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Biodiversity of arctic marine fishes: taxonomy and zoogeography

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Abstract Taxonomic and distributional information on each fish species found in arctic marine waters is reviewed, and a list of families and species with commentary on distributional records is presented. The list incorporates results from examination of museum collections of arctic marine fishes dating back to the 1830s. It also incorporates results from DNA barcoding, used to complement morphological characters in evaluating problematic taxa and to assist in identification of specimens collected in recent expeditions. Barcoding results are depicted in a neighbor-joining tree of 880 *COI* (cytochrome *c* oxidase 1 gene) sequences distributed among 165 species from the arctic region and adjacent waters, and discussed in the family reviews. Using our definition of the arctic region, we count 242 species with documented presence, if 12 species that likely are synonyms are excluded. The 242 species are distributed among 45 families.

Six families in Cottoidei with 72 species and five in Zoarcoidei with 55 species account for more than half (52.5%) the species. This study produced *COI* sequences for 106 of the 242 species. Sequence variability in the barcode region permits discrimination of all species. The average sequence variation within species was 0.3% (range 0–3.5%), while the average genetic distance between congeners was 4.7% (range 3.7–13.3%). The *COI* sequences support taxonomic separation of some species, such as *Osmerus dentex* and *O. mordax* and *Liparis bathyarcticus* and *L. gibbus*; and synonymy of others, like *Myoxocephalus verrucosus* in *M. scorpius* and *Gymnelus knipowitschi* in *G. hemifasciatus*. They sometimes revealed the presence of additional species that were not entirely expected, such as an unidentified species of *Ammodytes* in the western Gulf of Alaska, most likely *A. personatus*; and an unidentified *Icelus* species of the *I. spatula* complex with populations in the western Gulf of Alaska and the northern Bering and Chukchi Seas which could be a new species or a species in synonymy. Reviewing distribution, we found that for 24 species the patterns assigned by authors understated historical presence in the arctic region, and for 12 species they overstated presence. For instance, *Hippoglossoides robustus* is counted as an arctic–boreal species rather than predominantly boreal, and *Artediellus uncinatus* as predominantly arctic rather than predominantly boreal. Species with arctic, predominantly arctic, or arctic–boreal distributions composed 41% of the 242 species in the region, and predominantly boreal, boreal, and widely distributed species composed 59%. For some continental shelf species, such as the primarily amphiboreal *Eumesogrammus praecisus* and *Leptoclinus maculatus*, distributions appear to reflect changes, including reentry into Arctic seas and reestablishment of continuous ranges, that zoogeographers believe have been going on since the end of land bridge and glacial times.

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Introduction

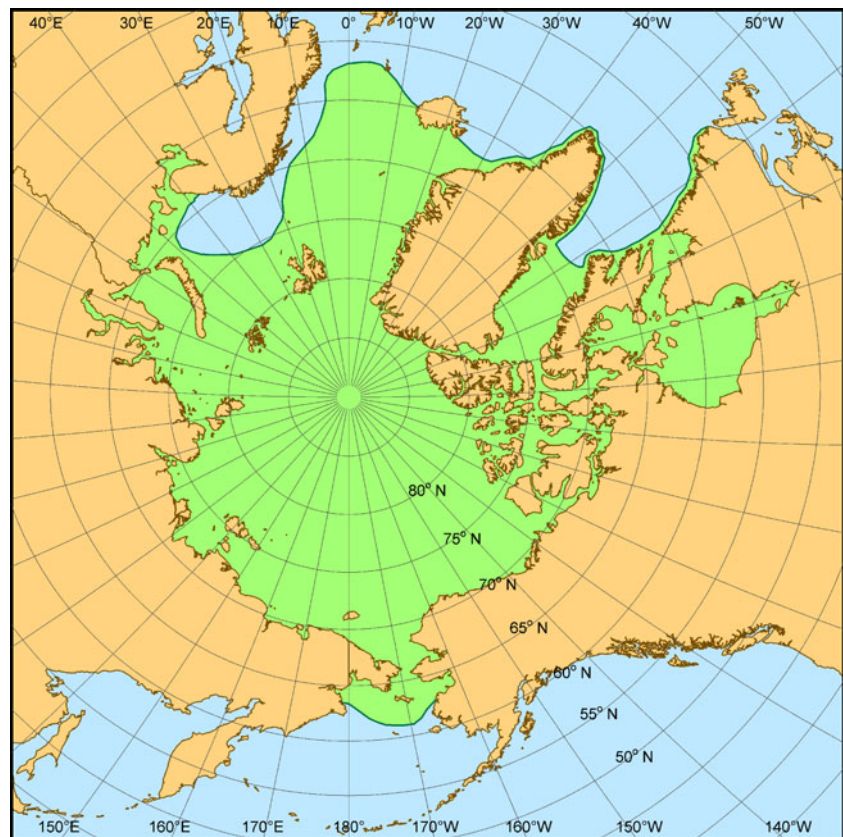
The way we classify organisms demonstrates our understanding of biodiversity at the most basic level. The classification of arctic marine fishes is somewhat unsettled, with the status of several species, genera, and even higher taxa controversial. The lack of nomenclatural stability and taxonomic resolution for some species has made it difficult to interpret the historical record of fish distribution and make temporal comparisons, and to identify fishes in the field and laboratory for modern assessments. Studies focusing on the taxonomy and geographic distributions of arctic marine fishes during the International Polar Year (IPY) and first Census of Marine Life (CoML) programs have advanced knowledge on those aspects of diversity to the extent that a review and synthesis are required. Such a synthesis is timely because it provides a critical component of the baseline for monitoring and detecting effects of climate change on biodiversity. This paper reviews advances in our taxonomic knowledge of species within the context of each family represented in arctic marine waters and provides an annotated list of species with notes on new records of

occurrence affecting known patterns of distribution. The family reviews and annotated list incorporate new information gained from DNA sequencing, examination of museum collections and records, and research fishing in the Arctic Ocean and adjacent arctic waters of the North Pacific and North Atlantic during the IPY and CoML (2001–2010).

Definition

By “arctic region” (Fig. 1) we mean the Arctic Ocean and its seas and adjacent waters of the North Atlantic and North Pacific southward to the arctic–boreal ichthyofaunal boundary. The position of the boundary is reflected in major differences in species composition associated with seafloor topography, such as sills and canyons, and water characteristics, such as temperature and salinity, that form barriers against fish movements. The boundary has a temporal dimension, in that it reflects historical patterns of distribution. Briggs (1974), in his comprehensive treatment of marine zoogeography for faunal regions of the world, defined the boundaries before the acceleration of climate change and retraction of the Arctic sea ice observed in recent decades. Wherever Briggs’ (1974) arctic–boreal boundary has been modified it has been done to add refinements from increased knowledge on historical patterns of distribution, not in response to any observed shifts in species composition attributed to recent climate change.

Fig. 1 Arctic marine ichthyofaunal region. See text for definition of boundary



In the North Atlantic, the arctic faunal region extends south to Cape Charles (52°13'N), Labrador, at the northern border of the Strait of Belle Isle (Briggs 1974, 1995). The region extends seaward at depths less than 50 m along the Canadian coast north approximately to Durban Island (67°05'N), along the Canada–Greenland Ridge, separating Baffin Bay from Davis Strait with depths less than 700 m, to near Aasiaat (68°40'N); along southern Greenland coasts at depths less than 50 m to about the middle of the Greenland–Iceland Ridge (67°N), separating the Greenland Sea and the North Atlantic Ocean with depths less than about 630 m, across to northern Iceland; along the Iceland–Faroe Ridge, with a maximum depth of 657 m, including the Faroe Trench; in the Norwegian Sea at depths more than 500 m nearly to Bear Island; and in the Barents Sea from 74–75°N nearly to southern Novaya Zemlya and including the White Sea west to the Murman Peninsula (Møller et al. 2005a, modified). Studies describing fish assemblages and associated hydrographic and topographic conditions at key locations along the Atlantic part of the boundary include Backus (1957) on Labrador; Kotthaus and Krefft (1967) on the Iceland–Faroe Ridge; Haedrich and Krefft (1978) on Denmark Strait and the Irminger Sea; Bergstad et al. (1999) on the slope of the eastern Norwegian Sea; Møller and Jørgensen (2000) and Jørgensen et al. (2005) on Baffin Bay and Davis Strait; Blindheim (2004) on the Greenland, Iceland, and Norwegian Seas; Loeng (1988), Fossheim et al. (2006), and Byrkjedal and Høines (2007) on the Barents Sea; and Loeng and Drinkwater (2007) on the Norwegian and Barents Seas.

In the North Pacific, the arctic region reaches south into the Bering Sea. Briggs (1974) considered the most likely historical boundary for arctic fishes in the Bering Sea to be at about Cape Olyutorskiy on the western side and Nunivak Island on the eastern side, but allowed that further research could show it to be farther north, as proposed earlier by Andriashev (1939). Andriashev's boundary proceeds from the southwestern part of the Gulf of Anadyr along the southern limit of the Anadyr–St. Lawrence cold patch (bottom temperatures negative or close to zero), dips south between St. Lawrence and St. Matthew islands, and curves northeast to the Yukon River Delta (Andriashev 1939). It curves strongly northeastward because the warm, northward flowing Alaska Coastal Current raises bottom temperatures near the Yukon Delta above tolerable limits for arctic fishes.

Origin of Arctic Ocean fishes

The geographic distributions of fish species and composition of regional fish faunas as they exist at present are products of the biogeographic history of the taxa and evolution of present climatic conditions. The biogeographic and climatic history of the Arctic Ocean has produced a fish fauna dominated by phylogenetically young families (e.g.,

Zoarcidae, Stichaeidae) (Andriashev 1954; Dunbar 1968). Old groups are thought to have been eliminated during the rapid cooling of the Middle Miocene (Savin 1977), and younger families to have invaded the Arctic mainly from the Pacific when the Bering Strait opened 3–3.5 million years ago. A few families appear to have invaded the Arctic from the Atlantic (e.g., Gadidae, Anarhichadidae). These theories are mainly based on current species diversity in the Atlantic, Arctic, and Pacific (Schmidt 1950; Briggs 1974), but are largely confirmed by phylogenetic studies (Møller and Gravlund 2003; Roa-Varóna and Orti 2009). At the time of this great biotic interchange (Briggs 2003), the Arctic Ocean was free of ice and boreal (cold–temperate) conditions still prevailed (Golikov and Scarlato 1989). Between 3.5 million years ago and the present, the Bering seaway apparently closed and reopened as many as ten times (Einarsson et al. 1967; Briggs 1974, 1995, 2003). The multiple Pliocene–Pleistocene glacial periods are thought to be the most important vicariance events in the evolution of Arctic fishes (Berg 1934; Andriashev 1939, 1949; Anderson 1982).

With continued cooling during the Pliocene and Pleistocene (Herman and Hubkins 1980), some Arctic Ocean species became extinct in the Arctic and relegated to warmer waters of the Pacific and Atlantic Oceans. This event created some amphiboreal sister species (e.g., *Hippoglossus hippoglossus* in the Atlantic and *H. stenolepis* in the Pacific), an observation first made by Berg (1918, 1934). True amphiboreal species, which have retained identity as a single species without extant populations between the Pacific and the Atlantic (e.g., *Aspidophoroides monopterygius*), are believed to reflect distribution before the last glaciation (Andriashev 1939; Walters 1955). After the last glacial period, which estimates indicate ended about 10,000–12,000 years ago, amphiboreal and other species with disjunct distributions could expand into the Arctic and reestablish continuous distributions (Walters 1955). The existence of naturally occurring amphiboreal species suggests either a recent separation or occasional gene flow between Pacific and Atlantic populations. Amphiboreality has been induced artificially in modern times by transplantation or stocking programs, such as for *Alosa sapidissima* and *Oncorhynchus gorbuscha*, and this mechanism has been proposed by Ursvik et al. (2007) to explain the recently discovered amphiboreality of *Gadus chalcogrammus*.

Rather than retreat south with cooling climate, another strategy for avoiding subzero temperatures seems to have been adaptation to brackish habitats (e.g., *Clupea pallasii*, *Lycodes jugoricus*, *Pleuronectes glacialis*). As Walters (1955:328) explained it, during the last glaciation fish could survive in the Arctic in brackish habitats wherever rivers continued to flow; “the rivers exerted a warming influence on the nearby salt waters and sustained ‘oases’ of elevated temperature.” Brackish water forms could follow close to the

retreating ice walls and most likely were the first fishes to move into deglaciated areas (Walters 1955). Another strategy was to adapt to deep ice-free waters (e.g., *Lycodes frigidus*, *Paraliparis bathybius*, *Triglops nybelini*); the so-called secondary deep-water fishes, as opposed to ancient deep-water forms (Andriashev 1953). Andriashev (1986, 1990) considered it unlikely that secondary deep-sea groups with Pacific ancestry could have penetrated the Arctic by way of the shallow waters of the northern Bering Sea and Bering Strait, and proposed trans-equatorial migration in deep cold waters as the means of reaching the Arctic for those groups. Dispersal in deep cold waters has been used to explain the antitropical distribution of many marine organisms (Ekman 1953) since the time of the polar explorer Sir James Ross, who observed that some of the animals caught during the Antarctic expedition of H.M.S. *Erebus* and *Terror* in 1839–1843 looked the same as those he had seen in the Arctic, and assumed they were able to migrate via abyssal, cold waters (Briggs 1995). Numerous examples now exist (Briggs 2003), including the discovery of a large Patagonian toothfish, *Dissostichus eleginoides*, off Greenland (Møller et al. 2003), that indicate that this type of deepwater migration does take place. In a more complex development of the “isothermic submersion” (Briggs 1995, 2003) theory, Andriashev (1986, 1990) proposed that secondary deep-water groups of Pacific origin (e.g., *Paraliparis*, *Careproctus*) migrated via the eastern Pacific to Tierra del Fuego, through Drakes Passage, and thence to the Arctic Basin via the Atlantic.

Knowledge on the current distribution of fishes is essential to understanding their biogeographic history. Fish fossils are relatively rare and current distributions must be studied to gain insight into prehistoric patterns. Regional monographs, checklists, and results of marine expeditions published during the IPY and CoML have reviewed the history of ichthyological research in the Arctic and adjacent waters and provided updated knowledge on geographic distribution for fishes of the Gulf of Alaska and Bering Sea to the Chukchi and Beaufort Seas (Mecklenburg et al. 2002, 2007); the Barents Sea (Dolgov 2006; Byrkjedal and Høines 2007; Karamushko 2008) and Kola Bay (Karamushko et al. 2009); the Kara Sea (Dolgov et al. 2009) and Baidaratskaya Bay (Semushin and Novoselov 2009); Baffin Bay and northern Davis Strait (Jørgensen et al. 2005); northeast Greenland (Christiansen 2003, 2006); all around Greenland (Møller et al. 2010); and Jan Mayen (Christiansen 2008; Wienerroither et al. 2010). A draft annotated checklist (Coad and Reist 2004) serves as a guide to the marine fishes of northern Canada while identifications are confirmed and the authors prepare a monograph.

Historical museum records

Voucher specimens serving to document the identifications of fishes caught by the various expeditions to the arctic

region are housed in museum collections around the world. Verifying fish identification in many of those collections to create a database of confirmed and reliable records of species occurrence for studies of zoogeography and climate change (e.g., Mecklenburg et al. 2006, 2007; Mecklenburg and Mecklenburg 2009), revealed numerous misidentified specimens, unreported specimens that extend known patterns of distribution, and even an entire, unreported collection of benthic and demersal fishes from a research expedition to the Chukchi Sea in 1973. The arctic marine fish museum vouchers study has focused mainly on collections from the northern Bering, East Siberian, Chukchi, and Beaufort Seas and the Canadian Arctic, including the Canadian high Arctic archipelago. Collections were examined at the California Academy of Sciences (CAS), San Francisco; Canadian Museum of Nature (CMN), Gatineau, Quebec; Hokkaido University Museum of Zoology (HUMZ), Hakodate, Japan; US National Museum of Natural History (USNM), Washington, D.C.; National Oceanic and Atmospheric Administration (NOAA), Alaska Fisheries Science Center (AFSC), Auke Bay Laboratory (ABL), Juneau, Alaska; University of Alaska Museum (UAM), Fairbanks; University of British Columbia (UBC), Vancouver; University of Washington (UW), Seattle; and Zoological Institute (ZIN), St. Petersburg, Russia. The large collections from around Greenland and adjacent Arctic seas at the Zoological Museum of the University of Copenhagen (ZMUC) and other museums with collections of eastern Arctic material studied by P.R.M. (e.g., Møller et al. 2010), have yielded similar discoveries of historical records affecting our understanding of arctic fish distributions. This paper reports many of the historical records of occurrence for the first time, mainly in Online Resource 1, where museum catalog numbers (e.g., CAS 228530) for specimens are cited to document limits of distribution or other noteworthy revision to geographic range not previously published. Locality, date, and other collection data associated with the records are given in Online Resource 2.

Recent ichthyological sampling

Investigations during the IPY and CoML that have provided most of the new records of occurrence reported here include, for the Pacific-arctic region: Bering Strait to northwestern Chukchi Sea in 2004 and Bering Strait to East Siberian and Chukchi Seas and Chukchi Borderland in 2009, for the Russian-American Long-Term Census of the Arctic (RUSALCA; NOAA and Russian Academy of Sciences) (<http://www.arctic.noaa.gov/aro/russian-american/>); northeastern Bering Sea and Bering Strait in 2006 (Norton Sound Economic Development Corporation); and eastern Chukchi Sea north to 70°N in September 2007 (NOAA, AFSC) and in August 2007

and 2008 (Hokkaido University Faculty of Fisheries and University of Alaska Fairbanks, School of Fisheries and Ocean Sciences). The investigations used bottom trawls. The September 2007 Chukchi Sea cruise also used a surface trawl and was the first time a large, commercial-sized surface net had been used for scientific sampling in the Chukchi Sea. Except for the RUSALCA 2004 cruise (Mecklenburg et al. 2007; Norcross et al. 2010), the ichthyological results from these cruises have not been published; reports are in progress. Presence of species in the catch is reported in this paper (Online Resource 1) if the information helps establish species' distributions.

Since 1996, annual surveys of *Reinhardtius hippoglossoides* and *Pandalus borealis* by the Greenland Institute of Natural Resources have been conducted in most of the Greenland EEZ, including northern Baffin Bay in 2001 and 2004 (Jørgensen et al. 2005). The same vessel covered the Canadian part of Baffin Bay in 1999, 2001, and 2004 (Chambers and Dick 2005). Material of most species was collected for ZMUC and the Canadian Museum of Nature (CMN). Several specific records from these cruises that provide noteworthy information on distribution were not previously reported.

Online Resource 2 provides collection data for recently collected material, as well as historical, cited by catalog number in this paper. Abbreviations for institutions and collections follow Fricke and Eschmeyer (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>).

DNA barcoding

Tissue samples and DNA sequences obtained from the recent cruise catches provide documentation for species identifications in addition to the specimens themselves, as well as insight into resolution of problematic taxonomy. Results from DNA barcoding [sequencing a standard region of the mitochondrial cytochrome *c* oxidase 1 gene (*COI*)] efforts conducted during the CoML are reported. The protocol for the barcoding method is described in Steinke et al. (2009). Ward et al. (2009) reviewed the benefits and limitations of DNA barcoding fishes. Limitations to barcoding include incomplete lineage sorting and introgressive hybridization, which often require additional genetic evidence such as supplemental nuclear loci to fully resolve species or an integrative approach that includes morphology and geography. The use of barcoding in fish taxonomy and identification has recently been demonstrated for southern Alaska skates (Spies et al. 2006) and fishes of Pacific Canada (Steinke et al. 2009). Our samples were sequenced by the Biodiversity Institute of Ontario, University of Guelph; other sequences were publicly available on the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007). Barcoding of fishes from the East Siberian,

Chukchi, Beaufort, and Bering Seas, Chukchi slope and Chukchi Cap, Aleutian Islands, and Gulf of Alaska was done from 691 tissue samples collected mostly by C.W.M.; 684 samples were successfully sequenced (BOLD project Fishes of Alaska and the Pacific-Arctic). Samples from Churchill, Hudson Bay, collected by D.S., yielded 97 *COI* sequences from marine species (BOLD project Actinopterygii of Churchill). We also used 78 sequences of fish caught in Baffin Bay and Davis Strait (BOLD project Arctic Fishes, provided by the Canadian Museum of Nature collection); and 21 sequences from various Bering Sea and eastern North Pacific sites (BOLD project NWFSC Marine Fish Voucher Collection, provided by the University of Washington collection). Online Resource 3 shows a neighbor-joining tree for *COI* sequences in the Pacific–Arctic, Hudson Bay (Churchill), Baffin Bay–Davis Strait, and UW collections (880 sequences). Online Resource 4 gives museum catalog numbers and collection data for the barcoded specimens.

Taxonomy and zoogeography of arctic marine fishes

Families are reviewed in the phylogenetic order presented by Nelson (2006). Documentation, including literature citations and museum catalog numbers, for geographic distributions (including those shown in Fig. 2) is provided in the annotated list of species (Online Resource 1). The DNA barcoding results are discussed here. Where fish size is given, it is total length (TL) unless specified otherwise.

Myxinidae (hagfishes)

Seven genera with about 70 species by Nelson's (2006) count, 73 species after adding new species described recently. Boreal, circumglobal; benthic; typically deep, on soft substrates. *Myxine glutinosa* is included on the list of arctic fishes from its occurrence in shallow waters of southern Greenland. In the eastern Atlantic, *M. glutinosa* reaches Varanger Fjord just outside the arctic region.

The name *Myxine limosa* Girard, 1859 for the western Atlantic population has been bounced back and forth in and out of synonymy with *M. glutinosa* (e.g., Garman 1899; Wisner and McMillan 1995; Fernholm 1998; Martini et al. 1998; Mok 2001; Moore et al. 2003). The strong morphological and distributional evidence provided by Møller et al. (2005b) should put this argument to rest in favor of treating *M. limosa* as a synonym of *M. glutinosa* Linnaeus, 1758.

Petromyzontidae (northern lampreys)

Eight genera, 34 species in cool zones generally north of 30°N (Nelson 2006). Anadromous and freshwater; parasitic and nonparasitic. Previously classified as a subfamily

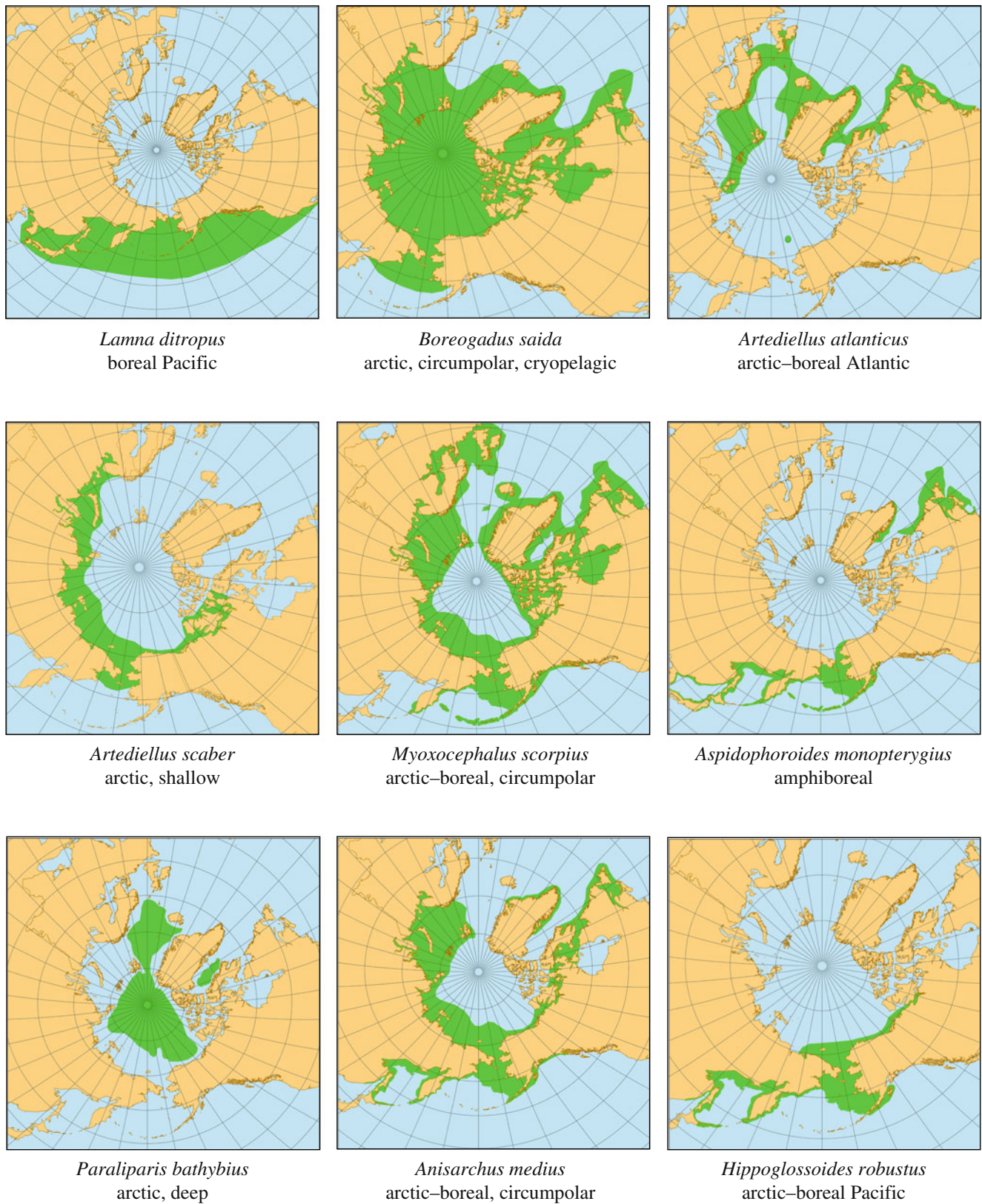


Fig. 2 Distribution patterns of nine fish species occurring in the arctic region

(Nelson 1994), the Northern Hemisphere lampreys are classified (Nelson 2006) as a separate family from the Southern Hemisphere lampreys following the phylogenetic study based on morphological data by Gill et al. (2003). Subgenera in *Lampetra* have been elevated to genera following Renaud (1997) and Gill et al. (2003). One species (*Lethenteron camtschaticum*) has a primarily arctic distribution extending southward into the North Pacific and eastern North Atlantic. Two boreal species have ranges extending into the arctic region; one from the North Pacific (*Entosphenus tridentatus*) and one from the North Atlantic (*Petromyzon marinus*).

Cetorhinidae (basking sharks)

One species (Compagno 2005). Epipelagic, coastal and oceanic, widely distributed in boreal and temperate seas. *Cetorhinus maximus* occurs rarely in the arctic region off northern Newfoundland and southwest and southeast Greenland, and reaches the margin of the arctic region off the Norway and Murman coasts.

Lamnidae (mackerel sharks)

Three genera, five species (Compagno 2005). Pelagic, neritic and oceanic, in tropical to temperate waters. Two lamnids occur rarely in southern waters of the arctic region; one species in the Pacific (*Lamna ditropis*), and one in the Atlantic (*L. nasus*). The catch of a young male *L. ditropis* at 66°06'N, 168°28'W in 2007 confirms the distribution of this species northward to Bering Strait (Figs. 2 and 3; Online Resource 1). Previously there were no firm records of *L. ditropis* north of about 60°N in the Bering Sea.

Squalidae (dogfish sharks)

Two genera with 19 species (Compagno 2005; Séret 2010). *Squalus acanthias* has a wide distribution in the Atlantic and Pacific and occasionally enters the arctic region. A specimen caught in a salmon gillnet in the southeastern Chukchi Sea near Kotzebue, Alaska (Mecklenburg et al. 2002) remains the only record of *S. acanthias* in the Pacific sector of the Arctic Ocean. Distribution in the Atlantic extends up to Umanak Fjord, off Baffin Bay, west coast of Greenland (Online Resource 1).

Somniosidae (sleeper sharks)

Sleeper sharks are recognized as a separate family rather than a subfamily of Dalatiidae (Compagno 1999, 2005; Nelson 2006). Seven genera with 17 species (Compagno 2005). Taxonomy of sleeper sharks remains problematic (Benz et al. 2007). Benthopelagic, widely distributed in

arctic and boreal seas. Three species have been recorded from arctic waters.

Somniosus microcephalus, inhabiting the eastern Arctic Ocean, is the only species of shark with significant presence in the arctic region. Skomal and Benz (2004) tracked *S. microcephalus* under sea ice using ultrasonic telemetry and discovered that they were not strictly a benthic or deepwater species but spent some time well above the bottom. In the Pacific, *S. pacificus* is abundant in the southern Bering Sea and might occasionally stray into the arctic region, where beachcast and floating carcasses have been found: at Norton Sound, eastern Bering Sea, in 1874 and 1876 (Turner 1886), and nearly 125 years later at Point Hope, eastern Chukchi Sea, in 1998 (Benz et al. 2004). *Centroscyrmnus coelolepis* was recorded for the first time in the arctic region in 2007, when a breeding female was caught in southern Baffin Bay (Møller et al. 2010).

Rajidae (skates)

Twenty-six genera, about 260 species (Nelson 2006; Séret 2010). Benthic, shallow to deep water, widespread in tropical to polar seas. Six are predominantly boreal species with a minor presence in the arctic region, while one has an exclusively arctic distribution.

Bathyraja parmifera and *B. spinicauda* are the only *Bathyraja* species in the arctic region, represented there by rare records. The northernmost record of *B. parmifera*, the most common skate in the southeastern Bering Sea and Aleutian Islands, was from Norton Sound, northeastern Bering Sea and was reported more than 125 years ago (Bean 1881a), until the summer of 2010 when the skate was found at several bottom-trawl survey stations between St. Lawrence Island and Norton Sound and carcasses washed up on the beach near Kivalina and Point Hope, on the Chukchi coast (Online Resource 1). Estimates of biomass and population numbers in the eastern Bering Sea indicate a nearly fourfold increase since 1975 (Hoff 2006). The center of distribution of skates in the eastern Bering Sea has shifted northward 90 km since the early 1980s (Mueter and Litzow 2008). In the Atlantic, *B. spinicauda* reaches southern Baffin Bay and is not uncommon in the southwestern Barents Sea.

The deepwater skates *Rajella bathyphila* and *R. fyllae* reach the southern margin of the arctic region on the slopes of the Atlantic and were recently found in Baffin Bay. *Dipturus linteus*, occurring at moderate depths on the fringes of the arctic region in the Atlantic, was found for the first time within the region in 2002 in the northern Barents Sea (Dolgov 2006). *Amblyraja radiata*, a more eurybathic species found as shallow as 20 m, reaches Baffin Bay, the Norwegian Sea off northeast Greenland, and the northern Barents Sea.



Lamna ditropis, male, ~1.75 m TL
Bering Strait, 0–55 m, 2007 (CAS 230160)



Osmerus dentex, 273 mm TL
Southeastern Chukchi Sea, 42 m, 2007 (CAS 230139)



Arctogadus glacialis, 221 mm TL
Chukchi Cap, 580–588 m, 2009 (ZIN 54854)



Gadus macrocephalus, 596 mm TL
Southeastern Bering Sea, ~50 m, 2005



Pleurogrammus monoptygius, 173 mm TL
Northeastern Bering Sea, 43 m, 2007 (CAS 230175)



Artediellus atlanticus, male, 142 mm TL
Chukchi slope, 365–370 m, 2009 (CAS 228530)



Enophrys dicerca, 164 mm TL
Southeastern Chukchi Sea, 41 m, 2009 (CAS 228554)



Trichocottus brashnikovi, 164 mm TL
Northeastern Bering Sea, 17 m, 2006 (CAS 230044)



Nautichthys pribilovius, 109 mm TL
Bering Strait, 53 m, 2007 (CAS 230152)



Cottunculus microps, 135 mm TL
Chukchi slope, 227–236 m, 2009 (CAS 228534)

Fig. 3 A sampler of marine fishes occurring in the arctic region: Lamnidae—Psychrolutidae

Abundant in deep waters from Baffin Bay to the Barents Sea, *Amblyraja hyperborea* is also known from more widely distributed but sparse records from other arctic seas. It likely is circumpolar (Mecklenburg et al. 2002), but descriptions of the geographic range of *A. hyperborea* (e.g., Stehmann and Bürkel 1984; Last and Stevens 1994) fail to mention the western Arctic Ocean. A few records have accumulated from this area: East Siberian Sea (Dolganov 1983); Chukchi slope north of Siberia (Tsinovsky 1981); western Beaufort Sea off Alaska and Amundsen Gulf, eastern Beaufort Sea, off Canada (Online Resource 1); and a tentative identification from photographs taken by remotely operated vehicle (ROV) on the Northwind Plain north of Alaska (Stein et al. 2005). Skates reported off Tasmania and New Zealand identified as *A. hyperborea* need further study (Last and Stevens 1994).

Genetic barcodes of skates from the Gulf of Alaska and southern Bering Sea (Spies et al. 2006) will help confirm identifications of Pacific skates when they are found farther north than usual.

Acipenseridae (sturgeons)

Four genera, 25 species (Birstein and Bemis 1997). Most are anadromous, spawning upriver and moving to river deltas and estuaries to feed. Potamodromous species, also called semianadromous, migrate within freshwater systems and are rarely found in the marine environment. Within species, both migratory and nonmigratory forms occur. *Acipenser baerii* and *A. ruthenus* live in arctic rivers of Europe and Siberia but are rarely found in saltwater owing to their potamodromous habit and the overall decline in populations from overfishing and pollution. *Acipenser oxyrinchus* and *A. sturio* barely reach the arctic region in the western Atlantic at Ungava Bay and in the eastern Atlantic in the White Sea, respectively (Online Resource 1). *Acipenser sturio* is listed as a critically endangered species on the IUCN Red List (Kottelat et al. 2009).

Evaluating the taxonomic status of *A. oxyrinchus*, Artyukhin and Vecsei (1999) concluded that North American *A. oxyrinchus* and European *A. sturio* are conspecific. The current view based on both molecular and morphological evidence is that they both are valid species (Ludwig et al. 2002, 2008; Kottelat and Freyhof 2007; Peng et al. 2007).

Notacanthidae (spiny eels)

Three genera, ten species (Nelson 2006). Deep-sea fishes found worldwide. Several older records of *Notacanthus chemnitzii* exist for the margins of the arctic region in the eastern Atlantic. A recent collection in Baffin Bay at 72°N (Jørgensen et al. 2005) places this species within the arctic region.

Anguillidae (freshwater eels)

One genus with 15 species, mostly catadromous; tropical and temperate seas (Nelson 2006). Two species, regarded as conspecific by some authors, spawn in the Sargasso Sea and reach southern waters of the arctic region in their migrations. *Anguilla anguilla* reaches the White Sea in the eastern Atlantic. *Anguilla rostrata*, endemic to the western Atlantic, reaches eastern Newfoundland and southwestern Greenland. The first occurrence recorded from Greenland since 1965 was in 2005 (Møller et al. 2010).

Clupeidae (herrings)

About 57 genera and 188 species, most of them primarily marine and some freshwater and anadromous, distributed among six subfamilies (Nelson 2006). The Clupeinae are represented by *Clupea harengus* and *C. pallasii* in the Atlantic and Pacific sectors of the arctic region, respectively, where both species are abundant. The Alosinae are represented by rare records of the boreal Atlantic species *Alosa sapidissima* in the marginal waters of the arctic region off Labrador and in the Bering Sea (introduced to the Pacific in the late 1800s).

Argentinidae (argentines or herring smelts)

Twenty-three species in two genera; Atlantic, Pacific, and Indian Oceans (Nelson 2006). Silvery, schooling fishes similar in appearance to smelts. *Argentina silus* was found in the arctic region for the first time in 2009 off Jan Mayen (Wienerroither et al. 2010) and has been increasing in abundance in the western Barents Sea (Dolgov 2006).

Microstomatidae (pencilsmelts)

About 38 species in 11 genera, two subfamilies; deep-sea fishes, widely distributed in tropical to temperate waters (Nelson 2006). *Bathylagus euryops* and another bathylagine, similar if not identical to *Melanolagus bericoides*, were recently recorded for the first time in the arctic region in Baffin Bay (Jørgensen et al. 2005; Møller et al. 2010). *Nansenia groenlandica*, a microstomatine, was found in the arctic for the first time in 2009 off Jan Mayen (Wienerroither et al. 2010).

Platyroctidae (tubeshoulders)

About 37 species in 13 genera (Nelson 2006); mesopelagic and bathypelagic midwater fishes in all oceans. Named for a tube on the shoulder which emits a blue-green luminous fluid. *Maulisia microlepis*, distributed in the North and South Atlantic Oceans (Quéro et al. 1984), was recently

recorded for the first time in the arctic region in Baffin Bay (Jørgensen et al. 2005).

Alepocephalidae (slickheads)

At least 90 species in about 23 genera (Nelson 2006); deep-sea fishes living in all oceans in close association with the bottom. The North Atlantic boreal species *Alepocephalus agassizii* was recently recorded for the first time in the arctic region in Baffin Bay (Jørgensen et al. 2005). In the eastern North Atlantic, there are records between Iceland and Greenland and west of the British Isles (Markle and Quéro 1984).

Osmeridae (smelts)

About 31 species in 11 genera in the Arctic, Atlantic, and Pacific Oceans, including marine, anadromous, and freshwater forms (Nelson 2006). Osmerid interrelationships have long been a matter of debate and study. Ilves and Taylor (2009) reconstructed osmerid phylogeny from molecular evidence and, mapping morphological characters onto their phylogeny, showed widespread homoplasy, which, they concluded, could be the source of systematic disagreement produced in previous works. Three anadromous species in *Osmerus* and the marine species *Mallotus villosus* are found in the arctic region.

Mallotus villosus, a circumpolar species and the only strictly marine osmerid species in the arctic region, has the broadest arctic distribution among the Osmeridae. *Osmerus dentex* (Fig. 3) occurs in the Pacific and in Arctic seas off Russia, Alaska, and western Canada. *Osmerus mordax* reaches the arctic region in the Atlantic north of the Strait of Belle Isle, and *O. eperlanus* occurs along coasts of the White and Barents Seas.

The western Atlantic and Pacific–Arctic populations of *Osmerus* have been classified as different subspecies, *O. mordax mordax* and *O. m. dentex*, on the basis of morphological and life history characteristics (Kljukanov 1969; Hart 1973; Scott and Crossman 1973; Haldorson and Craig 1984). From examination of mitochondrial DNA restriction fragment length and cytochrome *b* sequence polymorphism in regional forms of *Osmerus*, Taylor and Dodson (1994) treated these two forms as distinct species, *O. mordax* and *O. dentex*. The *COI* sequences also indicate they are distinct: *O. dentex* from arctic Alaska, the Barents and Kara Seas, and Primorski Kray, Russia, form a separate clade from *Osmerus mordax* from New Brunswick and Ontario, eastern Canada, with mean genetic distance between the groups of 8.5% (range 7.4–9.6%). *Osmerus eperlanus*, represented by specimens from the Baltic Sea, is genetically more similar to *O. dentex* than to *O. mordax* (Fig. 4a).

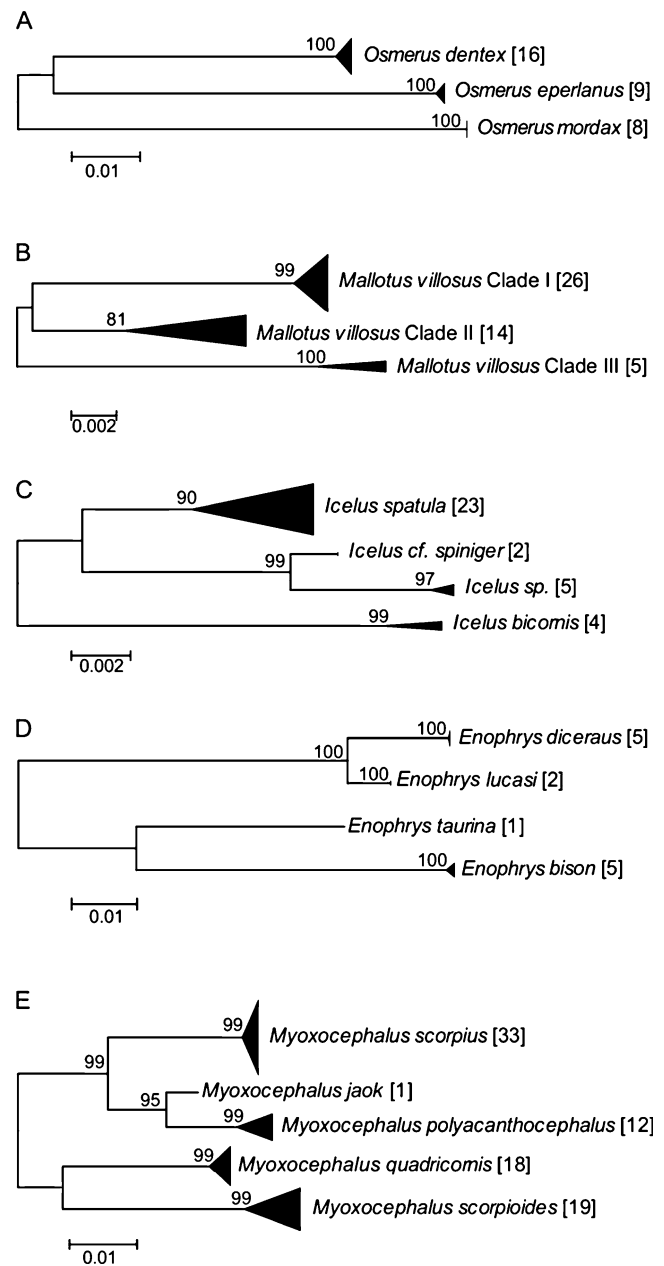


Fig. 4a–e Neighbor-joining trees of *COI* sequence divergences in five genera of fishes found in the arctic region. The samples are drawn from the entire BOLD database (publicly available sequences), including the samples used in Online Resource 3 as well as others. Sequence divergences were calculated using the Kimura two parameter (K2P) distance model (Kimura 1980). The trees shown were bootstrapped 1,000 times. Numbers at nodes represent bootstrap values (only values greater than 80 are shown). The number of specimens follows each species name. **a** The topology supports the taxonomic separation of *Osmerus dentex* and *O. mordax*, which are shown to be more divergent from each other than are *O. dentex* and *O. eperlanus*. **b** Northwest Atlantic (Clade I) and Pacific–Arctic (Clade II) clades of *Mallotus villosus* are closer to each other than they are to the Kara Sea clade (Clade III). **c** Two distinct populations in an unidentified *Icelus* clade are revealed. **d** The taxonomic separation of *Enophrys lucasi* and *E. diceraus* is supported. **e** Recognition of *Triglopsis*, often used for *Myoxocephalus quadricornis*, is not supported

Capelin of the North Pacific were described in 1784 as a species, *Salmo catervarius* Pennant, distinct from the Atlantic capelin, *Mallotus villosus* (Müller). Placed for a time in the synonymy of *M. villosus*, the Pacific capelin was later redescribed and again given full specific status, *M. catervarius*, by Schultz (1937). Walters (1955) reviewed western Arctic specimens and concluded they represented a subspecies, *M. villosus catervarius*, the view commonly held in recent years (e.g., Andriashev and Chernova 1994; Parin 2001). This does not mean that all Pacific and western Arctic capelin are the *catervarius* form or all in the Atlantic are the *villosus* form. Speciation in *Mallotus* is a complex problem with a long history. For instance, Schultz (1937) listed several specimens from the Gulf of Alaska that he thought could represent a different form than *M. catervarius*, and Sleggs (1933) reported morphological evidence indicating the possibility of races or specific differences in *M. villosus* from the Newfoundland region.

Recently, several lines of evidence have been applied in analyses of capelin relationships (e.g., Stergiou 1989; Dodson et al. 2007; Praebel et al. 2008; Skurikhina et al. 2010). Four highly divergent mitochondrial-DNA (mtDNA) clades were revealed in *M. villosus* from the North Atlantic, North Pacific, and Arctic Oceans by Dodson et al.'s (2007) analysis. Our own small sample of capelin *COI* sequences (Online Resource 3) is most similar in composition by locality (northern Bering Sea, Arctic Ocean) to their ARC (Arctic) clade. When *COI* sequences from our sample and others available in BOLD are combined for analysis (Fig. 4b), sequences from *M. villosus* from the Chukchi Sea, northern Bering Sea, Gulf of Alaska, and Davis Strait form a separate clade (Clade II, $n=14$) from those collected off Quebec, Newfoundland, Nova Scotia, New Brunswick, and Hudson Bay (Clade I, $n=26$), with an average genetic distance of 2.5% (range 1.9–3.1%). The *COI* sequences from specimens from the Kara Sea (Clade III, $n=5$) might represent a fifth clade, separated by 2.9% (2.3–3.5%) genetic divergence, not revealed in Dodson et al.'s (2007) study because of the lack of specimens from east of the Barents Sea. The presence of a *COI* sequence from Davis Strait in the same clade as those from the Chukchi and Bering Seas supports Dodson et al.'s (2007) hypothesized distribution pattern for the Arctic clade, from the Bering Sea to the Labrador Sea via the Beaufort Sea and Canadian Arctic. The microsatellite study by Praebel et al. (2008) showed complementary fine-scale structuring of *M. villosus* but did not include samples from within the greater portion of the geographic range of Dodson et al.'s (2007) Arctic clade.

Salmonidae (salmons, chars, and allies)

About 66 species in 11 genera and three subfamilies; Northern Hemisphere, freshwater and anadromous (Nelson

2006). Epipelagic at sea. Six species in Coregoninae (whitefishes) and nine in Salmoninae (salmons and chars) have significant presence in the arctic marine region. Specific information on occurrence of species of Pacific salmon in the arctic has been provided in recent reviews (Mecklenburg et al. 2002; Stephenson 2006). The five *Oncorhynchus* species of the North Pacific and *Salmo salar* of the North Atlantic spend periods of 1–6 years at sea before returning to natal streams to spawn. Recent molecular genetic studies (e.g., Brunner et al. 2001; Oleinik et al. 2004, 2007; Taylor et al. 2008) have helped resolve char taxonomy and phylogeny, including confirmation of the status of *Salvelinus taranetzi* as a distinct species.

Gonostomatidae (bristlemouths)

Four or five genera, 23 species; four genera if *Cyclothone* is a synonym of *Gonostoma*, but this problem has not been resolved (Nelson 2006). Widespread, primarily meso- and bathypelagic. *Cyclothone microdon* occurs from the Southern Ocean to the arctic region, reaching Baffin Bay and Iceland. Catches in 1999, 2001, and 2004 are the first from Baffin Bay (Online Resource 1).

Sternoptychidae (marine hatchetfishes)

Ten genera and about 67 species in two subfamilies (Nelson 2006). Pelagic, in Atlantic, Pacific, and Indian Oceans. *Argyropelecus hemigymnus* was found in the arctic region for the first time in 1997 off Jan Mayen, and records of *Maurollicus muelleri* off Jan Mayen date from 1980 to 2002 (Wienerroither et al. 2010).

Stomiidae (barbeled dragonfishes)

About 273 species in 28 genera and six subfamilies. Harold (2002) recognized all six subfamilies as separate families, but Nelson (2006) considered that this problem remains unresolved. Widespread, primarily meso- and bathypelagic. *Stomias boa* inhabits deep oceanic waters of the South Pacific, southern Indian, and North Atlantic Oceans, reaching southern Iceland and Baffin Bay. The first record for Baffin Bay is from 1999–2001 (Jørgensen et al. 2005).

Paralepididae (barracudinas)

About 56 species in 13 genera (Nelson 2006). Fast-moving pelagic fishes, generally meso- to bathypelagic. Two widely distributed barracudinas, *Arctozenus risso* and *Paralepis coregonoides*, are abundant in the marginal waters of the arctic region in the Atlantic (Jensen 1942). *Arctozenus risso* was recently caught north of 81°N between Svalbard and Franz Josef Land (Dolgov 2006).

Myctophidae (lanternfishes)

At least 240 species in about 32 genera (Nelson 2006). Mesopelagic, found in all oceans. *Benthoosema glaciale* and *Protomyctophum arcticum* spawn both north and south of the Polar Front in the Atlantic. *Lampanyctus macdonaldi* and *Myctophum punctatum* were recently found for the first time in the arctic region: *M. punctatum* in the Kara Sea in 2007–2008 (Dolgov et al. 2009), and both in the Jan Mayen fisheries zone in 2009 (Wienerroither et al. 2010).

Benthoosema glaciale is abundant in mesopelagic assemblages in the North Atlantic at least as far north as 60°N, where it has been found over the Iceland Basin, Reykjanes Ridge, and into the Irminger Sea (Fock and John 2006). Widespread records from the Arctic Ocean confirm the species' occurrence around the Arctic Basin, as suggested by Bolin (1959): nearly to 80°N off the northwest coast of Spitsbergen (Von Hofsten 1919); the Kara Sea (Dolgov et al. 2009); Baffin Bay (Jørgensen et al. 2005); and near Point Barrow, Alaska (Wilimovsky 1954; recently confirmed, Online Resource 1), which is the only record from the western Arctic.

Lampridae (opahs)

Two species, one genus. Pelagic, in temperate and warm waters worldwide. *Lampris guttatus* is the more widely distributed of the two species, reaching northern boreal or subarctic waters of the North Atlantic and North Pacific. The only record of *L. guttatus* from the arctic region is an opah found and photographed off the coast near Aasiaat, west Greenland, in 2005 (Møller et al. 2010). It reaches the northern Gulf of Alaska in the Pacific (Mecklenburg et al. 2002). Nelson (2006) explained the shift in spelling from Lamprididae to Lampridae.

Macrouridae (grenadiers)

About 350 species in 27 genera and four subfamilies (Nelson 2006). Mostly benthopelagic, widely distributed, at depths to 6,000 m or more. Two boreal Atlantic macrourids were found in the arctic region for the first time in 1999–2001, in Baffin Bay: *Coryphaenoides rupestris* and *Macrourus berglax* (Jørgensen et al. 2005). *Macrourus berglax* was caught again in Baffin Bay in 2004 (Online Resource 1).

Phycidae (phycid hakes)

Five genera with 25 species in subfamilies Gaidropsarinae and Phycinae (Nelson 2006). The two subfamilies recognized by Nelson (2006) are classified in Gadidae by Endo (2002). Three Atlantic rocklings (Gaidropsarinae) have

been recorded from the arctic region. The boreal Atlantic species *Ciliata septentrionalis* reaches Jan Mayen and the Barents Sea. The arctic–boreal species *Gaidropsarus ensis* is common in deep arctic Baffin Bay, more common than *G. argentatus*, whereas in the Barents Sea *G. argentatus* is more common.

Gadidae (cods)

About 31 species in 16 genera and three subfamilies (Nelson 2006). The Lotinae were classified as a separate family Lotidae by Endo (2002). Most cods are demersal or benthopelagic. Twelve species in Gadinae and one in Lotinae inhabit arctic marine waters. *Arctogadus glacialis* (Fig. 3) and *Boreogadus saida* (Fig. 2) are primarily distributed in the Arctic Ocean. The others are mainly boreal Pacific or Atlantic species with less of a presence in Arctic seas. Major changes in the composition of gadine genera in recent years mean patterns of species distribution are different.

Gadus macrocephalus (Fig. 3), following the recent DNA studies (see below) that indicate *G. ogac* Richardson, 1836, is a junior synonym, has a much broader distribution than formerly understood; not only north from the Pacific into the Chukchi Sea, but continuing eastward in the Arctic across Canada to Greenland and the White Sea. The White Sea cod, *G. callarias marisalbi*, was determined by Walters (1955) to be the same as *G. ogac*, although he followed Svetovidov (1948) in considering that these were subspecies of *G. morhua*, rather than of *G. macrocephalus* as indicated by the recent DNA studies. He pointed out that although *ogac* (= *G. macrocephalus*) and Atlantic cod (*G. morhua*) have different habitat preferences, they are sometimes found together and are able to maintain their separate identities.

Genetic studies have not yielded evidence to separate *G. macrocephalus* and *G. ogac* (Carr et al. 1999; Møller et al. 2002). *Gadus callarias marisalbi* Derjugin, 1920 has been treated as a subspecies of *G. morhua* (e.g., Svetovidov 1948; Evseenko et al. 2006) or a junior synonym of *G. ogac* (e.g., Renaud 1989; Cohen et al. 1990; Mecklenburg et al. 2002). If *G. ogac* is a synonym of *G. macrocephalus*, then *marisalbi* is also a synonym of *G. macrocephalus*. Differences in larval pigment patterns and egg chorion adhesiveness and smoothness observed in samples identified as *G. macrocephalus*, *G. ogac*, and *G. morhua marisalbi* (Evseenko et al. 2006) appear not to be significant at the specific level.

After many years in *Theragra*, where it was placed by Jordan and Evermann (1898:2535), the walleye pollock has been returned to its original genus as *Gadus chalcogrammus* Pallas, 1814 (Coulson et al. 2006; Carr and Marshall 2008). The Norwegian pollock, *Theragra finnmarchica* Koefoed,

1956, was shown to be a junior synonym of *G. chalcogrammus* (Ursvik et al. 2007; Byrkjedal et al. 2008). Ursvik et al. (2007) concluded that the Atlantic population resulted from recent transplanting from the Pacific, because, they stated, the species was not known from Bering Strait to Norway and they found records of marine species being transferred around 1930 from Vladivostok to Murmansk. However, several records now exist of this species north of Bering Strait in the Chukchi and Beaufort Seas (Online Resource 1), and Ursvik et al. (2007) found no records of this particular species being transplanted. *Gadus chalcogrammus* appears to be a true amphiboreal species with representatives both in the northeast Atlantic and North Pacific and lacking records in between. Atlantic catch records were reviewed by Christiansen et al. (2005), and Privalikhin and Norvillo (2010) reported on a single specimen found in the northeast Barents Sea. A review of *Gadus* to fully document the recent changes in nomenclature and assess implications for geographic distribution and history of the species is needed.

Jordan et al. (2003) provided meristic and morphometric evidence and a review of available records of *Arctogadus*, and synonymized *A. borisovi* in *A. glacialis*.

Lophiidae (goosefishes)

Four genera with 25 species, in Arctic, Atlantic, Indian, and Pacific Oceans, including the Mediterranean Sea (Nelson 2006). On the head, a fleshy fishing rod and lure attract prey toward the mouth. Abundance and distribution of *Lophius piscatorius*, a boreal eastern Atlantic species, in Icelandic waters have increased rapidly in recent years (Solmundsson et al. 2010).

Gasterosteidae (sticklebacks)

Five genera with about eight species, all in the Northern Hemisphere. Enormously diverse despite recognition of only eight species (Nelson 2006), the family presents numerous taxonomic problems, especially in the two species complexes distributed in the arctic region. *Gasterosteus aculeatus* and *Pungitius pungitius* are both found in coastal marine, brackish, and freshwater habitats in the region. Arctic populations of the predominantly boreal *G. aculeatus* complex are primarily distributed in the Atlantic side of the Arctic (Haglund et al. 1992a), with a few records from the Pacific side (Mecklenburg et al. 2002). Representatives of the *P. pungitius* complex are circumboreal and nearly circumpolar, lacking records from the Canadian high Arctic archipelago, Greenland, and Iceland (Haglund et al. 1992b).

Syngnathidae (pipefishes and seahorses)

About 232 species in 52 genera and two subfamilies. Typically in shallow water in warm temperate to tropical

waters of the Atlantic, Pacific, and Indian Oceans (Nelson 2006). *Entelurus aequoreus* has been dramatically increasing in abundance in its core area of distribution (eastern North Atlantic) since 2002 (Kirby et al. 2006; Fleischer et al. 2007) and has expanded its range into the arctic region. Previously found in the eastern North Atlantic from the Azores to southern Iceland and northern Norway (Dawson 1986), *E. aequoreus* has been found in recent years off Spitsbergen (Fleischer et al. 2007), Jan Mayen (Wienerroither et al. 2010), and in the Barents and Greenland Seas (Rusyaev et al. 2007). Abundance increased dramatically in the Barents Sea, peaking in 2007; however, the species disappeared as fast as it arrived and was absent from the Barents Sea–Svalbard region by 2009, when water temperatures were back to “normal” (Høines et al. 2009).

Scorpaenidae (rockfishes)

Systematists have proposed splitting the Scorpaenidae into several families, but consensus is lacking and the family remains intact, with six subfamilies, at least 56 genera, and about 418 species (Nelson 2006). Two species in the subfamily Sebastinae (*Sebastes norvegicus*, *S. mentella*) occur in the Atlantic-arctic region. Both were found to be widely distributed in the western Barents Sea up to about 76°N (south of Spitsbergen) in 2000 (Byrkjedal and Høines 2007). In the Pacific-arctic, early juveniles tentatively identified as *S. alutus* were found in the Chukchi Sea in 1971 (Quast 1972), but *Sebastes* species generally do not occur north of the Navarin Canyon, western Bering Sea. Records of late juveniles or adults north of Bering Strait are lacking.

Hexagrammidae (greenlings)

Thirteen species in five genera and five subfamilies, endemic to the North Pacific; intertidal area to depths typically less than 200 m; demersal, except for *Pleurogrammus monoptygius* adults, which are pelagic. Mecklenburg and Eschmeyer (2003) reviewed taxonomy and nomenclature. A molecular phylogenetic analysis of the family using multiple loci supported the recognition of *P. monoptygius* and *P. azonus* as distinct species (Crow et al. 2004). The latter is a western Pacific species. Three hexagrammids (*Hexagrammos octogrammus*, *H. stelleri*, *P. monoptygius*) have been recorded in arctic marine waters. *Pleurogrammus monoptygius* (Fig. 3) has been found farther north in the Bering Sea in recent years, with records at Bering Strait, than its historical pattern of distribution no farther north than Cape Navarin. *Hexagrammos stelleri* is occasionally caught in the eastern Chukchi Sea, and *H. octogrammus* reaches only to St. Lawrence Island, Bering Sea. Reports of an additional greenling (*H. lagocephalus*) in the arctic region were found to be based on misidentifications (Online Resource 1).

Cottidae (sculpins)

About 275 species in 70 genera (Nelson 2006). Relationships within Cottidae are not completely understood, and subfamilies are not well defined (Mecklenburg et al. 2002). Benthic, in coastal waters from shallow depths to about 290 m. The greatest diversity of cottids is found in the North Pacific. Thirty-one species live on the bottom in the arctic marine region.

The distribution and relative abundance of *Arteidiellus* species are not well understood, partly because they have not been well described and misidentifications are inevitable. *Arteidiellus gomojunovi* is an example. Although the presence of a small spinule on the inside of the first preopercular spine is a diagnostic character of *A. gomojunovi* in the most recent review and key (Nelson 1986), this spinule, which is sometimes multiple, is only variably present in *A. gomojunovi* and is also present in some *A. scaber*. Large nuchal tubercles and three distinct dark bands on the body are consistently present in *A. gomojunovi* and more readily identify this species (C.W.M., unpubl. data).

Arteidiellus scaber is endemic to the arctic region, occurring from the southern Barents Sea eastward at shallow depths in Siberian and American Arctic seas to the Boothia Peninsula (Fig. 2). *Arteidiellus atlanticus* is an arctic–boreal species with more presence in the Arctic proper (Fig. 2) than previously understood, with new records from the Pacific side of the Arctic and Greenland (Online Resource 1). *Arteidiellus atlanticus* caught by bottom trawl on the Chukchi slope in 2009 are the first record from the East Siberian–Chukchi–Beaufort region (Fig. 3). The nearest records to the west are from the upper slopes off the Kara Sea and western Laptev Sea, and to the east are from Hudson Strait and Baffin Bay. The *COI* sequences from our Chukchi slope sample and *A. atlanticus* from Baffin Bay are identical (Online Resource 3). *Arteidiellus camchaticus*, *A. gomojunovi*, *A. pacificus*, and *A. ochotensis* are boreal Pacific species that reach the fringe of the arctic region in the northern Bering Sea. In 1959, *A. ochotensis* was also found in the eastern Chukchi Sea. *Arteidiellus uncinatus* is a predominantly arctic species that reaches northward to Baffin Bay and northern Greenland.

Gymnocanthus tricuspis is circumpolar and is one of the most abundant benthic fish species in the arctic region. The boreal Pacific species *G. galeatus* is found infrequently, and *G. pistilliger* frequently, up to the northern Bering Sea.

Hemilepidotus jordani has been verified only as far north as Bering Strait, whereas *H. papilio* is common in the eastern Chukchi Sea. Both *Melletes* and *Hemilepidotus* have recently been in use as the genus for *H. papilio*. The amount of difference among the three hemilepidotine species (average 2.3%, range 1.6–3.0%) in our *COI* sequence sample (*H. papilio*, *H. zapus*, *H. jordani*; Online Resource 3) is similar to that for other species within a genus. Considering this result

and the species' morphology, we do not recognize the monotypic *Melletes* Bean, 1880, as either a genus (e.g., Parin et al. 2002; Tokranov et al. 2003) or subgenus (e.g., Peden 1979; Mecklenburg et al. 2007) for *H. papilio*. It is not clear from the recent review of the hemilepidotine species (Tokranov et al. 2003) why the authors consider the morphological differences between *H. papilio* and the others to be indicative of separation at the generic level. Mecklenburg et al. (2002) followed Peden (1979), who considered that a further degree of specialization in features common to *Hemilepidotus* species characterizes *H. papilio* and that *H. spinosus* also shows a level of differentiation indicating a different lineage, and recognized three subgenera of *Hemilepidotus* (*Calcilepidotus*, *Hemilepidotus*, *Melletes*) for the three lineages. (All three are represented in our *COI* sequences; Online Resource 3). However, as Peden (1979) cautioned, the suggested relationships needed to be tested. Recognition of genera and subgenera is somewhat subjective, but our data indicate that to recognize *Melletes* as a monotypic genus or to recognize the three subgenera proposed by Peden (1979) overstates the genetic and morphological differences and state of knowledge on hemilepidotine relationships.

Icelus bicornis is circumpolar and occurs as far north as sculpins have been found (Alert, Ellesmere Island). The taxonomic status of other *Icelus* populations in the arctic region needs further study. The most recent review of *Icelus* (Nelson 1984) concluded from morphological evidence that *I. spatula* is a single, highly variable species with several geographic variants. The specimens identified (using Nelson's key) as *I. spatula* that provided our *COI* sequences (Online Resource 3) from the East Siberian Sea and from the southern Chukchi Sea just north of Bering Strait are morphologically similar to Nelson's Arctic variant, whereas specimens that stood out while sorting catches at sea as possibly being different (*Icelus* sp.), from the northeastern Bering Sea, Bering Strait, and eastern Chukchi Sea south of Point Hope, fall into a separate clade and are morphologically most similar to Nelson's Bering Sea variant. The *COI* sequences from specimens identified as *Icelus* cf. *spiniger* from the Semidi Islands, western Gulf of Alaska, form a sister group in the clade with our *Icelus* sp. (Online Resource 3, Fig. 4c). The close genetic similarity (0.2% divergence, range 0.1–0.4%) of the *I. cf. spiniger* clade to the *Icelus* sp. clade was unexpected, since *I. spatula* and *I. spiniger* are morphologically so different and our *Icelus* sp. looked, in the field, more similar to *I. spatula*. For instance, they have different types of scales, those of the dorsal row in *I. spiniger* having one tall spine and in *I. spatula* and our *Icelus* sp. having multiple spines. The genital papilla of the males of *Icelus* cf. *spiniger* and *Icelus* sp. is the *I. spatula* type. The high genetic distance between the *I. spatula* and *Icelus* sp. (including *I. cf. spiniger*) clades (2.0%, range 1.6–2.4%) indicates two species are represented.

Gilbert and Burke (1912) described *I. spatula* from specimens collected in the Pacific Ocean off southeastern Kamchatka, described *I. uncinialis* from specimens collected in the Bering Sea between the Commander Islands and Petrel Bank, and referred to a third species, which they did not describe, with a range from the eastern Bering Sea to the Gulf of Alaska. Our *Icelus* sp. are not *I. uncinialis*, but are clearly different genetically from *Icelus* identified as *I. spatula*. These results indicate that one or more of the nominal species placed in the synonymy of *I. spatula* by Nelson (1984) are actually distinct species. The specimens in the barcode samples from the southern Chukchi Sea and East Siberian Sea to New Brunswick and Nova Scotia (Fig. 4c, $n=23$) which are similar to Nelson's Arctic variant should possibly be called something other than *I. spatula*, although it is least confusing to call them that for the present. The *Icelus* sp. in the barcode sample could be Gilbert and Burke's (1912) undescribed species. *Icelus spatula* sensu stricto might not be represented in the entire Barcode of Life Data System. Samples from the northwest Pacific off the Kamchatka Peninsula, where Gilbert and Burke's *I. spatula* was caught, could help resolve this part of the problem. A thorough review of *Icelus* with further testing of Nelson's (1984) species limits is needed.

The genus *Enophrys* comprises five species in the most recent revision of the genus (Sandercock and Wilimovsky 1968). *Enophrys diceraus*, with distribution extending into the Chukchi Sea, is the only *Enophrys* with known presence in the Arctic proper. *Enophrys lucasi* has occasionally been collected in the northern Bering Sea but not in the Chukchi Sea. Morphological differences between *E. lucasi* and *E. diceraus* are not great, and the status of *E. lucasi* as a species distinct from *E. diceraus* has been questioned by some (e.g., Evermann and Goldsborough 1907; Quast and Hall 1972; Neyelov 1979) and defended by others (e.g., Sandercock and Wilimovsky 1968; Peden and Wilson 1976; Mecklenburg et al. 2002). Verifying identifications in museum collections, we were able to distinguish the two consistently, in one or two cases only by fin ray counts (fewer anal fin rays in *E. lucasi*) but usually also by the tanglike lachrymal extensions in *E. diceraus* versus the shorter lachrymals in *E. lucasi*. The *COI* sequences of *E. diceraus* from the Bering and Chukchi Seas and *E. lucasi* from the western Gulf of Alaska and the Aleutian Islands (Fig. 4d) support the distinction, with a genetic distance of 2.3% (range 2.2–2.4%) between the species. Sequences from two other *Enophrys* species in BOLD, *E. taurina* and *E. bison*, form a separate clade from the *E. diceraus*–*E. lucasi* clade, with a genetic distance between the clades of 12% (range 10.5–13.7%). The greater genetic distance between *E. taurina* and *E. bison* (8.1%, range 8.0–8.2%) than between *E. diceraus* and *E. lucasi* parallels the greater morphological difference between *E. taurina* and *E. bison*.

Myoxocephalus jaok and *M. polyacanthocephalus* are boreal Pacific species with few records from the arctic region. Distribution of *Trichocottus brashnikovi* (Fig. 3), *Megalocottus platycephalus*, and *Microcottus sellaris* is predominantly boreal Pacific, with more numerous records from the northern Bering Sea and Chukchi Sea. *Myoxocephalus aenaeus* is the only representative of the boreal myoxocephalines in the Atlantic that approaches the arctic region, with a reported northern limit of range at Raleigh, Strait of Belle Isle (Jeffers 1932; Scott and Scott 1988).

Myoxocephalus quadricornis and *M. scorpioides* are distributed only in the arctic region at shallow depths. Recognition of *Triglopsis*, often used for the euryhaline *M. quadricornis* complex (e.g., Andriashev and Chernova 1994; Parin et al. 2002), is not supported by the *COI* sequences (Fig. 4e), with an average distance of 6.4% (range 5.1–9.2%), which is well within the range for the representatives of the genus *Myoxocephalus* (average 6.5%, range 2.1–10.5%). The *M. quadricornis* complex of species was found in a recent phylogenetic assessment using mtDNA sequence data to be deeply nested within the *Myoxocephalus* genus (Kontula and Väinölä 2003).

Myoxocephalus scorpius is distributed around the edges of the polar basin on the inner and middle areas of the continental shelves (Fig. 2), where it is one of the most abundant bottom fishes in research trawls. Abundance diminishes northward, toward the outer area of the shelf (e.g., Mecklenburg et al. 2007). The distribution of this species is believed to be secondarily circumpolar (Walters 1955). Species with this pattern likely were once present in the Arctic Ocean and adjacent waters of the North Pacific and North Atlantic, but became extinct in the Arctic as temperatures dropped and ice barriers and land bridges emerged. *Myoxocephalus scorpius* is thought to have reentered the Arctic postglacially from the Bering Sea and the North Atlantic, reestablishing this sculpin as a circumpolar species (Walters 1955). This prehistory, if correct, goes far toward explaining observed morphological variation over the geographic range of the species.

In the eastern Pacific and adjacent Arctic seas off Alaska, there appears to be a cline in external morphological features such that *M. scorpius* in the Pacific off southeastern Alaska and British Columbia are most like eastern Canadian and some European populations in, for example, having low or weak postocular and occipital spines and few or no prickly platelike scales on the dorsolateral surface of the body (C.W.M., unpubl. data). From the Kara Sea eastward to Greenland, including the Chukchi Sea, *M. scorpius* has the most strongly developed postocular and occipital spines and platelike scales and is classified by some taxonomists as a separate species, *M. verrucosus*. Bean (1881b) described *M. verrucosus* on the basis of a juvenile specimen which is attributable to *M. groenlandicus* (Cuvier,

1829), later recognized by some authors as *M. scorpius groenlandicus* (e.g., Walters 1955; Mecklenburg et al. 2007) (Table 1). We could retrieve *COI* sequences for *M. scorpius* from the Bering Sea eastward to the Hudson Bay (Fig. 4e), with only 0.5% (range 0–1.8%) intraspecific divergence. When running those against the ID engine of BOLD we were able to match them with specimens from the Baltic Sea, which lends support to the recognition of *M. scorpius* in the arctic region as a single circumpolar species with no distinct subspecies. Sequences from populations in the Sea of Okhotsk and Gulf of Alaska are needed for further resolution of *M. scorpius* taxonomy and zoogeography.

Triglops nybelini found north of Alaska on the Chukchi slope in 2009 (Online Resource 1) extend this arctic species' known distribution westward from Canadian Arctic seas, leaving only the East Siberian Sea as a gap in its probable circumpolar distribution. The arctic–boreal species *Triglops pingelii* is also circumpolar in Arctic seas. *Triglops murrayi* is found in the North Atlantic and adjacent waters of the Arctic Ocean.

Hemitripterae (sailfin sculpins)

Eight species in three genera (Mecklenburg 2003a), with seven species in the North Pacific and one in the North

Table 1 List of arctic marine fish species with taxonomic changes in the past 10 years (2001–2010) and relationships needing further study

Synonyms, recent or supported by new evidence:

- Arctogadus borisovi* Drjagin, 1932 = *Arctogadus glacialis* (Peters, 1872)
Aspidophoroides bartoni Gilbert, 1896 = *Aspidophoroides monopterygius* (Bloch, 1786)
Cottus groenlandicus Cuvier, 1829 = *Myoxocephalus scorpius* (Linnaeus, 1758)
Eumicrotremus eggvinii Koefoed, 1956 = *Eumicrotremus spinosus* (Fabricius, 1776)
Gadus callarias marisalbi Derjugin, 1920 = *Gadus macrocephalus* Tilesius, 1810
Gadus ogac Richardson, 1836 = *Gadus macrocephalus* Tilesius, 1810
Gymnelus barsukovi Chernova, 1999 = *Gymnelus viridis* (Fabricius, 1780)
Gymnelus bilabrus Andriashev, 1937 = *Gymnelus viridis* (Fabricius, 1780)
Gymnelus knipowitschi Chernova, 1999 = *Gymnelus hemifasciatus* Andriashev, 1937
Gymnelus platycephalus Chernova, 1999 = *Gymnelus hemifasciatus* Andriashev, 1937
Liparis liparis bathyartcticus Parr, 1931 = *Liparis bathyartcticus* Parr, 1931
Lycodes vahli gracilis Sars, 1867 = *Lycodes gracilis* Sars, 1867
Lycodes vahli vahli Reinhardt, 1831 = *Lycodes vahli* Reinhardt, 1831
Melletes papilio Bean, 1880 = *Hemilepidotus papilio* (Bean, 1880)
Myoxocephalus scorpius groenlandicus (Cuvier, 1829) = *Myoxocephalus scorpius* (Linnaeus, 1758)
Myoxocephalus verrucosus Bean, 1881 = *Myoxocephalus scorpius* (Linnaeus, 1758)
Myxine limosa Girard, 1859 = *Myxine glutinosa* Linnaeus, 1758
Osmerus mordax dentex Steindachner & Kner, 1870 = *Osmerus dentex* Steindachner & Kner, 1870
Salvelinus alpinus taranetzi Kaganowsky, 1955 = *Salvelinus taranetzi* Kaganowsky, 1955
Theragra chalcogramma (Pallas, 1814) = *Gadus chalcogrammus* Pallas, 1814
Theragra finnmarchica Koefoed, 1956 = *Gadus chalcogrammus* Pallas, 1814
Triglopsis quadricornis (Linnaeus, 1758) = *Myoxocephalus quadricornis* (Linnaeus, 1758)
Ulcina olrikii (Lütken, 1877) = *Aspidophoroides olrikii* Lütken, 1877

Relationships needing further study:

- Cottunculus konstantinovi* Myagkov, 1991 = *Cottunculus microps* Collett, 1875?
Cottunculus sadko Essipov, 1937 = *Cottunculus microps* Collett, 1875?
Gymnelus andersoni Chernova, 1998 = *Gymnelus retrodorsalis* Le Danois, 1913?
Gymnelus esipovi Chernova, 1999 = *Gymnelus retrodorsalis* Le Danois, 1913?
Gymnelus obscurus Chernova, 2000 = *Gymnelus viridis* (Fabricius, 1780)?
Gymnelus taeniatus Chernova, 2005 = *Gymnelus retrodorsalis* Le Danois, 1913?
Liparis bristolensis (Burke, 1912) = *Liparis tunicatus* Reinhardt, 1836?
Liparis herschelini (Scofield, 1898) = *Liparis tunicatus* Reinhardt, 1836?
Liparis koefoedi Parr, 1931 = *Liparis fabricii* Krøyer, 1847?
Liparis laptevi Popov, 1933 = *Liparis fabricii* Krøyer, 1847?
Liparis marmoratus Schmidt, 1950 = *Liparis tunicatus* Reinhardt, 1836?
Lycodes rossi Malmgren, 1865 = *Lycodes reticulatus* Reinhardt, 1835?

Atlantic; demersal, mostly shallow on the continental shelf. Two boreal Pacific species reach the Chukchi Sea. *Blepsias bilobus* records from the Chukchi Sea are from 1990, 2007, and 2009, although the species was documented in adjacent waters of the northwestern Bering Sea at Provideniya Bight as early as 1948. *Nautichthys pribilovius* (Fig. 3) is relatively common in the Chukchi Sea, with records from 1954 through 2009, and was recently found in the Beaufort Sea (Online Resource 1).

Psychrolutidae (fathead sculpins)

About 29 species in the family (Byrkjedal and Orlov 2007), demersal, distributed in the North Pacific, Atlantic, and Indian Oceans from intertidal depths to about 2,800 m (Nelson 2006). One predominantly boreal Pacific species, *Eurymen gyrinus*, is distributed northward to the Chukchi Sea. Another, *Psychrolutes paradoxus*, occurs as far north as Norton Sound, northern Bering Sea. *Cottunculus microps*, *C. sadko*, and *P. subspinosus* are primarily distributed in the arctic region. *Cottunculus konstantinovi*, from north Spitsbergen and known only from the holotype, is not clearly distinguished from *C. microps* (Parin et al. 2002), and *C. sadko* is likely the same as *C. microps* (Møller et al. 2010).

A *C. microps* (Fig. 3) collected in 2009 on the Chukchi slope north of Alaska is the first record from the western Arctic, or the second if *C. sadko*, with one published record from the Beaufort Sea (Nelson 1982), is a synonym. The *COI* sequence from the Chukchi slope *C. microps* falls within the same clade as *C. microps* from northern Davis Strait (Online Resource 3) and the Gulf of St. Lawrence in the BOLD system (not shown). The sequence from an unidentified *Cottunculus* collected in southern Davis Strait (Online Resource 3) identifies it as the boreal species *C. thomsonii*, falling within the same clade as three others in the BOLD system (not shown). The *C. microps* and *C. thomsonii* clades are separated by a genetic distance of 2.7% (range 2.4–2.8%).

Agonidae (poachers)

About 46 species in 21 genera, demersal, from the intertidal to 1,290 m, primarily distributed in the North Pacific. Reviewing the taxonomy of the Agonidae, Sheiko and Mecklenburg (2004) listed 47 species in 22 genera but allowed that some species and genera were poorly understood. This study (Online Resource 3) found that the genetic distance between the *Aspidophoroides monopterygius* clade and *Ulcina olrikii* is so small (1.4%, range 1.2–1.8%) that a separate genus cannot be supported, and the latter species is returned to *Aspidophoroides*, the genus in which it was described (Table 1). This distance in most

other fishes is one of congeners. The change reduces the number of genera in Agonidae from 22 to 21. Treating *A. bartoni* as a synonym of *A. monopterygius* (Table 1) brings the number of species down to 46.

Aspidophoroides bartoni has recently been classified as either a junior synonym of *A. monopterygius* (Kanayama 1991; Mecklenburg et al. 2002), or as a valid species (Sheiko and Fedorov 2000) with a range of *A. monopterygius* from western Greenland to New Jersey and of *A. bartoni* from the Chukchi Sea to the Gulf of Alaska and northern Sea of Japan (Sheiko and Mecklenburg 2004). From incomplete morphological evidence, Sheiko and Mecklenburg (2004) provisionally listed *A. bartoni* as a distinct species. However, the *COI* sequences (Online Resource 3) show almost no genetic divergence (0.2%, range 0–0.2%) at the barcode locus between what others might identify as *A. bartoni* from the Chukchi Sea and other *A. monopterygius* from the Atlantic Ocean.

Although *A. monopterygius* has been represented as widely distributed from the Pacific Ocean across the Arctic to the Atlantic (Kanayama 1991), no records were found to support such a distribution. The data support recognition of a single species with an amphiboreal distribution and significant presence in the adjacent waters of the arctic region, including the northern Bering Sea and Chukchi Sea, southwestern Greenland and Baffin Bay, and off Canadian coasts north of the Strait of Belle Isle (Fig. 2). The distribution of *A. monopterygius* is that of an amphiboreal species recolonizing Arctic seas, as proposed for a number of other species by Andriashev (1939) and Walters (1955).

Aspidophoroides olrikii and *Leptagonus decagonus* have broad distributions in Arctic seas. The distribution of other poachers extends northward from primary centers of abundance in the North Pacific (six species), North Atlantic (one species), or both (*A. monopterygius*). *Hypsagonus quadricornis* (Fig. 5) was found in the eastern Chukchi Sea in 2007. *Ocella dodecaedron* was found in the southeastern Chukchi Sea in 1976. *Pallasina barbata* appears to be somewhat more common in the southeastern Chukchi Sea, but perhaps only in recent years. *Podothecus veterinus* is abundant in the northern Bering Sea and Chukchi Sea. The distribution of *P. accipenserinus* extends up to the Chukotsk Peninsula where it overlaps the range of *P. veterinus*. Distinguished mainly by different numbers of snout barbels and a qualitative, overlapping difference in lateral expansion of the first preopercular spine, *P. veterinus* and *P. accipenserinus* show a genetic difference of 2.9% (range 2.8–3.2%). *Sarritor frenatus* has been recorded as far northward in the Bering Sea as the Gulf of Anadyr and outer Norton Sound, but rarely and only in old collections. *COI* sequences are not available from enough species of *Sarritor* and *Leptagonus* to contribute to resolution of the status of *Sarritor* as a possible



Hypsagonus quadricornis, 103 mm TL
Bering Strait, 53 m, 2007 (CAS 230150)



Careproctus reinhardti, 170 mm TL
Chukchi slope, 227–236 m, 2009 (ZIN 54800)



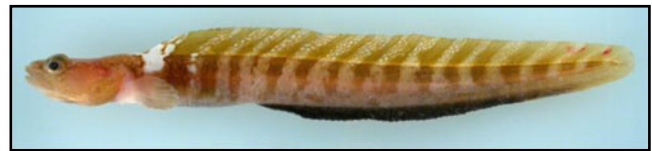
Liparis bathyarcticus, 244 mm TL
Northwestern Chukchi Sea, 151–152 m, 2009 (ZIN 54761)



Liparis tunicatus, 90 mm TL
Southeastern Chukchi Sea, 47 m, 2007 (CAS 230136)



Paraliparis bathybius, 198 mm TL
Canada Basin, about 2,500 m, 2005 (CAS 230368)



Gymnelus hemifasciatus, male, 128 mm TL
Northwestern Chukchi Sea, 80 m, 2009 (UAM 5520)



Gymnelus hemifasciatus, female, 101 mm TL
Southwestern Chukchi Sea, 34 m, 2004 (CAS 220475)



Gymnelus hemifasciatus, 79–156 mm TL
Northeastern Bering Sea, 51 m, 2007 (CAS 230181)



Gymnelus hemifasciatus, 72 mm TL
Northeastern Chukchi Sea, 51 m, 2007 (CAS 230107-01)



Gymnelus hemifasciatus, 159 mm TL
Northeastern Chukchi Sea, 51 m, 2007 (CAS 230107-02)



Gymnelus viridis, male, 174 mm TL
Northeastern Chukchi Sea, 45 m, 2007 (CAS 230055)



Gymnelus viridis, female, 172 mm TL
Northeastern Chukchi Sea, 45 m, 2007 (CAS 230053)

Fig. 5 A sampler of marine fishes occurring in the arctic region: Agonidae—Zoarcidae

synonym of *Leptagonus*. *Agonus cataphractus* barely reaches the arctic region in the White Sea, and perhaps off Jan Mayen (Wienerroither et al. 2010).

Cyclopteridae (lumpsuckers)

Six genera and 28 species were considered valid in the most recent lumpsucker taxonomic checklist pending results of further study (Mecklenburg and Sheiko 2003). With *Eumicrotremus eggvinii* recently shown to be a junior synonym of *E. spinosus* (Byrkjedal et al. 2007), the number of species is down to 27, and some of those still listed as valid likely are synonyms. Much work remains to be done to delimit genus and species boundaries in this family. Lumpsuckers are mostly benthic fishes with a suction disc on the chest made from modified pelvic fins.

Eight species of lumpsucker have been found in the arctic region. *Eumicrotremus orbis* and *Aptocyclus ventricosus* barely reach the arctic region in the northern Bering Sea. *Cyclopterus lumpus* is commonly found in the margins of the arctic in the North Atlantic and was found off northeast Greenland in 2009 (Hartz et al. 2009). *Cyclopteroopsis jordani* and *C. mecalpini* have been found only in the arctic region but are rare, whereas *E. derjugini* has been found in most seas of the Arctic Ocean. *Eumicrotremus andriashevi* is common in museum collections from the eastern Chukchi Sea and Bering Sea, but not reported in recent years; and *E. spinosus* is abundant in the high Arctic from the Canadian archipelago and northern Greenland to the Kara Sea.

Liparidae (snailfishes)

About 29 genera, 334 species were considered valid in the most recent taxonomic checklist, but with the stipulation that much work remained to be done and numbers would change (Chernova et al. 2004). Many species have been described or resurrected since then, including several from arctic waters (Chernova 2005a, b, 2008). Having a ventral suction disc like that of the lumpsuckers, snailfishes are sometimes classified in the same family (Cyclopteridae). Phylogenetic analyses using molecular and morphological characters indicated, among other significant findings, that the disc has been lost at least twice during evolution of the Liparidae (Knudsen et al. 2007). Adults of most arctic snailfishes live on the sea floor; a few are both benthic and pelagic.

The number depending on resolution of problematic taxonomy, 17–22 liparid species have been found in the arctic region. All but three are in *Liparis* and *Careproctus*. Four *Liparis* species have arctic circumpolar distributions primarily on the continental shelves and upper slopes: *Liparis bathyarticus*, *L. fabricii*, *L. gibbus*, and *L. tunicatus*. Two

are intertidal and shallow-water boreal species: *L. callyodon* in the Pacific and *L. atlanticus* in the Atlantic. Distribution of five other *Liparis* species is uncertain because of their lack of clear distinction from *L. tunicatus* and *L. fabricii* (Table 1). *Careproctus* in the arctic region are generally distributed deeper than *Liparis* species, on the continental slopes, and have arctic or predominantly arctic (*C. dubius*, *C. kidoi*, *C. knipowitschi*, *C. micropus*, *C. solidus*) or arctic–boreal (*C. derjugini*, *C. longipinnis*, *C. reinhardti*; Fig. 5) distributions. *Paraliparis bathybius* (Fig. 5) is widely distributed on Arctic Ocean slopes and basins (Fig. 2), whereas *P. violaceus* is known only from the holotype from the Nansen Basin. *Rhodichthys regina* is one of the most abundant snailfishes in Arctic basins.

Barcoded samples of *Liparis* from arctic waters form four clades with little in-group variation (Online Resource 3). The *COI* sequences from *Liparis tunicatus* and *L. fabricii* form a clade in sister-group relationship to an *L. gibbus* and *L. bathyarticus* clade, separated by a genetic distance of 5.5% (range 5.2–5.6%). Despite great differences among individuals in coloration, similar to those reported by Chernova (1991) for the Barents Sea and Mecklenburg et al. (2007) for the Chukchi Sea, and wide geographic (Bering, Chukchi, Beaufort, and East Siberian Seas) and bathymetric distributions, only one species in the *L. tunicatus* complex appears to be represented in our barcoded sample. *Liparis bathyarticus* (Fig. 5), recently resurrected from synonymy in *L. gibbus* (Chernova 2008), is separated from *L. gibbus* by a genetic distance of 3.1% (range 2.8–3.2%).

Liparis bristolensis and *L. herschelini* most likely are junior synonyms of *L. tunicatus* (e.g., Able and McAllister 1980; Mecklenburg et al. 2002), as is *L. marmoratus*. The *COI* sequences of specimens collected in 2007–2009 from the Chukchi and Bering Seas which were tentatively identified as *L. bristolensis* and *L. marmoratus* from external characters are the same as *L. tunicatus* sequences; all are included in the *L. tunicatus* clade in Online Resource 3. Chernova (2008) stated that the systematics of this group need further study and that her data were insufficient to clarify the status of the species. The resurrected junior synonyms and *L. marmoratus* need further study (Table 1).

Liparis laptevi and *L. koefoedi* were resurrected from synonymy in *L. fabricii* by Chernova (1998a, 2008). Despite wide geographic distribution (western Chukchi Sea, Chukchi slope, East Siberian Sea, and Davis Strait), as well as the presence of two or three slightly different-looking forms (e.g., some with little or no silvery coloration on the belly), in the barcoded specimens, the barcodes indicated only one species was present (Online Resource 3). Differences between *L. fabricii*, *L. laptevi*, and *L. koefoedi* (Chernova 2008) seem to be largely a matter of degree for which analysis of a larger number of specimens is required. As with *L. tunicatus* junior

synonyms, the resurrected junior synonyms of *L. fabricii* need further study (Table 1).

Zoarcidae (eelpouts)

Classification mainly follows Anderson and Fedorov (2004), who recognized about 240 valid species in four subfamilies, but much of zoarcid taxonomy is problematic. Zoarcids are the most diverse family in the suborder Zoarcoidei of the order Perciformes and exhibit a greater degree of character plasticity than the other zoarcoid families (Anderson 1994; Anderson and Fedorov 2004). They primarily inhabit the outer continental shelves and slopes of the North Pacific and North Atlantic. Not counting five probable junior synonyms (Table 1), 34 species of eelpout inhabit Arctic seas; 23 (68%) have arctic to arctic–boreal distributions, while 11 (32%) are boreal or predominantly boreal. Most (23) are in genus *Lycodes*.

Species of *Gymnelus* and *Lycodes* appear to exist as polymorphic populations in the arctic region (Anderson and Fedorov 2004). Most of nine recently described species of *Gymnelus* (Chernova 1998a, 1999a, b, 2000) were considered (Anderson and Fedorov 2004) to be probable ecophenotypes of three species with predominantly arctic distributions: *Gymnelus hemifasciatus*, *G. viridis*, and *G. retrodorsalis*. The *COI* sequences (Online Resource 3) indicate that gymnelines collected from the northern Bering Sea and Chukchi Sea in 2007–2009 belong to two species separated by only 1.2% sequence divergence (range 0.9–1.6%). The two clades are clearly separated, yet closely related. There is little ingroup variation (0.3% for *G. hemifasciatus* and 0.1% for *G. viridis*). The minor genetic variation seen is not consistent by coloration, sex, size, or geographic location. Primarily following Andriashev (1937) and Anderson (1982), and in step with established usage, these are *G. hemifasciatus* and *G. viridis* (Fig. 5). However, Chernova (1998b, 1999a, b; pers. comms.) has redescribed both species and restricts distribution of *G. hemifasciatus* to the western and northern Bering Sea and Pacific off Iturup Island, Kuril Islands, while identifying the common *Gymnelus* of the northern Bering Sea and Chukchi Seas as two new species, *G. knipowitschi* and *G. platycephalus*. The *COI* sequences from RUSALCA specimens identified as *G. platycephalus* from Chernova's (1999a) key fall into the *G. hemifasciatus* clade (Online Resource 3). The *COI* sequences from fish identified as *G. knipowitschi* from Chernova's (2000) key also fall within the *G. hemifasciatus* clade, supporting recognition of *G. knipowitschi* as a junior synonym. The *COI* sequences for fish in our sample identified as *G. barsukovi* and *G. bilabrus* from Chernova (2000) fall within the clade traditionally identified as *G. viridis* and indicate they are the same species. These results reflect the variability and lack of diagnostic strength

of characters recently used (Chernova 1998b, c, 1999a, b, 2000) to describe gymnelines. Variability in zoarcid head pore configuration was demonstrated previously by Anderson (1994). In *Lycodes*, for instance, the supratemporal commissure, heavily relied on as a diagnostic character to describe the new gymnelines, is present only in the young of shallow-dwelling species and obliterated in adults. The validity of *G. obscurus*, another possible synonym of *G. viridis*, and of *G. andersoni*, *G. esipovi*, and *G. taeniatus*, which are similar to *G. retrodorsalis* (Anderson and Fedorov 2004), also needs to be tested. The BOLD database has one barcode from a specimen identified as *G. viridis* from the western North Atlantic, from New Brunswick, and it is identical to our Chukchi Sea *G. viridis*. The available *COI* sequences indicate there might be another species close to *G. retrodorsalis*. This could be a known species, such as one of Chernova's, or an undescribed species.

Taxonomy and distribution of arctic *Lycodes* have been addressed in descriptions and redescriptions of several species in recent years, especially for species found around Greenland (Møller and Petersen 1997; Møller 2000, 2001a, b; Møller and Jørgensen 2000). Møller and Gravlund (2003) presented the first phylogenetic analysis of the genus *Lycodes*, employing DNA sequences of two mitochondrial genes. Worldwide, about half of the *Lycodes* species inhabit shallow to moderate depths on continental shelves and upper slopes, and half frequent depths greater than about 400 m; none is primarily intertidal (Mecklenburg et al. 2002; Møller and Gravlund 2003).

A large number of *Lycodes* species exhibit “profound character plasticity” and at least nine species were once subdivided into subspecies on the basis of characters now known to vary individually or within populations (Anderson 1994:70). Our studies indicate that character plasticity might be obscuring the relationships of one or more arctic *Lycodes* species. Møller and Jørgensen (2000) noted that the differences between *L. reticulatus*, *L. lavalaei*, *L. rossii*, and *L. raridens* need further study. From P.R.M.'s research for the monograph on fishes of arctic Canada in preparation (see Coad and Reist 2004) and our recent observations on fresh material, we consider it likely that *L. reticulatus* and *L. rossii* are the same (Table 1), and *L. lavalaei* and *L. raridens* are distinct species. Descriptions (e.g., Mecklenburg et al. 2002) of *L. rossii* suggest they might be small individuals (up to 310 mm) of *L. reticulatus* (up to 760 mm). *Lycodes raridens* differs from *L. reticulatus* and *L. rossii* in dentition, squamation, and coloration (Mecklenburg et al. 2002). The *COI* sequences clearly show that *L. raridens* is distinct from other *Lycodes* (Online Resource 3).

Some *Lycodes* species, as with *Gymnelus*, are difficult to distinguish even by specialists, and barcoding shows promise for a partial solution in the laboratory, if not in the field. Møller and Gravlund (2003) found small genetic

differences among *Lycodes* species in the Atlantic side of the Arctic, and concluded that this was an indication of recent radiations from the Pacific after the opening of Bering Strait 3.0–3.5 million years ago. In our *COI* tree (Online Resource 3), the Atlantic species *L. paamiuti* and *L. mcallisteri* hardly look different but are separated by an average genetic distance of 0.6% (range 0.4–0.7%) and numerous morphological characters.

Several new extensions of known distribution of *Lycodes* species are reported in this paper (Online Resource 1), but the discovery of *L. adolfi* (Fig. 6) on the continental slope off the Chukchi Sea in 2009 is most dramatic. Described fairly recently (Nielsen and Fosså 1993), *L. adolfi* is fairly abundant in the eastern Norwegian Sea (Byrkjedal et al. 2009) and was found on the eastern slope of the Yermak Plateau north of Spitsbergen in 2007–2009 (Byrkjedal et al. 2010). The Chukchi slope specimens are the first from the western Arctic.

The five *Lycenchelys* species known to occur in the arctic region have all been found in the eastern Arctic and mostly on the continental slopes. *Lycenchelys platyrhina* has been found as deep as 2,377 m (Soltwedel et al. 2009). *Lycodonus* species also live at great depths. *Lycodonus flagellicauda* is known from the Norwegian and Greenland Seas, whereas *L. mirabilis* is predominantly boreal western Atlantic and reaches north to Baffin Bay. *Zoarces viviparus*, inhabiting shallow depths down to about 40 m, is predominantly boreal eastern Atlantic, reaching north to the southern Barents Sea and White Sea.

Stichaeidae (pricklebacks)

Thirty-seven genera with 76 species, in six subfamilies (Mecklenburg and Sheiko 2004). Stichaeids occur in a variety of habitats from intertidal and subtidal to sandy and muddy sea floors far from shore in water depths down to 500 m and more. Most species are found in the North Pacific. Five have arctic–boreal distributions and seven are boreal or predominantly boreal.

Eumesogrammus praecisus (Fig. 6), with distribution continuous from the East Siberian Sea through the Beaufort Sea and Canadian Arctic to western Greenland, is appropriately characterized as arctic–boreal (Mecklenburg et al. 2002; Online Resource 1), rather than amphiboreal (Andriashev 1939, 1954) or boreal (Andriashev and Chernova 1994). It appears to have reentered the Arctic from the North Pacific as well as from the western North Atlantic. *Eumesogrammus praecisus*, *Leptoclinus maculatus*, *Lumpenus fabricii*, and *Stichaeus punctatus* all have distributions in the western Arctic (Online Resource 1) that appear to reflect pre-Wisconsinan patterns of continuous ranges in the Arctic (Walters 1955). *Anisarchus medius* (Fig. 2) likely reentered the western Arctic postglacially via Europe as well as Bering Strait (Walters 1955).

The Pacific population of *L. maculatus* is sometimes classified as a subspecies, *L. m. diaphanocarus* (Schmidt, 1904), separate from the Atlantic population, *L. m. maculatus* (Fries, 1838). The *COI* sequences in the BOLD database for *L. maculatus* do not indicate a real separation between the Pacific and Atlantic samples. The distance between the Bering–Chukchi–Beaufort samples and the East Siberian–northwest Chukchi samples (1.3%, range 1.1–1.5%) is as “large” as between the Bering–Chukchi–Beaufort and Atlantic groups (1.6%, range 1.2–1.8%). The East Siberian–northwest Chukchi clade is close (0.5%, range 0–0.5%) to the Atlantic group.

Pholidae (gunnels)

Three genera, 15 species (Mecklenburg 2003b). Like stichaeids, pholids occur primarily in the North Pacific. *Pholis fasciata* has a wide distribution in the western Arctic. Most gunnels are typically found in the intertidal area under rocks or in tidepools, but *P. fasciata* is typically found below the intertidal and often far offshore in water depths down to about 50 m. *Pholis gunnellus* and *Rhodymenichthys dolichogaster* reach the fringes of the arctic region in the North Atlantic and Bering Sea, respectively.

Anarhichadidae (wolffishes)

Two genera, five species; updated taxonomic synopsis in Mecklenburg (2003c). Benthic or benthopelagic. *Anarhichas orientalis* is abundant in the Chukchi Sea, and also present but less common in the Beaufort Sea. *Anarrhichthys ocellatus* was found once in the arctic region, at Norton Sound on the beach after a 20-year storm in 2004. In the North Atlantic, *A. lupus* and *A. minor* are distributed northward into the margin of the arctic region.

Anarhichas denticulatus found on the beach at Kaktovik in 2008 and frozen on the ice near Barrow in 2009 are the first from the Alaskan Beaufort Sea and Chukchi Sea (Fig. 6). If this high-salinity species has spread westward across Arctic America (Walters 1955) as records from Canada suggest, the Barrow record represents its westernmost penetration from the western North Atlantic.

Zaproridae (prowfishes)

One species; updated taxonomic synopsis in Mecklenburg (2003d). North Pacific. Adults benthopelagic; juveniles pelagic, often found near surface.

Zapora silenus was collected in the Bering Sea north of St. Lawrence Island and in the Chukchi Sea (Fig. 6), both for the first time, in 2007. One juvenile was caught at each of the two locations by surface trawl. It is difficult to assess the significance of these northern records. Juvenile *Z.*



Lycodes adolfi, 193 mm TL
Chukchi Cap, 580–588 m, 2009 (UAM 5529)



Lycodes palearis, 152 mm TL
Southeastern Chukchi Sea, 47 m, 2007 (CAS 230137-01)



Lycodes palearis, 186 mm TL
Southeastern Chukchi Sea, 47 m, 2007 (CAS 230137-02)



Lycodes raridens, 208 mm TL
Southwestern Chukchi Sea, 45 m, 2009 (UAM 5574)



Lycodes turneri, 145 mm TL
Southeastern Chukchi Sea, 40 m, 2009 (CAS 228548)



Eumesogrammus praecisus, 150 mm TL
Bering Strait, 53 m, 2007 (CAS 230149)



Stichaeus punctatus, 106 mm TL
Northeastern Chukchi Sea, 49 m, 2009 (UAM 5535)



Anarhichas denticulatus, ~1.2 m TL
Chukchi Sea, found on ice near Barrow, 2009 (UAM 5845)



Zaprora silenus, 139 mm TL
Northeastern Bering Sea, 49 m, 2007 (CAS 230187)



Hippoglossoides robustus, 197 mm TL
Northeastern Chukchi Sea, 49 m, 2007 (CAS 230127)



Limanda proboscidea, 140 mm TL
Southeastern Chukchi Sea, 41 m, 2009 (ZIN 54866)

Fig. 6 A sampler of marine fishes occurring in the arctic region: Zoarcidae—Pleuronectidae

silenus are pelagic, and surface trawling has been relatively infrequent in the Chukchi Sea. Adults have not been taken in bottom trawl investigations in the Chukchi Sea and northern Bering Sea, most likely because those waters are shallow, less than 100 m, and adults inhabit deeper waters of the outer shelf and upper slope.

Ammodytidae (sand lances)

Marine, benthic; eight genera and about 23 species (Ida et al. 1994; Nelson 2006). One arctic endemic species (*Ammodytes dubius*) plus one boreal species each from the Atlantic (*A. marinus*) and the Pacific (*A. hexapterus*) also inhabiting seas in the Arctic.

Our *COI* sequences from *Ammodytes* (Online Resource 3) indicate a different species than *A. hexapterus* is present in the western Gulf of Alaska, with a genetic distance between the Bering–Chukchi clade and the Semidi Islands clade of 3.8% (range 3.6–4.1%). The second species most likely is *A. personatus* Girard, 1856, described from specimens collected at Cape Flattery, Washington and at present generally regarded as an endemic western Pacific species despite the type locality. With confusion of *A. hexapterus* and *A. personatus*, the southern limit of *A. hexapterus* is uncertain.

Scombridae (mackerels and tunas)

Fifty-one species in 15 genera and two subfamilies (Collette et al. 2001; Collette 2003; Nelson 2006). Fast-swimming, pelagic fishes of tropical and subtropical marine waters. *Scomber scombrus* reaches the arctic region off Jan Mayen, with records dating from 1978 to 2007 (Wienerroither et al. 2010).

Pleuronectidae (righteye flounders)

About 60 species in 23 genera and five subfamilies (Nelson 2006). Phylogenetic studies and revisions of the Pleuronectidae were recently reviewed by Evseenko (2004), Nelson et al. (2004), and Nelson (2006). The Pleuronectidae has representatives in all oceans and is the only family of flatfishes (order Pleuronectiformes) occurring in the Arctic Ocean. Benthic, usually in shallow marine waters; burrow into the surface sediment to rest and wait for prey.

Ten pleuronectid species are present in Arctic Ocean seas as well as in adjacent boreal waters: *Hippoglossoides robustus* (Fig. 6), *H. platessoides*, *Hippoglossus stenolepis*, *Limanda aspera*, *L. proboscidea* (Fig. 6), *L. sakhalinensis*, *Platichthys stellatus*, *Pleuronectes glacialis*, *P. quadrituberculatus*, and *Reinhardtius hippoglossoides*. The only pleuronectid distributed in the high Arctic is *R. hippoglossoides*, with records reaching as far north as 75°N on the Chukchi slope and 77°N

off Greenland. Previously overlooked historical as well as recent records from the Arctic Ocean (Online Resource 1) and the presence of spawning populations in the arctic region (e.g., around Greenland; Møller et al. 2010) indicate that *R. hippoglossoides* is more appropriately typified as an arctic–boreal species than as boreal (e.g., Andriashev and Chernova 1994). Another eight pleuronectids are boreal species with northern limits of distribution in the margins of the arctic region: *Acanthopsetta nadeshnyi*, *Atheresthes evermannii*, *A. stomias*, *Hippoglossoides elassodon*, and *Lepidopsetta polyxystra* in the Bering Sea; and *Hippoglossus hippoglossus*, *Platichthys flesus*, and *Pleuronectes platessa* in the Atlantic.

Hippoglossoides robustus, reported to be absent north of Bering Strait prior to 1933 (Andriashev 1937), is resident in the Chukchi Sea and distributed eastward through the Beaufort Sea to Bathurst Inlet in the Canadian Arctic (Fig. 2), where it was found as early as 1965; and westward to the East Siberian Sea (Online Resource 1). In some years it is one of the three or four most abundant fish species in the Chukchi Sea (Mecklenburg et al. 2007). *Limanda proboscidea* was found to be distributed eastward to Bathurst Inlet from collections dating back to 1975 (Online Resource 1).

Hippoglossus stenolepis representing a new northern record, northwest of Point Franklin, Chukchi Sea, was discovered in an unreported collection of fishes from 1973. The four records of *H. stenolepis* from the Chukchi Sea are from 1973, 1990, 2004, and 2007. *Lepidopsetta polyxystra* was collected in 2007 in the northern Bering Sea west of Cape Rodney, a little north of previous records (Orr and Matarese 2000). *Limanda sakhalinensis* was recorded for the first time from the Chukchi Sea in 1990 (Barber et al. 1997), followed by additional catches in 2008 and 2009.

The *COI* sequences from *R. hippoglossoides* from the Chukchi slope to the northern Bering Sea match those from Atlantic *R. hippoglossoides* (Online Resource 3) and do not support recognition of separate subspecies, with a genetic divergence of just 0.3% (range 0–0.6%). On the other hand, a biochemical genetic analysis found genetic divergence considered significant at the subspecific level between Northwest Atlantic and Bering Sea *R. hippoglossoides* (Fairbairn 1981). Chiperezak et al. (1995) reviewed taxonomic history and distribution of *R. hippoglossoides*, and reported one of the first records from the Beaufort Sea. This and the other Arctic Ocean records cited above, suggest that genetic continuity is maintained by exchange along the upper continental slopes.

Summary

The total number of species with documented presence in the arctic region (Online Resource 1) is 254, or 242 if the 12 probable junior synonyms (Table 1) are not counted.

The more conservative number (242) is used in the rest of this summary. That number includes four arctic marine fish species (*Careproctus derjugini*, *C. kidoi*, *Lycodes mcallisteri*, *L. paamiuti*) described in the past 10 years, and three species recently resurrected from synonymy (*Osmerus dentex*, *Liparis bathyarticus*, *Lycodes gracilis*). Several other species were synonymized or had name changes confirmed by recent evidence (Table 1).

The 242 species are distributed among 45 families. The suborder Cottoidei is represented by six families (Cottidae, Hemitripterae, Psychrolutidae, Agonidae, Cyclopteridae, Liparidae) and 72 species, and the suborder Zoarcoidei by five families (Zoarcidae, Stichaeidae, Pholidae, Anarhichadidae, Zaproridae) and 55 species. Together, those two suborders account for more than half the species (52.5%). The ten families represented by the most species are Zoarcidae (34 species), Cottidae (31), Pleuronectidae (18), Liparidae (17), Salmonidae (16), Gadidae (13), Stichaeidae (12), Agonidae (10), Cyclopteridae (8), and Rajidae (7). The Anarhichadidae are represented by five species, and the other 34 families by four or fewer species (Online Resource 5).

Three fish species have been found in the arctic region only as floating or beached carcasses: *Somniosus pacificus* and *Anarhichthys ocellatus* in the Chukchi Sea and northeastern Bering Sea, respectively, and *Lampris guttatus* in southern Baffin Bay. The only records of skates from the Chukchi Sea are beached carcasses of the boreal Pacific species *Bathyraja parmifera*. *Benthoosema glaciale* and *Anarhichas denticulatus*, common in the North Atlantic, are known in the western Arctic only from dead or dying beached specimens or remains of prey found on the ice. Four of the 242 species are known only from the type specimens: *Porocottus quadrifilis*, *Careproctus solidus*, *Paraliparis violaceus*, and *Lycodes sagittarius*.

Thirty-one (12.8%) of the 242 species are diadromous or have diadromous populations. All 16 of the listed species in Salmonidae are anadromous, as well as three in Petromyzontidae, two in Acipenseridae, one in Clupeidae, three in Osmeridae, and the two arctic species in Gasterosteidae. Two species in Acipenseridae are potamodromous and rarely found in saltwater, and the two in Anguillidae are catadromous.

Evaluating distribution patterns (Online Resource 1), we changed the designations for several species from those used by other authors (e.g., Andriashev and Chernova 1994; Parin et al. 2002). For 24 species the previously assigned patterns understated presence in the arctic region, and for ten species they overstated presence. These changes reflect increased knowledge of historical species distributions, not new incursions of boreal species or other reactions to climate change. Counting up the number of species in each distribution pattern gives: arctic, 19.4% (47 species); predominantly arctic, 6.2% (15); arctic–boreal,

15.7% (38); predominantly boreal, 21.5% (52); boreal, 31.4% (76); widely distributed, 5.8% (14). Combining the three distributions with a major arctic component gives 41.3% (100 species) compared with the three boreal patterns with 58.7% (142). As in any typological approach, it was difficult to assign some species to one of the defined distribution patterns.

Divergence of *COI* sequences between congeneric taxa in this study averaged 4.7% (range 3.7–13.3%). Conversely, within-species variation for most taxa was low (adjusted mean, 0.3%; range 0–3.5%), matching the lowest levels of conspecific variation reported in barcoding studies on fishes (Ward et al. 2005; Hubert et al. 2008; Steinke et al. 2009; Zemlak et al. 2009). This allows their separation from other taxa included in this study (or any of the other 7,540 fish species in BOLD).

The *COI* sequences generated for this study support the taxonomic separation of some species and the synonymy of others. For instance, the validity of *Liparis bathyarticus*, recently resurrected from synonymy in *L. gibbus* (Chernova 2008), and of *Enophrys lucasi*, considered the same as *E. diceraus* by some authors, was confirmed. Lack of genetic divergence supports the synonymy of, for instance, *Aspidophoroides bartoni* in *A. monopterygius* (e.g., Kanayama 1991; Mecklenburg et al. 2002), and of *Myoxocephalus verrucosus* and *M. groenlandicus* in *M. scorpius* (e.g., Mecklenburg et al. 2002, 2007). The barcode data also support synonymy of *Gymnelus bilabrus* and *G. barsukovi* in *G. viridis*, and of *G. knipowitschi* and *G. platycephalus* in *G. hemifasciatus* (e.g., Anderson and Fedorov 2004). The *COI* sequences also revealed that *Icelus spatula* as presently described (Nelson 1984) contains more than one species. *Mallotus* clades revealed by mtDNA analysis (Dodson et al. 2007) were confirmed by the barcode data, and an additional clade was revealed. The *COI* sequences did not support some controversial generic distinctions (*Theragra* = *Gadus*, *Melletes* = *Hemilepidotus*, *Triglopsis* = *Myoxocephalus*, *Ulcina* = *Aspidophoroides*). Although there are limitations to the conclusions that can be drawn on species status based on sequences from a single locus (Ward et al. 2009), the *COI* results in combination with morphological characters and geographical information provide sufficient proof for potentially overlooked species and synonymies and shed a light on controversial cases.

Discussion

Comparing arctic marine fish distributions as they have been revealed by recent studies to the distributions reported earlier from more limited occurrence records and different species classifications, large differences are obvious. For instance, reviewing the distribution of 16 species that had

been found in the northern Bering Sea but not north of Bering Strait at the time of Andriashev's (1939) review of the zoogeography of Bering Sea fishes, we found that 11 of them are now well documented north of the strait and some have fairly significant presence in the Chukchi Sea (Online Resource 1): *Clupea harengus pallasii* (= *C. pallasii*), *Oncorhynchus kisutch*, *O. nerka*, *Gasterosteus aculeatus*, *Hexagrammos stelleri*, *Hypsogonus quadricornis*, *Leptagonus decagonus*, *Pallasina barbata*, *Eumesogrammus praecisus*, *Limanda aspera*, and *Pleuronectes quadrituberculatus*. Two are the same as previously named arctic species (*Gymnelus bilabrus* = *G. viridis*, *Lycodes coccineus* = *L. mucosus*). One is still known only from the holotype (*Porocottus quadrifilis*). The remaining two have not been found north of the strait: *Artediellus dydymovi gomojunovi* (= *A. gomojunovi*) and *Lepidopsetta bilineata*; northern records were referred by Orr and Matarese (2000) to *L. polyxystra*, which does not reach Bering Strait. Andriashev (1939) also listed numerous examples of amphiboreal species, present in boreal waters of the Pacific and Atlantic but not in intervening Arctic waters. Several of them are now known to have populations and continuous or nearly continuous distributions in Arctic seas, including *Leptagonus decagonus*, *Eumesogrammus praecisus*, *Leptoclinus maculatus*, and *Reinhardtius hippoglossoides*. The cruise results and verification of museum specimens in this study (Online Resource 1) and results published from other studies in recent years have produced numerous records that extend previously understood patterns of distribution. This study, for instance, reports the first records of *Lycodes adolfi* from the western Arctic; *L. raridens*, *Leptoclinus maculatus*, and *Hippoglossoides robustus* from the East Siberian Sea; *Artediellus atlanticus*, *Trigllops nybelini*, *Cottunculus microps*, and *Lycodes seminudus* on the Chukchi slope; *Trichocottus brashnikovi*, *Hypsogonus quadricornis*, and *Zaprora silenus* in the Chukchi Sea; and *Amblyraja hyperborea* in the Beaufort Sea off Alaska. First records in recent literature include *Centroscymnus coelolepis*, *Alepocephalus agassizii*, *Cyclothone microdon*, *Stomias boa*, *Lampris guttatus*, *Macrourus berglax*, and *Sebastes mentella* from Baffin Bay (Møller et al. 2010); and many others from around the Arctic cited in the annotated checklist (Online Resource 1). As well, a few cases of possible retraction of arctic species' distributions are evident from the historical record. For example, *Myoxocephalus scorpioides* has not been found south of the northern Bering Sea since the late 1800s. Records from farther south, at Herendeen Bay on the north side of the Alaska Peninsula in 1890 and Chignik on the south side of the Alaska Peninsula in 1896, might give witness to the colder conditions that prevailed in the arctic Pacific at that time (see Wang et al. 2006). Populations of the predominantly arctic species *Aspidophoroides olrikii* in deep fjords of Prince William Sound, Gulf of Alaska, likely are relicts of former colder times. Finally, some species reported from the arctic

were found not to occur in the region. For instance, specimens from Alaska identified as *Myoxocephalus stelleri* in museum collections were misidentified or had erroneous locality data (Online Resource 1); photographs attributed to *M. stelleri* from the northeastern Pacific, including the Bering Sea and Gulf of Alaska, on websites and supplied by authors when queried show *M. scorpius* and *M. polyacanthocephalus*.

Are all of the revised distribution patterns the result of increased research in the historical collections and increased research sampling in the Arctic, or are some of them due to recent movements of species in response to climate change? Which species are most apt to expand or contract their distribution in the face of climate warming? For some arctic–boreal, predominantly boreal, and boreal fish species, increasing records from the Arctic could reflect a continuing reentry that started after glaciation and land barrier times (Walters 1955). With accelerated warming, the pace of reentry of amphiboreal species into the Arctic from both the Pacific and the Atlantic could be expected to increase, and the species more rapidly to establish continuous or circumpolar distributions. It could be more difficult for purely boreal species with a longer prehistory of isolation in the North Pacific or North Atlantic to acclimate or adapt to conditions in the Arctic even if it warms by a few degrees. Other conditions need to be taken into account as well, such as availability of appropriate trophic structure, substrate, vegetation, and topography.

A review of all known captures of Pacific salmon (*Oncorhynchus* species) in the Canadian western Arctic (coastal eastern Beaufort Sea) up to 2003 concluded that there was no evidence of newly established populations and not enough information to state definitively that salmon are increasing in frequency as a direct result of climate change. Recent programs to gather information on salmon abundance gave a false impression, making salmon appear to be more abundant than historically (Stephenson 2006). This theme is repeated in study after study. Reviewing historical and new data for fish presence around Greenland, Møller et al. (2010) concluded that new species of fish caught in shallow, intensively fished waters are apt to actually be new in the area, whereas the many new records from deep waters are explained by recently increasing fishing efforts for deepwater species. Reviewing literature on boreal Atlantic fish species, Rose (2005) concluded that small pelagics, including *Mallotus villosus* and *Clupea harengus*, can react strongly and quickly to climate change because of their broad physiological limits and potential for fast population growth; fisheries in Icelandic and Greenland waters have provided verification. Species that inhabit deeper, hydrographically more stable waters would be less affected (Rose 2005). In some regions, trawling was hampered by ice until recent years when warming temperatures opened waters earlier covered by ice. The increased scientific

sampling that warming recently has made possible has resulted in several first records (e.g., Dolgov et al. 2009).

A few regions have comprehensive long-term fishery or ichthyological investigation records and can with assurance monitor and detect changes in the ichthyofauna. One such is Icelandic waters, which are a transitional area at the boundary between warm, saline Atlantic water and cold, lower-salinity Arctic water. There, in recent years, pronounced changes have occurred in the abundance and distribution of fish and invertebrates that demonstrate the truth of the general hypothesis that in the face of climate warming the abundance of southerly species will increase and cold-water species will retract their distributions (Solmundsson et al. 2010). Long-term fisheries research databases recently were used in an analysis of demersal fish and invertebrate communities in the southeastern Bering Sea that demonstrated the movement, since the early 1980s, of several boreal species' centers of distribution northward as sea ice and cold bottom water retreated (Mueter and Litzow 2008). The recent intensive research fishing in the northern Bering Sea and Chukchi Sea, along with efforts to build the historical baseline (e.g., Mecklenburg et al. 2007; Norcross et al. 2010; this study), have led to a dramatic improvement in our knowledge of this region, which previously was one of the most poorly understood regions ichthyologically in the Arctic and in the world. The RUSALCA, planned as a long-term monitoring effort, with cruises currently planned through 2012, will build on this effort. We should now, with some assurance, be able to identify species that most likely are new to the Arctic north of Bering Strait. Similar advances in our knowledge of fishes at the Polar Front and beyond in the IPY and CoML in other key locations have been made, including the Barents and Kara Seas (Dolgov 2006; Byrkjedal and Høines 2007; Dolgov et al. 2009), Jan Mayen (Christiansen 2006; Wienerroither et al. 2010), and Baffin Bay and Davis Strait (Jørgensen et al. 2005; Møller et al. 2010; this study). The TUNU–MAFIG (University of Tromsø) program of fisheries research cruises to northeast Greenland is the only program currently providing information on the practically unknown ichthyofauna of the Greenland Sea, and is planned as a long-term monitoring effort (Christiansen 2003, 2006). For the most part, the deep continental slopes and Arctic basins received less sampling attention in the IPY and CoML, but what was learned was highly instructive and should provide good cause for pursuing sampling in these less accessible regions in future.

Detecting species new to the arctic region will be easier than linking cause and effect. For instance, community-wide northward distribution shifts of demersal fish and invertebrate species in the southeastern Bering Sea were demonstrated which coincided with retreat of cold bottom water northward (Mueter and Litzow 2008). Although

measures of community composition and structure showed relationships with temperature suggesting warming climate as the primary cause of the changing biogeography, variability not explained by climate also showed a temporal trend and suggested that internal community dynamics also contribute to changing distributions. Whether the observed distributional changes and retreat of the cold bottom water are a result of decadal-scale trends or global warming, or both, is unknown (Mueter and Litzow 2008).

The number of species we count as arctic is lower than might be on other authors' lists, partly due to different opinions on the taxonomic status of certain species. In all, what we have found reinforces Dunbar's (1968) observation that species in the higher latitudes, with distribution over enormous geographic areas having similar environmental conditions, are few in number but morphologically variable within species compared with species in, for instance, the myriad of small tropical ecosystems each with its distinct species. Intraspecific variation in arctic species is often the cause of taxonomic controversy. In our study, the *COI* sequences grouped specimens together that would have been identified as different species based on differences in coloration, head pore configuration, head shape, and other morphology used by authors as diagnostic characters in *Gymnelus*, *Lycodes*, and *Liparis*. The *COI* results demonstrate the highly plastic nature of these characters in these genera, which other authors previously noted purely on the basis of morphology (e.g., Anderson 1994). A recent study using molecular genetic and morphological data demonstrated that, despite separation by a number of morphological characters, *Eumicrotremus eggvinii* is the same species as *E. spinosus* and that specimens identified as *E. eggvinii* are the males and *E. spinosus* are the females (Byrkjedal et al. 2007).

Some of the intraspecific diversity observed today in arctic species could be attributable to prehistoric patterns of distribution, with waves of colonization and recolonization as ice sheets and land bridges formed and disappeared. *Myoxocephalus scorpius* is a good example. Our *COI* data support the recognition of arctic *M. scorpius* as a single circumpolar species. Some of the several morphological differences which have been noticed and used to diagnose subspecies and species could be populational or regional differences reflecting the prehistory of *M. scorpius*. In pre-Wisconsinan times, it is hypothesized (Walters 1955), the species had a circumpolar distribution, then became extinct in the Arctic and relegated to refugia in the North Pacific and North Atlantic as the ice sheets advanced. With the later disappearance of the land bridge barriers and the ice sheets, *M. scorpius* "could have quickly entered the Arctic from both oceans, spreading eastward and westward as opportunity permitted. The North Atlantic and North Pacific stocks met to produce a circumpolar distribution"

(Walters 1955:350). *Mallotus villosus* is another species which appears to have reentered the Arctic to become circumpolarly distributed (Walters 1955). Both species have diminished abundance northward. Genetic clades in *Mallotus villosus* (e.g., Dodson et al. 2007; this study) could reflect longer periods of genetic isolation, and further morphological, geographical, and genetic studies with analysis of implications for taxonomic significance, including possible recognition of species, are indicated.

Efforts in the IPY and CoML to build the baseline for historical marine fish species distribution, coupled with the recent scientific surveys, have allowed a better estimation than previously could be made of which species might have expanded their distribution within or into the arctic region in recent years. For instance, *Hippoglossoides robustus* was shown to be distributed in the Arctic Ocean from the East Siberian Sea to the easternmost reaches of the Beaufort Sea off Canada, and to have achieved that distribution as early as 1965. On the other hand, *Hypsagonus quadricornis* was found in 2007 in the Arctic for the first time in a region of the Chukchi Sea that had been extensively sampled in prior years, and could be new to the Arctic. The annotated list of species (Online Resource 1) is full of such examples. The greater impediment now to determining the historical distribution of some species is unresolved taxonomy. Distribution of several species was clarified through resolution of taxonomic problems during the CoML, such as *Gadus macrocephalus* and *G. chalcogrammus*. The former was shown to be distributed from the Pacific to the Atlantic through Alaskan and Canadian Arctic seas when it was recognized that the Atlantic species *G. ogac* and White Sea cod *G. callarias marisalbi* were the same as the Pacific cod *G. macrocephalus* (Carr et al. 1999; Møller et al. 2002). Walleye pollock *Theragra chalcogramma* (= *G. chalcogrammus*) and Atlantic pollock *T. finnmarkica* were recognized to belong in genus *Gadus* and, moreover, to be the same species (Coulson et al. 2006; Ursvik et al. 2007; Byrkjedal et al. 2008; Carr and Marshall 2008). Unlike *G. macrocephalus*, *G. chalcogrammus* has not been reported in intervening waters. For some species of *Gymnelus*, *Careproctus*, *Cottunculus*, and *Liparis*, for instance, the lack of taxonomic resolution still obscures distribution patterns.

Despite the progress in taxonomic and distributional studies reviewed in this paper, it is clear that much remains to be done to elucidate and document the biodiversity of arctic marine fishes. Solid diagnostic morphological characters are still lacking for the adults, as well as the early life stages, of several species. Increased sampling in Arctic seas and collection of specimens for taxonomic research should continue to be a priority beyond the CoML. Geographic distributions are incompletely known due to insufficient sampling, especially in the western Arctic, unresolved

taxonomic issues, and difficulties encountered by specialist and nonspecialist alike in identifying some species. Barcoding has proved to be a valuable tool for fish identification, but barcodes are lacking for more than half the arctic fish species. For many of those that are barcoded, samples are needed from additional collection localities to test species limits and reveal cryptic species. Phylogenetic analyses of genera and species need to include populations from a wider range of arctic locations. To more fully comprehend the pace and directions of change in zoogeographic patterns of distribution in the arctic region, additional modern studies are needed like those on the origins of the “codmother,” trans-Atlantic vicariance, and midglacial population expansion (Carr and Marshall 2008), and the trans-Atlantic dispersal and evolution of the *Mallotus villosus* complex (Dodson et al. 2007) which analyze the distribution of arctic fishes through geological time using a multifaceted methodology.

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