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By Catherine W. Mecklenburg and Dirk Steinke



ABSTRACT. At the beginning of the Russian–American Long-Term Census of the Arctic (RUSALCA) program in 2003, the composition and characteristics of the Pacific Arctic marine fish fauna and distribution of the species were poorly known compared with knowledge on the fish fauna of warmer waters. The mission for ichthyological investigations in the RUSALCA program has been to provide information necessary to construct zoogeographic and taxonomic baselines against which change may be detected. Our methods have involved examining historical fish collections in museums and identifying fresh samples secured on RUSALCA scientific expeditions and those of other programs, and DNA barcoding. This paper presents the first modern, comprehensive, well-founded inventory of the marine fish species in the Pacific Arctic region and its subregions; evaluates each species' zoogeographic pattern, primary distribution, biotype, and life zone; and highlights some of the positive results of our investigations in the first decade of the program as well as new and persistent problems identified that need further investigation.

BACKGROUND

Because of the recent, rapid climate change in the region, the Chukchi Sea and adjacent marine waters of the Pacific-influenced sector of the Arctic Ocean were chosen as the focus of the Russian-American Long-Term Census of the Arctic (RUSALCA) program. For purposes of this synthesis of the ichthyofauna of the region, the Pacific Arctic includes the northern Bering Sea (generally north of St. Matthew Island, about 60°N latitude); the East Siberian, Chukchi, and Beaufort Seas; and the adjacent waters of the Arctic Ocean down to about the 1,500-m isobath (Figure 1). When the program started in 2003, relatively few ichthyological investigations had been carried out in the Pacific Arctic, particularly north of Bering Strait (about 66°N). Compared with available knowledge on the fish fauna of warmer waters, the composition and characteristics of the Pacific Arctic fish fauna and the geographic distributions of the species were poorly known. A compendium and review of the regional fish fauna (Mecklenburg et al., 2002) published shortly before the start of the RUSALCA program provided a valuable early baseline while revealing numerous inadequacies in knowledge and the need for continuing studies. The mission for ichthyological investigations in the RUSALCA program has been to generate and disseminate essential information on regional marine fish diversity and presence to a wide community

of users, providing current baselines against which change may be detected. Our methods, described in earlier papers (Mecklenburg et al., 2007, 2011, 2014), involve study of historical fish collections in museums, sampling by modern investigations including RUSALCA multidisciplinary expeditions, and review of the ichthyological and fisheries science literature combined with results from DNA barcoding. The basic quest is to determine the geographic distributions and taxonomic identity of the species in the region. This paper highlights some of the positive results of these investigations in the first decade of the program, as well as new and persistent problems identified and needing further investigation. The main purpose is to describe the state of the baseline for the Pacific Arctic.

Following the earlier studies to produce *Fishes of Alaska*, the compendium that includes Chukchi and Beaufort Sea fishes (Mecklenburg et al., 2002), we continued and expanded examination of specimens in museums around the world (e.g., Mecklenburg et al., 2006; Mecklenburg and Mecklenburg, 2009) as we participated in the Census of Marine Life, the International Polar Year, RUSALCA, and other efforts to document biodiversity in the Arctic. Catch records in the literature and museum records were reviewed for accuracy of identifications from our examination of voucher specimens (e.g., Norcross et al., 2013). We focused on museums with

significant collections of Arctic fishes, listed in Mecklenburg et al. (2011, 2014). The museum work has remained a critical focus of our studies. In this article, a few additional museum catalog numbers (e.g., CAS 228491) are cited. The collection abbreviations are: CAS, California Academy of Sciences, San Francisco; CMNFI, Canadian Museum of Nature, Gatineau, Quebec; HUMZ, Hokkaido University Museum of Zoology, Hakodate, Japan; UAM, University of Alaska Museum, Fairbanks; and USNM, National Museum of Natural History, Washington, DC. Efforts to accumulate records of fish presence by participation in RUSALCA and other research cruises, and from collections by other programs sent frozen to author Mecklenburg for identification, preservation, and archiving were also outlined previously (Mecklenburg et al., 2007, 2011, 2014).

The RUSALCA used small bottom-fishing otter trawls and beam trawls described in Mecklenburg et al. (2007, 2014) and Norcross et al. (2010). Most of the RUSALCA trawl stations (Figure 1) were west of the International Dateline in Russian waters, and some were north of the 200-mile limit in international waters. The RUSALCA focus on Russian waters is unique. The only other US bottom trawl fishing effort in Russian waters of the Chukchi Sea was accomplished by University of Alaska Museum curator James E. Morrow, participating in a multidisciplinary cruise of R/V *Alpha Helix* in 1973 (Figure 1). The UAM 1973 collection is unusual in that all specimens caught were saved and archived in the museum; typically, only a representative sample of voucher specimens is archived. The specimens were archived under the names given on the field labels, but identifications were not subsequently verified, and no analysis of the catch was conducted or published. The analysis, conducted in 2008–2010 by author Mecklenburg, provided a valuable addition to the RUSALCA baseline.

The most recent additions to our data on fish presence and morphology have been gained by participation in the 2013

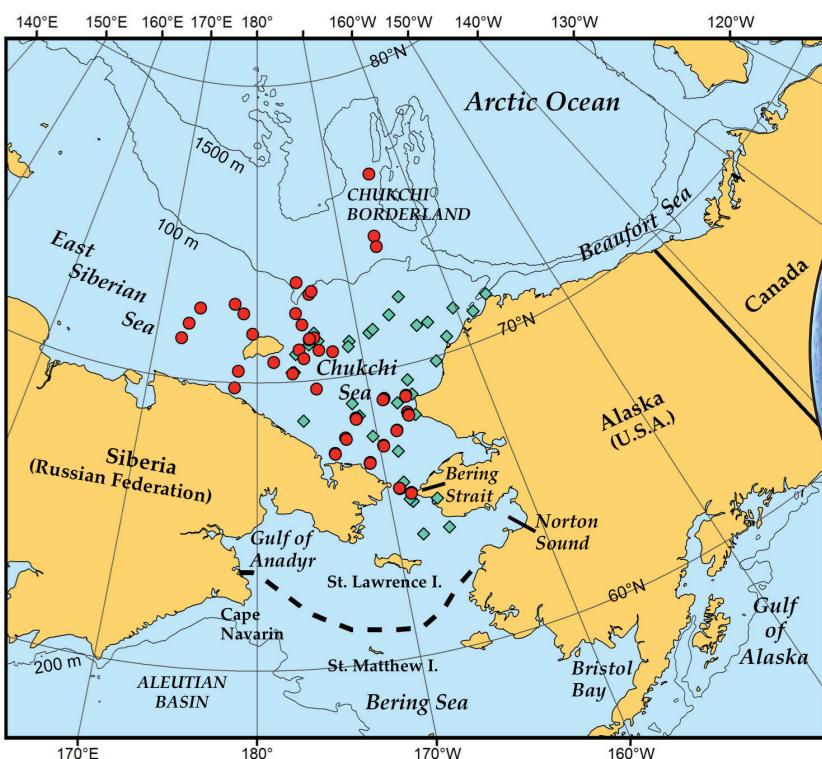


FIGURE 1. Map of Pacific Arctic region showing the southern limit of the Arctic region (heavy dashed line) and locations of the RUSALCA 2004, 2009, and 2012 (red dots, n = 54) and University of Alaska Museum 1973 (green diamonds, n = 34) bottom trawling sites. Some of the 2004 RUSALCA stations were resampled in 2009 and 2012, and having only slightly different geographic coordinates appear as single dots.

and 2015 University of Tromsø ichthyological cruises to northeastern Greenland (TUNU-V and TUNU-VI) and identification of specimens collected from the Beaufort Sea in 2011–2014 and provided by the University of Alaska Fairbanks and from the Bering Sea in 2011 provided by the Ted Stevens Marine Research Institute of the National Oceanic and Atmospheric Administration (NOAA), Alaska Fisheries Science Center (AFSC), Juneau, Alaska. Participation in the TUNU program (Christiansen, 2012; Christiansen et al., 2014) has helped provide the necessary pan-Arctic perspective against which to evaluate the Pacific Arctic species.

To supplement examination of morphology, a significant facet of our methodology has been DNA barcoding, which sequences a standard region of the mitochondrial cytochrome c oxidase 1 gene (COI) (Hebert et al., 2003; Bucklin et al., 2011). Tissue samples were sent to the Biodiversity Institute of Ontario, University of Guelph, Canada, for

barcoding as contributions to the Fish Barcode of Life initiative (Ward et al. 2009). Tissue collection and sequencing followed the protocol described by Steinke et al. (2009a). Sequence data were submitted to the Barcode of Life Data system (BOLD; <http://www.barcodinglife.org>; see Ratnasingham and Hebert [2007]) and to GenBank. Since publication of the barcode library presented in Mecklenburg et al. (2011), tissue sampling as part of the RUSALCA effort has expanded to include about 1,550 specimens (Figure 2). Reflecting a recent focus on studying relationships of the Pacific Arctic fish fauna to the Atlantic fauna, sampling from the Atlantic Arctic has particularly increased. Participation in the Norwegian TUNU cruises (Christiansen, 2012), as well as donations of tissues from the Zoological Museum of the University of Bergen, added barcodes from northeastern Greenland, around Jan Mayen and Svalbard, and the Barents and Norwegian Seas. The numbers of

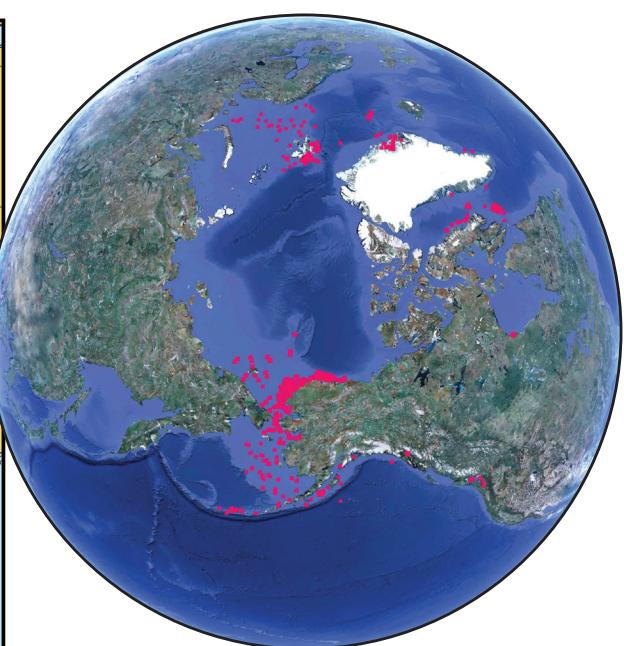


FIGURE 2. Collection localities for the 1,550 fish specimens tissue-sampled and sequenced for the RUSALCA studies. Sets from other sources are added as necessary to increase sample sizes or add species for individual analyses.

barcodes from the Bering, Chukchi, and Beaufort Seas were increased by author Mecklenburg's study of recent frozen collections from the Pacific Arctic as well as donations of tissues from the University of Washington fish collection. To date, we have barcoded 201 species. For the Pacific Arctic—the RUSALCA study area—we have barcoded 101, or 83%, of the 122 marine fish species known to occur in the region.

Specimen and collection data, sequences, specimen images, trace files, and GenBank accessions are provided in the public data sets on BOLD. Links to the data sets are provided in the text. Neighbor-joining (NJ) analyses and genetic distance calculations were executed with MEGA version 6.0 (Tamura et al., 2013). The Kimura 2-parameter (K2P) distance metric (Kimura, 1980) was employed for all sequence comparisons and analyses. Confidence in estimated relationships of NJ tree topologies was evaluated by a bootstrap analysis with 1,000 replicates using MEGA version 6.0. The samples discussed and used in the

NJ trees are drawn from the entire BOLD database (publicly available sequences), including the samples sequenced specifically for the RUSALCA program as well as sequences obtained through GenBank.

To understand the distributions of Pacific Arctic marine fishes, it is necessary to evaluate them in the context of the entire Arctic region. The circular and mediterranean structure of the Arctic Ocean with its seas requires a holistic approach (Wassmann, 2011). For our purposes, the Arctic region is defined as it pertains for marine fish species, with boundaries determined primarily by the southern limits of distribution of the Arctic species (Figure 3). We count at least 235 marine fish species in this region (Mecklenburg et al., 2011, 2013, and ongoing revision). The ichthyofauna is a combination of species endemic to the Arctic Ocean and its marginal seas and species that primarily inhabit warmer waters but have some presence in the Arctic. Of the total, 65 species occur only in the Pacific sector, 56 occur in both the Atlantic and the Pacific, and 114 are only in the Atlantic Arctic.

The Norwegian and Barents Seas in the Atlantic and the Bering and Chukchi Seas in the Pacific Arctic have been characterized as gateways to the Arctic (e.g., Christiansen et al., 2013) because they allow movement of species from boreal to Arctic regions. The Atlantic gateway is wide open and has been for much of its geological past, whereas the Pacific gateway includes the narrow Bering Strait, which has intermittently posed a barrier to fish movements as the Bering Land Bridge rose and submerged during glacial and interglacial periods (Briggs, 1995; Mecklenburg et al., 2011; Beszczynska-Möller et al., 2011). The physical environment of the Pacific Arctic has recently been detailed in Grebmeier and Maslowski (2014). The physical relationships of the region to the overall Arctic region, including the pathways of Pacific and Atlantic waters, which influence faunal distributions, are described in Woodgate et al. (2013).

THE PACIFIC ARCTIC ICHTHYOFAUNAL BASELINE

No complete lists of fish species with verified presence in the Pacific Arctic region were available prior to the syntheses in Mecklenburg et al. (2011, 2013). The closest in recent times was presented in Mecklenburg et al. (2002), which although focusing on the waters off Alaska also reviewed species presence in the adjacent Russian waters of the Chukchi Sea and the Canadian waters of the Beaufort Sea. Most lists have narrower regional coverage or are older and based on relatively sparse data. The list of Chukchi Sea fishes in Andriashev (1952) is useful for making broad comparisons but only when accounting for misidentifications due to the outdated state of knowledge and conclusions on species presence based on relatively few expeditions. The recent list in Datsky (2015) is largely uncritical, based largely on earlier lists and reporting documentation for fish presence only in general terms (such as “literature and online databases”), and includes several unsubstantiated claims of species presence and depths, many of them previously corrected in, for instance, the annotated list in Mecklenburg et al. (2011). Several papers report presence in the catches of individual ichthyological or fishery investigations. For instance, Rand

and Logerwell (2011) reported a preliminary list of species taken in a NOAA AFSC trawl survey in 2008 in the Alaskan Beaufort Sea, and Lin et al. (2012, 2014) reported trawl catches by the Chinese National Arctic Research Expedition (CHINARE) of 2010 in the northern Bering Sea and Chukchi Sea. The present paper reports species presence in the entire Pacific Arctic region and its sub-regions from complete reviews of the literature and examination of historical and recent collections.

Only marine species are included in the assessment. Freshwater and anadromous fishes are not included because they are not a focus of RUSALCA, which operates in late summer and fall, when sea-running species such as the Pacific salmons (Salmoninae) have returned to their natal streams, and conducts sampling in waters farther offshore than the nearshore waters inhabited by amphidromous and anadromous species like the ciscoes and other whitefishes (Coregoninae). Occasionally, anadromous sticklebacks (Gasterosteidae) and Arctic smelt (*Osmerus dentex*, Osmeridae), and the basically freshwater pond smelt (*Hypomesus olidus*, Osmeridae), are caught, but these are incidental. We include pelagic marine species from presence in investigations conducted by

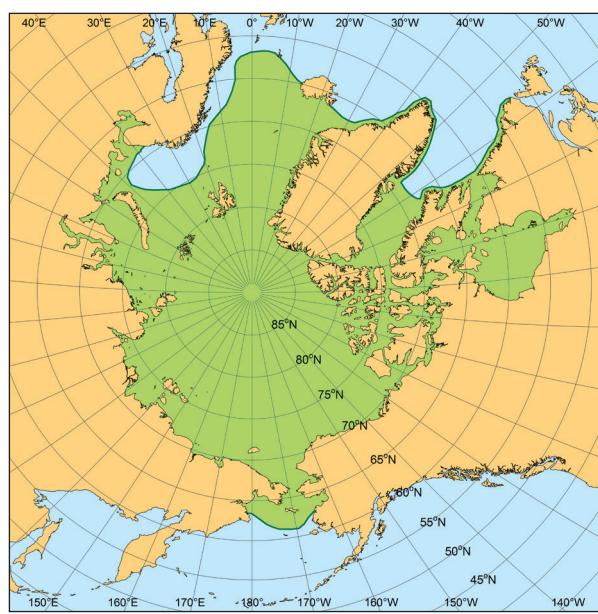


FIGURE 3. The Arctic region, defined as it pertains for marine fish species. Arctic marine fish species are rarely found outside of this region, so the boundary reflects the limits of distribution of Arctic species and not the extent to which boreal species have penetrated into the region. Modified from Mecklenburg et al. (2011, 2013)

programs that use pelagic nets, such as the pelagic surveys by NOAA AFSC divisions in Seattle, Washington, and Juneau, Alaska, because RUSALCA has used bottom trawls only, except for ichthyoplankton. Species presence in the ichthyoplankton is studied by other RUSALCA investigators and will be reported elsewhere. Larvae of species nonresident in the Chukchi Sea sometimes drift northward beyond Bering Strait. Essentially, therefore, the RUSALCA fish diversity studies have focused on adult fishes and on relatively large juveniles, which, if they are of species that develop in the ichthyoplankton or in the water column, have settled to the bottom.

Presence of Species and Higher Taxa

The simplest measure of biodiversity is the number of species, also called species richness. In all, we count 122 marine species in the Pacific Arctic (Table 1). This is 52% of the total number of marine species (235) counted for the entire Arctic region (Mecklenburg et al., 2013, revision in progress). The Table 1 list is accurate according to current knowledge, but the total number likely will change as taxonomic studies advance and new species are discovered. A few taxonomic issues among the snailfishes and eelpouts, for instance, are highlighted later in this paper. Species that have been found on continental slopes elsewhere in the Arctic, such as the eelpouts *Lycodonus flagellicauda* and additional *Lycenchelys* species, are likely to be found in the Pacific Arctic with retreat of the sea ice and intensified sampling.

The marine fish species of the Pacific Arctic are distributed among 10 orders and 23 families, compared with 19 orders and 44 families represented in the entire Arctic region. The makeup of the orders and families followed here is from the classification in Nelson (2006). Recent studies on the phylogeny and relationships of the higher taxa may result in taxonomists adopting changes (e.g., Smith and Busby, 2014).

The top 10 most speciose families account for 93 (77%) of the species present in the Pacific Arctic region. The sculpins (Cottidae) and eelpouts (Zoarcidae), with 27 and 20 species, respectively, are by far the most speciose families in the region. Snailfishes (Liparidae) are represented by 11 species, and flounders (Pleuronectidae), pricklebacks (Stichaeidae), and poachers (Agonidae) by 10 species each. Cods (Gadidae) and lump suckers (Cyclopteridae) are represented by five species each, and greenlings (Hexagrammidae) and fathead sculpins (Psychrolutidae) by three species each. The same families have historically had the highest numbers of species in the region. The remaining 13 families are represented by only one or two species (Table 1).

The fish fauna varies with the sub-regions of the Pacific Arctic (Table 1). The assemblages on the continental shelf of each of the seas differ from each other and from the assemblages in the deeper waters of the adjacent slopes and basins. When counting species, most authors combine the slope area with the shelf in the Chukchi Sea (e.g., Lin et al., 2014), and this practice combines assemblages. It makes, for instance, the deepwater species *Lycodes seminudus* and *Artediillus atlanticus* appear to be abundant in the shallow Chukchi Sea (with an average depth of 50 m), whereas they truly are restricted to the deeper waters. To grossly separate the assemblages, therefore, we show presence in Table 1 for the continental slopes separately from the Chukchi and Beaufort shelves. It should also be noted that for the purpose of counting species, we define Bering Strait, which marks the separation of the Chukchi and Bering Seas, as a line from Cape Dezhneva, Russia, to Cape Prince of Wales, USA. Some authors define the strait as a broader region or do not clearly discriminate between catches north and south of it. For instance, although larvae of masked greenling *Hexagrammos octogrammus* and gray starsnout *Bathyagonus alascanus* have

been reported from the Chukchi Sea (Logerwell et al., 2015), NOAA AFSC records show they were caught south of Bering Strait. In Table 1, species caught as adults or juveniles only as far northward as Bering Strait, such as salmon shark *Lamna ditropis*, shortraker rockfish *Sebastes borealis*, and Atka mackerel *Pleurogrammus monopterygius*, are not counted as Chukchi Sea species. Species are not counted as present in a region if their presence is known only from dead specimens, such as beached carcasses.

For each subregion, Table 1 includes only those marine species that have their presence documented by our own sampling, voucher specimens in museum collections, or records reported in the literature with adequate supporting information. The number of marine fish species documented for the Chukchi Sea shelf is 71 (Table 1, Figure 4). In the adjacent deeper waters of the continental slope down to about 1,500 m, an additional 34 species are present. The East Siberian Sea shelf, also with 34 species, is relatively depauperate compared with the Chukchi Sea and, indeed, with all other Arctic seas. Christiansen et al. (2013) estimate that the Kara and Laptev Seas have 60 and 50 marine species, respectively. The shelf of the Beaufort Sea has 56 species, similar to the Canadian Arctic archipelago with 57 species. The northern Bering Sea has the largest number of species in the Pacific Arctic region, with 97. With a total of about 385 species in the Bering Sea overall, there is great potential for expansion of populations northward and an increase in the number of species in the northern Bering Sea and Chukchi Sea.

The RUSALCA bottom trawls, sampling in Bering Strait, the Chukchi and East Siberian Seas, and the Chukchi Borderland in 2004, 2009, and 2012, took 54 species (Table 1). The relative abundance of the continental shelf species in the RUSALCA trawls fluctuated but did not exhibit any definite temporal trend. In the RUSALCA surveys, as well as in other scientific sampling efforts on the

TABLE 1. Marine fish species in subregions of the Pacific Arctic arranged by orders and families. The total number of species is 122. Orders and families follow the classification in Nelson (2006). X's indicate confirmed presence of species in the subregions from recent ichthyological and fisheries sampling or examination of historical collections. Asterisks indicate species taken by the RUSALCA trawl nets in 2004, 2009, or 2012. Authors and dates of publication of the original species descriptions given with the scientific names follow Eschmeyer's *Catalog of Fishes* online.

SCIENTIFIC NAME	COMMON NAME	BERING SEA N OF 60°	EAST SIBERIAN SEA	CHUKCHI SEA SHELF	BEAUFORT SEA SHELF	ADJACENT ARCTIC SLOPES
ORDER Lamniformes	Lamniforms					
FAMILY Lamnidae	Mackerel sharks					
<i>Lamna ditropis</i> Hubbs & Follett, 1947	salmon shark	X				
ORDER Squaliformes	Squaliforms					
FAMILY Squalidae	Dogfish sharks					
<i>Squalus suckleyi</i> (Girard, 1855)	spotted spiny dogfish	X	X			
FAMILY Somniosidae	Sleeper sharks					
<i>Somniosus pacificus</i> Bigelow & Schroeder, 1944	Pacific sleeper shark	X	X			
ORDER Rajiformes	Rajiforms					
FAMILY Rajidae	Skates					
<i>Amblyraja hyperborea</i> (Collett, 1879)	Arctic skate					X
<i>Bathyraja parmifera</i> (Bean, 1881)	Alaska skate	X	X			
ORDER Clupeiformes	Clupeiforms					
FAMILY Clupeidae	Herrings					
<i>Clupea pallasi</i> Valenciennes, 1847	Pacific herring	X*	X	X	X	
ORDER Osmeriformes	Osmeriforms					
FAMILY Osmeridae	Smelts					
<i>Mallotus catervarius</i> (Pennant, 1784)	Pacific capelin	X*	X	X*	X	
ORDER Myctophiformes	Myctophiforms					
FAMILY Myctophidae	Lanternfishes					
<i>Benthosema glaciale</i> (Reinhardt, 1837)	glacier lanternfish					X
ORDER Gadiformes	Gadiforms					
FAMILY Gadidae	Cods					
<i>Arctogadus glacialis</i> (Peters, 1872)	polar cod	X	X	X	X*	
<i>Boreogadus saida</i> (Lepechin, 1774)	Arctic cod	X*	X*	X*	X	X*
<i>Eleginus gracilis</i> (Tilesius, 1810)	saffron cod	X*	X	X*	X	
<i>Gadus chalcogrammus</i> Pallas, 1814	walleye pollock	X*		X*	X	X*
<i>Gadus macrocephalus</i> Tilesius, 1810	Pacific cod	X	X	X		
ORDER Scorpaeniformes	Scorpaeniforms					
FAMILY Scorpaenidae	Rockfishes					
<i>Sebastodes alutus</i> (Gilbert, 1890)	Pacific ocean perch	X				
<i>Sebastodes borealis</i> Barsukov, 1970	shortraker rockfish	X				
FAMILY Hexagrammidae	Greenlings					
<i>Hexagrammos octogrammus</i> (Pallas, 1814)	masked greenling	X				
<i>Hexagrammos stelleri</i> Tilesius, 1810	whitespotted greenling	X*		X	X	
<i>Pleurogrammus monopterygius</i> (Pallas, 1810)	Atka mackerel	X				
FAMILY Cottidae	Sculpins					
<i>Artediellus atlanticus</i> Jordan & Evermann, 1898	Atlantic hookear sculpin					X*
<i>Artediellus camchaticus</i> Gilbert & Burke, 1912	clownfin sculpin	X				
<i>Artediellus gomojunovi</i> Tarantet, 1933	spinyhook sculpin	X				
<i>Artediellus ochotensis</i> Gilbert & Burke, 1912	Okhotsk hookear sculpin	X				
<i>Artediellus pacificus</i> Gilbert, 1896	hookhorn sculpin	X				
<i>Artediellus scaber</i> Knipowitsch, 1907	hamecon	X	X*	X*	X	
<i>Enophrys diceraus</i> (Pallas, 1788)	antlered sculpin	X*		X*	X	
<i>Enophrys lucasi</i> (Jordan & Gilbert, 1898)	leister sculpin	X				
<i>Gymnocanthus galeatus</i> Bean, 1881	armorhead sculpin	X				
<i>Gymnocanthus pistilliger</i> (Pallas, 1814)	threadfin sculpin	X				

Table continued next page...

TABLE 1. Continued...

SCIENTIFIC NAME	COMMON NAME	BERING SEA N OF 60°	EAST SIBERIAN SEA	CHUKCHI SEA SHELF	BEAUFORT SEA SHELF	ADJACENT ARCTIC SLOPES
<i>Gymnoanthus tricuspid</i> (Reinhardt, 1830)	Arctic staghorn sculpin	X*	X*	X*	X	
<i>Hemilepidotus jordani</i> Bean, 1881	yellow Irish lord	X				
<i>Hemilepidotus papilio</i> (Bean, 1880)	butterfly sculpin	X*		X*		
<i>Icelus bicornis</i> (Reinhardt, 1840)	twohorn sculpin		X	X	X	X
<i>Icelus spatula</i> Gilbert & Burke, 1912	spatulate sculpin	X*	X*	X*	X	X
<i>Icelus spiniger</i> Gilbert, 1896	thorny sculpin	X*		X*		
<i>Megalocottus platycephalus</i> (Pallas, 1814)	belligerent sculpin	X		X	X	
<i>Microcottus sellaris</i> (Gilbert, 1896)	brightbelly sculpin	X		X		
<i>Myoxocephalus jaok</i> (Cuvier, 1829)	plain sculpin	X		X		
<i>Myoxocephalus polyacanthocephalus</i> (Pallas, 1814)	great sculpin	X*		X		
<i>Myoxocephalus quadricornis</i> (Linnaeus, 1758)	fourhorn sculpin	X	X	X	X	
<i>Myoxocephalus scorpioides</i> (Fabricius, 1780)	Arctic sculpin	X	X	X	X	
<i>Myoxocephalus scorpius</i> (Linnaeus, 1758)	shorthorn sculpin	X*	X	X*	X	
<i>Porocottus mednius</i> (Bean, 1898)	Aleutian fringed sculpin	X				
<i>Trichocottus brashnikovi</i> Soldatov & Pavlenko, 1915	hairhead sculpin	X*		X*	X	
<i>Triglops nybelini</i> Jensen, 1944	bigeye sculpin					X*
<i>Triglops pingellii</i> Reinhardt, 1837	ribbed sculpin	X*	X	X*	X	X
FAMILY Hemiripteridae						
Sailfin sculpins						
<i>Blepsias bilobus</i> Cuvier, 1829	crested sculpin	X		X*		
<i>Nautichthys pribilovius</i> (Jordan & Gilbert, 1898)	eyeshade sculpin	X*		X*	X	
FAMILY Psychrolutidae						
Fathead sculpins						
<i>Cottunculus microps</i> Collett, 1875	polar sculpin					X*
<i>Eurymenes gyrinus</i> Gilbert & Burke, 1912	smoothcheek sculpin	X		X		
<i>Psychrolutes paradoxus</i> Günther, 1861	tadpole sculpin	X				
FAMILY Agonidae						
Poachers						
<i>Aspidophoroides monoptyerus</i> (Bloch, 1786)	alligatorfish	X		X*		
<i>Aspidophoroides olrikii</i> Lütken, 1877	Arctic alligatorfish	X*	X	X*	X	X
<i>Hypsagonus quadricornis</i> (Valenciennes, 1829)	fourhorn poacher	X		X		
<i>Leptagonus decagonus</i> (Bloch & Schneider, 1801)	Atlantic poacher	X		X*	X	X
<i>Occella dodecaedron</i> (Tilesius, 1813)	Bering poacher	X		X		
<i>Pallasina barbata</i> (Steindachner, 1876)	tubenose poacher	X*		X		
<i>Percis japonica</i> (Pallas, 1769)	dragon poacher	X				
<i>Podothecus accipenserinus</i> (Tilesius, 1813)	sturgeon poacher	X				
<i>Podothecus veterinus</i> Jordan & Starks, 1895	veteran poacher	X*		X*	X	
<i>Sarrtor frenatus</i> (Gilbert, 1896)	sawback poacher	X				
FAMILY Cyclopteridae						
Lumpsuckers						
<i>Aptocyclus ventricosus</i> (Pallas, 1769)	smooth lump sucker	X				
<i>Eumicrotremus andriashevi</i> Perminov, 1936	pimpled lump sucker	X		X		
<i>Eumicrotremus derjugini</i> Popov, 1926	leatherfin lump sucker			X	X	
<i>Eumicrotremus orbis</i> (Günther, 1861)	Pacific spiny lump sucker	X				
<i>Eumicrotremus spinosus</i> (Fabricius, 1776)	Atlantic spiny lump sucker					X
FAMILY Liparidae						
Snailfishes						
<i>Careproctus phasma</i> Gilbert, 1896	spectral snailfish	X				
<i>Careproctus reinhardti</i> (Krøyer, 1862)	sea tadpole					X*
<i>Careproctus spectrum</i> Bean, 1890	stippled snailfish	X				
<i>Liparis bathyarticus</i> Parr, 1931	nebulous snailfish	X	X	X*	X	X
<i>Liparis callyodon</i> (Pallas, 1814)	spotted snailfish	X				
<i>Liparis fabricii</i> Krøyer, 1847	gelatinous seasnail	X	X*	X*	X	X*
<i>Liparis gibbus</i> Bean, 1881	variegated snailfish	X*	X	X*	X	
<i>Liparis ochoensis</i> Schmidt, 1904	Okhotsk snailfish	X				
<i>Liparis tunicatus</i> Reinhardt, 1836	kelp snailfish	X*	X*	X*	X	
<i>Paraliparis bathybius</i> (Collett, 1879)	black seasnail					X
<i>Rhodichthys regina</i> Collett, 1879	threadfin seasnail					X

Table continued next page...

TABLE 1. Continued...

SCIENTIFIC NAME	COMMON NAME	BERING SEA N OF 60°	EAST SIBERIAN SEA	CHUKCHI SEA SHELF	BEAUFORT SEA SHELF	ADJACENT ARCTIC SLOPES
ORDER Perciformes	Perciforms					
FAMILY Zoarcidae	Eelpouts					
<i>Gymnelus hemifasciatus</i> Andriashev, 1937	halfbarred pout	X*	X*	X*	X	
<i>Gymnelus viridis</i> (Fabricius, 1780)	fish doctor	X*	X	X*	X	
<i>Lycenchelys kolthoffi</i> Jensen, 1904	checkered wolf eel					X
<i>Lycodes adolfi</i> Nielsen & Fosså, 1993	Adolf's eelpout					X*
<i>Lycodes brevipes</i> Bean, 1890	shortfin eelpout	X				
<i>Lycodes eudipleurostictus</i> Jensen, 1902	doubleline eelpout					X
<i>Lycodes frigidus</i> Collett, 1879	glacial eelpout					X
<i>Lycodes jugoricus</i> Knipowitsch, 1906	shulupaoulk		X		X	
<i>Lycodes marisalbi</i> Knipowitsch, 1906	White Sea eelpout			X	X	
<i>Lycodes mucusosus</i> Richardson, 1855	saddled eelpout	X*		X*	X	
<i>Lycodes palearis</i> Gilbert, 1896	wattled eelpout	X		X*	X	
<i>Lycodes pallidus</i> Collett, 1879	pale eelpout		X			X
<i>Lycodes polaris</i> (Sabine, 1824)	polar eelpout	X	X*	X*	X	X
<i>Lycodes raridens</i> Taranetz & Andriashev, 1937	marbled eelpout	X	X*	X*	X	X
<i>Lycodes reticulatus</i> Reinhardt, 1835	Arctic eelpout			X	X	
<i>Lycodes rossi</i> Malmgren, 1865	threespot eelpout			X	X	
<i>Lycodes sagittarius</i> McAllister, 1976	archer eelpout					X
<i>Lycodes seminudus</i> Reinhardt, 1837	longear eelpout					X*
<i>Lycodes squamiventer</i> Jensen, 1904	scalebelly eelpout					X
<i>Lycodes turneri</i> Bean, 1879	estuarine eelpout	X		X*	X	
FAMILY Stichaeidae	Pricklebacks					
<i>Acantholumpenus mackayi</i> (Gilbert, 1896)	blackline prickieback	X		X	X	
<i>Alectrias electrolophus</i> (Pallas, 1814)	stone cockscomb	X				
<i>Anisarchus medius</i> (Reinhardt, 1837)	stout eelblenny	X*	X*	X*	X	
<i>Chirolipophis decoratus</i> (Jordan & Snyder, 1902)	decorated warbonnet	X				
<i>Chirolipophis snyderi</i> (Taranetz, 1938)	bearded warbonnet	X		X		
<i>Eumesogrammus praecisus</i> (Krøyer, 1836)	fourline snakeblenny	X*	X	X*	X	
<i>Leptoclinus maculatus</i> (Fries, 1838)	daubed shanny	X*	X*	X*	X	X*
<i>Lumpenus fabricii</i> Reinhardt, 1836	slender eelblenny	X*	X*	X*	X	
<i>Lumpenus sagitta</i> Wilimovsky, 1956	snake prickieback	X				
<i>Stichaeus punctatus</i> (Fabricius, 1780)	Arctic shanny	X*	X	X*	X	
FAMILY Pholidae	Gunnels					
<i>Pholis fasciata</i> (Bloch & Schneider, 1801)	banded gunnel	X*		X*	X	
<i>Rhodymenichthys dolichogaster</i> (Pallas, 1814)	stippled gunnel	X				
FAMILY Anarhichadidae	Wolfishes					
<i>Anarhichas denticulatus</i> Krøyer, 1845	northern wolffish			X	X	X
<i>Anarhichas orientalis</i> Pallas, 1814	Bering wolffish	X		X*	X	
FAMILY Zaproridae	Prowfishes					
<i>Zaprora silenus</i> Jordan, 1896	prowfish	X		X		
FAMILY Ammodytidae	Sand lances					
<i>Ammodytes hexapterus</i> Pallas, 1814	Pacific sand lance	X	X	X*	X	
ORDER Pleuronectiformes	Pleuronectiforms					
FAMILY Pleuronectidae	Righteye flounders					
<i>Hippoglossoides robustus</i> Gill & Townsend, 1897	Bering flounder	X*	X*	X*	X	
<i>Hippoglossus stenolepis</i> Schmidt, 1904	Pacific halibut	X		X		
<i>Lepidotsetta polyxystra</i> Orr & Matarese, 2000	northern rock sole	X				
<i>Limanda aspera</i> (Pallas, 1814)	yellowfin sole	X*		X*	X	
<i>Limanda proboscidea</i> Gilbert, 1896	longhead dab	X		X*	X	
<i>Limanda sakhalinensis</i> Hubbs, 1915	Sakhalin sole	X*		X*		
<i>Liopsetta glacialis</i> (Pallas, 1776)	Arctic flounder	X	X	X	X	
<i>Platichthys stellatus</i> (Pallas, 1787)	starry flounder	X		X	X	
<i>Pleuronectes quadrifiliger</i> Pallas, 1814	Alaska plaice	X		X		
<i>Reinhardtius hippoglossoides</i> (Walbaum, 1792)	Greenland halibut	X*	X	X*	X	X*

Chukchi Sea shelf, including the 1973 University of Alaska Museum investigation, the same species were the most abundant in most years. In the combined catches for those expeditions (Table 2), the top 10 species were Arctic staghorn sculpin *Gymnocanthus tricuspidatus*, Arctic cod *Boreogadus saida*, slender eelblenny *Lumpenus fabricii*, Arctic alligatorfish *Aspidophoroides olrikii*, ribbed sculpin *Triglops pingelii*, shorthorn sculpin *Myoxocephalus scorpius*, Bering flounder *Hippoglossoides robustus*, stout eelblenny *Anisarchus medius*, Pacific sand lance *Ammodytes hexapterus*, and hamecon *Artediellus scaber*. In some years, polar eelpout *Lycodes polaris*, spade sculpin *Icelus spatula*, Arctic shanny *Stichaeus punctatus*, or kelp snailfish *Liparis tunicatus* were among the top 10. The deepwater species, for instance Adolf's eelpout *Lycodes adolfi*, longear eelpout *L. seminudus*, and polar sculpin *Cottunculus microps*, were taken in low numbers, reflecting the small number of tows (three) made in the Chukchi Borderland in 2009, which was the only

one of the RUSALCA cruises to reach the northern deep waters. Similarly, RUSALCA trawled in offshore waters, so nearshore species like threaded sculpin *Gymnocanthus pistilliger*, belligerent sculpin *Megalocottus platycephalus*, and starry flounder *Platichthys stellatus* were among the least abundant species and were taken only in the 1973 UAM trawls, which sampled at a few nearshore locations.

Biotypes and Life Zones

Four biotypes, also called lifestyles or ecological types, are represented among the Pacific Arctic marine fishes: pelagic, cryopelagic, demersal, and benthic (Table 3). Pelagic species move freely in the water column. The most numerous in the RUSALCA and 1973 UAM trawls was Pacific capelin *Mallotus catervarius*, with an average number of fish caught ranking it in sixteenth place of all species. The pelagic species would not be expected to be present in great numbers on those expeditions because fishing was done with bottom rather than surface

or midwater trawls. The salmon shark *Lamna ditropis* was taken only once, by surface trawl in Bering Strait. Glacier lanternfish *Benthosema glaciale* is known in the region from only a couple of dead and dying specimens washed ashore in a storm at Point Barrow.

The Arctic cod *Boreogadus saida* and polar cod *Arctogadus glacialis* are special cases and are variously considered to represent pelagic or demersal biotypes or to be in a special category by themselves, the cryopelagic (ice-associated). However, their habitat varies with depth. Within the shelf area, *B. saida* is found sparsely among the ice, instead living almost constantly in the near-bottom layers where it is exploited by bottom trawling. In the deeper waters over the continental slopes and the central Arctic basins, the fish concentrate near the surface, at the sea ice. Observations near Greenland indicate that bottom habitat deeper than 800 m is not suitable for them (Karamushko, 2012). The situation for *A. glacialis* is similar, except that this species is not as often found on the inner shelf (Aschan et al., 2009). Catches by the RUSALCA otter trawl in the deeper waters of the Chukchi Borderland and nearby slope in 2009 reflect this behavior. The net took 686 *B. saida* at the shallowest station (227–236 m), 39 at the intermediate depth (365–370 m), and one at the deepest station (580–588 m). Four specimens of *A. glacialis* were taken on the intermediate depth station and only two at the deepest station (Mecklenburg et al., 2014).

Demersal species, also called benthopelagic species, live on and near the seafloor but also actively swim in the water column. They typically range more widely than the benthic species and are more often found in schools or other groups; they include spotted spiny dogfish *Squalus suckleyi*, walleye pollock *Gadus chalcogrammus*, Atka mackerel *Pleurogrammus monopterygius*, and northern wolffish *Anarhichas denticulatus*. In the entire circumpolar region encompassing the Arctic Ocean and its marginal seas, the marine fishes

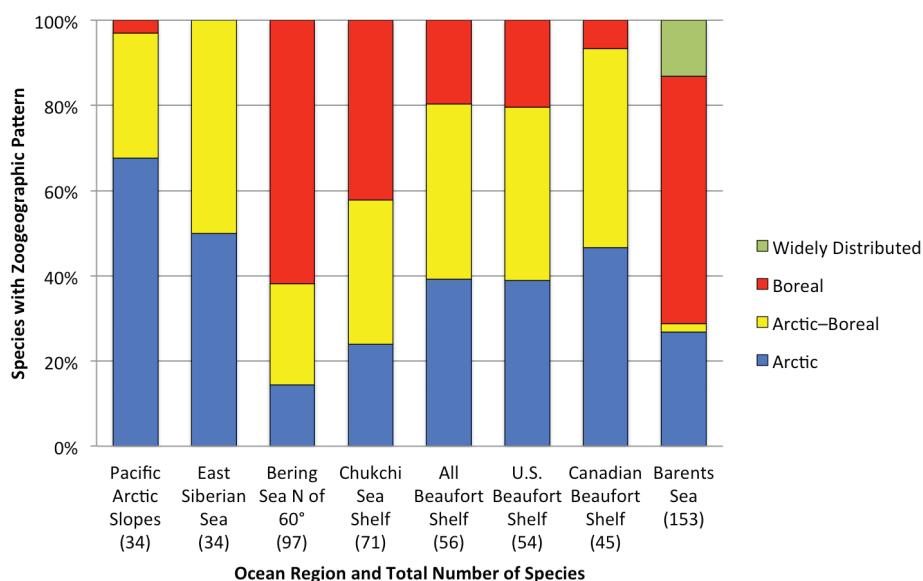


FIGURE 4. Proportions of marine fish species of each major zoogeographic pattern in Pacific Arctic subregions and the Barents Sea. The deep waters of the Arctic continental slopes have the most typically Arctic fish fauna, while the gateway seas, including the northern Bering, Chukchi, and Barents Seas, have the highest proportions of boreal species. None of the widely distributed species, those that are distributed in the warm waters of two oceans or in the Southern Hemisphere, have entered the Pacific Arctic. A = Arctic, AB = Arctic–boreal, B = boreal, WD = widely distributed. Data for the Barents Sea are from Christiansen et al. (2013).

are predominantly associated with the seafloor. The situation is no different in the Pacific Arctic region, with 94% (115) of species found on the bottom (benthic) or closely associated with it (demersal).

Benthic species live in close contact with the bottom and include species that burrow in the substrate. Sculpins (Cottidae), eelpouts (Zoarcidae), and flounders (Pleuronectidae) of the Pacific Arctic are almost exclusively benthic.

A few species are difficult to categorize. For instance, gelatinous seasnail *Liparis fabricii*, which is typically found in continental shelf waters on the bottom but has been found in midwater far out at sea over depths as great as 2,500 m (Mecklenburg et al., 2007, 2014), is labeled demersal here. Greenland halibut *Reinhardtius*

hippoglossoides is wide-ranging and swims with its ventral surface downward, unlike other flounders, and could be considered demersal rather than benthic.

Checklists of fishes often give minimum and maximum depths of occurrence recorded for each species, but these extremes do not generally reflect the typical life zones of the species and can be misleading. For instance, extreme depths listed for benthic species can be for winter, when the fish move down from the shelf, or for pelagic species can be for bottom depths although the fish were actually caught somewhere in the water column. Minimum depths given as 0 m can be for larvae in the plankton, fish in the intertidal zone or tidepools, or estimates for fish taken in beach seines. Some

depths reported may represent misidentifications. Table 3 gives life zones as categories of the major biotypes using a system modified from Parin et al. (2014). Depths are indicated by prefixes: epi-, 0–200 m; meso-, 200–1,500 m; bathy-, 1,500–3,000 m; and abysso-, deeper than 3,000 m. Shallow-water benthic and demersal fishes are in many cases characterized not by the prefix epi- but by the terms littoral, meaning the intertidal zone; sublittoral, the narrow coastal area of the continental shelf; and eulittoral, the offshore shelf zone. In some cases, pelagic fishes are characterized as neritic, found mainly on the continental shelf; nerito-oceanic, both over the shelf and in deeper waters; or oceanic. In a few cases, the categories given for species by

TABLE 2. Fishes caught in Bering Strait and the Chukchi Sea in the 2004, 2009, and 2012 RUSALCA and 1973 University of Alaska Museum (UAM) bottom trawls, ranked by total numbers of specimens. The UAM expedition was the only one to trawl for fishes in Russian as well as US waters of the Chukchi Sea other than the RUSALCA expeditions. A few postlarval and juvenile specimens too small to identify with confidence are not included in the counts.

RANK	SPECIES	NUMBER OF FISH	PERCENTAGE (%)	RANK	SPECIES	NUMBER OF FISH	PERCENTAGE (%)
1	<i>Gymnophanthis tricuspidis</i>	16,144	32.97	25	<i>Limanda sakhalinensis</i>	14	0.03
2	<i>Boreogadus saida</i>	6,672	13.63	26	<i>Pholis fasciata</i>	9	0.02
3	<i>Lumpenus fabricii</i>	5,542	11.32	26	<i>Aspidophoroides monopterygius</i>	8	0.02
4	<i>Aspidophoroides olrikii</i>	5,342	10.91	27	<i>Arctedius atlanticus</i>	7	0.01
5	<i>Triglops pingelii</i>	4,840	9.89	27	<i>Icelus spiniger</i>	7	0.01
6	<i>Myoxocephalus scorpius</i>	4,533	9.26	27	<i>Eumesogrammus praecisus</i>	7	0.01
7	<i>Hippoglossoides robustus</i>	1,494	3.05	27	<i>Arctogadus glacialis</i>	6	0.01
8	<i>Anisarchus medius</i>	778	1.59	27	<i>Limanda proboscidea</i>	6	0.01
9	<i>Ammodytes hexapterus</i>	676	1.38	27	<i>Myoxocephalus quadricornis</i>	4	0.01
10	<i>Arctedius scaber</i>	567	1.16	27	<i>Gymnelus viridis</i>	4	0.01
11	<i>Eleginus gracilis</i>	392	0.80	27	<i>Lycodes adolfi</i>	4	0.01
12	<i>Liparis tunicatus</i>	360	0.74	27	<i>Lycodes seminudus</i>	4	0.01
13	<i>Lycodes polaris</i>	319	0.65	27	<i>Clupea pallasi</i>	3	0.01
14	<i>Stichaeus punctatus</i>	303	0.62	27	<i>Gymnophanthis pistilliger</i>	3	0.01
15	<i>Icelus spatula</i>	188	0.38	27	<i>Lycodes turneri</i>	3	0.01
16	<i>Mallotus catervarius</i>	86	0.18	28	<i>Triglops nybelini</i>	2	0.00
17	<i>Leptocephalus maculatus</i>	68	0.14	28	<i>Pleuronectes quadrifasciatus</i>	2	0.00
18	<i>Lycodes palearis</i>	64	0.13	28	<i>Sebastes borealis</i>	1	0.00
19	<i>Liparis fabricii</i>	53	0.11	28	<i>Hexagrammos stelleri</i>	1	0.00
20	<i>Podothecus veterus</i>	47	0.10	28	<i>Megalocottus platycephalus</i>	1	0.00
20	<i>Limanda aspera</i>	47	0.10	28	<i>Myoxocephalus jaok</i>	1	0.00
21	<i>Gadus chalcogrammus</i>	45	0.09	28	<i>Myoxocephalus polycanthocephalus</i>	1	0.00
21	<i>Lycodes mucosus</i>	42	0.09	28	<i>Blepsias bilobus</i>	1	0.00
22	<i>Liparis gibbus</i>	40	0.08	28	<i>Cottunculus microps</i>	1	0.00
22	<i>Gymnelus hemifasciatus</i>	39	0.08	28	<i>Leptagonus decagonus</i>	1	0.00
22	<i>Trichocottus brashnikovi</i>	37	0.08	28	<i>Pallasina barbata</i>	1	0.00
23	<i>Enophrys diceratous</i>	32	0.07	28	<i>Careproctus reinhardti</i>	1	0.00
23	<i>Nautichthys pribilovius</i>	32	0.07	28	<i>Anarhichas orientalis</i>	1	0.00
24	<i>Lycodes rariensis</i>	26	0.05	28	<i>Hippoglossus stenolepis</i>	1	0.00
24	<i>Liparis bathyartcticus</i>	25	0.05	28	<i>Platichthys stellatus</i>	1	0.00
24	<i>Hemilepidotus papilio</i>	23	0.05	28	<i>Reinhardtius hippoglossoides</i>	1	0.00
				Total		48,963	

TABLE 3. Zoogeographic patterns, primary distributions, biotypes, and life zones of marine fishes in the Pacific Arctic region. For zoogeographic patterns, A = Arctic, MA = mainly Arctic, A–B = Arctic–boreal, MB = mainly boreal, B = boreal. See definitions for zoogeography, biotypes, and life zones in the text. A few species lack documentation of presence in some seas but are assumed to be circumpolar based on known presence in adjacent seas; these species are indicated by asterisks in the primary distribution column.

SCIENTIFIC NAME	ZOOGEOGRAPHY	PRIMARY DISTRIBUTION	BIOTYPE	LIFE ZONE
Lamnidae				
<i>Lamna ditropis</i>	B	Pacific	Pelagic	Epipelagic, nerito-oceanic
Squalidae				
<i>Squalus suckleyi</i>	B	Pacific	Demersal	Epibenthopelagic
Somniidae				
<i>Somnioides pacificus</i>	B	Pacific	Demersal	Mesobenthopelagic
Rajidae				
<i>Amblyraja hyperborea</i>	A	Circumpolar	Benthic	Meso-bathybenthic
<i>Bathyraja parvifera</i>	B	Pacific	Benthic	Epi-mesobenthic
Clupeidae				
<i>Clupea pallasi</i>	A–B	Pacific	Pelagic	Neritic
Osmeridae				
<i>Mallotus catervarius</i>	A–B	Western Pacific–Beaufort; Davis Strait	Pelagic	Neritic
Myctophidae				
<i>Benthosema glaciale</i>	A–B	Atlantic; rare Pacific	Pelagic	Mesopelagic
Gadidae				
<i>Arctogadus glacialis</i>	A	Circumpolar	Cryopelagic	Nerito-oceanic
<i>Boreogadus saida</i>	A	Circumpolar	Cryopelagic	Nerito-oceanic
<i>Eleginops gracilis</i>	A–B	East Siberian–Chukchi; Pacific	Demersal	Eulittoral
<i>Gadus chalcogrammus</i>	MB	Amphiboreal	Demersal	Eulittoral
<i>Gadus macrocephalus</i>	A–B	Chukchi–western Greenland; Pacific	Demersal	Eulittoral
Scorpaenidae				
<i>Sebastodes alutus</i>	B	Pacific	Demersal	Epi-mesobenthopelagic
<i>Sebastodes borealis</i>	B	Pacific	Demersal	Mesobenthopelagic
Hexagrammidae				
<i>Hexagrammos octogrammus</i>	B	Pacific	Demersal	Littoral
<i>Hexagrammos stelleri</i>	MB	Pacific	Demersal	Sublittoral
<i>Pleurogrammus monopterygius</i>	B	Pacific	Demersal	Eulittoral
Cottidae				
<i>Artediellus atlanticus</i>	A–B	Eastern Canada–Chukchi; Atlantic	Benthic	Mesobenthic
<i>Artediellus camchaticus</i>	B	Western Pacific	Benthic	Eulittoral
<i>Artediellus gomojunovi</i>	B	Western Pacific	Benthic	Eulittoral
<i>Artediellus ochoensis</i>	B	Western Pacific	Benthic	Sublittoral
<i>Artediellus pacificus</i>	B	Pacific	Benthic	Eulittoral
<i>Artediellus scaber</i>	A	Siberian seas–western Canada	Benthic	Sublittoral
<i>Enophrys diceraus</i>	MB	Pacific	Benthic	Eulittoral
<i>Enophrys lucasi</i>	B	Pacific	Benthic	Sublittoral
<i>Gymnoanthus galeatus</i>	B	Pacific	Benthic	Eulittoral
<i>Gymnoanthus pistilliger</i>	MB	Pacific	Benthic	Eulittoral
<i>Gymnoanthus tricuspidis</i>	A	Circumpolar	Benthic	Eulittoral
<i>Hemilepidotus jordani</i>	B	Pacific	Benthic	Eulittoral
<i>Hemilepidotus papilio</i>	MB	Western Pacific	Benthic	Littoral–sublittoral
<i>Icelus bicornis</i>	MA	Circumpolar	Benthic	Eulittoral
<i>Icelus spatula</i>	A–B	Circumpolar; Pacific & western Atlantic	Benthic	Eulittoral
<i>Icelus spiniger</i>	MB	Pacific	Benthic	Eulittoral
<i>Megalocottus platycephalus</i>	MB	Western Pacific	Benthic	Sublittoral
<i>Microcottus sellaris</i>	MB	Western Pacific	Benthic	Littoral
<i>Myoxocephalus jaok</i>	MB	Pacific	Benthic	Eulittoral
<i>Myoxocephalus polyacanthocephalus</i>	B	Pacific	Benthic	Eulittoral
<i>Myoxocephalus quadricornis</i>	MA	Circumpolar	Benthic	Littoral
<i>Myoxocephalus scorpiooides</i>	A	East Siberian–western Greenland	Benthic	Littoral
<i>Myoxocephalus scorpius</i>	A–B	Circumpolar; Atlantic & Pacific	Benthic	Eulittoral
<i>Porocottus mednus</i>	B	Western Pacific	Benthic	Sublittoral
<i>Trichocottus brashnikovi</i>	MB	Western Pacific	Benthic	Sublittoral
<i>Triglops nybelini</i>	A	Circumpolar*	Benthic	Mesobenthic
<i>Triglops pingelii</i>	A–B	Circumpolar; Atlantic & Pacific	Benthic	Sublittoral

Table continued next page...

TABLE 3. Continued...

SCIENTIFIC NAME	ZOOGEOGRAPHY	PRIMARY DISTRIBUTION	BIOTYPE	LIFE ZONE
Hemitripteridae				
<i>Blepsias bilobus</i>	B	Pacific	Demersal	Sublittoral
<i>Nautichthys pribilovius</i>	MB	Pacific	Demersal	Eulittoral
Psychrolutidae				
<i>Cottunculus microps</i>	A–B	Circumpolar; Atlantic	Benthic	Mesobenthic
<i>Eurymenis gyrinus</i>	MB	Western Pacific	Benthic	Eulittoral
<i>Psychrolutes paradoxus</i>	B	Pacific	Benthic	Eulittoral
Agonidae				
<i>Aspidophoroides monopterygius</i>	MB	Amphiboreal	Benthic	Eulittoral
<i>Aspidophoroides olrikii</i>	MA	Siberian seas–western Greenland	Benthic	Eulittoral
<i>Hypsagonus quadricornis</i>	B	Pacific	Benthic	Eulittoral
<i>Leptagonus decagonus</i>	A–B	Nearly circumpolar; Atlantic & Pacific	Benthic	Eulittoral
<i>Occella dodecaedron</i>	B	Western Pacific	Benthic	Sublittoral
<i>Pallasina barbata</i>	MB	Pacific	Demersal	Sublittoral
<i>Percis japonica</i>	B	Western Pacific	Benthic	Epi-mesobenthic
<i>Podothecus accipenserinus</i>	B	Pacific	Benthic	Epi-mesobenthic
<i>Podothecus veterinus</i>	A–B	Western Pacific	Benthic	Eulittoral
<i>Sarritor frenatus</i>	B	Pacific	Benthic	Eulittoral
Cyclopteridae				
<i>Aptocyclus ventricosus</i>	B	Pacific	Pelagic	Epi-mesopelagic
<i>Eumicrotremus andriashevi</i>	A–B	Pacific	Benthic	Sublittoral
<i>Eumicrotremus derjugini</i>	A	Circumpolar*	Benthic	Eulittoral
<i>Eumicrotremus orbis</i>	B	Pacific	Benthic	Eulittoral
<i>Eumicrotremus spinosus</i>	MA	Eastern Beaufort–Kara; Atlantic	Benthic	Eulittoral
Liparidae				
<i>Careproctus phasma</i>	B	Pacific	Benthic	Eulittoral
<i>Careproctus reinhardtii</i>	A	Atlantic & Pacific	Benthic	Mesobenthic
<i>Careproctus spectrum</i>	B	Pacific	Benthic	Eulittoral
<i>Liparis bathyarcticus</i>	MA	Circumpolar; Pacific & Atlantic	Benthic	Eulittoral
<i>Liparis callyodon</i>	B	Pacific	Benthic	Littoral
<i>Liparis fabricii</i>	A	Circumpolar	Demersal	Eulittoral
<i>Liparis gibbus</i>	A–B	Barents–Chukchi; Pacific	Benthic	Eulittoral
<i>Liparis ochotensis</i>	B	Western Pacific	Benthic	Epi-mesobenthic
<i>Liparis tunicatus</i>	A	Circumpolar	Benthic	Sublittoral
<i>Paraliparis bathybius</i>	A	Circumpolar	Demersal	Bathybenthopelagic
<i>Rhodichthys regina</i>	A	Circumpolar	Demersal	Bathybenthopelagic
Zoarcidae				
<i>Gymnelus hemifasciatus</i>	A–B	Barents–Beaufort; Pacific	Benthic	Eulittoral
<i>Gymnelus viridis</i>	MA	Kara–Greenland; Pacific	Benthic	Eulittoral
<i>Lycenchelys kolthoffi</i>	A	Eastern Canada–Laptev; Beaufort	Benthic	Mesobenthic
<i>Lycodes adolfi</i>	A	Circumpolar*	Benthic	Mesobenthic
<i>Lycodes brevipes</i>	B	Pacific	Benthic	Eulittoral
<i>Lycodes eudipleurostictus</i>	A	Circumpolar	Benthic	Mesobenthic
<i>Lycodes frigidus</i>	A	Circumpolar	Benthic	Bathybenthic
<i>Lycodes jugoricus</i>	A	Barents–Boothia Peninsula	Benthic	Sublittoral
<i>Lycodes marisalbi</i>	A	Amphi-Arctic	Benthic	Eulittoral
<i>Lycodes mucosus</i>	A	Chukchi–western Greenland	Benthic	Sublittoral
<i>Lycodes palearis</i>	MB	Pacific	Benthic	Eulittoral
<i>Lycodes pallidus</i>	A	Circumpolar*	Benthic	Epi-meso-bathybenthic
<i>Lycodes polaris</i>	A	Barents–western Greenland	Benthic	Eulittoral
<i>Lycodes raridens</i>	A–B	Pacific	Benthic	Eulittoral
<i>Lycodes reticulatus</i>	A	Eastern Canada–Kara; Beaufort	Benthic	Epi-mesobenthic
<i>Lycodes rossi</i>	A	Eastern Canada–Laptev; Beaufort	Benthic	Eulittoral
<i>Lycodes sagittarius</i>	A	Kara–Laptev; Beaufort	Benthic	Meso-bathybenthic
<i>Lycodes seminudus</i>	A	Circumpolar*	Benthic	Mesobenthic
<i>Lycodes squamiventer</i>	A	Greenland–Svalbard; Beaufort	Benthic	Bathybenthic
<i>Lycodes turneri</i>	MA	Northern Bering & Chukchi	Benthic	Sublittoral

Table continued next page...

TABLE 3. Continued...

SCIENTIFIC NAME	ZOOGEOGRAPHY	PRIMARY DISTRIBUTION	BIOTYPE	LIFE ZONE
Stichaeidae				
<i>Acantholumpenus mackayi</i>	MB	Pacific	Benthic	Sublittoral
<i>Alectrias electrolophus</i>	B	Western Pacific	Benthic	Littoral
<i>Anisarchus medius</i>	A–B	Circumpolar; Pacific	Benthic	Eulittoral
<i>Chirolipophis decoratus</i>	B	Pacific	Benthic	Sublittoral
<i>Chirolipophis snyderi</i>	MB	Pacific	Benthic	Sublittoral
<i>Eumesogrammus praecisus</i>	A–B	East Siberian–western Greenland	Demersal	Eulittoral
<i>Leptoclinus maculatus</i>	A–B	East Siberian–Barents; Pacific & Atlantic	Benthic	Eulittoral
<i>Lumpenus fabricii</i>	A–B	Barents–western Greenland; Pacific	Benthic	Sublittoral
<i>Lumpenus sagitta</i>	B	Pacific	Benthic	Sublittoral
<i>Stichaeus punctatus</i>	A–B	East Siberian–western Greenland; Pacific	Demersal	Sublittoral
Pholidae				
<i>Pholis fasciata</i>	A–B	Chukchi–western Greenland; Pacific	Benthic	Sublittoral
<i>Rhodymenichthys dolichogaster</i>	MB	Western Pacific	Benthic	Littoral
Anarhichadidae				
<i>Anarhichas denticulatus</i>	A–B	Chukchi–Barents; Atlantic	Demersal	Eulittoral
<i>Anarhichas orientalis</i>	MB	Pacific	Demersal	Sublittoral
Zaproridae				
<i>Zaprora silenus</i>	B	Pacific	Demersal	Eulittoral
Ammodytidae				
<i>Ammodytes hexapterus</i>	A–B	East Siberian–Hudson Bay; Pacific	Demersal	Eulittoral
Pleuronectidae				
<i>Hippoglossoides robustus</i>	A–B	East Siberian–Beaufort; Pacific	Benthic	Eulittoral
<i>Hippoglossus stenolepis</i>	B	Pacific	Benthic	Eulittoral
<i>Lepidotsetta polyxystra</i>	B	Pacific	Benthic	Epi-mesobenthic
<i>Limanda aspera</i>	MB	Pacific	Benthic	Eulittoral
<i>Limanda proboscidea</i>	MB	Pacific	Benthic	Sublittoral
<i>Limanda sakhalinensis</i>	MB	Western Pacific	Benthic	Eulittoral
<i>Liopsetta glacialis</i>	MA	Barents–Beaufort; Pacific	Benthic	Sublittoral
<i>Platichthys stellatus</i>	A–B	Chukchi–Beaufort; Pacific	Benthic	Sublittoral
<i>Pleuronectes quadrituberculatus</i>	MB	Pacific	Benthic	Eulittoral
<i>Reinhardtius hippoglossoides</i>	A–B	Amphi-Arctic–boreal	Benthic	Mesobenthic

Parin et al. (2014) or other authors are more appropriate for the boreal western Pacific, such as in the Sea of Okhotsk or the Sea of Japan, and categories have been modified to describe occurrence in the Pacific Arctic.

With the greatest area of the Pacific Arctic occupied by the continental shelf, and most (115, or 94%) of the marine fishes being benthic or demersal, the main life zones exploited are the eulittoral (54, or 44%) and the sublittoral (28, or 23%). The littoral zone in the Arctic is limited, with tidal amplitudes less than 0.1 m in the Chukchi and Beaufort Seas (Huang et al., 2012). Consequently, littoral fish species diversity in the Arctic is very low compared with more southerly latitudes. In the Pacific Arctic, only six species are strictly littoral: masked greenling

Hexagrammos octogrammus, brightbelly sculpin *Microcottus sellaris*, fourhorn sculpin *Myoxocephalus quadricornis*, Arctic sculpin *M. scorpioides*, spotted snailfish *Liparis callyodon*, and stippled gunnel *Rhodymenichthys dolichogaster*. Of those, only *M. quadricornis* and *M. scorpioides* are found north of Bering Strait. The seafloor in deep waters of the region is home mostly to meso- and bathybenthic species like the Arctic skate *Amblyraja hyperborea* and glacial eelpout *Lycodes frigidus*, and two bathy-benthopelagic species, the black seasnail *Paraliparis bathybius* and the threadfin seasnail *Rhodichthys regina*, move freely above the bottom. Only five pelagic species inhabit the Pacific Arctic: salmon shark *Lamna ditropis* near the surface both over the shelf and offshore in

oceanic waters; Pacific herring *Clupea pallasii* and Pacific capelin *Mallotus catervarius* over the shelf; glacier lanternfish *Benthosema glaciale* mainly at 200–1,500 m and rising to near the surface at night; and smooth lump sucker *Aptocyclus ventricosus* over the shelf and down to about 500 m offshore. *Lamna ditropis* has reached Bering Strait, while *A. ventricosus* occurs northward to about the latitude of St. Lawrence Island. The two cryopelagic cods, *Boreogadus saida* and *Arctogadus glacialis*, occupy both the neritic and the oceanic life zones.

Zoogeographic Patterns

The species are further categorized in terms of their distribution according to zoogeographic pattern (Table 3), which is the total geographic range of a

species. The definitions of the zoogeographic patterns pertinent for fish species in the Arctic region are derived largely from Andriashev (1939), Andriashev and Chernova (1995), Mecklenburg et al. (2011, 2013), and Christiansen et al. (2013):

1. Arctic: distributed and spawning mainly in Arctic waters (0° C or below) and only infrequently found in adjacent boreal waters. *Boreogadus saida*, which rarely occurs south of about 60° N in the northern Bering Sea, is a typical indicator species for the Arctic region (Briggs, 1995).
2. Mainly Arctic: commonly distributed in Arctic waters but also occurring in adjacent boreal waters. An example is the Arctic flounder *Liopsetta glacialis*, found mainly from the Barents Sea eastward to the Beaufort Sea and, infrequently, southward in the Pacific to the southern Bering Sea.
3. Arctic–boreal: distributed in both Arctic and boreal waters and spawning at both subzero and positive temperatures. *Anisarchus medius*, for instance, is common from the seas of the Arctic Ocean to the Sea of Japan, Gulf of Alaska, and Gulf of St. Lawrence.
4. Mainly boreal: characteristic of boreal waters and common also in the border regions of the Arctic. The butterfly sculpin *Hemilepidotus papilio* is most common from the Sea of Okhotsk and Kuril Islands to the Aleutian Islands and southern Bering Sea, and is fairly common from the Gulf of Anadyr and Norton Sound to the eastern Chukchi Sea. Spawning populations are not known to occur in the Chukchi Sea.
5. Boreal: distributed in boreal waters and spawning at positive temperatures. The Pacific halibut *Hippoglossus stenolepis* is abundant from the Sea of Japan, the Aleutian Islands, and California to the Bering Sea and has been recorded only rarely, and as small juveniles, from the eastern Chukchi Sea.
6. Widely distributed: species that are common in both boreal and subtropical waters and in the warm waters of

at least two oceans or are known also from the Southern Hemisphere. No widely distributed species have penetrated into the Arctic region from the Pacific. The nearest is the snubnosed spiny eel *Notacanthus chemnitzii*, which has reached the Gulf of Alaska off northern British Columbia (Peden, 2002) and is otherwise distributed in the Pacific off Oregon, California, and Japan, in the Atlantic off Greenland, and in the oceans of the Southern Hemisphere; although, it should be noted, populations in the Pacific and Atlantic may be different species (McCusker et al., 2012).

The summaries of the primary distribution of each Pacific Arctic species (Table 3) provide further detail on the zoogeographic patterns. The boreal species are endemic to the Pacific, including the Bering Sea. The Arctic species are circumpolar or distributed in some portion of the Arctic. For Arctic–boreal species, the oceans where boreal populations occur are indicated, such as both Pacific and western Atlantic for spatulate sculpin *Icelus spatula* and Pacific for slender eelblenny *Lumpenus fabricii*. Distributions are stated from west to east, as in Barents Sea–Beaufort Sea.

For comparisons, it is convenient to group the Arctic and mainly Arctic and the boreal and mainly boreal patterns. In the entire Arctic region, with 235 species, 67 (28.5%) are Arctic, 31 (13.2%) Arctic–boreal, 120 (51.1%) boreal, and 17 (7.2%) widely distributed. The Pacific Arctic by itself has 122 species, with 35 (28.7%) Arctic, 27 (22.1%) Arctic–boreal, and 60 (49.2%) boreal. The proportions of species exhibiting each zoogeographic pattern in each of the Pacific Arctic subregions (Tables 1 and 3) are included in Figure 4, which also includes one of the Atlantic Arctic gateway seas, the Barents Sea.

Differences are reflected in the proportions of species in the various zoogeographic patterns (Table 3 and Figure 4), with the gateway seas having the largest proportions of boreal species.

The Atlantic gateway, in addition, has a large proportion of widely distributed species, whereas such species are lacking in the Pacific gateway. Moving away longitudinally from the gateways, larger numbers of Arctic species and fewer boreal species are found, as in the East Siberian Sea and the Beaufort Sea. The influence of warm waters from the Pacific flowing into the Beaufort Sea is seen in the higher proportion of boreal species in the US Beaufort Sea compared with the lower proportion in the Canadian Beaufort. The Arctic slopes and basins, including those of the Pacific Arctic, retain the most typical Arctic fish fauna with practically no boreal species. All of the Pacific Arctic slope fish species, except for one, occur in both the Pacific and the Atlantic Arctic regions. The one apparent exception is the marbled eelpout *Lycodes raridens*, which, being a eulittoral species, is not typically found on the slopes. Presence of the deepwater species, such as the eelpouts *L. adolfi*, *L. sagittarius*, and *L. seminudus*, on the slopes in both regions may be related to the presence of relatively warm Atlantic water at mid-depths around the Arctic.

ADVANCES AND REMAINING PROBLEMS IN DETERMINING THE BIODIVERSITY BASELINE

One challenge to determining the baseline against which we may assess future change in the distribution of fishes in the Arctic has been the unsettled nature of scientists' understanding regarding species identities. Add differences of opinion stemming from different schools of thought on the definition of species (see, e.g., de Queiroz, 2005; Mallet, 2008) and the significance of different lines of research to the fact that the Arctic fish fauna was poorly known to begin with, and one can see that the problem is compounded and understand why RUSALCA has invested significant effort in attempting to resolve the identity of species. With increased accessibility and sampling in the region as the sea ice retreats and nations focus on research in the Arctic,

and with new tools for studying the phylogenetic relationships of the species including DNA sequencing, researchers have come to a better understanding of the biodiversity baseline.

A review of Arctic fish taxonomy and zoogeography (Mecklenburg et al., 2011) used data from DNA barcoding in addition to morphological characters to suggest solutions and highlight problems concerning the identification of species. The analysis also added further confirmation of certain previous taxonomic actions. The following examples add further information to the resolution of some of the problems brought out, and raise additional questions on other taxa. It is not meant to be an exhaustive treatment but to update the earlier review and illustrate the need for continuing study to define the diversity of the Arctic fishes.

Our own data have not added insight on the taxonomy of the few elasmobranchs that occur in the Pacific Arctic (Table 1), but it should be mentioned that the spotted spiny dogfish *Squalus suckleyi* of the North Pacific has been resurrected from synonymy in the widely distributed species *S. acanthias* (Ebert et al., 2010). The COI sequences of specimens from Honshu and Hokkaido as well as British Columbia and Washington are identical, supporting the wide North Pacific distribution of *S. suckleyi*.

Within the smelts, family Osmeridae, the mounting evidence warrants resurrection of the Pacific population of capelin

from synonymy in *Mallotus villosus*, as *M. catervarius*. The species was originally described from Bering Island and Kamchatka material by Pennant (1784) as *Salmo catervarius* and by Pallas (1814) as *S. socialis*. Schultz (1937) redescribed the Pacific population and gave it full species status as *M. catervarius*. Recent taxonomic usage has favored treatment as a subspecies, *M. villosus catervarius* (Walters, 1955; Andriashov and Chernova, 1995; Parin et al., 2014). The COI sequences of *Mallotus* specimens from the western Gulf of Alaska to the Bering and Chukchi Seas were found to be identical (Mecklenburg et al., 2011), and the combined sample, including all publicly available sequences (<http://dx.doi.org/10.5883/DS-MALLOT>), supported other molecular genetic studies that found highly divergent clades around the Arctic (e.g., Dodson et al., 2007; Præbel et al., 2008). We now have sequences from more regions, including, for *M. catervarius* ($n = 26$), the Pacific off Kamchatka and the western Beaufort Sea, summarized in Figure 5. The clade with sample size of 10 includes sequences from eastern Greenland and the Kara Sea and is labeled *M. villosus* since that species was originally described by Müller (1776) from Icelandic material. The clade with 30 sequences, labeled *Mallotus* sp., comprises material from Hudson Bay, the Gulf of St. Lawrence, and waters off Newfoundland, Labrador, and Nova Scotia. Fabricius (1780) used the name

Salmo arcticus for capelin he described from western Greenland, and that name might have been used, as *M. arcticus*, for the clade of 30, but Fabricius's name is preoccupied by Pallas's (1776) *Salmo arcticus*, now called *Thymallus arcticus* (grayling) (William N. Eschmeyer, Catalog of Fishes online and pers. comm., June 12, 2015). That aside, we hesitate to identify a name with this clade pending further studies clarifying the relationships of the clades. For instance, Dodson et al.'s (2007) analysis revealed four divergent *Mallotus* clades. In our sample, *Mallotus villosus* and *M. catervarius* are separated by a genetic distance of 2.7%, *Mallotus* sp. and *M. catervarius* by 2.4%, and *Mallotus* sp. and *M. villosus* by 3.1%. More COI sequences are needed, especially from the eastern Beaufort Sea and eastern Arctic of Canada, but altogether the morphological and molecular data suggest a distribution of *M. catervarius* from the northwestern Pacific, the eastern Gulf of Alaska, and the Bering Sea to the Laptev and East Siberian Seas and across Arctic Alaska and Canada to Davis Strait. Further studies are needed to determine the details of distribution of *M. catervarius* and elucidate morphological characters distinguishing it from other *Mallotus* species. Rumyantsev (1947) and Lindberg and Legeza (1965) described morphological characters they believed distinguished the Pacific and Atlantic populations, although they opted for maintaining them as subspecies whereas Schultz (1937) concluded the differences warranted recognition as separate species. The nomenclature needs further research to determine appropriate names for the primarily Atlantic species. Neotypes will have to be selected, since type material for *M. catervarius* and *M. villosus* is lacking.

Among the cods present in the Pacific Arctic, *Boreogadus saida* exhibits relatively little genetic variation despite its broad circumpolar distribution. The barcode sample (<http://dx.doi.org/10.5883/DS-GADIDS>), with numerous sequences from the East Siberian and Chukchi Seas

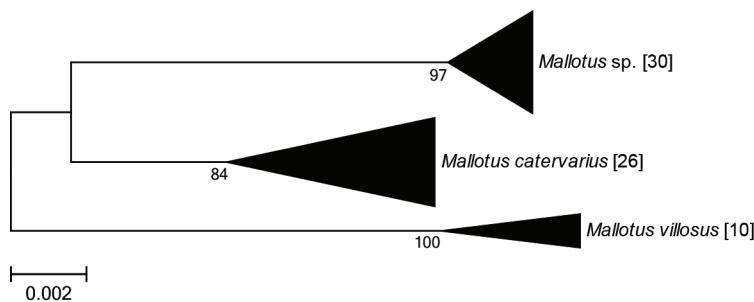


FIGURE 5. Neighbor-joining tree for COI (mitochondrial cytochrome c oxidase 1 gene) sequences in capelin (*Mallotus*, family Osmeridae). Triangles indicate the relative number of individuals sampled (height) and sequence divergence (width). Numbers at nodes represent bootstrap values. The number of specimens follows each species name. The scale bar represents Kimura 2-parameter (K2P) distance. The topology shown in this tree supports recognition of three species in *Mallotus*: *M. catervarius* primarily in the Pacific, and *M. villosus* and an unidentified species of *Mallotus* in the Atlantic.

eastward to the Greenland Sea, illustrates the low variation (Figure 6). Although genetic variation at both the pan-Arctic and regional scales has been found and *B. sonda* is clearly not genetically homogeneous across its range, the general structure is weak and population subdivisions, although they may exist, have not been revealed (Nelson and Bouchard, 2013). No division into subspecies or species has been proposed, and its Arctic zoogeographic pattern is clear (Figure 7).

In contrast, Pacific cod *Gadus macrocephalus* populations have been interpreted to represent two distinct species, for instance, most recently in Stroganov et al. (2011) by use of microsatellites. Microsatellites are used for population genetic analysis but are seldom used alone for species hypothesis testing. The barcode sequences from a large number of both putative species, *G. macrocephalus* and *G. ogac* (Figure 6), show little variability and support earlier studies indicating that, at most, *G. ogac* is a subspecies of *G. macrocephalus* (Carr et al., 1999; Møller et al., 2002). Thus, *G. macrocephalus* is not endemic to the Pacific but has a distribution extending from the western and eastern Pacific through the Bering, Chukchi, and Beaufort Seas across the Arctic to eastern Canada and Greenland. Differences in egg and larval pigmentation (Evseenko et al., 2006) correspond with subspecies and should not be taken to indicate distinct species. Similarly, differences in breeding tubercles on the scales are attributable to population-level differences. Most recently, a further assessment of the situation using additional morphometric, biochemical, and molecular methods (Stroganov, 2015) supports the synonymy of *G. macrocephalus* and *G. ogac*. We also note that Cohen et al. (1990) and Mecklenburg et al. (2011) did not synonymize the Atlantic cod *G. morhua* and *G. macrocephalus*, as claimed by Stroganov (2015). We were referring to *G. callarias marisalbi* Derjugin, 1920, which Cohen et al. (1990) included in the synonymy of the ogac and thereby extended its range

FIGURE 6. Neighbor-joining tree for COI sequence divergences in the six species of cods (family Gadidae) present in the Pacific Arctic region. The topology shown here supports the amphiboreal distribution of *Gadus chalcogrammus*, with identical sequences from both the Atlantic and the Pacific; the synonymy of *G. ogac* in *G. macrocephalus* and its distribution from the Pacific to the western Atlantic; and recognition of *Arctogadus glacialis* and *Boreogadus saida* as circumpolar species with low intraspecific variability. *Eleginops gracilis* is endemic to Pacific Arctic and boreal waters. For additional explanation see caption to Figure 5.

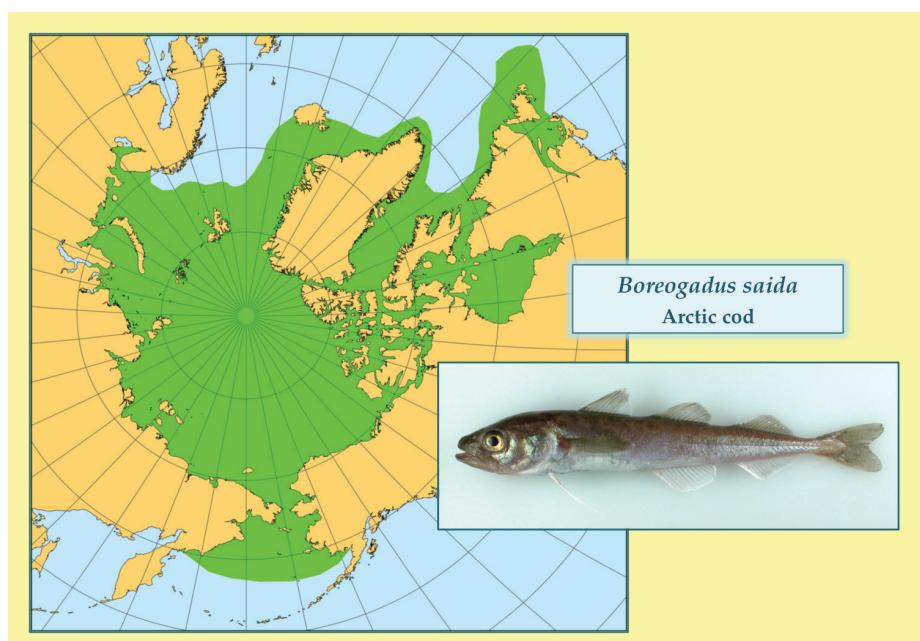
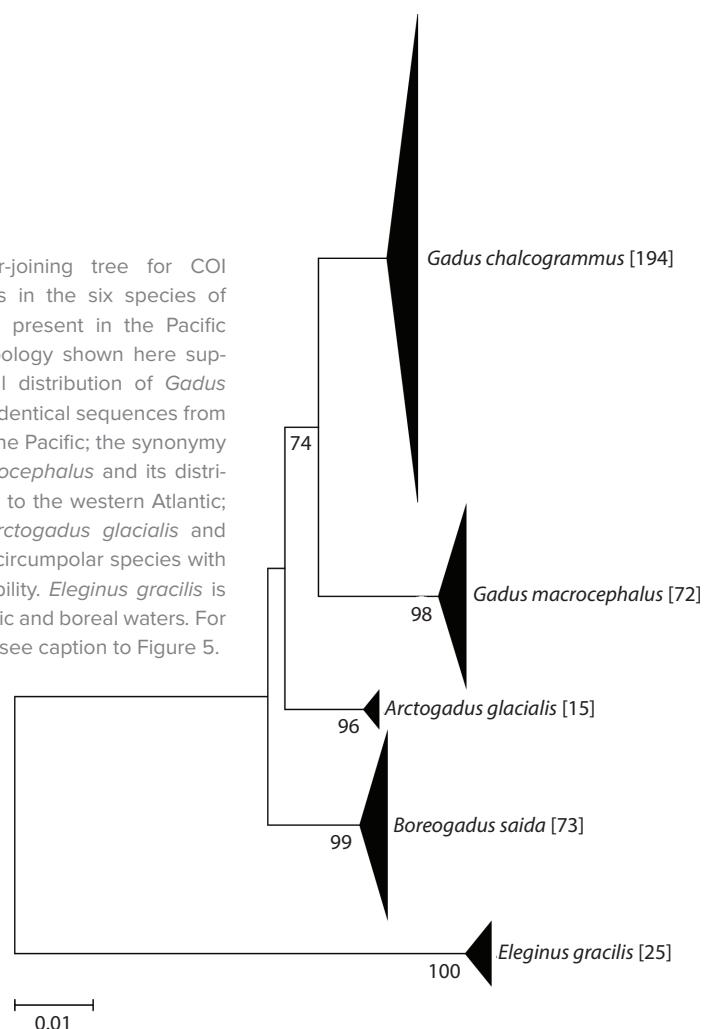


FIGURE 7. World distribution of Arctic cod *Boreogadus saida*. This cod is considered an indicator species for the Arctic region since it is abundant and rarely occurs outside the limits of the region (shown in Figure 3). In Europe, this cod is called the polar cod, and in North America is called Arctic cod. Genetically, the species is remarkably homogenous with no distinct regional subspecies or populations.

to the White Sea. In Stroganov (2015), all cods in the White Sea are grouped as “White Sea cod” without providing scientific species names. Since the

presence of ogac (*G. macrocephalus*) in the White Sea is uncertain and requires further study (it could coexist there with *G. morhua*), we give the established

range of *G. macrocephalus* to be eastward only to Greenland.

The genetics of the Atlantic population of walleye pollock *Gadus chalcogrammus*, originally described under the name *Theragra finnmarchica* by Koefoed (1956), and its synonymy with the Pacific population are well studied and established (Coulson et al., 2006; Ursvik et al., 2007; Byrkjedal et al., 2008). Although the Atlantic population may be regarded as a subspecies on the basis of geographic separation (Figure 8), there is little morphologically to distinguish it from the Pacific population. Slight differences in the number of pyloric caeca and the number of gill rakers on the first arch in Atlantic and Pacific samples have been attributed to population variation (Byrkjedal et al., 2008). Differences in body proportions recently described (Privalikhin and Norville, 2010; Zhukova and Privalikhin, 2014) are not significant at the species level but reflect dietary and environmental differences. The COI sequences (Figure 6) from the RUSALCA 2009 Chukchi slope and shelf specimens match those reported from other collections in the Pacific as well as the Atlantic Arctic (e.g., Byrkjedal et al., 2008; Mecklenburg et al., 2011, 2014). The genetic and morphological identity of the Atlantic and Pacific populations and the presence of individuals of mature size on the continental slopes in each region suggest that genetic interchange may occur along the continental slopes of Eurasia (Mecklenburg et al., 2014).

The polar cod *Arctogadus glacialis* (Figure 9) has been considered by most authors on the basis of both morphology and genetics (e.g., Jordan et al., 2003; Aschan et al., 2009; Mecklenburg et al., 2011, 2014) to be a single circumpolar species but has recently been presented from vaguely defined, nonparallel characteristics of appearance (Chernova, 2014) as representing a complex of as many as eight species. The RUSALCA 2009 specimens were identified as a different species and as many as five species of *Arctogadus* were indicated to be present nearby in the

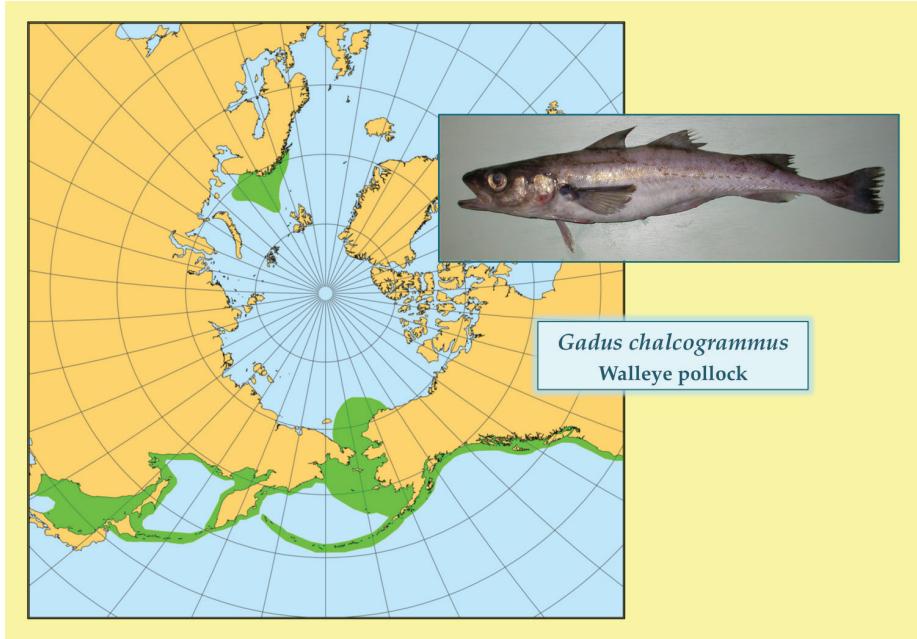


FIGURE 8. World distribution of walleye pollock, also called Alaska pollock, *Gadus chalcogrammus*. Until recently, the population in the Barents and Norwegian Seas was classified in a difference genus and species, *Theragra chalcogramma*. The wide geographic separation between the populations raises the question of how they maintain identity as one species. Discovery of mature walleye pollock on the slope of the Chukchi Sea by RUSALCA suggests they may maintain continuity by genetic interchange along the continental slopes.

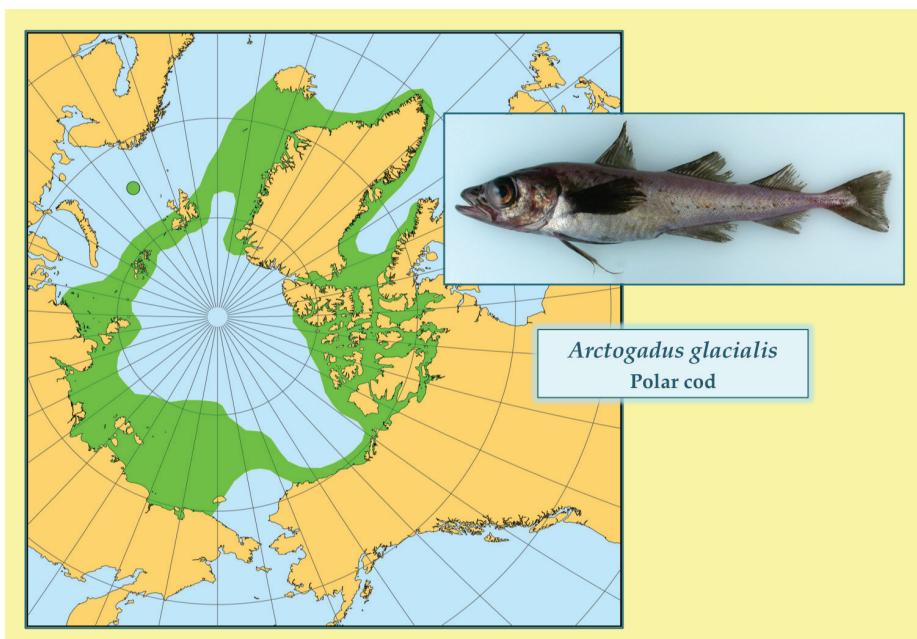


FIGURE 9. World distribution of polar cod *Arctogadus glacialis*. In Europe this cod is called the Arctic cod, and in the Pacific Arctic the polar cod. Slight morphological differences suggest to some authors that the species represents a complex of species, with as many as five present in the Pacific Arctic. DNA sequences (barcodes) support only one, circumpolar species.

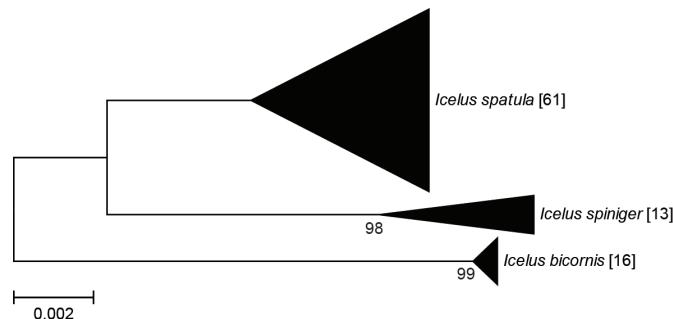
Arctic Ocean north of the Chukchi and East Siberian Seas. However, the COI sequences (Figure 6) of specimens from the Chukchi Borderland to Greenland support classification of *Arctogadus glacialis* as a single species, not a complex.

Among the sculpins, family Cottidae, the identity of two clades in *Icelus* was unresolved in the earlier review (Mecklenburg et al., 2011). The clades, labeled *Icelus* sp. and *Icelus* cf. *spiniger*, were separated by a low amount of genetic divergence (0.2%). Additional specimens from the Gulf of Alaska to the northern Chukchi Sea were recently barcoded and together with the previous material (<http://dx.doi.org/10.5883/DS-ICELUS>) were found to represent one species (Figure 10). The Gulf of Alaska and southern Bering Sea specimens are morphologically not distinguishable from *I. spiniger*, whereas those from the northern Bering Sea and Chukchi Sea are a variant with atypical scales (bearing one tall spine and several short spines) in the dorsal row. The appearance of the northern variant is close to that of *I. spatula*. They are so similar it will be difficult to distinguish them from each other without benefit of a microscope or COI sequencing. The relationship of *I. spiniger* to *I. spatula* should be reevaluated. In the most recent systematic review, several variants in *I. spatula* were described whereas *I. spiniger* was presented as without variants (Nelson, 1984). Both *I. spatula*, with sequences from the Chukchi, East Siberian, and Beaufort Seas as well as Svalbard and the Barents Sea, and *I. spiniger*, with sequences from the Gulf of Alaska to the Chukchi Sea, are shown to be highly variable in their COI sequences (0.5% and 0.4%, respectively), while the third Pacific Arctic species, *I. bicornis*, despite the presence of specimens from the Alaskan Beaufort Sea, northeast Greenland, Jan Mayen, Svalbard, and the Barents Sea, is less variable at 0.2%.

The circumpolar distribution of shorthorn sculpin *Myoxocephalus scorpius* (Figure 11) was shown to be supported by

numerous COI sequences, but sequences from the Gulf of Alaska were lacking (Mecklenburg et al., 2011). The barcode sample (<http://dx.doi.org/10.5883/DS-MYOXO>) now includes sequences from the southeastern Gulf of Alaska at Tee Harbor from specimens caught on sport fishing gear in 2012, as well as the Bering Sea to the East Siberian, Chukchi, and Beaufort Seas and eastward to Hudson Bay, southeastern Greenland, Svalbard, and the Barents Sea, as well as the Baltic Sea (Figure 12). The Tee Harbor specimens (CAS 235305) were identified

as *M. scorpius* from the presence of plate-like spiny scales with depressed centers below the first dorsal fin, postocular and occipital protuberances, warty skin on the top of the head, uppermost preopercular spine not reaching the edge of the opercle, 18 pectoral-fin rays, and large size (a ripe female was 38 cm in total length), among other characters. Gulf of Alaska specimens are the most lightly armored population of *M. scorpius*; at one time, they were believed to represent a distinct species, but they were not described as such when it was realized that they are



a variant of *M. scorpius* (Mecklenburg et al., 2002:405–406). In the Pacific Arctic, populations in the northern Bering Sea and the Chukchi Sea are most heavily armored (Figure 11). A barcoding study separate from ours found similar results (McCusker et al., 2012), with intraspecific diversity weakly expressed in clades. The most viable explanation for this distributional pattern is a retreat of populations into glacial refugia with later reentry into the Arctic due to deglaciation (Walters, 1955; Mecklenburg et al., 2011), especially since, in our large sample, infraspecific variation was low (0.3%; n = 91) and no clades corresponding to regions were revealed.

Although the taxonomic situation with *M. scorpius* has been addressed several times recently (e.g., Mecklenburg

et al., 2002, 2007, 2011), the name *M. verrucosus*, a nominal species described in the nineteenth century by Bean (1881), as *Cottus verrucosus*, from a small (88 mm total length) juvenile Bering Sea specimen without scales or other developed adult characters (USNM 27547), continues to appear in the literature. For instance, *M. verrucosus* is listed in a table and presented as a distinctly different species from *M. scorpius* in a recent phylogenetic tree (Knope, 2013). However, the author was not able to confirm the identification of the specimens (Matthew L. Knope, Stanford University, *pers. comm.*, September 15, 2014). This is perhaps not surprising, as specimens of *Microcottus sellaris*, *Megalocottus platycephalus*, *Enophrys diceraus*, and *E. lucasi* were misidentified or mixed up,

while an invalid combination, *Triglops quadricornis*, was applied to *Triglopsis* (= *Myoxocephalus*) *quadricornis*.

It is mystifying why, if a different name had to be given for the Pacific members of the species, *M. verrucosus* became the name applied by researchers in the Pacific region, based as it was on the small juvenile specimen without adult characters, when Bean (1881) in the same publication provided a good description of the adult under the name *Cottus humilis*. The 240 mm holotype (USNM 27972) has all the characteristics typical of *M. scorpius*. However, it was mistakenly placed in the synonymy of *M. jaok* in Neyelov (1979).

The frog sculpin *M. stelleri* continues to be erroneously reported from the Pacific Arctic (e.g., Johnson et al., 2012), so it is important to repeat the statement that it is not an eastern Pacific species (Mecklenburg et al., 2011). It is endemic to the northwestern Pacific. In the eastern Pacific, *M. polyacanthocephalus* and *M. scorpius* have often been mistaken for *M. stelleri*. The similarity of appearance is reflected in the close relationship of these species, especially between *M. stelleri* and *M. polyacanthocephalus* (Figure 12).

In another sculpin genus, *Triglops*, our COI sequences (Mecklenburg et al., 2011) clearly distinguished among the three Arctic species *Triglops nybelini*, *T. pingelii*, and *T. murrayi* (Figure 13), in contrast to the failure of barcoding to discriminate them in a different study (McCusker et al., 2012). Genetic distances in our expanded sample (<http://dx.doi.org/10.5883/DS-TRIGLOP>) were 3.2% between *T. nybelini* and *T. pingelii*, 2.5% between *T. nybelini* and *T. murrayi*, and 3.4% between *T. pingelii* and *T. murrayi*. The three species have historically been confused and, as suggested by the authors, misidentification is the most likely explanation for the failure of barcoding to separate them in the McCusker et al. (2012) study. Pietsch (1994) gave a detailed accounting of their rather complex taxonomic history and provided morphological characters for distinguishing among them.

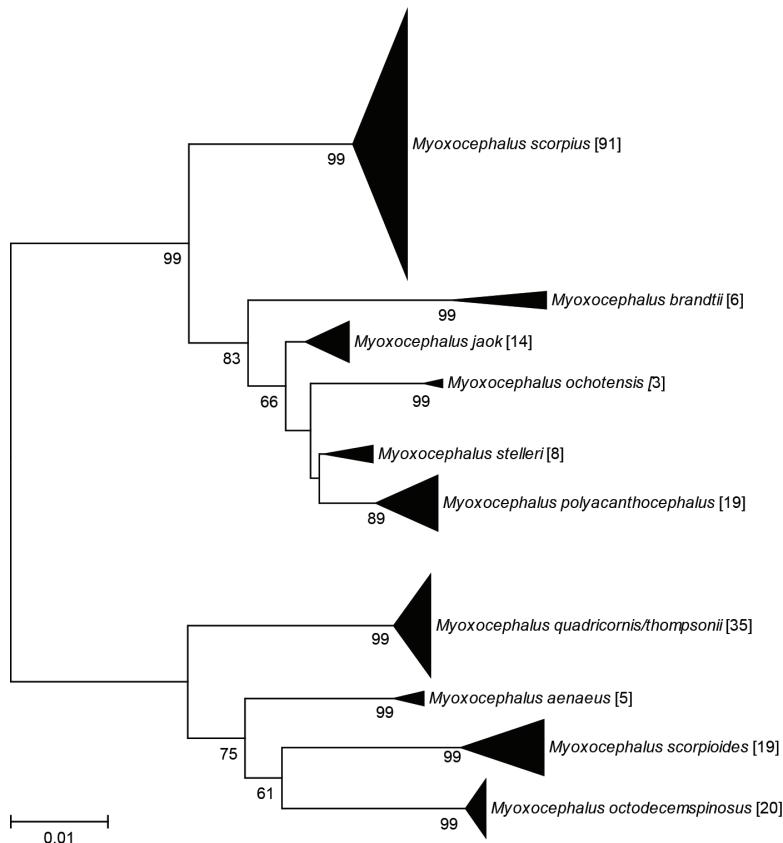


FIGURE 12. Neighbor-joining tree for COI sequence divergences in *Myoxocephalus* sculpins (family Cottidae) present in the North Pacific and North Atlantic Oceans and the Arctic region. The topology shown here supports the presence of one circumpolar species of shorthorn sculpin *M. scorpius*. Barcodes from the eastern Gulf of Alaska, the Bering, East Siberian, Chukchi, and Beaufort Seas and eastward to Hudson Bay, southeastern Greenland, Svalbard, the Barents Sea, and the Baltic Sea are included in the sample. The similarity of *M. polyacanthocephalus* and *M. stelleri* is reflected by their positions in the tree; the latter species does not occur in the eastern Pacific or Arctic but is often misidentified as *M. polyacanthocephalus* or *M. scorpius*. For additional explanation see caption to Figure 5.

The poachers, family Agonidae, present no particular problems. Most authors appear to recognize the close similarity of *Aspidophoroides monopterygius* and *A. olrikii* demonstrated by the morphology as well as the COI sequences, and include *olrikii* in *Aspidophoroides*, its originally assigned genus, rather than in the later-assigned genus *Ulcina*. Similarly, based on both morphology and the COI sequences, most authors treat *Pallasina aix* as a junior synonym of *P. barbata* (e.g., Mecklenburg et al., 2002, 2011).

Recent reviews of the lump suckers, family Cyclopteridae, pointed out several taxonomic problems (Mecklenburg et al., 2002; Mecklenburg and Sheiko, 2003). Since then, we have sequenced several specimens identified as various species (<http://dx.doi.org/10.5883/DS-EUMICRO>). The results, summarized in Figure 14, support the morphology in indicating that some species are synonyms of others, and that others have justifiably been described as distinct species. Specimens which had been identified as Atlantic spiny lumpsucker *Eumicrotremus spinosus* and submitted to the Barcode of Life for sequencing produced sequences in two distinct clades separated by a genetic distance of 0.8%. It is evident from review of the photographs submitted with some of them and a survey of the literature on cyclopterids that the two species represented are *E. spinosus* and the Newfoundland spiny lumpsucker *E. terraenovae*. The latter species has rarely been reported since it was described and named by Myers and Böhlke (1950) from a specimen taken off Newfoundland. Mecklenburg and Sheiko (2003) examined the holotype and reported other specimens from reexamination of material identified as *E. spinosus* in Garman (1892) and Goode and Bean (1896), and others not previously reported in the literature from Newfoundland and the Gulf of Maine. The 15 sequences in the *E. spinosus* clade are from southern Baffin Bay, eastern Greenland, and the northern Barents Sea, whereas the 12 in the *E. terraenovae* clade are from the southern

Gulf of St. Lawrence and offshore of Newfoundland and Nova Scotia. A recent guide to Gulf of St. Lawrence fishes (Nozères et al., 2010) uses photographs of *E. terraenovae* (with, for instance, interorbital tubercles not arranged in four regular rows) for identifying *E. spinosus* and reports *E. terraenovae* to be a rare species. The confusion is perhaps understandable. Authors have dismissed *E. terraenovae* as a valid species, going back to Lindberg and Legeza (1955) who considered it a junior synonym of *E. andriashevi*, and Leim and Scott (1966) and Scott and Scott (1988) who dismissed it as similar to *E. spinosus*. Ueno (1970) considered *E. terraenovae* a potentially valid species and Mecklenburg et al. (2002) gave characters for *E. spinosus* that clearly distinguish it from *E. terraenovae* as well as its close relatives in the Pacific Arctic.

In the western Atlantic, *E. spinosus* and *E. terraenovae* appear to be sympatric (author Mecklenburg's unpublished data).

Pimpled lump sucker *Eumicrotremus andriashevi*, originally described by Perminov (1936) as a "forma" of Pacific spiny lumpsucker *E. orbis* and subsequently treated as a subspecies, is separated from *E. orbis* by a distance of 2.9%. The former is distributed northward into the Chukchi Sea, whereas *E. orbis* is distributed south of Bering Strait. Sequences for papillose lump sucker *E. barbatus* from the Aleutian Islands unexpectedly fell within the *E. orbis* clade (Figure 14), and it is evident that the relationship between these two forms needs to be reevaluated. Sexual dimorphism, ecophenotypic, or other variation could be involved. For instance, from analyses including both morphological and

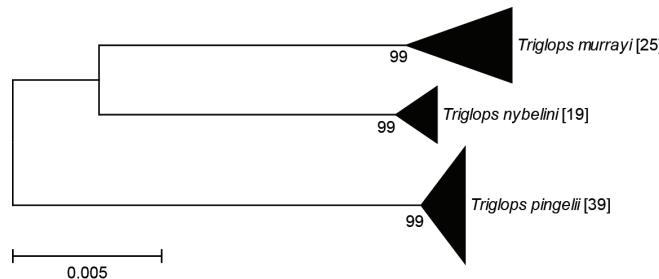


FIGURE 13. Neighbor-joining tree for COI sequence divergences in *Triglops* sculpins (family Cottidae) present in the Arctic region. The topology shown here supports the separation of the three species, whereas historically, from the morphology, and in a different barcode study, taxonomists have had difficulty discriminating between them. For additional explanation see caption to Figure 5.

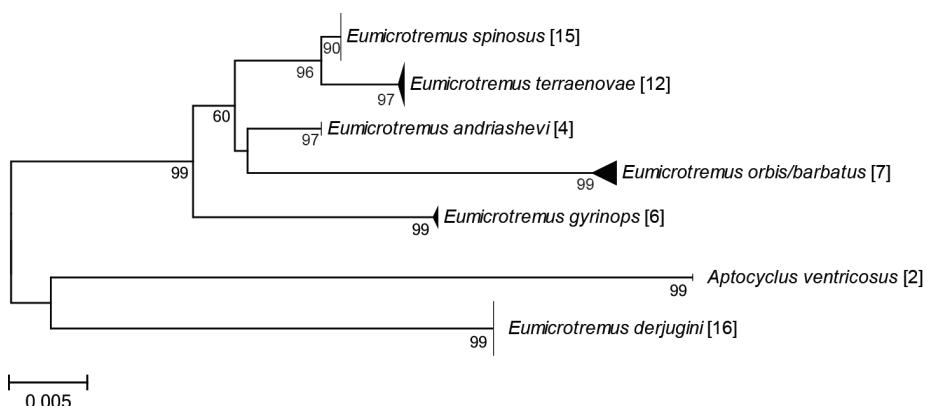


FIGURE 14. Neighbor-joining tree for COI sequence divergences in lump suckers (family Cyclopteridae). The topology shown here supports separation of Atlantic spiny lumpsucker *Eumicrotremus spinosus* from the commonly misidentified Newfoundland lump sucker *E. terraenovae*; the separation of pimpled lump sucker *E. andriashevi*, once considered to be a subspecies of Pacific spiny lumpsucker *E. orbis*; and some implications for the taxonomy of other species discussed in the text. For additional explanation see caption to Figure 5.

molecular genetic characteristics, it was demonstrated that, for some populations at least, the Atlantic Arctic nominal species *E. eggvinii* is the female of *E. spinosus* (Byrkjedal et al., 2007).

The Alaskan lump sucker *E. gyryinops* clade (Figure 14) includes sequences from specimens identified when submitted for sequencing as *E. phrynooides*, *E. birulai* (= *E. asperrimus*), and *Lethotremus muticus*. Mecklenburg and Sheiko (2003) examined the types and suggested *E. gyryinops* as the senior synonym of *E. phrynooides*. The COI sequences, as well as closely similar morphology (e.g., Mecklenburg et al., 2002), indicate that *E. asperrimus* and *L. muticus* might also belong in the synonymy. *Eumicrotremus phrynooides* is not found in the Arctic region, but it is an interesting example of the value of DNA sequencing in identifying potential synonymies.

The 16 sequences from leatherfin lump sucker *E. derjugini* form a remarkably invariable clade (Figure 14), despite the wide geographic coverage represented, from the Beaufort Sea to Baffin Bay and the Arctic Ocean and Barents

Sea off Svalbard. The smooth lump sucker *Aptocyclus ventricosus*, rarely found in the northern Bering Sea and not known north of the Gulf of Anadyr, appears most closely related to *E. derjugini*, although its morphology and pelagic way of life are markedly different from all other lump-suckers in the region.

Table 1 lists 11 snailfish (Liparidae) species in the Pacific Arctic, with six species in *Liparis*, three in *Careproctus*, and one each in *Paraliparis* and *Rhodichthys*. All six *Liparis* species (<http://dx.doi.org/10.5883/DS-LIPARIS>) have been sequenced (Figure 15). The recent elevation of the nebulosus snailfish *Liparis bathyartcticus* from its status as a subspecies of the variegated snailfish *L. gibbus* (Chernova, 2008) is amply supported by DNA evidence (Mecklenburg et al., 2011; McCusker et al., 2012; this study) as well as morphology. However, the data also confirm that both species are common in the Chukchi Sea, not just *L. bathyartcticus* as indicated in Chernova (2009a,b). The relative size of the anterior and posterior nostrils was given to be a distinguishing character (Chernova,

2008), but we found the species to be more consistently identifiable by the length of the gill openings and body coloration.

Specimens of *Liparis* identified by coworkers as *L. herschelius* and *L. marmoratus* from coloration, proportions, and relative amounts of gelatinous tissue all had COI sequences identical to the kelp snailfish *L. tunicatus*. From those observations and examination of specimens in the historical collections, we follow Able and McAllister (1980), Able (1990), Mecklenburg et al. (2002, 2011), and Parin et al. (2014) in retaining *L. herschelius* in the synonymy of *L. tunicatus*, and Chernova (2008) and Parin et al. (2014) in considering that *L. marmoratus*, if it is a valid species, is restricted to the Sea of Okhotsk. Specimens identified as *L. bristolensis* from the Chukchi Sea were determined by Able and McAllister (1980) to be *L. tunicatus*, and there was no indication in the RUSALCA or other recent investigations of its presence. If *L. bristolensis* is a valid species, its distribution is from Bristol Bay southward. The amount of intraspecific variation among the 48 COI sequences for *L. tunicatus* from the Bering Sea to the East Siberian, Chukchi, and Beaufort Seas is remarkably low (0.1%).

Gelatinous seasnail *Liparis fabricii* may be a species complex (Chernova, 2008, 2009b), but only one species is represented in our trawl collections from the East Siberian Sea eastward to the Arctic Ocean off Svalbard (Mecklenburg et al., 2014). Variability within our large barcode sample of 41 was low (0.2%) (Figure 15). Following Able and McAllister (1980), Able (1990), Mecklenburg et al. (2002, 2014), and Parin et al. (2014), we include *L. koefoedi* as a synonym of *L. fabricii*.

The fifth *Liparis* species in the Pacific Arctic is the Okhotsk snailfish *L. ochotensis*, primarily a western Pacific species with some presence in the eastern Bering Sea (Mecklenburg et al., 2002). Five small specimens (45–46 mm, UAM 4768) were taken in Norton Sound by a NOAA survey in 2011. They are uniformly brownish with black dorsal and

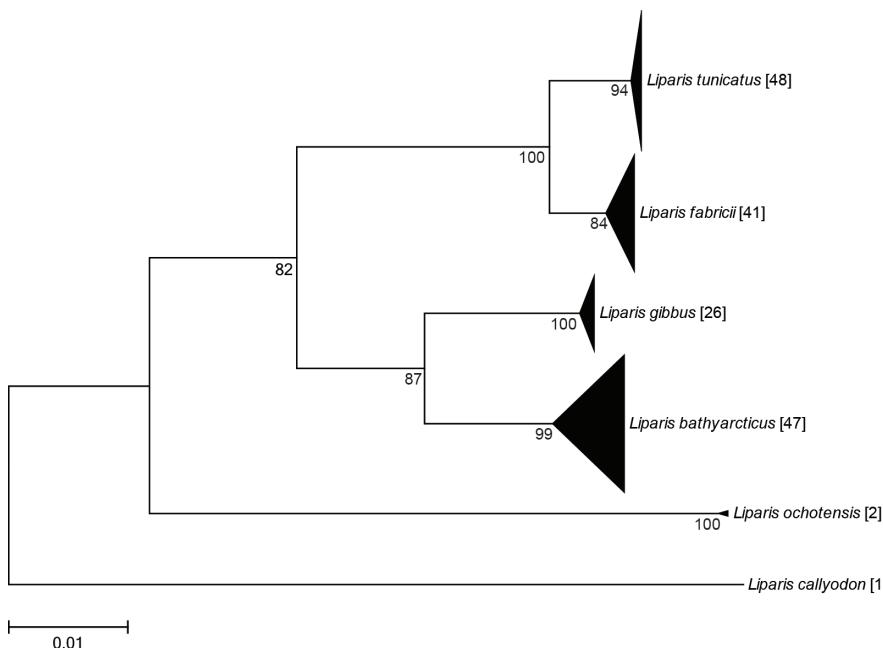


FIGURE 15. Neighbor-joining tree for COI sequence divergences in *Liparis* snailfishes (family Liparidae) present in the Pacific Arctic region. The topology shown here supports the separation of variegated snailfish *L. gibbus* and nebulosus snailfish *L. bathyartcticus* as distinct species, and does not support the presence of more than one species in kelp snailfish *L. tunicatus* and in gelatinous seasnail *L. fabricii*. Taxonomists have proposed that the latter two species are complexes containing several species each. For additional explanation see caption to Figure 5.

anal fins and a pale peritoneum, the dorsal fin extending onto the caudal fin for about one-third of its length, and the anal fin onto the caudal for about two-thirds of its length. Their unique COI sequence combined with the morphological appearance prevents confusion with any other species in the region. Datsky (2015) listed *L. ochotensis* from the Chukchi Sea but not *L. gibbus*, which is very similar in appearance, and presence of *L. ochotensis* in the Chukchi Sea is unconfirmed. Lin et al. (2012, 2014) listed both species from the Bering Sea and noted that their *L. ochotensis* specimen, taken southeast of St. Lawrence Island, extended its known distribution northward. Specimens identified by Mamoru Yabe (HUMZ, Hokkaido, Japan) and Morgan S. Busby (NOAA AFSC, Seattle, Washington) and reported in Mecklenburg et al. (2002) were caught farther north in the Bering Sea, to 63°20'N, 173°20'W, northwest of St. Lawrence Island (HUMZ 85934).

The sixth *Liparis* species present in the Pacific Arctic region is the spotted snailfish *L. callyodon*, an intertidal species not known north of the Gulf of Anadyr, St. Lawrence Island, and Norton Sound, and represented by one sequence from the Gulf of Alaska in our barcode sample (Figure 15).

Three *Careproctus* species are listed in Table 1, but the identity of all specimens of *Careproctus* represented in recent collections in the Pacific Arctic has not been resolved (<http://dx.doi.org/10.5883/DS-CAREPRO>). Specimens collected by RUSALCA from the Chukchi Borderland and by other programs from the Beaufort Sea, Baffin Bay, the Atlantic off Nova Scotia, and the fjords of northeast Greenland, all with identical COI sequences, were reported under the name *C. reinhardtii* (Mecklenburg et al., 2011, 2014). Since then, the barcoded specimens from the Beaufort Sea have been included in material used to describe a new species (Orr et al., in press). With the COI sequences identical in so many specimens from around the Arctic and morphological appearances being very

similar, it is possible that Orr et al.'s new species is the same as specimens already named and described and should bear another name. The material used to describe the new species was not compared to any of the barcoded material available from other studies and identified as other *Careproctus* species, and barcoding was not part of the methodology. We prefer to leave this as an unresolved question requiring further study. The two other *Careproctus* species listed for the Pacific Arctic (Table 1) are *C. spectrum* and *C. phasma*, which are present in the fringes of the Arctic region in the Bering Sea (Mecklenburg et al., 2002; Orr et al., in press). The relationship of these species to the others also should be reevaluated and COI sequencing should be part of the analysis.

Reevaluation needs to consider the possibility that *Careproctus* is a case where COI sequencing cannot discriminate among species. Cases where different but sympatrically occurring species share closely similar or identical barcodes have been reported in prior studies (e.g., Knebelsberger et al., 2014; Steinke et al., 2009a,b). Three processes may account for these findings. First, some may be recently diverged sister taxa where COI has not yet accumulated any

sequence differences (incomplete lineage sorting). In such cases, more extensive sequence information might allow resolution. Second, these taxa may share mtDNA because of hybridization. They may be in the indeterminate zone between differentiated populations and distinct species (de Queiroz, 2005), or well-formed species that are losing genetic identity due to secondary contact and introgression. Third, however, some of the pairs with overlapping barcodes may in fact be a single species.

Table 1 lists 20 eelpout species, family Zoarcidae, for the Pacific Arctic, with two *Gymnelus*, one *Lycenchelys*, and 17 *Lycodes*. For the entire Arctic, our data (<http://dx.doi.org/10.5883/DS-GYMNE>) support the presence of five species of *Gymnelus* (Figure 16). The two inhabiting Pacific Arctic waters are the half-barred pout *G. hemifasciatus* and the fish doctor *G. viridis*. Both are highly variable in appearance and have high genetic variability. *Gymnelus hemifasciatus*, for instance, has two sexually dimorphic variants with different coloration (Figure 17). DNA barcoding and morphological analysis (Mecklenburg and Anderson, 2015) confirmed that there are only those two species in the RUSALCA study area compared with six that were described and

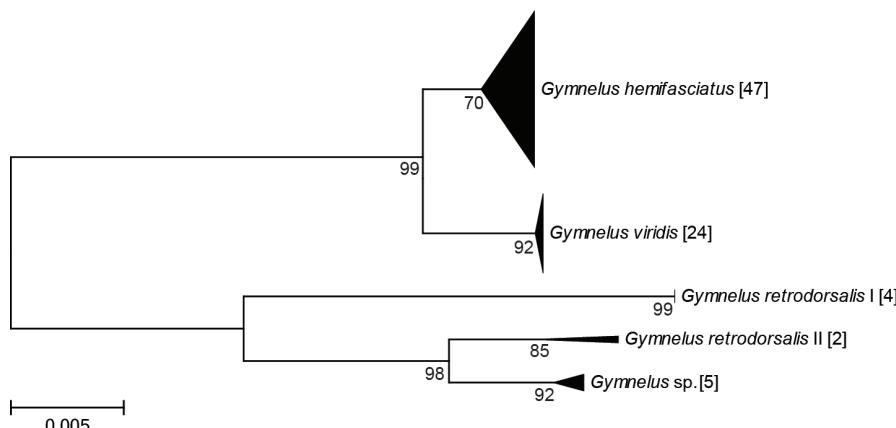


FIGURE 16. Neighbor-joining tree for COI sequence divergences in *Gymnelus* eelpouts (family Zoarcidae) present in the Arctic. Recent publications have named new species and resurrected older names that would at least double the number of species indicated to be present by our studies. In an analysis using morphological and molecular evidence, Mecklenburg and Anderson (2015) show that three of the described species are synonymous with fish doctor *G. viridis* and two are the same as halfbarred pout *G. hemifasciatus*. For instance, despite the presence of specimens identified by others as three different species, the topology shown here reveals little variability in the *G. viridis* clade. For additional explanation see caption to Figure 5.

given different names previously. The effect is that *G. bilabrus*, *G. barsukovi*, *G. knipowitschi*, and *G. platycephalus*, recently redescribed or named in Chernova (1998a, 1999a,b), are not included in the inventory of Pacific Arctic marine fishes (Table 1). Mecklenburg and Anderson (2015) suggest that the two main phenotypes of *G. hemifasciatus* are maintained by exploiting different habitats and are an example of mosaic sympatry (Mallet, 2008) with, in the same region, one form preferring a mostly muddy substrate and the other preferring rougher substrate with a high proportion of gravel. The other three *Gymnelus* clades (Figure 16) are from Atlantic Arctic material and have not been identified with certainty. We have not seen the specimens ourselves, and photographs are available for only a few. The two clades labeled *G. retrodorsalis* I (from Canada off Baffin Island, Arctic Ocean north of Spitsbergen, and Barents Sea) and *G. retrodorsalis* II (eastern Greenland), with specimens having markedly retrograde positions of the dorsal fin, could be *G. andersoni*, described by Chernova (1998b), and the well-established species *G. retrodorsalis*,

described by Le Danois (1913). The *Gymnelus* sp. clade (from southwest Greenland), with specimens having the dorsal fin closer to the pectoral fin, is some other species, perhaps *G. esipovi* or *G. taeniatus*, both described by Chernova (1999b), or an undescribed species.

The 17 species of *Lycodes* in the Pacific Arctic are all valid species except perhaps for the threespot eelpout *L. rossi*, which might be the same as the Arctic eelpout *L. reticulatus* (e.g., Mecklenburg et al., 2011:128). Both species have broad distributions in the Arctic. Results from morphological observations and DNA barcoding (<http://dx.doi.org/10.5883/DS-LYCODES>) are confusing, with sequences of specimens from the Beaufort Sea identified as *L. rossi* always falling into the *L. reticulatus* clade. Earlier, small genetic differences between the two forms were found in specimens from Svalbard and Baffin Bay (Møller and Gravlund, 2003). The reticulated (*L. reticulatus*) and unreticulated (*L. rossi*) forms could represent species in a complex of cryptic species, or they could represent phenotypes of one species. Pending resolution, both *L. reticulatus*

and *L. rossi* are listed in Table 1.

Although the barcoding study by McCusker et al. (2012) failed to discriminate among *L. reticulatus*, the longear eelpout *L. seminudus*, and the polar eelpout *L. polaris*, in our study they were separated by considerable genetic distances (1.8–3.2%). Variation in the appearance of each of those species is great enough that they are frequently misidentified. Misidentification was suggested as the most likely explanation for the failure to discriminate among them in the McCusker et al. (2012) analysis.

For sand lances, family Ammodytidae, the earlier sample of COI sequences (Mecklenburg et al., 2011) indicated that the Pacific sand lance *Ammodytes hexapterus* actually comprised two species. We suggested that the second species, from the Gulf of Alaska, was most likely *A. personatus*, which was described from specimens collected at Cape Flattery, Washington State (Girard, 1856), but has generally been regarded as endemic to the western Pacific (despite its eastern Pacific type locality). This meant that the southern limit of *A. hexapterus* was uncertain and the



FIGURE 17. From their various color patterns, these halfbarred pouts *Gymnelus hemifasciatus* may look like different species, but other morphological features together with their DNA sequences show that they are the same species. Ecological differences may help maintain the different phenotypes, with the form on the left preferring a mostly muddy substrate and the one on the right preferring rougher substrate with a high proportion of gravel (Mecklenburg and Anderson, 2015).

distribution of *A. personatus* needed reevaluation. The *A. hexapterus* clade also included specimens from Hudson Bay, which confirmed the range of *A. hexapterus* eastward across the Arctic. Most recently, Orr et al. (2015) included the Hudson Bay and other barcodes along with additional new data in a systematic review of *Ammodytes* and gave a distribution for *A. hexapterus* in the eastern Pacific southward to the southern Bering Sea and confirmed the identification of the Gulf of Alaska population as *A. personatus*. Both species co-occur in the southeastern Bering Sea, where barcoding should prove a useful tool for distinguishing between them. Mecklenburg et al. (2011) reported genetic distances of 3.6–4.1% between *A. hexapterus* and *A. personatus*. Orr et al. (2015), with a larger sample, found a minimum genetic distance of 2.7% (15 of 560 base pairs).

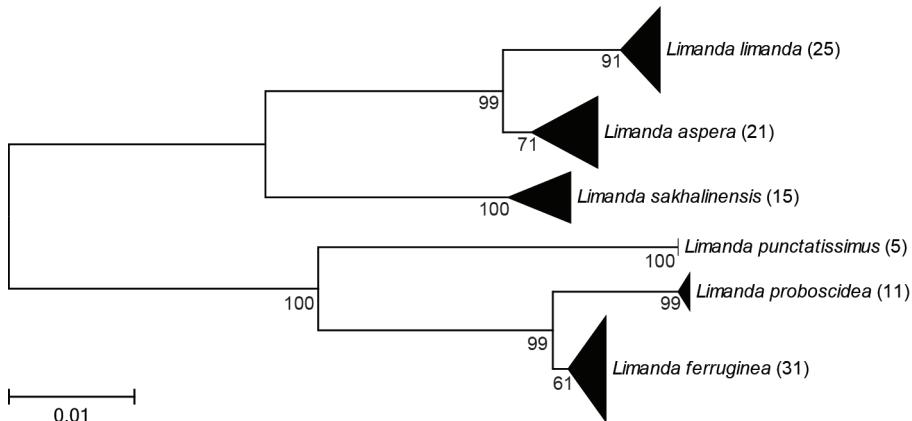
The classification of the righteye flounders, family Pleuronectidae, has been scrutinized and changes have been proposed in recent years by various authors (e.g., Sakamoto, 1984; Lindberg and Fedorov, 1993; Cooper and Chapleau, 1998; Orr and Matarese, 2000; Evseenko, 2004; Kartavtsev et al., 2007). Three of the changes involve Pacific Arctic flounders. The first involves names of species in *Limanda* (Figure 18). North American ichthyologists have typically classified longhead dab in *Limanda proboscidea* (e.g., Cooper and Chapleau, 1998; Mecklenburg et al., 2002, 2013; Nelson, 2006; Page et al., 2013), but DNA barcoding supports an alternative view (<http://dx.doi.org/10.5883/DS-LIMANDA>), which is to resurrect Gill's (1861) genus *Myzopsetta* for this and two Atlantic species currently classified in *Limanda*. Andriashov (1954) and Lindberg and Fedorov (1993) distinguished two species groups in the genus *Limanda* on the basis of six external and osteological characters, and Andriashov (1954) treated them as subgenera: *Limanda*, with *L. limanda*, *L. aspera*, and *L. sakhalinensis*, and subgenus *Myzopsetta*, with *L. ferruginea*,

L. punctatissima, and *L. proboscidea*. In a checklist of Kamchatka fishes, Sheiko and Fedorov (2000) treated the subgenus *Myzopsetta* as a full genus. DNA barcodes in a smaller sample than ours from four of the *Limanda* species also fell into two major clades (McCusker et al., 2012). A thorough revision of the genus *Limanda* sensu lato should be undertaken. While the barcode methodology focuses on identifying species, not higher taxa, it is clear from the separation of the two groups by DNA sequences, along with the morphological differences, that there is merit in restoring the genus *Myzopsetta*.

The second change for flounders of the Pacific Arctic is the genus name for the Arctic flounder. North American authors have treated it in *Pleuronectes* (e.g., Cooper and Chapleau, 1998; Mecklenburg et al., 2002, 2013; Nelson, 2006; Page et al., 2013). Following Russian authors including, recently, Evseenko (2004) and Parin et al. (2014), and the recent phylogenetic analysis based on morphology of 15 species in *Liopsetta*, *Pleuronectes*, and *Pseudopleuronectes* (Voronina and Chanet, 2014), the name is *Liopsetta glacialis*.

The third change is a proposal by Kartavtsev et al. (2007) on the basis of a cytochrome *b* analysis of western Pacific material to place the Bering flounder *Hippoglossoides robustus* in the synonymy

of the flathead sole *H. elassodon*. The proposal is not entirely new. Fadeev (1978) and other authors writing earlier considered *H. robustus* to be a subspecies, *H. elassodon robustus*. In our barcode collection, we have noticed that every time a tissue sample is submitted under the name *H. elassodon*, it falls within the clade we identify as *H. robustus*. Adding sequences from GenBank produces the same results; tissues identified with either species fall within the same clade. Larvae from the Gulf of Alaska and the Bering Sea, which coworkers identified as *H. elassodon* and *H. robustus*, respectively, are identical in appearance (personal observations of author Mecklenburg), and there is little to distinguish between adults of the two nominal species (e.g., Wilimovsky et al., 1967; Mecklenburg et al., 2002). The North Pacific Fishery Management Council manages them together as a “unit stock” (e.g., Stockhausen et al., 2008). Our inclination is to treat them as one species. The name *H. elassodon* Jordan and Gilbert, 1880, has priority and would be the name applied, but we await further confirmation from studies of eastern Pacific material. (The statement in Parin et al. [2014] that differences between the two putative species are “confirmed by molecular genetic data” is due to a misinterpretation of correspondence from author Mecklenburg.)



RANGE EXTENSIONS

What is a range extension? An obvious meaning is that a species has extended its distribution beyond some previously known limit. Alternatively, a range extension can mean that new knowledge has revealed an incomplete previous understanding of a species' distribution. To know if the presence of a species at some locality represents a range extension, the baseline distribution of the species must be well documented. Determining baseline patterns for marine species in Arctic waters is important for assessing effects of climate change, including true range extensions such as northward shifts in the latitudinal range of boreal species, which have been observed in recent years (e.g., Mueter and Litzow, 2008; Fossheim et al., 2015), or increased interchanges of species between the North Pacific and North Atlantic, which have been proposed as likely potential effects (Wisz et al., 2015). Although one focus of RUSALCA has been to establish a time series for the Chukchi Sea, it has not been possible to correlate species occurrences with environmental changes. This is because of the previous lack of focus on assessing what species were present in the region prior to RUSALCA, as well as the inconsistency of the localities sampled each year due to constraints of time and weather. Unfortunately, and especially for the Pacific Arctic, much of our understanding of species presence is based on opportunistic sampling and study of historical collections with no coherent time series, compounded by different concepts of species and nomenclatural preferences among taxonomists obscuring geographic distributions. Although authors often report greater numbers of species in recent compilations, compared with early assessments, as evidence of range extensions enabled by climate change (e.g., Datsky, 2015), for most species in the Pacific Arctic, it is not possible to determine whether observed differences are due to the fact of accumulated knowledge through increased sampling or to true effects of climate change.

With the baselines established through the RUSALCA program, we can begin to answer such questions.

In an earlier review of distributions based on historical museum records, recent ichthyological sampling including the RUSALCA investigations, and taxonomic assessments aided by DNA barcoding (Mecklenburg et al., 2011) we found that for 24 continental shelf species the zoogeographic patterns assigned by authors understated presence in the Arctic region. Conversely, evidence was found to be lacking to confirm presence of several species that were reported to be present in the region. In 2009 the RUSALCA venture into the Chukchi Borderland, where bottom trawling from a ship had not previously been accomplished, yielded first or rare records from the continental slope of six species (Mecklenburg et al., 2014). The following discussion highlights and presents new information on some of the more interesting cases involving reputed and possibly true range extensions.

Numerous elasmobranchs are present in the Atlantic Arctic, yet few inhabit the Pacific Arctic (Lynghammar et al., 2013). Only one, the Arctic skate *Amblyraja hyperborea*, inhabits the Arctic Ocean, while four are endemic to the Pacific (Table 1). A single specimen of salmon shark *Lamna ditropis* was taken at Bering Strait in 2007 (Mecklenburg et al., 2011), but no catches near or north of the strait have been reported since then. The only record of spotted spiny dogfish *Squalus suckleyi* in Arctic waters is old (Mecklenburg et al., 2002, 2011), and there are also no new reports of it in Arctic waters. The other two Pacific species have recently been found farther north than previously reported: Pacific sleeper shark *Somniosus pacificus* and Alaska skate *Bathyraja parmifera*. In October 2014, a female *S. pacificus* (UAM 8611) was taken by a seal hunter in the southeastern Chukchi Sea northeast of Shishmaref in a lagoon ($66^{\circ}20'N$, $165^{\circ}47'W$), and photographs of *S. pacificus* were taken on the Russian side of the southern Chukchi

Sea in the same year (Gay Sheffield, University of Alaska, Nome, Alaska, *pers. comm.*, October 20, 2014). Previously, only a few dead specimens had been found in the Chukchi Sea and northern Bering Sea (Mecklenburg et al., 2011).

Until recently, *Bathyraja parmifera* (Figure 19) had only been caught live as far north as Norton Sound, which is south of Bering Strait. There were one or two beachcast specimens that could have washed northward into the Chukchi Sea from fisheries bycatch discarded in the Bering Sea, including one found on the beach near the village of Kivalina in August 2010. The only record of live *B. parmifera* in the northern area of the Bering Sea was from Norton Sound, and that was back in 1875 (Turner, 1886). In 2010, *Bathyraja parmifera* was taken live at several stations in the northern Bering Sea, where it had not been known to occur in recent history (Mecklenburg et al., 2011). In 2012, a live adult *B. parmifera* was taken by bottom trawl in the southeastern Chukchi Sea (James W. Orr, NOAA AFSC, *pers. comm.* with photograph, May 10, 2013), and is the only live adult reported from the Chukchi Sea.

Such cases could represent expansion of populations northward or occasional feeding forays. The Chukchi Sea is much shallower than the normal bathymetric range exploited by either *S. pacificus* or *B. parmifera* for reproduction, but both are known to feed in shallow waters, population numbers of skates have been increasing (Hoff, 2006), and distribution centers of skates have been expanding northward in the eastern Bering Sea (Mueter and Litzow, 2008).

It is difficult to assess how discovery of egg cases of *B. parmifera* in the Arctic should be interpreted with respect to movement of populations into the Arctic. An egg case of *B. parmifera* was collected in 2012 in the Chukchi Sea east of Wrangel Island, Russia (James W. Orr, NOAA AFSC, *pers. comm.*, May 10, 2013), and a University of Alaska Fairbanks program found an egg case, which we barcoded, on the Beaufort slope in 2012 (UAM 4769),

at practically the same location as *Amblyraja hyperborea* adults. Both were old egg cases, indicated by wear and lack of the fresh covering, and egg cases can drift. However, the only known spawning and nursery area for *B. parmifera* is in the southern Bering Sea on the outer shelf at the edge of the Aleutian Basin (Hoff, 2008), and it is hard to see how the egg cases could have drifted so far northward, across the broad Chukchi shelf and onto the slope. Although egg cases of *B. parmifera* have been reported from the high Arctic north of the Chukchi Sea (Lin et al., 2012, 2014), from photographs provided to us they were determined to belong to *A. hyperborea*. Nevertheless, some overlap of the species along the Chukchi and Beaufort Sea slopes may be indicated and it should not be assumed that all observations or specimens of skates from the Chukchi and Beaufort slope are *A. hyperborea*.

Recent discoveries of *A. hyperborea* confirm the circumpolar distribution of this skate (Mecklenburg et al., 2002, 2011) and show it to be common in the Pacific Arctic (Figure 20). Earlier reports mention adult skates and egg cases of *A. hyperborea* taken eastward in the Canadian Beaufort, but no voucher specimens were saved (Stewart et al., 1993) and the identification cannot be verified. A juvenile specimen identified as *B. parmifera* from the Beaufort Sea was determined to be *A. hyperborea* (Mecklenburg et al., 2011). Several large juveniles and adults were taken in bottom trawls in the Chukchi Borderland in 2010 (Lin et al., 2012, 2014) and on the slope of the Alaskan Beaufort Sea in 2012–2014 (e.g., CAS 236458, UAM 3684–3687). Beaufort Sea and Greenland Sea specimens yielded identical COI sequences.

The dramatic retreat of the Arctic sea ice in September 2009 allowed the RUSALCA expedition to reach north of the US 200-mile limit to the continental slope in the Chukchi Borderland, where three tows of the otter trawl provided first and rare records for the Pacific Arctic of several fish species. This was a clear

demonstration of the value of fishing in previously undersampled regions. Fishing in the region had been accomplished only rarely, from drifting American and Soviet ice stations in 1959–60 and 1978–79, and never by trawling from a

ship. Among the RUSALCA catch were the first record for the Pacific Arctic of Adolf's eelpout *Lycodes adolfi*, the second record of Atlantic hookear sculpin *Artediellus atlanticus*, and rare records of sea tadpole *Careproctus reinhardti*, polar

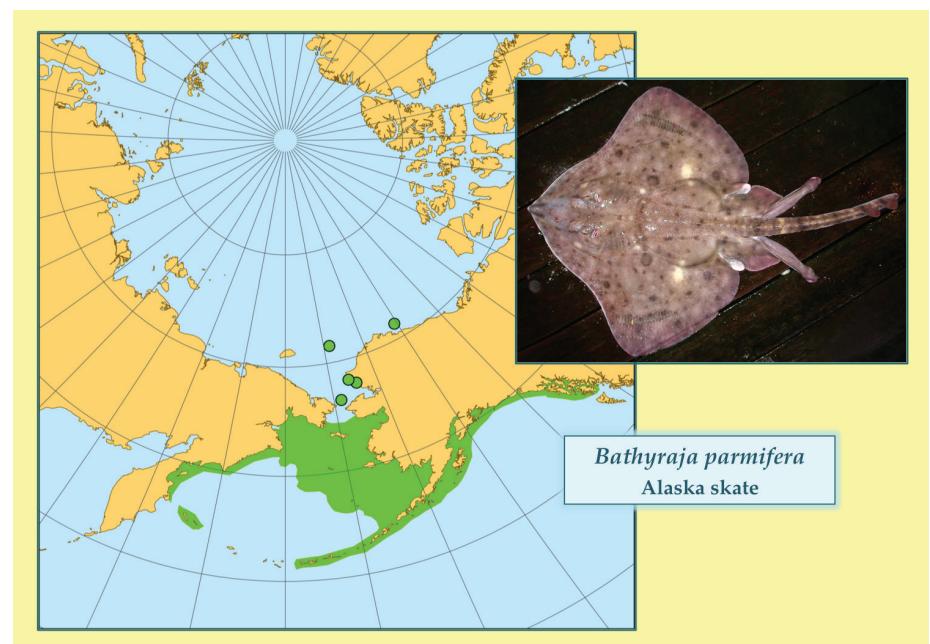


FIGURE 19. The Alaska skate *Bathyraja parmifera* might be an example of a species that has extended its range northward in recent years and entered the Chukchi Sea. One live specimen was taken in the southern Chukchi Sea in 2012, but other records from the Chukchi have been of old egg cases and beachcast carcasses that could have drifted northward from the Bering Sea.

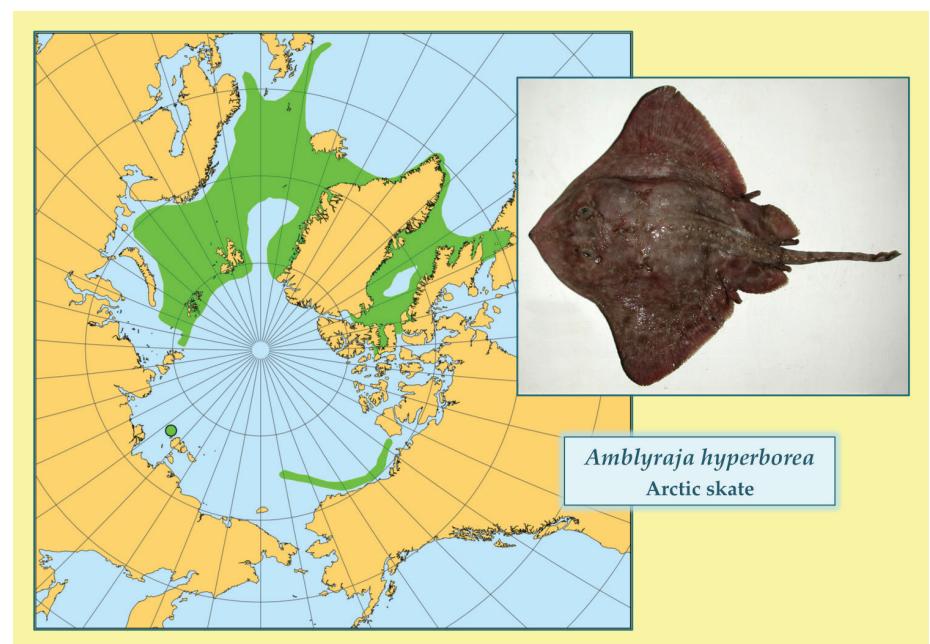


FIGURE 20. The Arctic skate *Amblyraja hyperborea* was not found on the slopes of the Chukchi and Beaufort Seas off Alaska until recently. Catches in 2010–2012 indicate it is common on Pacific Arctic slopes. Historical records from the literature and in museum collections and recent catches elsewhere in the Arctic, as well as the COI sequences, make it clear that *A. hyperborea* is circumpolar.

sculpin *Cottunculus microps*, bigeye sculpin *Triglops nybelini*, and longear eelpout *Lycodes seminudus*. One of the most interesting results was that all of the 12 species caught also occur in the Atlantic Arctic (Mecklenburg et al., 2014). The identities of fishes collected more recently in nearby deep waters of the Chukchi and Beaufort Seas indicate that some of the species that, in 2009, were first or rare records for the region are actually relatively common in the Pacific Arctic. For all of them, the DNA sequences from the Pacific Arctic match those of specimens from the Atlantic Arctic. Three of the Chukchi Borderland species are highlighted below.

The seven specimens of *Artediellus atlanticus* taken by RUSALCA in 2009 were believed to compose the first record of this species in the region (Mecklenburg et al., 2014). However, shortly before that, in a Russian publication, Neyelov (2008) reported a specimen from the slope off the western Chukchi Sea that previously had been misidentified as *A. scaber*. That made the RUSALCA catch the second record of *A. atlanticus* from the region.

In 2010, CHINARE (Lin et al. 2012, 2014) collected 11 specimens at one station on the Chukchi slope. This species still has not been recorded from the adjacent Beaufort Sea despite recent sampling (Figure 21), but it is likely to be found there as sampling continues.

The one specimen of *Cottunculus microps* taken by the RUSALCA otter trawl in 2009 was the only record from the Chukchi Sea slope (Mecklenburg et al., 2014). The only other confirmed record from the Pacific Arctic comprised a few specimens collected in 1972 from the slope of the Beaufort Sea and published under a different name, *C. sadko* (Nelson, 1982). A recent morphological and molecular analysis of Atlantic Arctic material shows *C. microps* and *C. sadko* to be the same species (Byrkjedal et al., 2014). In 2010, CHINARE (Lin et al. 2012, 2014) collected 11 specimens from the Chukchi slope. Two other Pacific Arctic records were unconfirmed as far as the species identification, but photographs and available data indicate they too are *C. microps*; one in the Canadian high Arctic archipelago from 1975 (CMNFI

1975-0010.1), and one photographed on the Northwind Ridge northeast of the Chukchi Borderland in 2002 (Stein et al., 2005). In 2013 and 2014, several *C. microps* were taken on the Beaufort Sea slope (e.g., CAS 238091–238093). From the accumulated Pacific Arctic records and the remainder of the species' distribution, it is clear that *C. microps* has a circumpolar distribution on the continental slopes and is common in the Pacific Arctic (Figure 22).

Lycodes adolfi taken by RUSALCA in 2009 in the Chukchi Borderland are the first recorded from the Pacific Arctic (Mecklenburg et al., 2011, 2014). The species is relatively new to science (Nielsen and Fosså, 1993), and additional discoveries have been especially important for determining its distribution. It has only been caught on the continental slopes, not in shallower water (Figure 23). The RUSALCA discovery, and catches on the Chukchi slope in 2010 (Lin et al., 2012, 2014) and the Beaufort slope in 2012–2014 (e.g., CAS 236445; UAM 3257, 47975, 47849) are indication not only of the probable circumpolar nature of its distribution along Arctic slopes, but that it is abundant in the Pacific Arctic.

The first record for the Pacific Arctic of another eelpout, the checkered wolf eel *Lycenchelys kolthoffi*, is another significant extension of known range revealed by bottom trawling in sparsely sampled areas. One specimen (183 mm, UAM 373804) was taken in a bottom trawl in the Alaskan Beaufort Sea near the border with Canada at 70°28'N, 141°09'W at a depth of 500 m, in 2014 by trans-boundary investigations conducted by the University of Alaska Fairbanks. This record helps fill the gap in the species' documented presence in the Arctic between the Laptev Sea and Hudson Strait and indicates that *L. kolthoffi* is a circumpolar species.

The righteye flounders, family Pleuronectidae, have presented some interesting examples of extensions of known range that have been attributed to climate change but are not actual

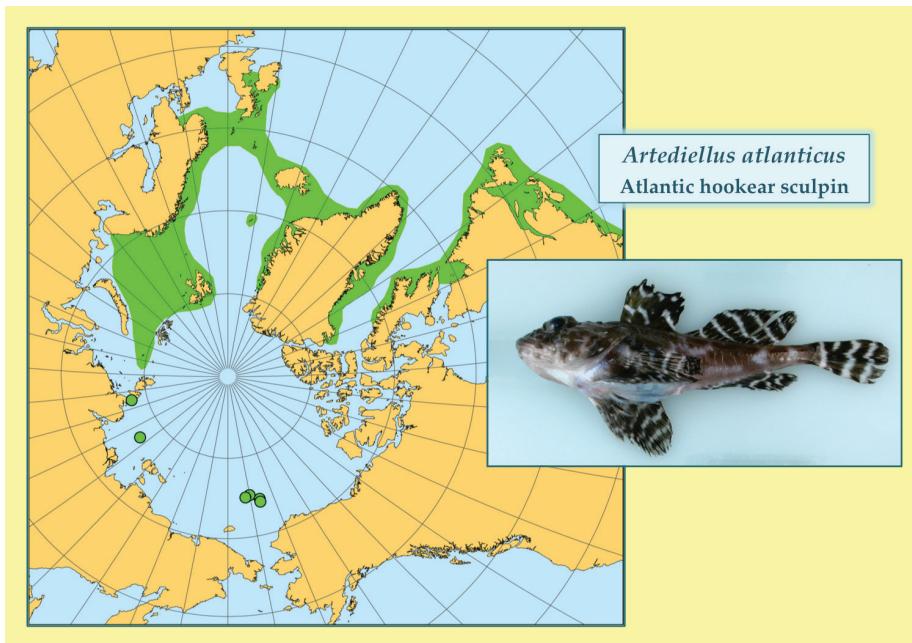


FIGURE 21. Specimens of Atlantic hookear sculpin *Artediellus atlanticus* caught by RUSALCA in 2009 in the Chukchi Borderland are the second record of this species in the region. There has been one additional record from the slope of the Chukchi Sea since then, but none from the Beaufort Sea. The COI sequences from the RUSALCA specimens and *A. atlanticus* from the Atlantic Arctic are identical.

extensions of the species' distribution. The collection history of Bering flounder *Hippoglossoides robustus* (Mecklenburg et al., 2011), one of the most abundant fish species in the Pacific Arctic, has shown it to occur eastward to Dease Strait in the Canadian Arctic, where it was found as early as 1965, and to spawn in the Pacific Arctic although previously perceived to be transported there as larvae and juveniles by the Alaska Coastal Current. Presence and distribution of eggs, larvae, and juveniles found in the Chukchi Sea by the RUSALCA investigations (Norcross et al., 2010) provide further documentation of the Arctic–boreal nature of this species. Furthermore, as mentioned in the preceding section, *H. robustus* should be formally placed in the synonymy of *H. elassodon*, with a total distribution southward to California.

The scaleye plaice *Acanthopsetta nadesnyi* was listed among the Pacific Arctic ichthyofauna (Mecklenburg et al., 2002, 2011) from published records (Lindberg and Fedorov, 1993) and unpublished records provided in personal communications, but has been removed from the list (Table 1). From reexamination of specimens and discussions with Sergei A. Evseenko (Russian Academy of Sciences, *pers. comm.*, April 25, 2013) it became apparent that *A. nadesnyi* in the northern Bering Sea had been confused with *Limanda sakhalinensis*. A review of the records and distribution of *A. nadesnyi* in the western Pacific is given in Parin et al. (2014).

The Kamchatka flounder *Atheresthes evermanni* and the arrowtooth flounder *A. stomias* are sometimes included on lists of Chukchi Sea fishes (e.g., Datsky, 2015), but examination of museum specimens and recent catches indicates they are distributed northward only to Cape Navarin or the southern Gulf of Anadyr (Mecklenburg et al., 2011; Parin et al., 2014). Juveniles of Greenland halibut *Reinhardtius hippoglossoides* have been confused with *Atheresthes* in the Pacific Arctic.

New discoveries will undoubtedly add

extensions of known range and increase the number of species documented in the Pacific Arctic, especially in previously unsampled or sparsely sampled areas,

but caution should be taken to avoid misidentifications and premature reports. Fish species in understudied areas tend to be unfamiliar to field and laboratory

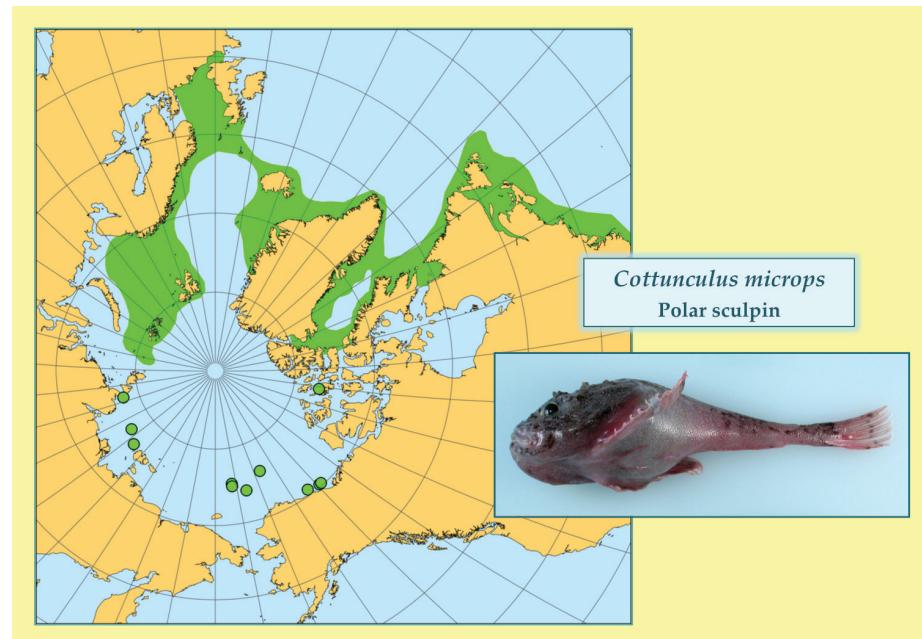


FIGURE 22. A polar sculpin *Cottunculus microps* taken by RUSALCA in 2009 is the first record of this species for the slope of the Chukchi Sea, and only the second record for the Pacific Arctic. It is now known to be common in the region, from additional specimens taken by other programs on the Chukchi and Beaufort slopes in 2010–2014. The COI sequences match those from Atlantic Arctic *C. microps*.

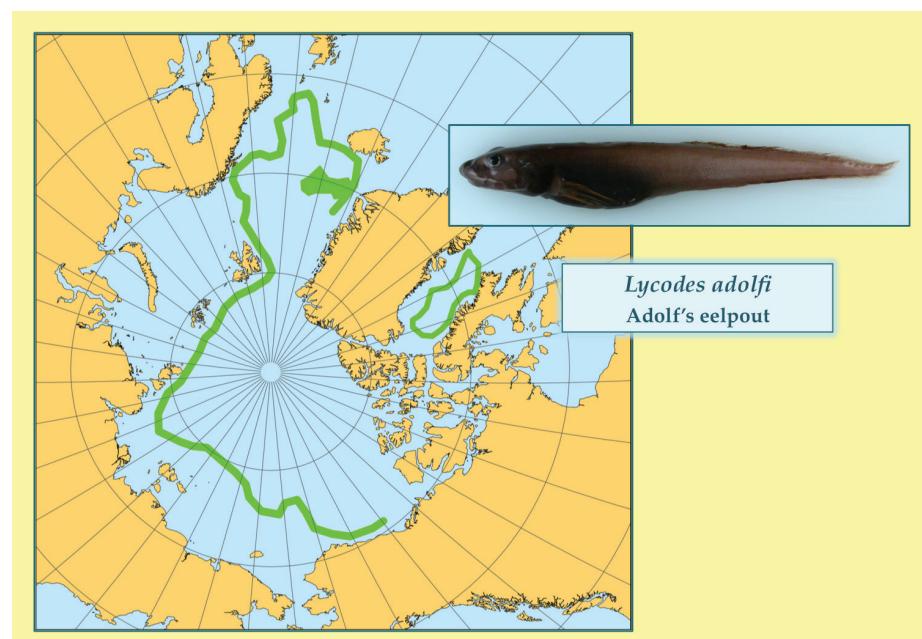


FIGURE 23. Several Adolf's eelpout *Lycodes adolfi* taken by RUSALCA in 2009 in the Chukchi Borderland compose the first record of this species from the Pacific Arctic. Catches by other programs on the Beaufort slope in 2011–2014, as well as the Chukchi slope in 2010, confirm the circum-polar nature of its distribution and demonstrate it is abundant in the Pacific Arctic. The COI sequences are identical to those of Atlantic Arctic *L. adolfi*.

workers, and misidentifications are frequent. For instance, *Liparis fabricii* was reported to be common in the 2010 CHINARE collection from the Chukchi and Bering Seas, whereas few *L. tunicatus* were taken (Lin et al. 2012, 2014). Previously, there had been only one record of *L. fabricii* from the Bering Sea, whereas *L. tunicatus* is known to be common there (e.g., Mecklenburg et al. 2011). It is evident that in the CHINARE collection, both *L. fabricii* and *L. tunicatus* were misidentified. In another example, in large collections taken by bottom trawl in the Beaufort Sea in 2011–2014 and provided to author Mecklenburg for identification or borrowed for study, more than 30% of specimens had been misidentified. Some of the other Beaufort Sea specimens have not been available for study. For instance, the identification of an eelpout as *Lycenchelys micropora* (UAM 48022) is doubtful, but the specimen could not be found when it was requested. This species is known from southern British Columbia to Mexico except for one specimen from the Aleutian Basin (Mecklenburg et al., 2002). The lost UAM specimen was more likely to be an Arctic species such as another *Lycenchelys kolthoffi* or one not yet recorded from the Pacific Arctic but potentially present like *L. muraena*, *L. platyrhina*, or *Lycodonus flagellicauda*, all known or tentatively identified from as close to the region as the Laptev Sea.

CONCLUSION

Misconceptions stemming from lack of knowledge on the identity and distributions of Pacific Arctic marine fish species are common. Without a sound baseline against which to make comparisons, change cannot be detected. The inventory of species resulting from the RUSALCA studies and presented herein provides that baseline. The studies of historical and recent collections and DNA barcoding have proved their worth in resolving taxonomic problems and determining geographic distributions of the fishes. The same methodology needs to continue as we seek answers to remaining questions,

many of them highlighted in this paper, on the identity of species.

Overall, the information presented in this paper forces the conclusion that for accurate identification of the fish species in the Pacific Arctic, which would enable changes in diversity to be detected, up-to-date, comprehensive reference tools are required. Because of all the changes in taxonomy and new knowledge on distributions, the *Fishes of Alaska* compendium (Mecklenburg et al., 2002) can no longer serve as the main reference for the Chukchi and Beaufort Sea fishes. Even combining that compendium with information more recently gained and reported (e.g., Mecklenburg et al., 2007, 2011, 2014) would not provide a complete reference. Although numerous cases have been described in the works cited and in the preceding pages, it has not been possible to address all the important recent changes and persisting problems in taxonomy and zoogeography. Another problem is that the accumulated information is scattered among many, sometimes highly technical, publications. Complete updated information on the taxonomy and zoogeography needs to be paired with other types of information such as on morphology and habitat, and all this information must be available in a single work. An atlas and identification guide currently nearing completion for Pacific Arctic marine fishes will answer the need for this sector of the Arctic region. It has been funded largely by the NOAA Arctic Research Program as part of the RUSALCA effort. Members of the Marine Fish Expert Network of the Circumpolar Biodiversity Monitoring Program (CBMP) of the Arctic Council have identified the same need on a pan-Arctic scale. Joining with other international experts, including those in the CBMP, and with funding from the Norwegian Ministry of Foreign Affairs as well as the NOAA Arctic Research Program, we are building on the Pacific Arctic atlas and guide to produce a reference covering the entire Arctic region. The works in progress will

enable fish specialists as well as non-experts to more accurately identify fish obtained by future monitoring efforts. They will provide baseline references for identifying marine fish species of the Arctic region and evaluating changes in diversity and distribution. Completion of a pan-Arctic barcode reference library will provide a critical component of the overall baseline and is a significant focus of the research plan. Some species and life stages cannot be identified without barcoding. The references under development will be critical to help prevent errors and inform future research. ☐

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