidia belyaevi</i> , <i>E. heckeri</i> , <i>E. glacialis</i> , and <i>Kolga hyalina</i>	Brittle star <i>Ophiocten sericeum</i> ; amphipods <i>Ampelisca eschrichti</i> and <i>Anony nugax</i> ; bivalve <i>Macoma calcarea</i> ; polychaetes <i>Eteone longa</i> , <i>Aglaothamus malmgreni</i> , and <i>Lumbrineris fragilis</i>	Sirenko, 2001; Piepenburg et al., 2011; Rogacheva, 2007, 2011
Fish	243	<i>Arctidiellus scaber</i> , <i>Arctogadus glacialis</i> , <i>Paraliparis bathybius</i> , <i>Rhodichtys regina</i> , <i>Lycodes frigidus</i> , and <i>L. adolfi</i>	<i>Boreogadus saida</i> , <i>Arctogadus glacialis</i> , <i>Gymnocanthus tricuspis</i> , <i>Myoxocephalus scorpius</i> , <i>M. quadricornis</i> , and <i>Lycodes polaris</i>	Mecklenburg et al., 2011, and pers. comm., February 16, 2011
Seabirds	64	Ivory gull, thick-billed murre, Dovekie, Kittlitz's murrelet, horned puffin, Heuglin's Gull, and various seabird subspecies	Glaucon and Iceland gull; Arctic tern; parasitic and long-tailed jaeger	Huettmann et al., 2011
Marine mammals	16	Polar bear; narwhal, beluga, and bowhead whales; walrus; ringed seal; bearded seal	Ringed seal; bearded seal	Huntington and Moore, 2008; Kovacs et al., 2011

occur even in the central Arctic. Two additional species are reported from the Russian shelves (Sirenko, 2001), while subarctic species are bound to the warm water inflow regions. At least 40 pelagic Radiolaria occur in Arctic waters (Sirenko, 2001), with *Amphimelissa setosa* being dominant in near-surface waters of the Chukchi, Beaufort, Barents, Iceland, and Greenland Seas (Itaki et al., 2003). For other pelagic taxa such as naked Amoeba and Ciliata, the species inventory remains poorly studied, although at least 75 species of pelagic ciliates are known for the Russian Seas (Sirenko, 2001).

Metazoan zooplankton communities are much better characterized, being highly structured by depth in the central Arctic, with no zoogeographical barrier apparent between the Eurasian and Canadian basins (Kosobokova et al., 2011). Diversity indices in that study increased with depth to a maximum within the Atlantic Water layer (i.e., 500–1,000 m depth), followed by a decrease in the deepest strata. Pacific and Atlantic expatriates account for basin-scale differences in the community composition of (only) the upper-layer zooplankton. Regionally, zooplankton communities tend to be structured by the distribution of water masses as traced by temperature and salinity characteristics (e.g., Wassmann et al., 2006; Błachowiak-Samołyk, 2008; Hopcroft et al., 2010).

The current inventory of metazoan holozooplankton is just over 350 species (Sirenko et al., 2010), with nearly 200 species largely restricted to the shelves and 174 listed from the central basins (Kosobokova et al., 2011). This number is very similar to the current species estimate for Antarctic

zooplankton (~ 340; DeBroyer and Danis, 2011; DeBroyer, *pers. comm.*, February 21, 2011). Arctic crustaceans comprise the dominant group (218 species) with Copepoda as the largest order (161 species), followed by the Cnidaria (76 species). The inventory is now assumed to be nearly complete with the exception of the deeper-water layers in the basins, where both unrecorded and new species continue to be found (Figure 3). Examples of those species include very small copepods in the family Discoidae (Andronov and Kosobokova, 2011), a jellyfish found to be rather common based on remotely operated vehicle (ROV) imagery (Raskoff, 2010), and several yet undescribed ctenophores (Figure 3). Only 15–20% of all zooplankton species are endemic to the Arctic (e.g., Kosobokova et al., 2011; Table 1). COI sequences, so-called barcodes, for over 40 Arctic plankton species accurately discriminated and identified known species of 10 taxa of Arctic holozooplankton, and as yet suggest no cryptic species (Bucklin et al., 2010; sequences available in GenBank; barcoding of additional species is ongoing).

Benthic Realm

Although mostly neglected in primary production estimates, benthic diatom photosynthesis may be more important than previously assumed. For example, these algae accounted for 16% of the total primary production in a Greenlandic fjord (Glud et al., 2002). An inventory of Arctic benthic microalgae, however, has not yet been compiled on a pan-Arctic scale, with regionally published diatom species lists from sediment cores considered inconclusive with regard to the benthic

(versus pelagic) origin of the species (Wulff et al., 2009). Nonetheless, pennate diatoms, such as species of the genera *Navicula*, *Nitzschia*, and *Pinnularia*, appear to dominate the taxonomic composition (e.g., Horner and Schrader, 1982; Glud et al., 2002), with some species thriving both on the sediment and in the sea ice.

In addition to microalgae, macroalgae can be abundant in shallow waters where suitable substrate occurs. About 160–210 seaweed species have been recorded in the Arctic to date (Wilce, 1994; Archambault et al., 2010; Mathieson et al., 2010; Sirenko et al., 2010). Forty percent are brown algae (phaeophytes), and 30% each are red (rhodophytes) and green (chlorophytes) algae (Mathieson et al., 2010). Fewer than 20 of these seaweeds are considered Arctic endemics (Wilce, 1990, and recent work of Wilce). An example of a recently described species is *Chukchia pedicellata*, a minute brown alga growing on blades of the kelp *Saccharia latissima* (Wilce et al., 2009). Macroalgal species richness is much lower than in other regions of the globe, except for the Antarctic, with regional latitudinal and longitudinal differences attributed to factors such as availability of coastal rocky habitat, salinity, and ice scouring (Wiencke et al., 2007; Mathieson et al., 2010).

Benthic bacteria contribute significantly to the degradation of organic matter at the seafloor, and also serve as a food source. Over 450 clones of benthic bacteria were obtained from Pacific-Arctic Ocean sediments, including members of the α , γ , and δ -Proteobacteria, Acidobacteria, Bacteroidetes, and Actinobacteria (Li et al., 2009). First assessments of viral and fungal communities have only

recently begun. For example, in the Kara Sea, 46 different species of Zygomycota, Ascomycota, and anamorphic fungi representing 24 genera were found in 18 seafloor cores (Bubnova, 2010). Four new fungi species isolated from Arctic driftwood beached in Svalbard (Pang et al., 2011) suggest room for discovery in this taxon.

Most benthic faunal communities depend on food supplied from the water column, with sediment and water mass characteristics being additional prominent environmental forcing factors. In nearshore habitats, ice scouring and low or variable salinity results in reduced species richness and biomass, dominated

by a few oligochaete and amphipod taxa (Weslawski et al., 1993). The global distribution of benthic biomass (Wei et al., 2010) shows comparatively high benthic biomass on some Arctic shelves that provides major feeding grounds for mammals and sea birds (e.g., Grebmeier et al., 2006a; Opper and Huetmann, 2010). Metazoan community abundance, biomass, and species richness tend to decrease with water depth with no mid-depth peak in species richness, contrary to other regions and to Arctic zooplankton distribution (e.g., Bluhm et al., 2011). Modern Arctic fauna of Pacific affinity is most prominent on the Chukchi Sea shelf and in nearby

shallow areas, while that of Atlantic affinity occurs both on the shelves and in the deep sea across the entire Arctic (recent work of author Gebruk and Alexander Mironov, P.P. Shirshov Institute, Moscow). Regional differences in diversity appear to be more prominent on the shelves than in the deep sea with no distribution barrier effect apparent from the mid-Arctic ridges (Bluhm et al., 2011; Piepenburg et al., 2011).

For Arctic macro- and megabenthic shelf fauna (excluding fishes), Piepenburg et al. (2011) listed 2,636 species (with a predicted total number of 3,900–4,700 species) with highest species numbers for crustaceans (847 taxa), closely followed by annelids (668 taxa). By region, species numbers were highest in the Barents Sea. An updated inventory of deep-sea (> 500 m) benthos (including protists and meiofauna) yielded 1,125 taxa (1,240 when including the Greenland-Iceland-Norwegian Seas; Bluhm et al., 2011). This species list is more than 400 taxa greater than the previous one by Sirenko (2001) and is again dominated by crustaceans (366 taxa), followed by foraminiferans, annelids, and nematodes. About 60% of the deep-sea taxa overlapped with shelf taxa (Bluhm et al., 2011). Combining the above shelf and deep-sea taxon lists with Sirenko's 2001 list, the total known benthic species richness is on the order of ~ 4,600. This number is not vastly different from the known and verified ~ 5,800 benthic invertebrate taxa currently listed in the Antarctic Register of Marine Species (DeBroyer and Danis, 2011; DeBroyer, *pers. comm.*, February 21, 2011).

The endemism rate in the Arctic benthos is significantly lower on the Arctic shelves than the > 50% rate



Figure 3. Examples of undescribed and recently described Arctic species: (a) the sea cucumber *Elpidia belyaevi* (Rogacheva, 2007), (b) the bristle worm *Terebellides irinae* (Gagaev, 2009), (c) an undescribed harpacticoid copepod crustaceans of the genus *Cervi*, (d) an undescribed ctenophore of the genus *Bathyctena*, and (e) the moss animal *Septentriopora karasi* (Kuklinski and Taylor, 2008). Photo credits: (a) A. Rogacheva, P.P. Shirshov Institute, Russia, (b) B. Bluhm, University of Alaska Fairbanks, USA, (c) T. Kihara, German Biodiversity Institute, Germany, (d) K. Raskoff, Monterey Peninsula College, USA, (e) P. Kuklinski, Institute of Oceanology, Poland

estimated for the Arctic deep sea (Vinogradova, 1997). This number, however, should be viewed cautiously, and likely as inflated, because of globally inadequate investigation of the deep seafloor. In the Arctic deep sea, for example, half of the taxa found in analysis of ~ 6,000 records only occurred at one or two locations (Bluhm et al., 2011). Recently, new Arctic benthic species were described from a broad range of taxa and regions, for example a pan-Arctic deep-sea sea cucumber (Rogacheva, 2007), three mollusks from the Chukchi Sea shelf (Chaban, 2008; Sirenko, 2009), several polychaetes from the Canada Basin (e.g., Gagaev, 2009), and several bryozoans and a hydroid from a well-investigated Svalbard fjord (e.g., Ronowicz and Schuchert, 2007; Kuklinski and Taylor, 2008; Figure 3).

Publicly available sequence data such as COI barcodes for over 330 (with more in progress) of Arctic benthic invertebrate species (<http://www.boldsystems.org>) are beginning to be applied to biogeographic and other questions. For example, recent molecular studies document the presence of numerous cryptic species and identify locations of Arctic glacial and periglacial marine refugia for a range of taxa (summarized in Hardy et al., 2011). Barcode sequences for shelf species of polychaetes and echinoderms have also revealed high population connectivity across the Arctic as well as connectivity to both the Atlantic and Pacific faunas. The degree of gene flow differs, however, between taxa, with, for instance, greater gene flow over larger spatial scales in echinoderms than in polychaetes (Carr, 2010; Corstophine, 2010; Hardy et al., 2011).

VERTEBRATES

Fishes occur in all three realms of the Arctic, with the highest species richness in the benthic and demersal fishes (87%) versus the pelagic fishes (13%) (Catherine Mecklenburg, California Academy of Sciences, *pers. comm.*, February 16, 2011). Habitat preference in these bottom-oriented fishes is primarily driven by sediment type, bottom salinity, and bottom temperature, while water-column temperature and salinity characterize ichthyoplankton distribution patterns much like they influence zooplankton communities (e.g., Norcross et al., 2010). Two fish species, Arctic and polar cod, are closely associated with Arctic sea ice where they serve as energy transmitters from the sea ice system to higher trophic level predators (e.g., Lønne and Gabrielsen, 1992). Many temperate fishes are intolerant to the low temperatures of bottom waters in ice-covered regions, and thus the sea ice extent with its interannual and decadal-scale variability reasonably corresponds in spatial extent to the (hence, also variable) boundary between Arctic and subarctic demersal and benthic fish communities (Wyllie-Echeverria and Wooster, 1998; Mecklenburg et al., 2011).

An updated Arctic fish inventory contains 242 species (excluding 12 likely synonyms) distributed among 45 families, with sculpins (Cottoidei: 72 species) and eelpouts (Zoarcoidei: 55 species) accounting for more than half of all species (Mecklenburg et al., 2011). Thirty-one species are listed as diadromous and the remaining species as marine. The authors note that their list of species reflects significant changes in taxonomy and increased knowledge of species geographic distributions since previous compilations (e.g., Andriashev

and Chernova, 1995). COI sequences obtained for 165 species from the Arctic region and adjacent waters permitted discrimination of all sequenced species, supporting the separation of several species and the synonymy of several other species whose taxonomic status has been debated (Mecklenburg et al., 2011). Fishes with Arctic, predominantly Arctic, or Arctic-boreal distributions composed 41% of the 242 species in the region, while the remainder were considered boreal, predominantly boreal, or widely distributed species. New Arctic fish species continued to be described in the first decade of this century, for example, *Lycodes paamiuti* (Møller, 2001) and *Careproctus kidoi* (Knudsen and Møller, 2008). New studies continue to change the inventory, with, for example, resurrection of the North Pacific spiny dogfish, *Squalus suckleyi*, from synonymy in *S. acanthias* (Ebert et al., 2010), raising the count to 243 species (Catherine Mecklenburg, California Academy of Sciences *pers. comm.*, February 16, 2011). The reason for the overall low species richness of Arctic fish fauna is thought to be related to the relatively young evolutionary age of the Arctic habitat.

Arctic seabirds are dependent on marine resources from the Arctic for all or most of their energy requirements while they are in the region (Gaston, 2004). A total of ~ 450 bird species are known to breed or have bred in the Arctic region as defined by CAFF (CAFF, 2001; Zoeckler, in press). Of these, 256 species have significant populations in the Arctic, and 175 are water related. The Seabird Working Group of CAFF identified 64 Arctic seabird species (Petersen et al., 2008; Zoeckler, in press), about 16 species of

which have circumpolar distributions. Uncertainty on the subspecies level and taxonomic splitting (see Huettmann et al., 2011, for a taxonomic crosswalk of 27 pelagic seabird species) affect not only the species richness estimates but also specific conservation and risk assessments. Species that forage on the open ocean are mostly alcids, gulls, skuas, and terns (e.g., Huettmann et al., 2011). Other taxa tied to marine food webs are sea ducks, as well as the species-rich shorebirds, loons, some geese, cranes, and most Arctic raptors, including owls and ravens. It should be noted that many terrestrial and coastal birds of the Arctic can often be found on the sea ice, and crossing oceans. Many Arctic seabirds are connected with southern areas by seasonal migrations (Huettmann et al., 2011), for example, the Arctic tern, some skuas, and jaegers travel between the Arctic and Antarctic, and the sooty shearwater and Wilson's storm petrels migrate between New Zealand/Chile and the North Pacific, including Alaska, as well as the North Atlantic.

The life cycles, distribution, and migration patterns of many Arctic marine mammals are also intricately coupled to the seasonal pattern of sea ice melt and formation (e.g., Moore et al., 2000). A total of 16 marine mammals occur in the Arctic: nine species are ice-associated year-round with an additional seven species occurring seasonally or occasionally (Huntington and Moore, 2008). Eight of the 16 species are cetaceans and seven are seals, plus the polar bear. Arctic foxes are regularly observed far out on sea ice but have not been classified as marine mammals. Recent diversity-related research on Arctic marine mammals has focused on delineating genetic population structure

of some species (references cited in O'Corre-Crowe, 2008), while data on metapopulations, species culture, and population size and structure of other species are sparse (Kovacs et al., 2011). Analysis of molecular data from multiple studies on seven Arctic marine mammal species suggests that small and isolated subarctic populations tend to have lower genetic diversity than larger Arctic populations (O'Corre-Crowe, 2008). Behavioral aspects, widely recognized to be essential for defining marine mammal population structures, are still virtually unstudied for most species.

RECENT CHANGES IN BIODIVERSITY AND BIOMASS

A proper assessment of changes in biodiversity requires solid baselines on species occurrences, abundance, and biomass. To date, however, only a few time series of biological variables have been collected in the Arctic, and for a limited number of taxa and regions; nonetheless, they demonstrate substantial interannual and interdecadal variability or change in pelagic and benthic habitats at virtually all trophic levels. Changes include shifts in distribution ranges (Figure 2), and/or biomass and trophic cascades (examples outlined below), but also—primarily investigated in mammal species—variances in body condition, reproductive output, or diet (examples in Kovacs et al., 2011; Wassmann et al., 2011). The largest number of reported changes are for marine mammals and seabirds, where studies often tend to focus on individual species and populations rather than communities and ecosystems as a whole. Within the invertebrates, documented distribution shifts are more numerous in the benthic realm than the pelagic realm because the typically longer benthic life

spans result in less seasonally modulated abundance and distribution that integrate changes over longer time periods (e.g., Blacker, 1957). As an example, the benthic community structure in Kongsfjorden (Svalbard) varied with the phases of the North Atlantic Oscillation and its local manifestations between 1980 and 2003 (Beuchel et al., 2006). To date, most of the observed changes are near the Arctic margins rather than in the central Arctic (Figure 2), but it remains unclear whether this is a bias from higher observation density in subarctic areas or is due to truly larger environmental changes in those areas.

At the lowest trophic level, increased ice-free conditions extend the distribution of Atlantic phytoplankton species northward. An example is *Emiliania huxleyi* that now occurs along the northern sector of the western Eurasian shelves (Hegseth and Sundfjord, 2008; Figure 2). The recent occurrence of the North Pacific planktonic diatom *Neodenticula seminae* in the North Atlantic (Figure 2) is also interpreted as an effect of climate warming (Reid et al., 2007), presumably by transport in a pulse of Pacific water through the Canadian Arctic Archipelago and/or Fram Strait. At intermediate trophic levels, switches from long-lived, slow-growing Arctic benthic species to faster-growing temperate species in Svalbard reflect increasing water temperatures (e.g., Weslawski et al., 2010). Similarly, northern range extensions in some epifaunal crabs, chitons, and bivalves in the Chukchi Sea (Sirenko and Gagaev, 2007) and community-wide northward distribution shifts of fish in the Bering Sea (Mueter and Litzow, 2008) are tied to warming water. The reappearance of the blue mussel in Svalbard after a thousand

years of absence appears to be a direct consequence of a warmer environment (Berge et al., 2005; Figure 2). The contraction of the distribution center of female snow crab to the north in the Bering Sea (Ohrensantz et al., 2004) and a probable increase of that species in the Chukchi Sea (Bluhm et al., 2009; Figure 2) might eventually influence the distribution of the commercial fishery.

At still higher trophic levels, examples of population changes include declines of seabird numbers such as those of nesting ivory gulls (a species strongly associated with sea ice) in the Canadian Arctic by as much as 80% relative to the 1980s (Gilchrist and Mallory, 2005). Sabine's Gull and Kittlitz's Murrelet populations have dropped, and Thick-billed Murres have been declining for several decades (CAFF, 2010). Other southern species seem to increase northerly; for example, declines of various populations of king and common eiders in the Beaufort Sea between 1976 and 1996 have also been documented, with yet undetermined causes (Suydam et al., 2000). Spectacled eiders nesting in southwest Alaska declined by 96% between the early 1970s and the early 1990s and stabilized afterward at those low levels (e.g., Petersen et al., 2000), while trends in the large Siberian spectacled eider breeding populations remain unknown. A 30+ year time series on seabirds of Cooper Island, off the coast of Arctic Alaska, demonstrated the arrival and successful nesting of black guillemots and later horned puffins (Divoky, 1982) at the island when the environment had warmed enough to provide sufficient snow-free days for laying eggs and raising chicks (Moline et al., 2008). Beginning in the 1990s, the number of breeding pairs of black guillemots declined again, possibly because

the sea ice that provides critical foraging habitat for the species retreated earlier and farther offshore. Other species such as Skuas, Horned and Tufted Puffin, some gull species, and the otherwise temperate Northern Gannets seem to have moved north, with the latter species now breeding in the White Sea (e.g., Krasnov and Barrett, 1997; Piatt and Kitaysky, 2002).

Marine mammals have frequently been suggested as "ecosystem sentinels" because they integrate change across trophic levels as well as large areal and temporal scales (Moore, 2008). Distribution changes in Arctic pinnipeds and cetaceans have been linked to ice extent and ice availability plus related factors (e.g., Kovacs et al., 2011). To give only a few examples from the growing body of literature, northward expansions are recorded for the Pacific gray whale in the Chukchi and Beaufort Seas (e.g., Moore, 2008) and for orcas in the Canadian Arctic (e.g., Ferguson, 2009). Other populations, in contrast, such as bowhead whales in the Chukchi and Beaufort Seas, have been rather stable with regard to their distribution (George et al., 2004). Population size has changed in some populations (summarized by O'Corre-Crowe, 2008) with declines and distribution changes, for example, in many polar bear (Aars et al., 2006) and some walrus populations (Born, 2005), but increasing numbers can be seen in other populations such as western Arctic bowhead whales between 1979 and 2001 (George et al., 2004). Other documented changes in seals and whales include shifts in prey composition and declines in body condition and reproductive success (e.g., reviewed by Kovacs et al., 2011). The hooded seal, polar bear, and narwhal are regarded as the

most sensitive to climate change, based on population size, geographic range, habitat specificity, diet diversity, migration, site fidelity, sensitivity to changes in sea ice, sensitivity to changes in the trophic web, and maximum population growth potential (Laidre et al., 2008).

While changes in species distribution ranges appear primarily tied to water temperatures, changes in biomass (other than those related to harvests) result from a combination of shifts in energy flow or benthic-pelagic coupling, and environmental conditions. For example, the biomass of jellyfish increased in the Bering Sea throughout the 1990s, followed by a biomass collapse in 2000, with subsequent stabilization (Brodeur et al., 2008). These dynamics were linked to ice cover, wind mixing, and sea surface temperatures as well as prey availability, specifically juvenile walleye pollock and zooplankton. Associated phytoplankton communities switched between coccolithophore blooms in warmer years and diatoms in colder years (Stockwell et al., 2001). Emerging trends with regard to benthic invertebrate biomass are not coherent and include (1) decreasing infaunal and/or amphipod biomass in the northern Bering Sea (Moore et al., 2003; Dunton et al., 2005; Grebmeier et al., 2006b; Coyle et al., 2007), (2) increased epifaunal biomass in the northern Bering and southern Chukchi Seas (Feder et al., 2005; Hamazaki et al., 2005; Bluhm et al., 2009), and (3) no change of infaunal biomass in yet other areas such as a High Arctic fjord (Renaud et al., 2007). The examples of biomass decrease could perhaps be interpreted in support of the prediction that the current benthos-favoring pelagic-benthic coupling will shift toward a pelagic-dominated

system (e.g., Carroll and Carroll, 2003; Grebmeier et al., 2006b). Regionally, however, biomass changes can also be evidence of spatial community-wide shifts, specifically northward displacement as documented in the Bering Sea (Mueter and Litzow, 2008).

KNOWLEDGE GAPS

Arctic regions contain a complex variety of habitats, most of which are difficult to access. Despite a recent increase in overall interest and research effort, observational gaps still remain for some geographic areas (Figure 1a), taxa, and habitats. The decades-long lack of interest and the logistical challenges posed by filling these gaps are now leading to uncertainties about the biodiversity patterns (Figure 1b) and the extent of ongoing changes. Compiling information on the status quo and making informed predictions into the future require open data sharing in online data systems, as, for example, outlined in the data policy of the International Polar Year 2007–2009 and followed by some of its projects (e.g., Bluhm et al., 2010b), with regrettably overall weak compliance to date (Carlson, 2011).

Incomplete species/OTU lists are clearly largest in the microbial realm, including fungi. For the bacteria and archaea, diversity estimates are largely based on the scaling of a limited number of observations (Lovejoy et al., 2011). The recent inventory of marine pelagic and sea ice unicellular eukaryotes (Poulin et al., 2011) demonstrated the largest gap in knowledge to be in the diversity of small cells (< 20 µm), which represented less than 20% of their assessment; however, their effort did not include lesser-known groups such

as pelagic ciliates or benthic microalgae. On higher trophic levels, including seabirds and marine mammals, gaps still exist in the knowledge of species distributions and population numbers, as well as their temporal trends, sensitivities, and reasons for change (other than a human role per se) (Huettmann et al. 2011; Kovacs et al., 2011).

Regional gaps still exist in the deep sea, in particular at depths over 1,000 m, despite considerable sampling effort in the past decade (e.g., Soltwedel et al., 2005; Bluhm et al., 2011). Of the shelf seas, the East Siberian Sea is probably the most understudied in terms of biodiversity, although an intense study by the Zoological Institute in St. Petersburg is ongoing. Large gaps also exist in the vast area of the Canadian Arctic Archipelago (Carr, 2011) and northern Greenland, both of which still remain heavily ice-covered. Examples of underexplored habitats include the deep-sea ridge systems spanning thousands of kilometers across the Arctic as well as special features such as pockmarks and seamounts. In the sea ice realm, pressure ridge biodiversity studies are only now starting to emerge (Hop and Pavlova, 2008; Gradinger et al., 2010b), although this habitat may play an increasingly important role in light of the diminishing ice cover. Ironically, while nearshore habitats have been extensively studied, they are typically only well investigated in the vicinity of field stations and not at broader scales that capture the full range of habitat types and heterogeneities.

OUTLOOK


Recent updates of Arctic species inventories across all taxonomic levels demonstrate the presence of close to

8,000 eukaryotic species (i.e., excluding Eubacteria and Archaea). Cautious estimates predict that several thousand benthic invertebrate species still remain to be recorded (Bluhm et al., 2011; Carr, 2011; Piepenburg et al., 2011). It is clear that Arctic ecosystems will be subjected to a variety of pressures in the future (e.g., ACIA, 2005; Johnsen et al., 2010), and prediction of future Arctic “species richness” in time and space is complicated by an interplay of factors capable of either increasing or decreasing the overall species richness in the coming decades (Weslawski et al., 2011). Species richness can increase, for example, when northward-advected boreal species mix with Arctic residents, and when perennial algae and associated fauna replace seasonal communities in previously ice-scoured nearshore areas (Vermeij and Roopnarine, 2008; Weslawski et al., 2008, 2011). Species richness can decrease through habitat homogenization and increasing sedimentation associated with glacial melt and increased river runoff, and when biota associated with multiyear ice loses its habitat (e.g., Kędra et al., 2010; Weslawski et al., 2011). Species richness might even stay stable if, for example, southern species replace functionally similar Arctic species, or because existing adaptations to seasonally low food availability, variable temperatures, and other factors might buffer Arctic biota against some degree of change (Pertsova and Kosobokova, 2010; Weslawski et al., 2011).

Species richness, therefore, may not be the most desirable single metric with which to evaluate biodiversity changes, and should be considered along with many other metrics. The competition of Arctic endemics and primarily Arctic-distributed biota with temperate

taxa is inevitable, and is expected (if not already observed; see above) to lead to the reduction of “typical” Arctic populations, species, communities, and/or habitat (e.g., Weslawski et al., 2008; CAFF, 2010). The examples of ongoing changes on species and communities levels demonstrate the value and necessity of related surveys that are systematic and methodologically comparable in nature. Such surveys are required on both regional and pan-Arctic scales to detect change and inform both short-term and long-term conservation and management plans. As stressed also by CAFF (2010) and UNEP, these plans should include identifying and protecting biologically important marine areas (Johnsen et al., 2010; Huettmann and Hazlett, 2010).

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