

Prepared in cooperation with Bureau of Ocean Energy Management,
Environmental Studies Program (OCS Study, BOEM 2016-048)

Alaska Arctic Marine Fish Ecology Catalog



Scientific Investigations Report 2016–5038

U.S. Department of the Interior
U.S. Geological Survey

Cover: Photographs of various fish studied for this report. Background photograph shows Arctic icebergs and ice floes. Photograph from iStock™, dated March 23, 2011.

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By Lyman K. Thorsteinson and Milton S. Love, editors

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U.S. Department of the Interior
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U.S. Department of the Interior
SALLY JEWELL, Secretary

U.S. Geological Survey
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Conversion Factors

[Inch/Pound to International System of Units]

Multiply	By	To obtain
Length		
foot (ft)	0.3048	meter (m)
mile (mi)	1.609	kilometer (km)

[International Systems of Units to Inch/Pound]

Multiply	By	To obtain
Length		
centimeter (cm)	0.3937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Area		
square meter (m ²)	0.0002471	acre
square kilometer (km ²)	247.1	acre
hectare (ha)	0.003861	square mile (mi ²)
square kilometer (km ²)	0.3861	square mile (mi ²)
Flow rate		
cubic kilometer per year (km ³ /yr)	0.000811	acre-foot per year (acre-ft/yr)
kilometer per day (km/d)	0.6214	mile per day (mi/d)
Mass		
gram (g)	0.03527	ounce, avoirdupois (oz)
kilogram (kg)	2.205	pound avoirdupois (lb)
Density		
kilogram per hectare (kg/ha)	0.06242	pound per cubic foot (lb/ft ³)
gram carbon per square meter (g C/m ²)	62.4220	pound per cubic foot (lb/ft ³)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$^{\circ}\text{F} = (1.8 \times ^{\circ}\text{C}) + 32.$$

Temperature in degrees Fahrenheit (°F) may be converted to degrees Celsius (°C) as follows:

$$^{\circ}\text{C} = (^{\circ}\text{F} - 32) / 1.8.$$

Datum

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).

Abbreviations

ACW	Alaska Coastal Water
ADFG	Alaska Department of Fish and Game
AFGP	antifreeze glycoprotein
AFP	antifreeze protein
AFS	American Fisheries Society
AFS-ASIH	American Fisheries Society-American Society of Ichthyologists and Herpetologists
AFSC	Alaska Fisheries Science Center
AI	Aleutian Islands
AIC	Akaike information criterion
AMAP	Arctic Monitoring and Assessment Programme
AO	Arctic Oscillation
AW	Anadyr Water
AOOS	Alaska Ocean Observing System
ArcOD	Arctic Ocean Diversity
BSW	Bering Sea Water
BOEM	Bureau of Ocean Energy Management
C	carbon
Cl ⁻	chloride
CO ₂	carbon dioxide
CoML	Census of Marine Life
CPUE	catch-per-unit-effort
DBO	Distributed Biological Observatory DIDSON. Dual Frequency Identification Sonar
DOI	U.S. Department of the Interior
EBSA	Ecological and Biologically Sensitive Area
eDNA	environmental DNA
EIS	Environmental Impact Statement
EEZ	U.S. Exclusive Economic Zone
EBS	Eastern Bering Sea
EPA	U.S. Environmental Protection Agency
FL	fork length
GAM	Generalized Additive Model
GI	gonadosomal index
GOA	Gulf of Alaska
IARPC	Interagency Arctic Research Policy Commission
IDW	Inverse Distance Weighted interpolation
ITIS	Integrated Taxonomic Information System
LME	large marine ecosystem
M	natural mortality
Ma	million years
MCA	Metabolic Cold Adaptation

Abbreviations—Continued

MMS	Minerals Management Service
Na ⁺	sodium
NEPA	National Environmental Policy Act
NOAA	National Oceanic and Atmospheric Administration
NPFMC	North Pacific Fisheries Management Council
NPRB	North Pacific Research Board
NSF	National Science Foundation
OA	ocean acidification
OBIS	Ocean Biogeographic Information System
OCS	Outer Continental Shelf
OR1	Online Resource 1
psu	practical salinity unit
RACE	Research Assessment and Conservation Engineering
rm	intrinsic rate of increase
RUSALCA	Russian-American Long-term Census of the Arctic
SDM	species distribution model
SL	standard length
SST	sea surface temperature
T	Trophic Index
TL	total length
tm	age at first maturity
UAF	University of Alaska, Fairbanks
USCGC	U.S. Coast Guard Cutter
USGS	U.S. Geological Survey
VBGM	von Bertalanffy growth model
WFRC	USGS Western Fisheries Research Center
YOY	young-of-the-year

Chapter 1. Alaska Arctic Marine Fish Ecology Catalog—Chukchi and Beaufort Seas

By Lyman K. Thorsteinson¹

Abstract

The marine fishes in waters of the United States north of the Bering Strait have received new and increased scientific attention over the past decade (2005–15) in conjunction with frontier qualities of the region and societal concerns about the effects of Arctic climate change. Commercial fisheries are negligible in the Chukchi and Beaufort Seas, but many marine species have important traditional and cultural values to Alaska Native residents. Although baseline conditions are rapidly changing, effective decisions about research and monitoring investments must be based on reliable information and plausible future scenarios. For the first time, this synthesis presents a comprehensive evaluation of the marine fish fauna from both seas in a single reference. Although many unknowns and uncertainties remain in the scientific understanding, information presented here is foundational with respect to understanding marine ecosystems and addressing dual missions of the U.S. Department of the Interior for energy development and resource conservation. This chapter describes the Department’s information need with respect to planned offshore oil and gas development, provides an overview of the *Alaska Arctic Marine Fish Ecology Catalog*, and presents regional background information, synthesis methodologies, and definitions for commonly used terms and concepts throughout the report.

Introduction

Accurate natural resource inventories and knowledge of baseline conditions for Arctic resources and ecosystems are essential for estimating effects of the U.S. Department of the Interior (DOI) offshore oil and gas-leasing program. The exploration and development of these offshore resources is managed by the DOI Bureau of Ocean Energy Management (BOEM). This document, *Alaska Arctic Marine Fish Ecology*

Catalog, addresses a specific need of BOEM to inform its decision making with respect to the fisheries ecosystems in Arctic Outer Continental Shelf (OCS) Planning Areas. This report is a compilation of species accounts of the marine fishes known from United States sectors of the Chukchi and Beaufort Seas. Certain diadromous (for example, Pacific salmon, char, and whitefishes) species are treated as marine fishes (McDowall, 1987) because much of their life cycle is in marine and brackish environments. This synthesis of information is meant to provide current information and understanding of this fauna and its relative vulnerability to changing Arctic conditions.

The National Environmental Policy Act (NEPA) requires the BOEM to prepare an Environmental Impact Statement (EIS) for each offshore oil and gas lease sale area offered through the DOI leasing program. The EISs provide an assessment of the potential environmental effects associated with major development proposals and communicate this information to decision-makers and the broader public (Wood, 2008). In complying with the NEPA, the BOEM relies on the best available science to evaluate potential effects on regional ecosystems and living resources. Our objectives were to review and synthesize current fish biology, ecology, and fisheries information to assist BOEM’s NEPA analysts in assessing environmental effects from planned future offshore oil and gas development on the Arctic OCS.

BOEM’s NEPA analysts require detailed information about the biodiversity, life history, and population ecology of regional biota to assess adversity of impact in the EIS process. For Arctic marine fishes, impact is evaluated in terms of potential declines in abundance or changes in geographic distribution and recovery of populations to pre-impact status (thresholds of significance analysis, see Miner and Rivasplata, 1994, and Musick, 1999). To illustrate, adverse effects would require three or more generations for a population to recover (Bureau of Ocean Energy Management Regulation and Enforcement, 2011). The population understanding required for a robust EIS analysis is similar to what is required to assess Essential Fish Habitat under provisions of the Magnuson-Stevens Fishery Conservation and Management Act.

¹U.S. Geological Survey.

2 Alaska Arctic Marine Fish Ecology Catalog

The compilation of species information provides BOEM's NEPA analysts and others with a single, authoritative scientific reference about the biology and ecology of marine fishes in the United States Chukchi and Beaufort Seas. Biodiversity is broadly assessed with respect to current understanding of (1) classification and taxonomy, (2) abundance and geographic distribution, and (3) life history and population ecology. A focus of this study has been on new information and discoveries about this fauna since the publication of *Fishes of Alaska* (Mecklenburg and others, 2002). As such, the species checklist, geographic distribution maps, and depth profiles represent new biodiversity products to science. This synthesis is unique because it is based on confirmed species occurrences in United States sectors of the Chukchi and Beaufort Seas. Confirmation is an important process because it assures the reliability of resource information in management areas of direct concern to decision makers. For most species, the link between occurrence and abundance remains tenuous given the nature of sampling conducted to date. As such, quantitative aspects of the dynamics of fish populations and their interactions with the Arctic marine environment are hindered by inadequacies of existing data and relative lack of Alaskan records. The emphasis on population dynamics and ecologic relationships in the species accounts provides an important basis for assessment of outstanding needs.

Although knowledge about the marine fish fauna in the Alaska Arctic is among the poorest in the state, it has been slowly improving over time. However, much life history information presented in this report was acquired from scientific observations outside Alaska. As such, basic

taxonomic science and population understanding is needed to support modern assessments and potential fisheries in the Arctic high seas. The goals of this report are to present the most current information about what is known about the marine fishes in the Arctic area of the United States with a special focus on geographic distributions, vertical structure, abundance, and life history parameters of key populations. The section, "Outline of Species Accounts" in [chapter 3](#) serves as a users' guide to information presented in the individual species descriptions.

Study Area

The primary geographical boundaries encompass Arctic OCS Planning Areas (Bureau of Ocean Energy Management (2012) in the U.S. Chukchi and Beaufort Seas (hereafter Chukchi and Beaufort Seas, [fig. 1.1](#)) and the U.S. Exclusive Economic Zone (EEZ) including the Arctic Management Area. The eastern boundary of the Beaufort Sea EEZ extends to the north and offshore of the Alaska-Canada Border. The Chukchi Sea extends from Point Barrow in Alaska and the Beaufort Sea in the east to the United States–Russia Maritime Boundary in the west. The Bering Strait forms the southern boundary of the Chukchi Sea. Some chapters, especially those addressing species descriptions ([chapter 3](#)) and discussing species diversity and possible geographic origins ([chapter 4](#)), include comparative information from adjacent seas and broader basin and ocean considerations, respectively.

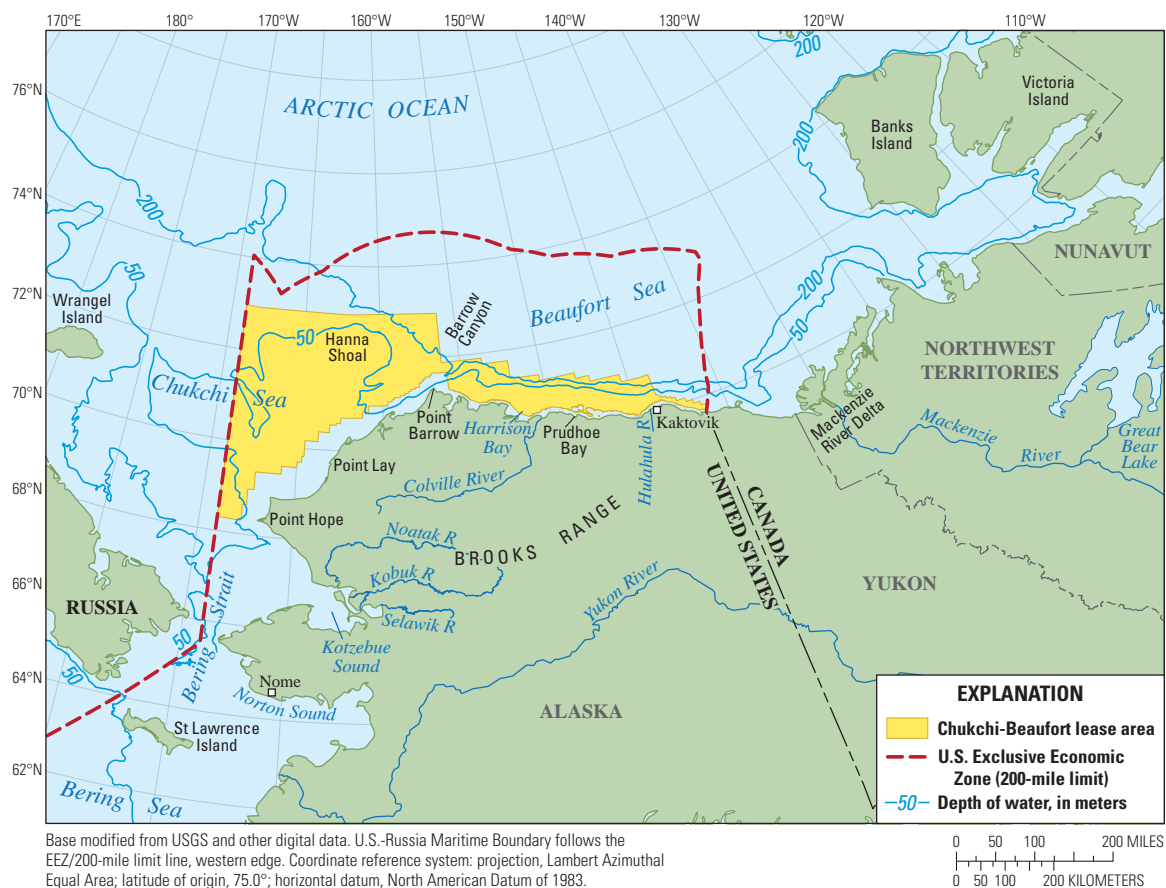


Figure 1.1. Bureau of Ocean Energy Management administrative boundaries for Outer Continental Shelf oil and gas leasing in the Chukchi and Beaufort Seas, Alaska.

Environmental Setting

Physical and biological components of the Arctic marine environment as they relate to marine regional descriptions of fish habitats and their use by fish and other biota were described by DeGange and Thorsteinson (2011)². The descriptions of physical oceanography, substrates, and biological productivity supporting marine fish habitats and populations are primarily based on this review. Information about the distribution of Arctic marine birds and mammals, potential competitors and predators of marine fishes, is not reported here but is available in DeGange and Thorsteinson (2011).

Regional Oceanography

Large-scale features of the Chukchi and Beaufort Seas oceanography were reviewed by Weingartner and others (2008). Surface circulation in the Beaufort Sea is dominated by the southern edge of the perpetual clockwise Beaufort Gyre of the Canadian Basin (fig. 1.2). The subsurface Beaufort Undercurrent Atlantic water masses and flows in the opposite direction, to the east, over the shelf (fig. 1.2). Bering Sea waters generally follow topography, moving north across the Chukchi Sea shelf and to the east over the shelf edge and slope (fig. 1.2). Currents in the shallower waters of the inner Beaufort Sea Shelf (fig. 1.2) primarily are wind driven and, thus, can flow either east or west. Because the predominant wind direction during the summer ice-free season is from the east, near-shore flow generally is from east to west.

Oceanographers have observed regional, seasonal, and interannual variability in water mass properties in the Chukchi and Beaufort Seas. Generally, the temperature and salinity characteristics of the major water masses are:

- Alaska Coastal Water—warm (2–13 °C), low salinity (to 32.2 practical salinity units [psu]);
- Bering Sea Water—warm (>0.0 °C); well-mixed and moderate salinity (about 32.5 psu);

- Anadyr Water—cold (<0.0 °C), marine salinities (32.8–33.2 psu);
- Siberian coastal waters—cold (<0.0 °C), low salinity (24 psu);
- Atlantic Water (at depths > 220 m)—warm (>0 °C), highly salinity (>34 psu); and
- Beaufort Gyre—cold (<0.0 °C), moderate to high salinity (31–34 psu).

In the Chukchi Sea, the summer water masses are cold in the east and warm in the west. Similarly, warm brackish waters (5–10 °C, <15 psu) occur adjacent to Alaska's north coast during summer (to about 10 km off the coast) and cold marine waters (<1 °C, 28 psu) farther offshore.

Under persistent east winds, bottom marine water can move onshore, where it is forced to the surface. This upwelling of marine water can cause some otherwise brackish and warm areas along the coast to become colder and more saline. This replacement of brackish with marine waters results in the transport of warmer, less saline waters offshore.

The Chukchi Sea receives water that flows northward through the Bering Strait, driven by the 0.5 m drop in sea level between the Aleutian Basin of the Bering Sea and the Arctic Ocean (fig. 1.2). Coachman and others (1975) provide a good overview of the northward movement of Bering Sea waters into the Chukchi Sea. Three distinct water masses, each of different origin, move northward through the Bering Strait. Anadyr Water, cold, high salinity, nutrient-laden oceanic water that originates along the slope of the Bering Sea Shelf, flows northward through Anadyr Strait, west of St. Lawrence Island and into the central Chukchi Sea (fig. 1.2). As much as 72 percent of the water transported through the Bering Strait in the summer may come through Anadyr Strait. Alaska Coastal Water originates in the Gulf of Alaska. This low salinity, seasonally warm water hugs the Alaska coast as it transits the Bering Sea into the Chukchi Sea. Alaska Coastal Water is influenced by freshwater run-off from major rivers in western Alaska. Bering Shelf Water is the resident water mass of the central shelf region south of St. Lawrence Island. This water mass is intermediate with respect to its hydrographic properties when compared to Anadyr Water and Alaska Coastal Water, is advected northward on both sides of St. Lawrence Island, and then flows through the Bering Strait where it mixes with the other water masses. These waters are an important source of plankton and carbon in the Chukchi and Beaufort Seas, and influence the seasonal distribution and abundance of marine biota and migration behaviors of many species (Piatt and Springer, 2003; Hopcroft and others, 2008; Weingartner and others, 2008; Crawford and others, 2012). The deep waters offshore in the northern Chukchi Sea also are a potentially important source of nutrient-rich waters.

²This review of large-scale physical oceanography was guided by DeGange and Thorsteinson (2011) who presented information previously reported in Minerals Management Service (2008) and Weingartner and others (2008). The summaries of primary and secondary levels of ecosystem production are from Bluhm and others (2008), Hopcroft and others (2008), Stockwell and others (2008), and Yager and others (2008). Other key references included Carmack and Wassmann (2006); Grebmeier and Maslowski, 2014; Moore and Staben, 2015; and Grebmeier and others (2015).

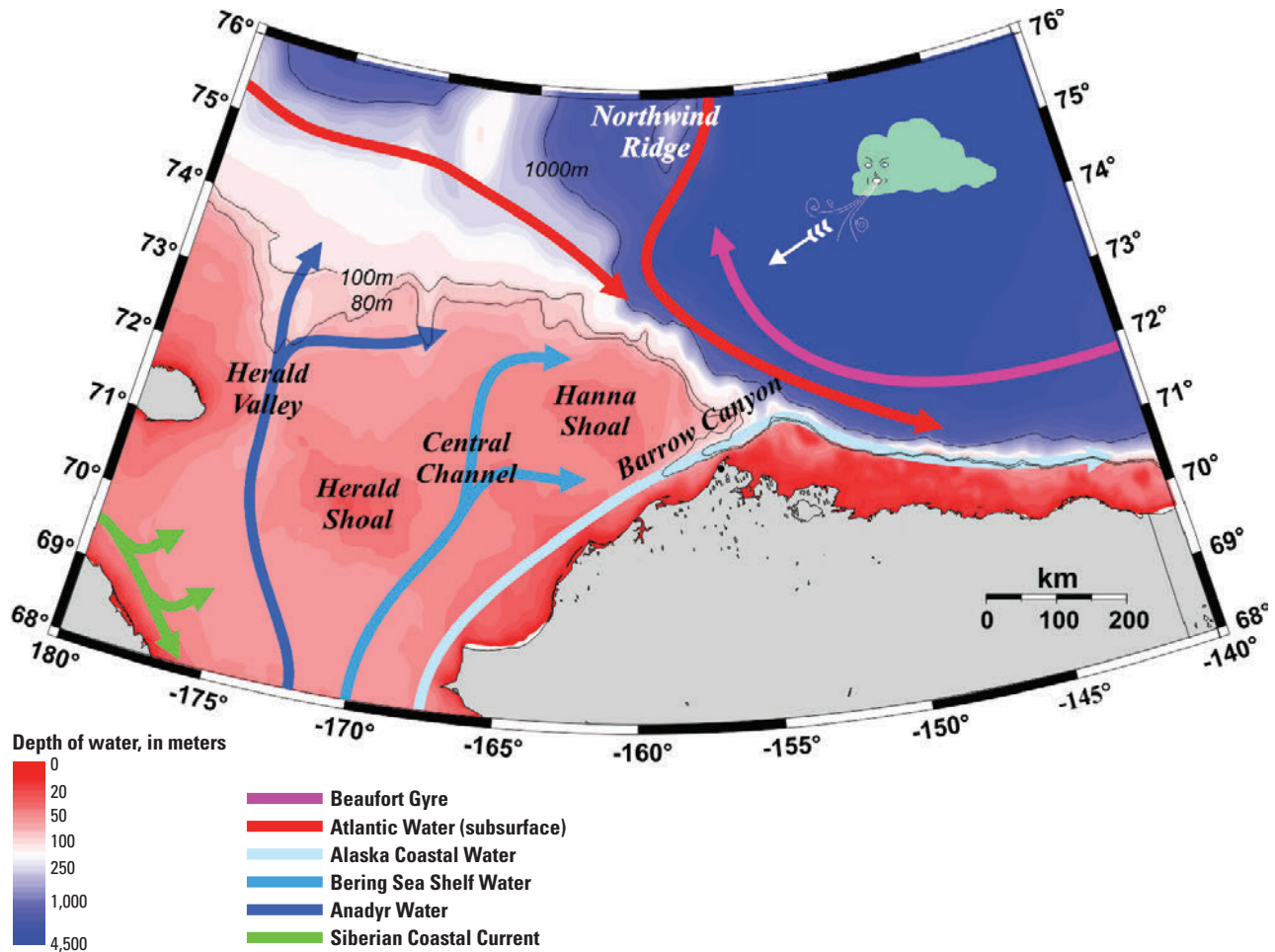


Figure 1.2. Schematic circulation map of the northern Chukchi Sea and western Beaufort Sea. From Weingartner and others (2008).

Bering Sea Cold Pool

Mecklenburg and others (2011) described the boundaries of an “arctic region” to include the Arctic Ocean and its seas and adjacent waters of the North Atlantic and North Pacific southward to an ichthyofaunal boundary (Arctic–Boreal species in [chapter 2](#)). Mecklenburg and others (2011, p. 110) reported that, “...position of the boundary is reflected in major differences in species composition associated with seafloor topography, such as sills and canyons, and water characteristics, such as temperature and salinity, that form barriers against fish movements.” In the northern Bering Sea, the location of the 2 °C isotherm during summer months, generally south of St. Lawrence Island, demarks this zoogeographic boundary and the northern edge, or ecotone, of marine waters associated with the Bering Sea cold pool (bottom temperatures ≤ 2 °C) that relates to the seasonal presence of sea ice (see [chapters 4](#) and [5](#)).

Sea Ice Dynamics

The presence of ice in the Arctic is one of the most important physical conditions to deal with for developing offshore OCS oil and gas resources. The seasonal sea ice cycle is a pervasive force in the Arctic, influences human activities and many aspects of the region’s natural history, and demonstrates great seasonal and inter-annual variability off the coast of Alaska. Generally, there are two forms of sea ice: fast ice that is anchored along the shore and free-floating pack ice that moves with winds and currents. Shore fast and pack ice interact to cause an extensive, somewhat predictable, system of flaw leads (swathes of open water in between ice) and polynyas off the coasts of the Chukchi and Beaufort Seas eastward to the Canadian Archipelago. These flaw leads and polynyas become more prevalent in spring and are biologically significant features with respect to the timing and location of seasonal movements and northward migrations of wildlife species, such as bowhead whales and marine birds.

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Maximum sea-ice cover occurs in March or early April, lagging minimum insolation in late December by 3 months because of the heat capacity of the ocean and the cold atmosphere. During these months, essentially all of the Beaufort and Chukchi Seas are ice-covered (fig. 1.3). Winter ice extent in the Arctic has decreased since the late 1970s (fig. 1.3) along the southern margins of sea-ice extent, but not severely (fig. 1.4). Maximum retreat of the sea ice occurs in September, again lagging maximum insolation by about 3 months. The extent of sea-ice loss in Septembers since the satellite record began has been remarkable (fig. 1.5). By September, in normal years, the ice pulls away from the Arctic coasts of Canada, Alaska, and Siberia, leaving a nearly continuous, relatively ice-free corridor that varies in width around the permanent ice pack. In recent years (2010–15), the ice-free corridor has expanded to hundreds of kilometers in the East Siberian Sea and offshore of the northern Alaska

coast. The contrasts between 1980, a representative year with extensive ice cover, and 1987, when sea-ice extent in the Arctic was at a record minimum, and the long-term median ice edge are evident (fig. 1.5).

In addition to decreases in sea-ice extent during late summer and autumn, the amount of multi-year compared with summer sea ice in the Arctic also is changing; conditions are moving toward an abundance of younger and thinner sea ice (figs. 1.3–1.6). The longer sea ice remains in the Arctic Ocean the thicker it becomes because of additional freezing and deformation. The thinning of Arctic Ocean sea ice has occurred largely because of the export of older, thicker sea ice out of the Arctic through Fram Strait, east of Greenland. This is important because young, thin ice is more vulnerable to the melting that results from warm air and water temperatures, perpetuating a feedback cycle because the open ocean absorbs solar insolation.

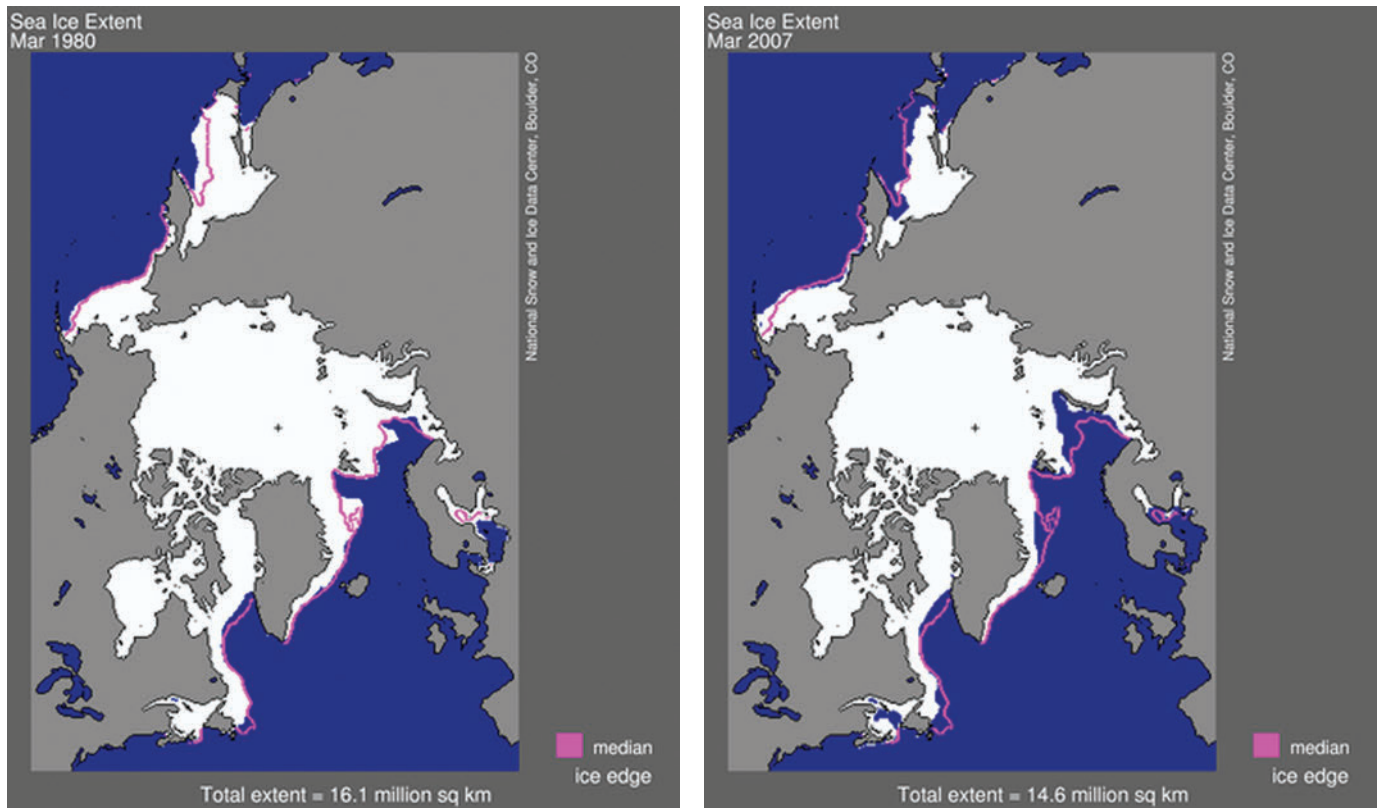


Figure 1.3. Extent of sea ice for single months and single years, using 1980 as an example of an extensive ice cover year, and 2007 as the record minimum year—maximum winter extent. The border plots the long-term median ice edge based on data from 1979 to 2000. From National Snow and Ice Data Center, 2011a, monthly sea ice extent for 1980 and 2007: National Snow and Ice Data Center database, accessed April 15, 2011, at <http://nsidc.org/>.

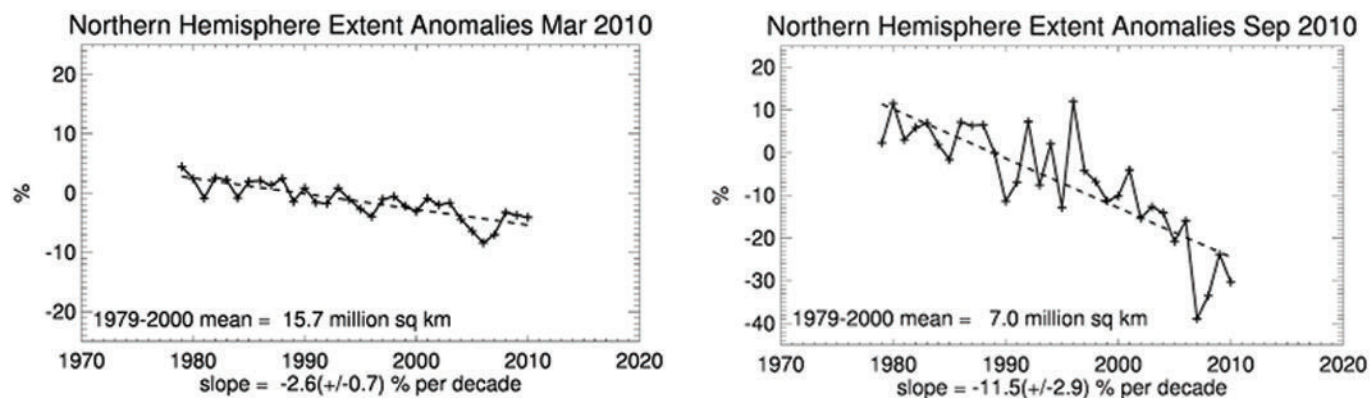


Figure 1.4. Sea-ice extent anomalies for March (maximum sea-ice extent) and September (minimal sea-ice extent) expressed as percentage-departure from average (that is, anomalies as compared to the 1979–2000 mean). From National Snow and Ice Data Center (2011b).

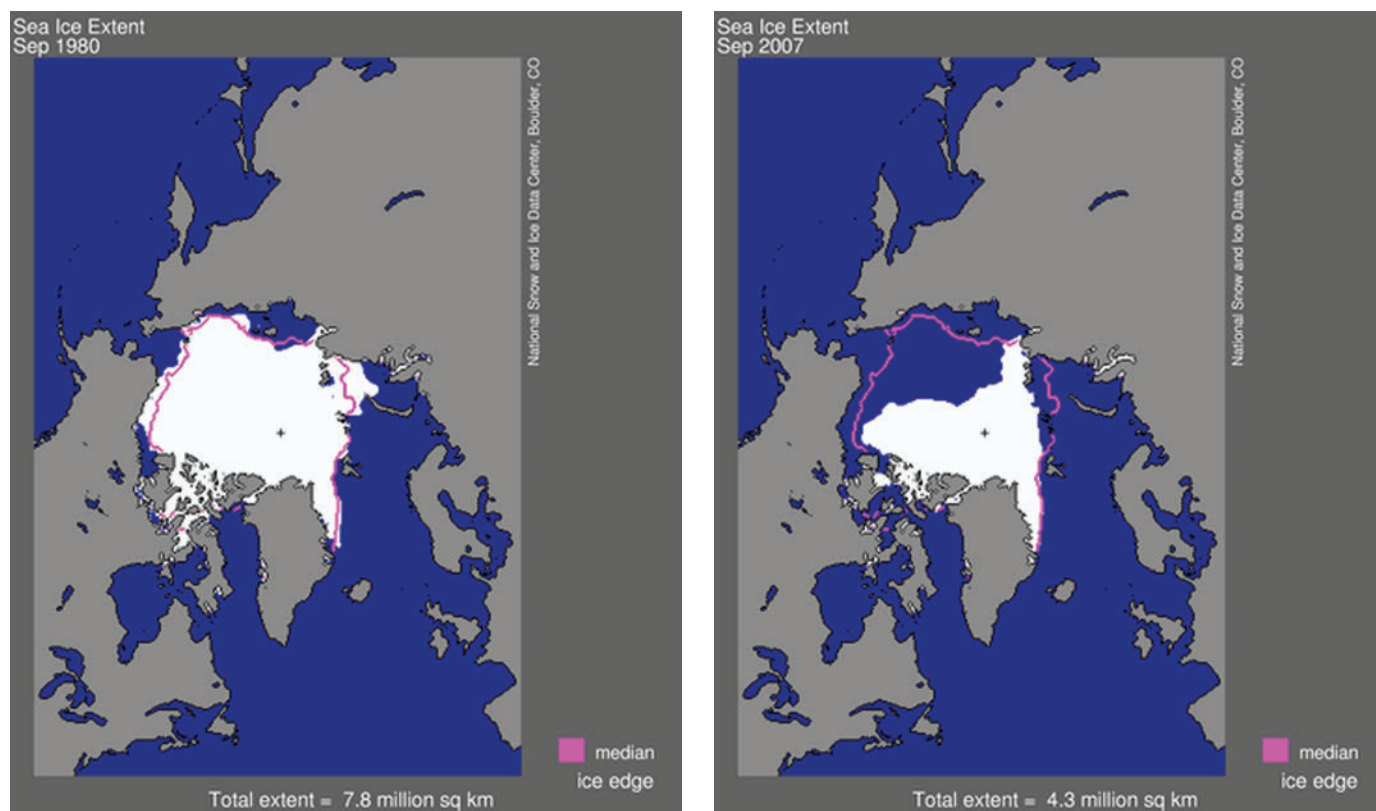


Figure 1.5. Extent of sea ice for single months and single years, using 1980 as an example of an extensive ice cover year, and 2007 as the record minimum year. The border plots the long-term median ice edge based on data from 1979 to 2000. Source: National Snow and Ice Data Center (2011a).

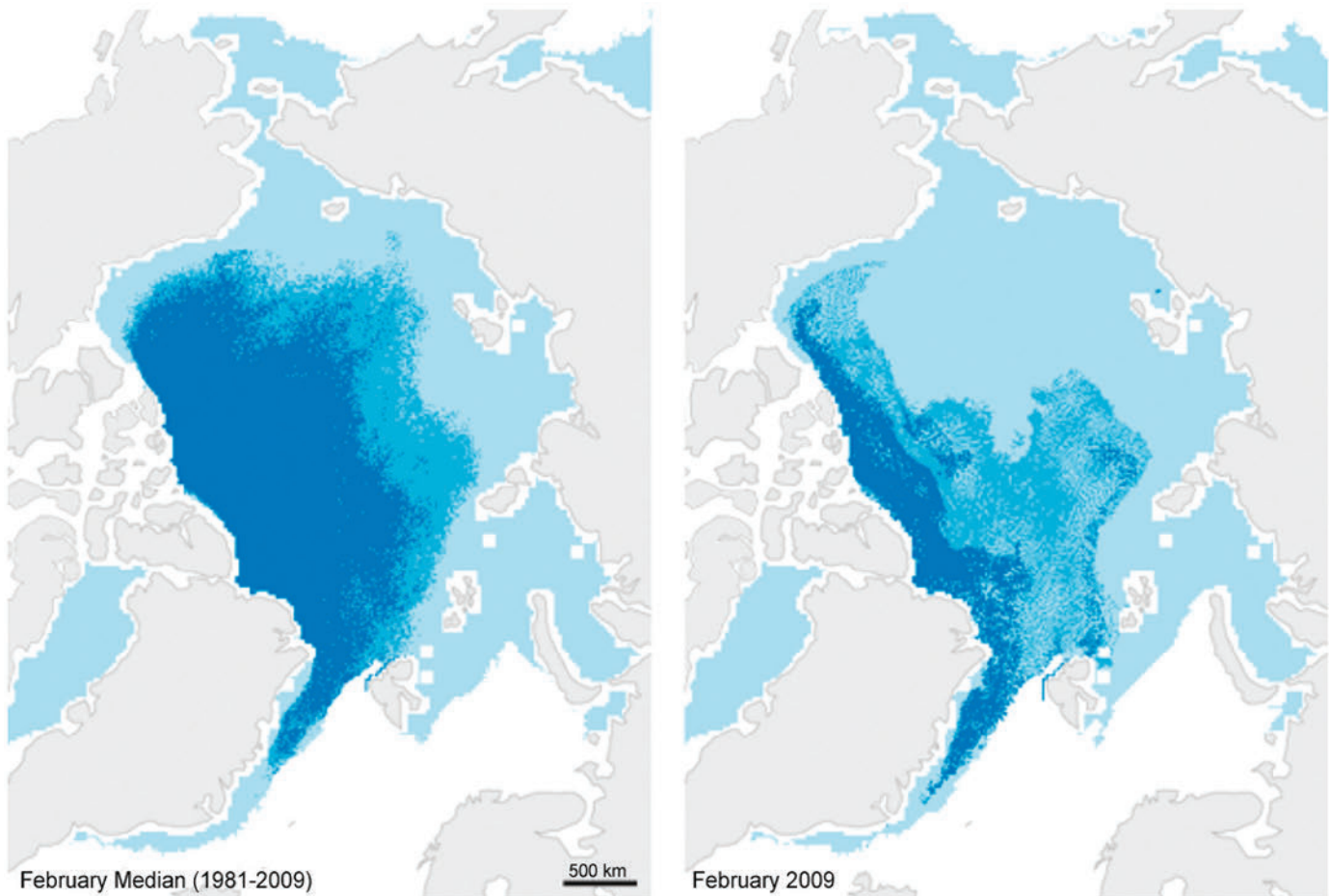
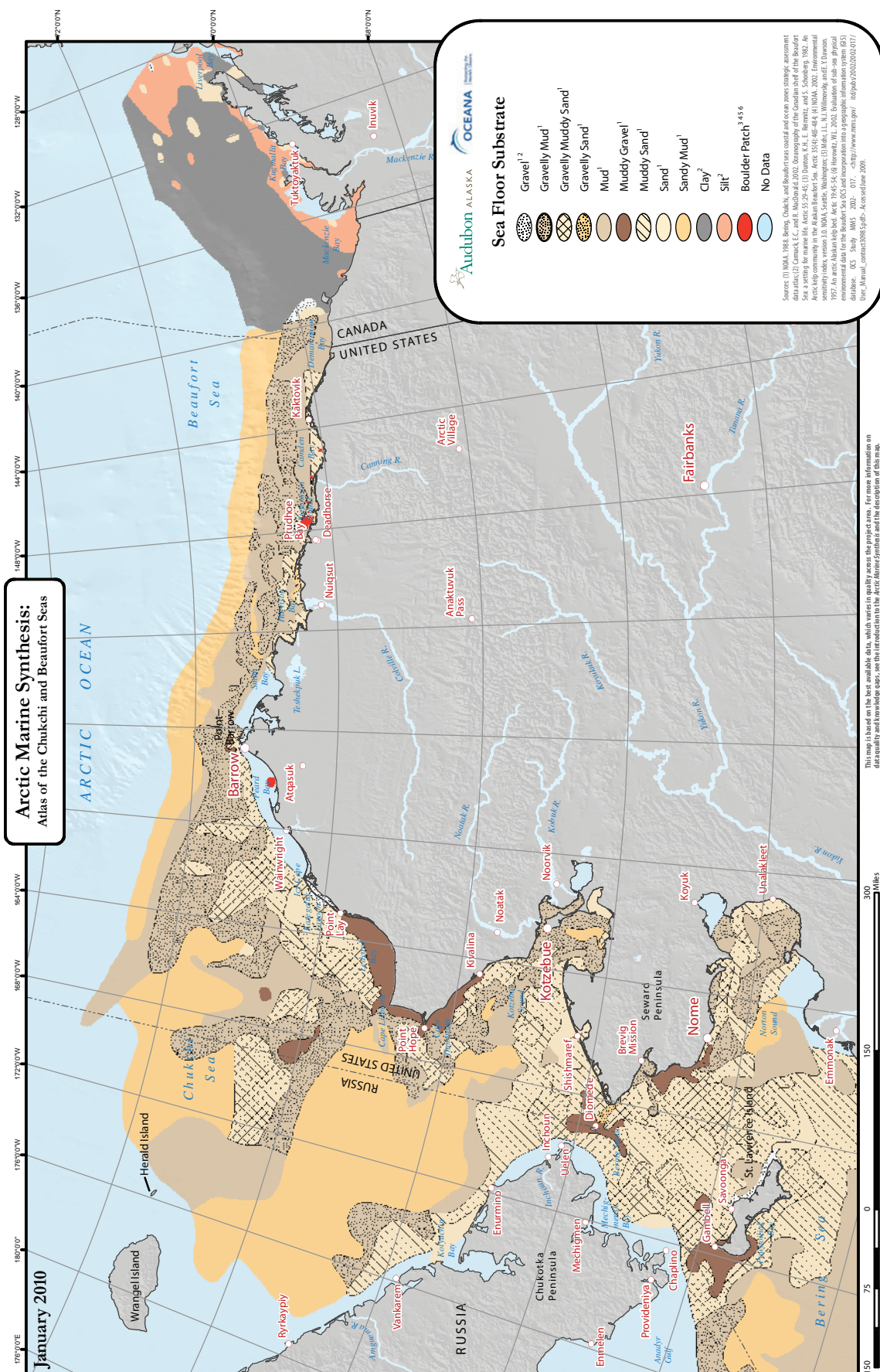


Figure 1.6. Old and new ice in the Arctic for February. These maps show the median age of February sea ice from (A) 1981 to 2009 and (B) February 2009. As of February 2009, ice older than 2 years accounted for less than 10 percent of the ice cover. Dark blue indicates ice greater than 2 years old; medium blue indicates 2-year-old ice; pale blue indicates annual ice. From National Snow and Ice Data Center (2011c), accessed April 15, 2011, at http://nsidc.org/sotc/sea_ice.html.

Seafloor Substrates

Soft sediments dominate the sea floors of the continental shelves of the Beaufort and Chukchi Seas. These are largely combinations of muds, sands, and gravels (fig. 1.7). These soft-sediment bottoms support high densities and biomass of benthic invertebrates, particularly in the extensive shallow shelf areas of the Chukchi Sea where productivity is high (for example, Hanna Shoal and Barrow Canyon [fig. 1.1]).

Only two areas with hard substrates have been identified in the entire region (Smith, 2010) (fig. 1.7)—one in Peard Bay, southwest of Barrow, and the other in Steffansson Sound near Prudhoe Bay that is known as the “boulder patch” (Dunton and others, 1982). The boulder patch is characterized as sediment with greater than 10 percent boulder cover. It provides attachment habitat for the endemic kelp *Laminaria solidungula* and other macroalgae, which are the primary carbon source for consumers living there.



Benthos

Benthic food supply originates in surface waters and is highly seasonal in the Arctic. Densities of sediment particles and their nutritional values range vastly from the nutrient rich waters of the northern Bering and Chukchi Seas to the oligotrophic deep waters of the Arctic Basins. Less is known about the benthos from the Beaufort Sea although preliminary data from ongoing BOEM surveys suggest there is much less biomass and diversity, and that different ecological processes occur ([appendix A](#)). Generally, however, comparisons of energy fluxes show that the benthic systems receive more energy in the Arctic than from temperate and tropical systems.

Much of the broad, shallow shelf of the Chukchi Sea is strongly influenced by northward flowing nutrient-rich Pacific Ocean water through the Bering Strait, resulting in high benthic biomass, which is among the highest worldwide in soft-sediment macrofaunal communities (for example, Grebmeier and Maslowski, 2014; [fig. 1.8](#)). Specifically, the south-central Chukchi Sea has the highest algal and faunal biomass on the combined Bering Sea and Chukchi Sea shelf because of the high settlement rates of organic production that is not grazed by microbes and zooplankton. These rich benthic communities, tied to high pelagic production and advection, serve as prey for various diving sea birds and marine mammals, a key feature of the productive Chukchi Sea. About 1,200 species are known from the Chukchi Sea fauna to date with amphipods, clams, and polychaetes dominating infaunal community. Important macrofauna prey species for higher trophics include bivalves taken by walrus, in particular *Macoma* spp. and *Mya truncata*, and benthic amphipods used by gray whales and bearded seals. Within the epifauna, ophiuroids dominate abundance and biomass in much of

the surveyed Chukchi Sea, and other patchily distributed echinoderms (especially asteroids), gastropods, ascidians, sponges, cnidarians, and bryozoans are locally abundant.

The comparatively narrow Beaufort Sea Shelf is influenced by large freshwater inflow from numerous small rivers and streams, the larger Colville and Mackenzie Rivers ([fig. 1.1](#)), and permafrost resulting in estuarine conditions in the nearshore. Because of this freshwater flow, non-marine sources of carbon may play an increasingly important role for the benthic food web in parts of the nearshore Beaufort Sea. The Beaufort Sea floor is dominated by soft sediments ([fig. 1.7](#)), but high ice cover and associated scouring, along with glacial erratics, have left coarser sediments (gravel and boulders) in various areas of the Beaufort Sea. The Alaskan part of the Beaufort Sea coast is fringed by sandy barrier islands forming numerous shallow lagoons with average depths less than 5 m and ecological traits different from those in the open water. Compared to the Chukchi Sea, productivity and benthic biomass in the Alaskan Beaufort Sea are dramatically lower. Consequently, benthic-pelagic coupling is not as pronounced as in the Chukchi Sea and food chains are shorter. Much less is known about the slopes of the Chukchi Sea and especially the Beaufort Sea, and the adjacent basins (Bluhm and others, 2008). The existing investigations of the slopes and abyssal infaunal benthos in the western Arctic revealed low abundances and biomass values relative to the shelves, especially with increasing water depth and distance from the shelves. At taxonomic levels of phylum and orders, the soft-bottom deep Arctic macrofauna appear to be similar to the shelf communities: polychaetes, bivalves, and crustaceans are dominant, but on a family, genus, and species level, inventories differ from the shelves.

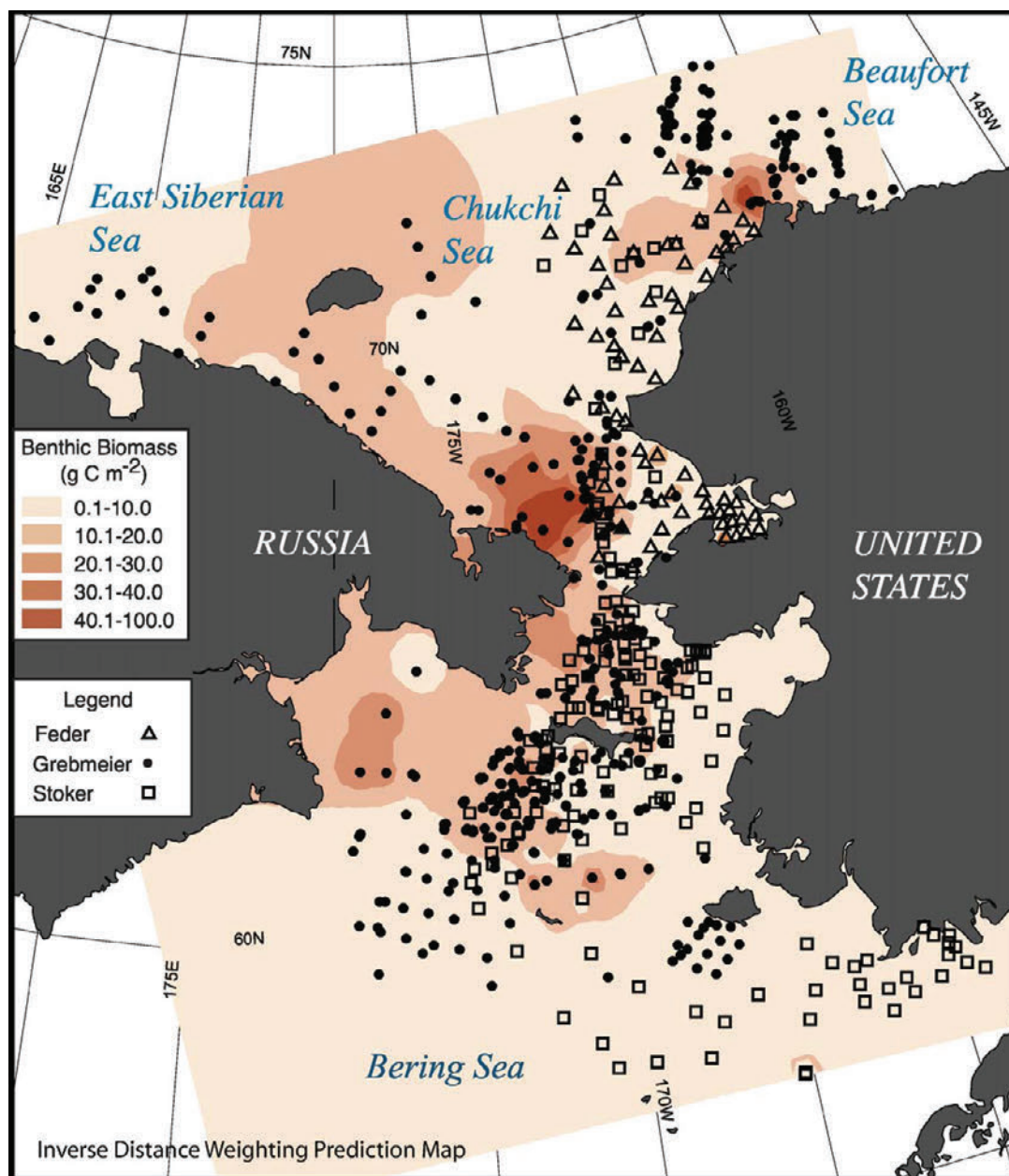


Figure 1.8. Benthic biomass distribution in the Chukchi and northern Bering Seas. From Grebmeier and others, 2006a. Feder and Stoker station locations reference historical sampling stations by University of Alaska-Fairbanks researchers in the Bering and Chukchi Seas as part of NOAA's Outer Continental Shelf Environmental Assessment Program. (g C m⁻², grams of carbon per square meter.)

Primary and Secondary Production

In the Arctic, the combination of cold temperature, the occurrence of sea ice, and the extreme seasonal variations in light regimes controls phytoplankton growth and governs its spatial and temporal growth patterns. The stabilizing effect of sea ice allows production to occur near the surface under low light intensities. A large number of planktonic algae thrive in Arctic waters, but there seem to be relatively few truly Arctic species. Estimates of phytoplankton biomass vary widely depending on the region, with the highest amounts in the Chukchi Sea. Algal production and biomass in the Arctic primarily are controlled by light, stratification, and nutrient fields. On the shelves, advection and turbulent mixing of nutrients through the Bering Strait and local nutrient remineralization sustain extremely high primary production values on the Chukchi Sea Shelf (fig. 1.9). Much of the production is not grazed, falls to the sea floor, and fuels benthic communities. In addition to phytoplankton, ice algae contribute to the total primary production of the Arctic Ocean with higher production values in first-year ice compared to multi-year ice. The contributions of ice algae to total primary production range from less than 1 percent in coastal regions to as much as 60 percent in the central Arctic Ocean.

Secondary producers include the microbes, protists, and zooplankton that consume phytoplankton and algae. Compared to phytoplankton and mesozooplankton, much less is known about the composition, distribution, and rates of activity of microbes and protists in the Arctic Ocean, and this confounds the ability to estimate the effect of climate change or other disturbances on food webs and basic biogeochemical processes. Biomass of heterotrophic microbes in Arctic surface waters shows a strong response to seasonal changes in phytoplankton stocks. In the Chukchi Sea, concentrations of bacteria are low in spring, increase over the course of the bloom, and are highest in late summer. Heterotrophic protists include nanoflagellates, ciliates, and dinoflagella.

Recent work in the Gulf of Alaska, the Bering Sea, and shelf and slope regions of the western Arctic Ocean has confirmed the role of these organisms, known as microzooplankton, as consumers of phytoplankton in sub-Arctic and Arctic food webs. Although it is likely that phytoplankton and sea ice algae still represent a crucial food source for the larger zooplankton, use of microzooplankton as food is recognized as being of similar import, particularly during periods when phytoplankton standing stock is low or of poor quality. Because strong local pulses of primary production are a frequent characteristic of high-latitude oceans, including the Chukchi and Beaufort Seas, the response of microbes (including both bacteria and protists) to these pulses determines the rate of remineralization and the fraction of total production exported to the benthos. Weak microbial activity in the Arctic contributes to the high degree of benthic-pelagic coupling in many shelf regions of the Arctic and the consequent strength of demersal ecosystems.

Zooplanktons are the major grazers of the primary production in the Arctic and determine the resources available to many higher trophic levels, such as fishes, seabirds, and marine mammals. In the Chukchi Sea, large quantities of Pacific zooplankton enter the region through the Bering Strait, in a complicated mixture of water masses. The influx of the rich Pacific water determines the reproductive success of both the imported and resident zooplankton communities. Both inter-annual and long-term variation in climate will affect the relative transport of these various water masses and hence the composition, distribution, standing stock, and production of zooplankton and their predators in the Chukchi Sea. Zooplankton abundance and community structure also affect the amount and quality of carbon exported to the benthic communities in this region. In contrast, the Beaufort Sea primarily is Arctic in character, with cross-shelf exchange mechanisms more important in determining the relative contribution of “oceanic,” “shelf,” and “estuarine” species. In the Eastern Beaufort Sea, the outflow of the McKenzie River has significant effect on both the composition of the zooplankton and its productivity. Thus, the Beaufort Sea is responding to a fundamentally different set of factors than the Chukchi Sea, even if they are both driven by similar climate-related variations and trends.

Although copepods typically predominate throughout the Arctic, there is a broad assemblage of other planktonic groups. Euphausiids are less abundant and diverse in Arctic waters than elsewhere, but can be important prey for higher trophic levels such as bowhead whales, birds, and fishes. Larvaceans (Appendicularians) have been shown to be abundant in Arctic polynyas, and are transported in high numbers through the Bering Strait into the Chukchi Sea. Similarly, important and common predatory groups, such as the chaetognaths, amphipods, ctenophores, and cnidarians have been reported on in detail by only a few surveys. Hyperiid amphipods also can be common in Arctic waters and, like chaetognaths, have a potential to graze a large proportion of the *Calanus* population. Relatively little is known of the abundance, composition, or ecology of the delicate gelatinous zooplankton, such as jellyfish. There are indications that climate change has resulted in increased numbers of jellyfish in the Bering Sea in recent years. Scientists have recorded jellyfish piled up several feet deep along shorelines near Barrow, Alaska. The ecological effect of these predators is substantial and underestimated in polar waters.

The ongoing reduction of the sea-ice cover will have major effects on the ecosystems and biogeochemical fluxes on the extensive continental shelves of the Arctic Ocean. Many processes involved in the regulation of the vertical and trophic fluxes of particulate organic carbon, and the production of dissolved organic carbon, are controlled by the zooplankton. Knowledge of zooplankton community ecology, especially the temporal and spatial distribution patterns of the different classes of zooplankton, is needed to understand the role of sea-ice variability in dictating fluxes of biogenic carbon on and off the shelves.

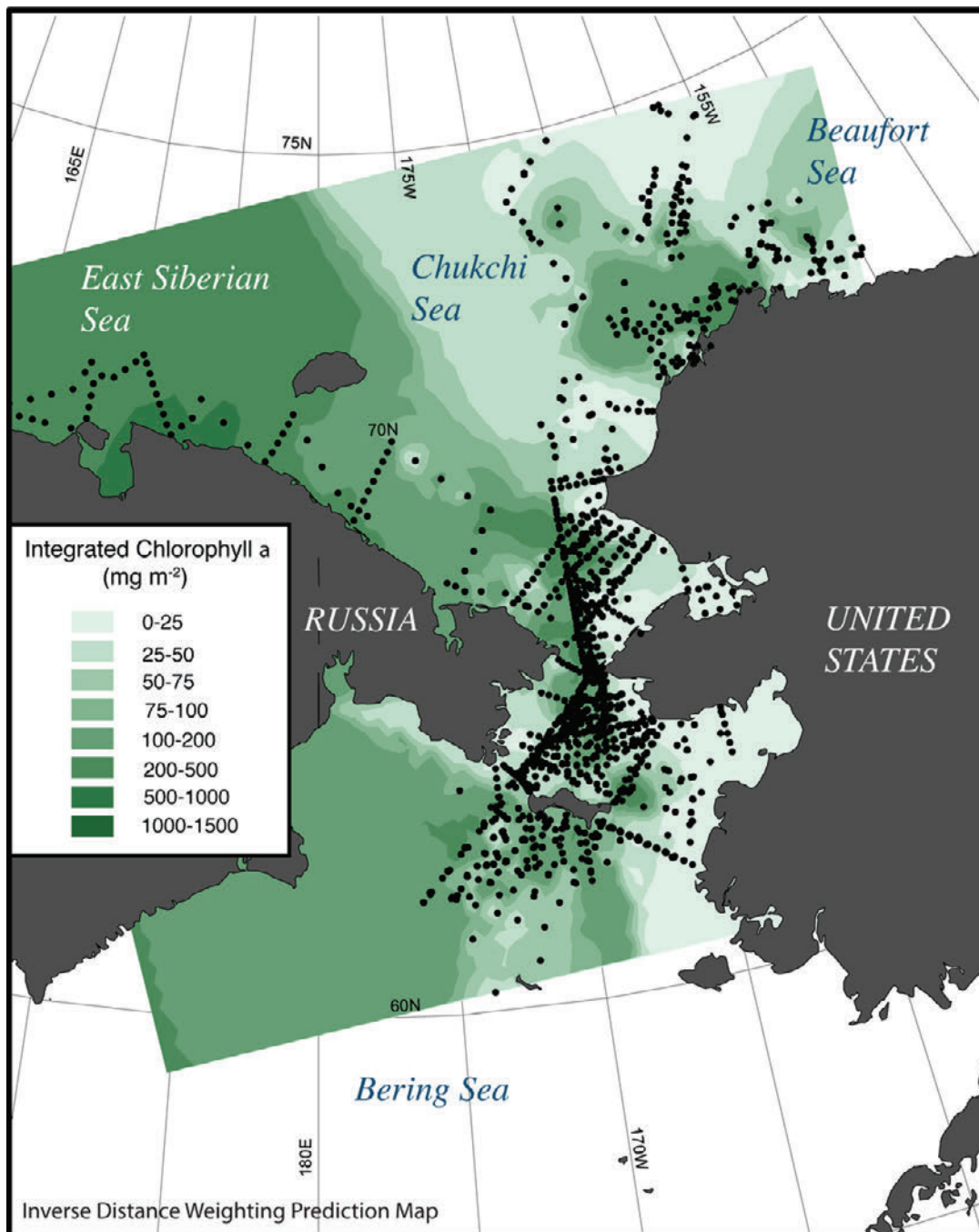


Figure 1.9. Contours of integrated chlorophyll *a* concentrations, in milligrams per square meter [mg m^{-2}] based on discrete measurements at sampling locations in the northern Bering Sea, east Siberian Sea, and Chukchi and Beaufort Seas, April–September 1976–2004 (Grebmeier and others, 2006a).

Environmental Context Within the Pacific Arctic Region

The information summarized in the section, “[Environmental Setting](#)” focused on the United States Chukchi and Beaufort Seas, and included relevant physical and biological information from the Pacific Arctic Region. The description of the Pacific Arctic Region includes the northern Bering Sea, Chukchi and Beaufort Seas, East Siberian Sea, and western sectors of the Canadian Arctic Archipelago (for example, Grebmeier and others, 2015). Regional information, from data collections outside the United States, was included because large scale understanding of physical and biological processes (for example, the delineation of boundaries for the Arctic Large Marine Ecosystem [Protection of the Arctic Marine Environment, 2013] evaluates interactions and connections at scales of the northeast Pacific and Arctic Ocean) is needed to address historical and ecological biogeography objectives of this study ([chapter 4](#)). Additional focus and synthesis on the environmental features of the Pacific Arctic Region address scale issues by drawing special attention to the importance of shelf geography and advection on regional ecology (this chapter) as it pertains to marine fish distributional patterns described in [chapters 3 and 4](#).

Geographic relations between advection, sea ice, and stratification properties were reviewed by Carmack and Wassmann (2006) to classify shelf typologies and compare regional connections between physical habitats and biota in Arctic seas. Inflow, interior, and outflow shelves were described for the Pacific Arctic Region and collectively these shelf types were estimated to cover $2,145 \times 10^3 \text{ km}^2$ or approximately 35 percent of the entire shelf area of the Arctic Ocean ($6,048 \times 10^3 \text{ km}^2$). Continental shelf area is greatest in the East Siberian Sea (16 percent of total Arctic Ocean shelf area) followed by the Chukchi Sea (10 percent), Beaufort Sea (3 percent), and Canadian Arctic Archipelago (about 2 percent). The total volume of seawater over Arctic shelves is $829 \times 10^3 \text{ km}^3$ of which 7 percent is associated with the East Siberian Sea, 6 percent the Chukchi Sea, about 4–5 percent in the Canadian Arctic Archipelago, and 3 percent the Beaufort Sea.

The northern Bering/Chukchi Sea is a shallow inflow shelf (mean depth = 58 m) as the transport of Pacific water through the Bering Strait connects Pacific and Arctic Oceans ($S \sim 32 \text{ psu}$, $V_T \sim 1 \text{ Sv}$) ([fig. 1.2](#); salinity and annual mean volume as reported by Woodgate and others, 2015). As these waters flow across the Chukchi shelf they are responsive to atmospheric forcing and are strongly modified by geophysical and physical processes before their subduction along the break and upper slope. Freshwater transport from rivers, ice (primarily first year ice), and stratified waters of the Bering Sea is significant and supports strong seasonal stratification and high primary productivity in the Chukchi Sea. The Bering Sea inflows, especially from upwelled deep waters, are rich in nutrients and biogenic materials such as phytoplankton, zooplankton, and meroplankton. Large herbivores are not

abundant in the zooplankton community overlying shelf waters and the grazing efficiency is low. The advection of freshwater and suspended organic matter combined with high primary production and inefficient cropping over shallow depths results in tight pelagic-benthic coupling and high standing stocks of benthic communities (Renaud and others, 2008). As a consequence of the large vertical flux of locally and advected carbon, the Chukchi shelf (and southwestern Beaufort Sea) are also the site of substantial denitrification and high benthic biomass in offshore areas compared to the more river-influenced central and eastern Beaufort Sea. Benthic ecosystems and short food chains are adaptations to the fluxes and cycling of carbon as evidenced in the composition and life history traits of the benthos and seasonal migrations of large numbers of benthic feeding animals in the Bering Strait and Chukchi Sea each year.

The East Siberian Sea (mean depth = 48 m) and Beaufort Sea are interior shelves (mean depth = 80 m). According to Carmack and Wassman (2006), interior shelves are shallow and characterized by strong effect of major Arctic rivers (for example, Kolyma and Mackenzie Rivers). Interior shelves exhibit a positive estuarine flow (plume spreading) in summer and a negative estuarine circulation (brine release) in winter. During summer, sediments and organic matter are transported to the nearshore in a highly variable mix of riverine, estuarine, and marine waters. The horizontal exchange of water masses is thus considerable and variation in salinity is significant. Carmack and others (2015) defined the brackish water mass that forms near the coast ($\leq 30 \text{ m}$) as the River Coastal Domain. In deeper waters beyond the shelf break, boundary currents flow to the east and contain Arctic water derived from Atlantic and Pacific origins. Interior shelf waters are turbid (large terrigenous loads) and seafloors featureless except in large river areas where small valleys continue across the bed. The interior shelves are characterized by a predominance of landfast ice that melts during summer and flaw polynyas in winter. Primary production and the general biological activity are low over offshore areas of the interior shelves due to high turbidity, export of surface waters below the ice cover, and nutrient limitation due to stratification. Suspended biomass of planktonic organisms is thus low, but that of benthic organisms is relatively high. This relates to benthic foods from marine advection and local production and significant imports from littoral and riverine sources. Shoreline erosion delivers large amounts of peat to coastal waters and represents a major source of carbon in lagoonal food webs (Dunton and others, 2005; 2006; 2012). During winter, the lagoons freeze to depths about 2–5 m, often to the bottom, a disruption so great that the epibenthic community at the base of their food webs must re-colonize them annually.

The Beaufort Sea is a narrow interior shelf. The primary production in some of the coastal lagoon ecosystems of the United States Beaufort Shelf is less than 10 grams of carbon per meter ($\text{g C m}^2/\text{yr}$) as light penetration in spreading and meandering river plumes is extremely limited. Land fast ice cover is persistently strong and severely limits primary

production. Primary production on the adjacent Canadian Beaufort Shelf with its mixture of land fast and multi-year ice, flow polynyas, stamukhi, and higher light penetration outside the river plumes, is high, in the range of 30 to 70 g C m²/yr. High freshwater inputs from numerous rivers and streams produce an environment that is decidedly estuarine in character, especially during the late spring and the summer months. Coastal erosion and river discharge are largely responsible for introducing high concentrations of suspended sediment from upland regions into the nearshore zone and often trapped in nearshore lagoons. Shelf energetics are characterized by a relatively low autochthonous production and a rich terrestrial, allochthonous carbon supply, especially in more productive regions. Benthic biomass is relatively rich in terrestrial carbon. Zooplankton populations, however, are poorly developed in the inner coastal region and the brackish waters that form along the coast each summer allows access to more marine foraging areas outside of the lagoons by several species of amphidromous fishes of importance in traditional economies.

In contrast the East Siberian Sea is a wide interior shelf. The wide interior shelves may extend far offshore (about 800 km) before reaching the shelf break. Most of the trophic dynamics in this sea remain to be resolved. This sea is heavily covered by land fast ice, is shallow (<50 m), and is exposed to most of the discharge of freshwater to the Arctic Ocean when the Lena River is considered. As a consequence, total primary production is low and the contribution from ice algae is probably significant. Stratification is strong during the productive season and the biota is dominated by benthos. High chlorophyll *a* concentrations in the sediments indicate a tight coupling between sympagic and pelagic primary production and nutrient supply to the benthos throughout the entire Laptev Sea. However, pronounced regional differences exist in the magnitude of primary production. The shallow nature of the ecosystem implies that the effect of zooplankton on carbon flux is limited and may increase toward the shelf break. Preliminary carbon budgets indicate that a high proportion of primary production is channeled through the benthic food web. As in the case of the narrow interior shelves input of allochthonous organic carbon seems to be required to balance the overall carbon demand. Despite its refractory nature, the supply of riverine dissolved organic carbon and particulate matter of terrestrial origin, mediated by microbial food webs, may be significant for this shelf.

The Canadian Arctic Archipelago is a network outflow shelf (mean depth = 124 m). Outflow shelves allow Arctic Water to drain back into the North Atlantic. The Canadian Arctic Archipelago is a complicated network of channels, straits, and sounds, and water mass transit times are long enough for thermohaline and biogeochemical changes to occur en route. There are no large rivers in this system, but moderately sized rivers enter from the Canadian mainland; there is other, local freshwater run-off. Stratification derives primarily from ice melt. Land fast ice in the region is regular, but strongly variable with regard to depth, time of melt, and

snow-cover. The archipelago is ice-covered during most of the year with extensive, but variable ice melt and stratification observed during summer and early autumn. Primary production on outflow shelves is spatially variable. Over the southern parts of outflow shelves the primary production can be significant and is highly seasonal, quickly nutrient limited, and highly variable between years. The comparatively great depth implies that much of the carbon flux is channeled through plankton, with additional supplies from sympagic biota. Existing measurements of total primary production in the entire Archipelago suggest that it may support as much as 32 percent of the total primary production of pan-Arctic shelves. The zooplankton dynamics are even more variable, probably because of irregular advection episodes through the Archipelago. Ice fauna and flora are rich in the Archipelago and close pelagic–benthic coupling results in rich benthic communities in the shallow sections. However, primary production is generally low and the transport of organic matter (mostly of terrestrial origin) and ice biota by multi-year ice and the Transpolar Drift is significant along longitudinal outflow shelves. Interannual comparisons of ice algae production in Barrow Strait (to the east of M'Clure Strait, Canada) reveal strong year-to-year variability, ranging from 2 to 23 g C m² y⁻¹ (Smith and others, 1988). Thus, this outflow shelf probably experiences similar significant variability in its planktonic/sympagic primary production.

A conceptual model for the Pacific Arctic Region relates observed patterns in ecosystem structure and function to advection and related functional attributes (fig. 1.10; Grebmeier and others, 2015). The patterns are consistent with shelf processes described by Carmack and Wassman, (2006) denoting significance to areas of convergence in the Chukchi and Beaufort Seas and along the shelf break, large freshwater influences from the Mackenzie River and through the Bering Strait, and within different water masses of the Chukchi Sea. The conceptual model also is consistent with information about the physical environment and the marine resources in this chapter and portrays the role of advection more clearly with respect to seasonality and patterns in species distribution and abundance and further description of biological connections between Chukchi and Beaufort Sea shelves and other Pacific Arctic environments (for example, northern Bering Shelf and nearshore waters).

Two other conceptual models also inform current understanding of the present state: (1) a food web model linking physical factors to biological distribution and abundance and food web relationships (Wiese and others, 2013); and (2) a marine-pulsed model focusing on the seasonality of production cycles and biological activity as they relate to connections between riverine exports, benthic–pelagic coupling and remineralization, advection, winds and episodic upwelling events, and sea ice coverage (Moore and Stabeno, 2015). The advection, food web, and marine-pulsed models are complementary, building on the unifying constructs of the contiguous domain, and depict current understanding and suggest how energy pathways and efficiencies in benthic

and pelagic communities could be affected by the changes in meteorology (temperature, winds and cloudiness), sea ice (timing and extent of open water) hydrology (freshwater discharge), hydrography (stratification and halocline), and plankton dynamics (timing, intensity, magnitude, and production) and related ecological efficiencies (energy transfers between trophic levels).

Advection is a key forcing function for the Arctic marine environment in general and the Pacific Arctic Region in particular (Grebmeier and others, 2015). In this conceptual

model, advection of water, ice, and biological constituents through the Bering Strait creates the energetic pathways and connections that affect much of the region and influence regional productivity and abundance of biota. Sea ice is a primary forcing factor in the region and is inherently connected to advection. Because of a steep decadal decline in seasonal sea ice coverage in the Chukchi Sea, it is thought to be among the most vulnerable Arctic continental seas for ecosystem change (Wiese and others, 2013; Grebmeier and others, 2015).

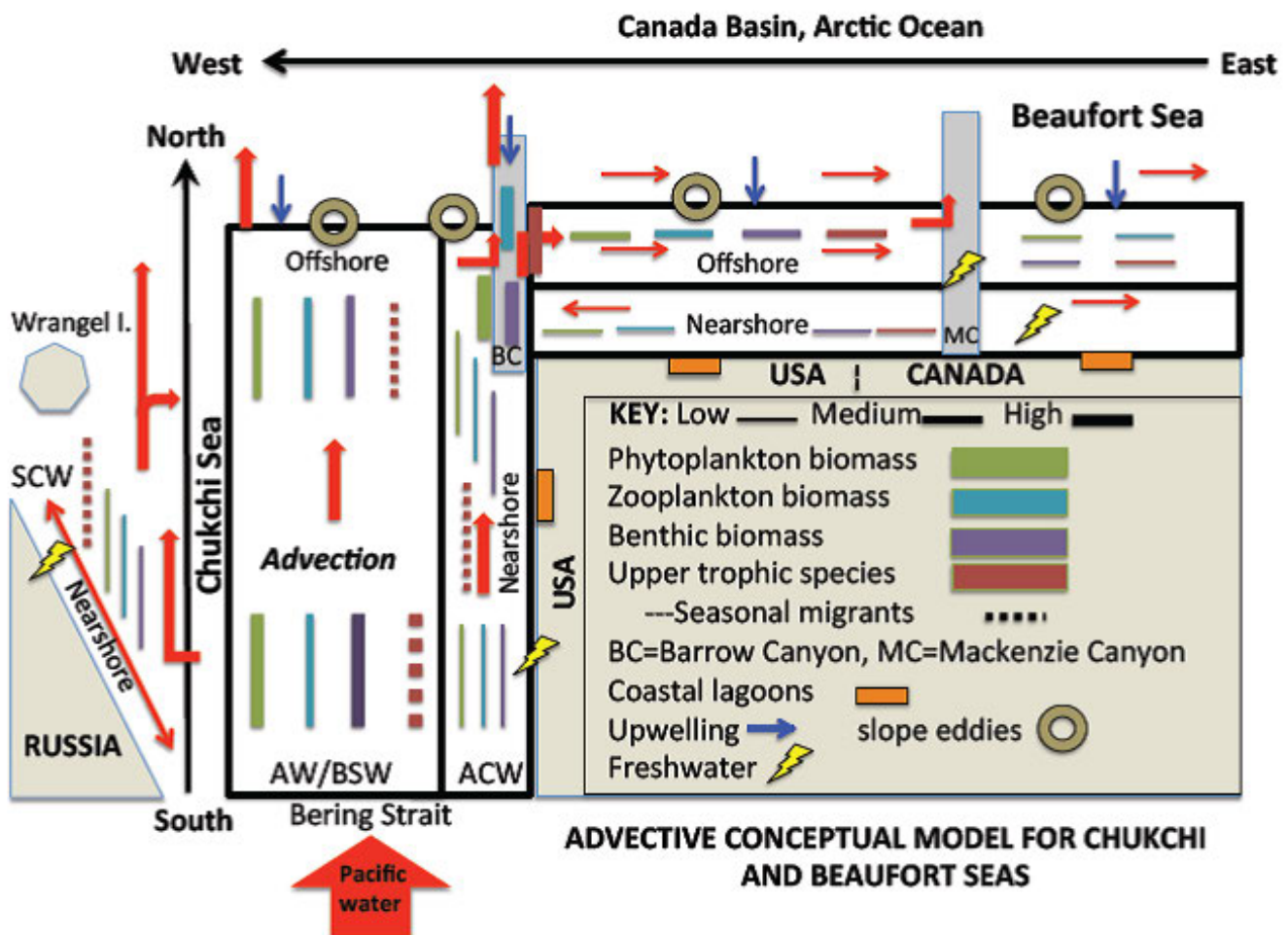


Figure 1.10. Advection conceptual model for Pacific Arctic Region (emphasis on Chukchi and Beaufort Seas, Alaska). (From Grebmeier and others, 2015). A 30-meter contour separates nearshore and offshore regions. The inflow of Pacific water masses (Anadyr Water [AW], Bering Shelf Water [BSW], and Alaska Coastal Water [ACW]) is critical to ecosystem dynamics, for example benthic ecosystem functioning, and transport processes in this conceptual framework. The East Siberian Coastal Current, not shown, while important, may be of less significant to the United States Chukchi and Beaufort Sea marine ecosystem dynamics.

Methods, Sources, and Terminology

Standard methods of literature review for published and unpublished data sources were followed. The search process for data and information included reviews of: current and historical studies; peer-reviewed journal and monographs; regional guides; museum specimens; technical reports and survey databases; searchable Web-based databases; oral communications; limited new data collection; and use of defensible unpublished scientific data.

Unless otherwise noted we conformed with conventions of scientific and common nomenclature used by Nelson and others (2004), Nelson and Bouchard (2013), Love and others (2005), Mecklenburg and others (2011), Maslenikov and others (2013), and Mecklenburg and Steinke (2015). This publication includes a key list of Arctic species referred to as the Online Resource 1 (OR1). The American Fisheries Society-American Society of Ichthyologists and Herpetologists (AFS-ASIH) recently completed an update to its list of common and scientific names (Page and others, 2013). In this report, *Boreogadus saidi* refers to Arctic Cod instead of Polar Cod (Page and others, 2013). *Arctogadus glacialis* is called Ice Cod. Other changes in nomenclature as they pertain to differences in taxonomy since the *Fishes of Alaska* (Mecklenburg and others, 2002) was published are noted. The *Fishes of Alaska* is a critical companion document to this report for the physical description of species including the key diagnostic features of anatomy for proper identifications.

Synthesis Methods

The preparation of species accounts involved several interrelated tasks including (1) documenting marine fish biodiversity; (2) defining terminology relative to the fauna and environment; (3) developing a standard template for information delivery (outline of species accounts); (4) acquiring and reviewing biological, ecological, and economic data and information; (5) producing species accounts; (6) synthesizing environmental (physical, biological, and ecological) information; and (7) managing the scientific review. The second and third tasks were most challenging because of limitations in existing data and the related need for consistent, reliable information in each species account. Pilot efforts involved the development of prototype species accounts and their review and improvement in an iterative process that introduced an evolutionary quality to product formation and information portrayal. The pilots highlighted the need for clarity in usage of standard terminologies being applied to Arctic baselines.

The fifth synthesis task involved an in-depth analysis of the collective body of the biological and ecological information presented in the species accounts to give it proper context to the biogeography of the fauna. Synthesis efforts were framed using historical and ecological components of

biogeography (Nelson, 2006) to describe patterns of species occurrence, habitat and population relationships, and the ecosystem processes that affect the distribution and abundance of marine fishes in the Chukchi and Beaufort Seas. These environmental influences reflect physical, biological, and ecological attributes and interactions in the region and include human uses, such as fisheries, that can affect the population dynamics, community dynamics, and species presence in an area. In addition to providing information about environmental constraints (limiting factors) to marine fish populations, the BOEM requested more generalized information about the region's physical setting, adaptation and acclimation, life history strategies, marine fish assemblages, foraging and feeding behaviors, seasonality, growth and reproduction, predation and disease, population abundance and production, and human uses. We were asked to consider potential effects of climate change and, in light of all of the above, provide our impressions of information needs and research directions. Our opinions on potential effects of climate change should be viewed as hypotheses and, our thoughts on information needs are directed at the Arctic scientific community, in general, and no single organization, in particular. In many instances, these opinions were directed at deficiencies in understanding of species biology and ecology and basic information needs for any assessment or management action.

Biodiversity Assessment

The assessment of regional biodiversity included: (1) developing and updating an Arctic marine fish checklist; (2) reviewing recent (since *Fishes of Alaska* was published) ichthyologic sampling and management documents; (3) searching online databases; (4) systematic investigations that include documenting current taxonomic understanding with genetic information, historical museum collections, and voucher specimens; (5) acquiring digital images (photographic and line drawings); (6) creating visualization products that include distribution maps and vertical species profiles; and (7) conducting peer reviews.

Arctic Marine Fish Checklist

A provisional working list of marine fishes inhabiting the Chukchi and Beaufort Seas was initially prepared. This important first list incorporated new discoveries and taxonomic resolutions from ichthyologic sampling, genetic analysis, and museum studies conducted since the regional monograph *Fishes of Alaska* (Mecklenburg and others, 2002) and checklist of fishes (Love and others, 2005) were published. The list included only marine fish species confirmed from the region and greatly benefited from recently completed and ongoing field, laboratory, and museum research establishing new baselines for marine fish in the Pacific Arctic Region (Mecklenburg and Steinke, 2015). It was evident to BOEM and the U.S. Geological Survey (USGS) that much

new information on species distribution and occurrence had been collected in the decade following publication of the *Fishes of Alaska* and, as noted by Mecklenburg and Steinke (2015), this reference is no longer complete for the region. An important objective of this study was to illustrate the relationship of the final checklist to Mecklenburg and others (2002), which remains an important companion document and primary source for taxonomic information and identification guides for Alaskan fishes.

In addition to Mecklenburg and others (2002), other key references included reviews and syntheses on the taxonomy and zoogeography of Arctic marine fishes by Mecklenburg and others (2007), Mecklenburg and others (2011, 2013, 2014), Mecklenburg and Steinke (2015), and Maslenikov and others (2013). A new atlas and identification guide for the marine fishes of the Pacific Arctic Region is an important source of information about the diversity, taxonomy, and geographic distribution of marine fishes in the Chukchi and Beaufort Seas (Mecklenburg and others, 2016).

Scientific Reviews

Recent publications, technical reports, and unpublished data were reviewed for new species occurrences and expansions in range. Survey results from fish sampling in the Chukchi Sea (Mecklenburg and others, 2007, 2011; Norcross and others, 2009, 2013a) and Chukchi Borderlands (for example, Mecklenburg and others, 2013; Longshan and others, 2014) and industry research (Gallaway and Norcross, 2011; Norcross and others, 2013b) were reviewed. Surveys from the southwestern Beaufort Sea (Johnson and others, 2010; Parker-Stetter and others, 2011; Rand and Logerwell, 2011; and Johnson and others, 2012) were reviewed for new information from nearshore and shelf waters. Additionally, National Oceanic and Atmospheric Administration (NOAA), University of Alaska-Fairbanks (UAF), and RUSALCA scientists are involved in ongoing fishery investigations for BOEM's Alaska OCS Region in the Chukchi and Beaufort Seas. Taxonomic support provided to these studies and other research (for example, Mecklenburg and Steinke, 2015) and analysis of previously unprocessed samples from WEBSEC-71 (1971) (Hufford, 1974) was a source of new records from the Beaufort Sea.

Relevant environmental analyses and Arctic resource management plans done by the BOEM (Minerals Management Service [MMS], 2008) and North Pacific Fishery Management Council (NPFMC, 2009), respectively, were reviewed in this assessment of biodiversity, human uses, and environmental relationships. The DOI synthesis of priority science needs for continued oil and gas development in the Arctic was consulted for information about the region's environmental setting, living resource information, and USGS-identified research needs (Holland-Bartels and

Pierce, 2011). A supplemental draft EIS addressing possible offshore oil and gas development in the U.S. Chukchi and Beaufort Seas was reviewed for species and community assemblage information (National Oceanic and Atmospheric Administration, 2013). A significant study of subsistence use and traditional ecological knowledge of whitefish in the southeastern Chukchi Sea (Georgette and Shiedt, 2005) provided an important source of information about Inupiat taxonomy and seasonal use of whitefishes in the Noatak, Kobuk, and Selawik Rivers of Kotzebue Sound (fig. 1.7).

Searchable Databases

The exploration of the Arctic is at the forefront of ecological research to document and understand marine ecosystems and population ecologies with respect to climate change, possible commercial fisheries, and other stressor effects. In recent years, active research in conjunction with RUSALCA, Census of Marine Life (CoML) programs [that is, Pan-Arctic Inventory/Arctic Ocean Diversity (ArcOD) and Marine Barcode of Life] has emphasized fishery objectives for resource inventory. In this capacity, data for this report were from the Global Marine Life Database, Census of Marine Life Community Database, and CoML bibliographic database (for example, Mecklenburg and others, 2007 and Mecklenburg and Mecklenburg, 2009). Other searchable Web-based databases used included: FishBase; BOEM Arctic Fisheries Database; United Nations Ocean Biogeographic Information System (OBIS Database); Encyclopedia of Life; World Register of Marine Species; Catalogue of Life Species; and Integrated Taxonomic Information System (ITIS). NOAA's on-line database services provide access to life history and distributional information for nearshore atlases; offshore fishery resources were accessed at the National Oceanic and Atmospheric Administration Web site (<http://alaskafisheries.noaa.gov>). The automated database at the University of Washington School of Fisheries and Ocean Sciences provided key access to type specimens and mapping tools.

The BOEM database, "Alaska Scientific and Technical Publications" (<http://www.boem.gov/Alaska-Scientific-Publications/>), was a significant resource for marine fishery, subsistence, and socioeconomic data. A summary of ongoing and recently completed BOEM fishery studies is provided in [appendix A](#). A major synthesis by Braund and Kruse (2009) provided an authoritative review of subsistence harvest patterns for fish and wildlife patterns over the past 30 years (from the mid-1980s). During this period, the OCS subsistence studies and this synthesis focused on coastal harvest patterns in the Alaska North Slope villages of Wainwright, Barrow, Nuiqsut, and Kaktovik. An early study by Craig (1987) provided important baseline documentation of subsistence patterns and Inupiat taxonomy from the Chukchi and Beaufort Seas.

Systematic Investigations

Recent information about the taxonomy and biogeography of Alaskan Arctic fishes has come from numerous analyses using field and museum studies, DNA sequencing, and exhaustive literature review, as well as efforts to synthesize the accumulated results for the Pacific Arctic region; particularly the works of Mecklenburg and others (2006, 2007, 2011, 2013, 2014, 2016), Mecklenburg and Mecklenburg (2009), and Mecklenburg and Steinke (2015). Voucher specimens provide a crucial link to historical data sets, allowing determination of existing baselines and accurate identification of new field collections. Museum collections housing the specimens are globally located and managed by many institutions. The following collections are some of those studied for the works just cited: California Academy of Sciences, San Francisco; Canadian Museum of Nature, Gatineau, Quebec; Hokkaido University Museum of Zoology, Hakodate, Japan; U.S. National Museum of Natural History, Washington, D.C.; NOAA, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska; University of Alaska Museum, Fairbanks, Alaska; University of British Columbia, Vancouver, Canada; University of Washington, Seattle; and Zoological Institute, St. Petersburg, Russia. Detailed data on voucher specimens examined, including the authors' verified or redetermined identifications, have been published (for example, Mecklenburg and others, 2006; Mecklenburg and Mecklenburg, 2009; and Mecklenburg and others, 2011, Online Resources 1 and 2) and the most recent results are available from the museums' online search databases. In many instances, the museum studies have revealed previously misidentified or unreported specimens and have led to extensions or contractions in known patterns of distribution; these results are reported here in abbreviated form from the authors' more detailed works. The origins, classification, diversity, human uses, and vulnerabilities of circumpolar freshwater and marine Arctic fishes were reviewed as part of the most recent Arctic Biodiversity Assessment (Christiansen and others, 2013).

Genetic Analyses

Mecklenburg and others (2011, 2014, 2016) and Mecklenburg and Steinke (2015) described the DNA analyses (barcoding) performed on Arctic fish specimens as part of the CoML, RUSALCA, and other fisheries investigations. This analytical tool has provided critical information to ichthyologists to help resolve taxonomic problems, assist difficult identifications, and, in many instances, generate hypotheses about potential population structuring. Many of the Arctic fishes that have been barcoded were collected in the Chukchi and Beaufort Seas and in other parts of Alaska. Online Resources 3 and 4 of Mecklenburg and others (2011) provide museum catalog numbers and collection data for barcoded specimens. That collection has been increased, and

data on additional specimens may be found on the Barcode of Life Data System (BOLD) Web site from links supplied by Mecklenburg and Steinke (2015).

Other sources of genetic identification information were found in the literature review. Research on Pacific salmon has been extensive in Alaska including north through Kotzebue Sound. BOEM and other organizations including the North Pacific Research Board (NPRB) are funding new research on the genetic diversity and population structure of Arctic Gadidae (for example, Arctic, Saffron, and Ice cod) and the new results and ongoing studies are, or will, assist in addressing existing taxonomic complexities (for example, see [appendix A](#) and Nelson and Bouchard, 2013).

Digital Images

Many recent high-quality images of marine fishes were obtained from active Arctic researchers who photographed freshly sampled specimens in the field. For example, most of the images in this report are products of research of Mecklenburg and others (2016). Each photograph is properly attributed with names of providers and date and location of sample collection.

Distribution Maps and Vertical Species Profiles

ArcGIS geographic range maps were developed for each confirmed species from the Chukchi and Beaufort Seas. Vertical distribution profiles were created in Adobe software to portray specific information in a generalized life cycle schemata depicting water column distributions of life stages over continental shelf and slope habitats. The maps and profiles depicting geographic distributions and vertical distribution information are composite products from multiple sources of data collection and observation. A BOEM study with objectives of compiling existing fishery data sets for the Chukchi and Beaufort Seas into an electronic format was not completed in time for use herein. Although the data were acquired through traditional sources, easier access to, and manipulation of these data, in concert with the results of ongoing fishery research, would improve the efficiency and number of Alaskan records in future updates.

Peer Review

USGS standards for science quality (USGS Fundamental Science Practices) were followed (<http://www.usgs.gov/fsp/>) for this study and report. The USGS process includes technical and policy reviews for technical reports and journal publications. For this report, we relied on external subject matter experts due to the diversity of species and ecological topics addressed. The USGS reviews were supported by BOEM technical reviews that included additional internal and external scientists having appropriate ichthyologic expertise.

Operational Definitions

In some cases, especially in the species accounts and synthesis discussions, highly technical information relative to various aspects of marine biogeography is presented. In several disciplinary areas, especially those dealing with quantitative population ecology, special attention to defining the scientific terminology used was needed. To facilitate consistency and understanding, a glossary of key terms was developed as an aide for users. The glossary ([chapter 7](#)) defines many of the more complex terms and quantitative relationships used in the species accounts. Each definition is appropriately cited so that, if they are not clear, additional sources can be quickly accessed and referenced. Other terms commonly used to describe spatial relationships in biogeography, involve ecological scaling considerations of importance to conservation and are described in the section, “[Geospatial Terminology](#).” The terms described in this chapter are used widely throughout the report and, for that reason, are introduced here. Abundance terminology represented a special case where the derivation of a unique classification scheme for the Arctic region was necessary and developed in [chapter 2](#) with application to other chapters as well.

Geospatial Terminology

This study focuses on the biological geography of marine fishes in Alaska’s Arctic Ocean and describes their distribution and abundance using various spatial terms. Some have zoogeographic meaning (for example, realm and province) and others refer to common descriptions of a species occurrence by scale (for example, region, area, and local). The mapping classifications for biogeographic realms and faunal provinces used herein are as described by Lourie and Vincent (2004) and Spalding and others (2007), respectively. The Arctic region, as described by Briggs and Bowan (2012), adds additional clarity to the boundaries of marine provinces by considering the zoogeography of fishes of fishes. For Alaska, Sigler and others (2011) described three provinces that relate to conventional management areas in the United States segments of the northern Bering Sea and the Chukchi and Beaufort Seas.

In each case, the biogeographic concepts relate to ecological patterns and processes, and thus to conservation. Lourie and Vincent (2004, p. 1,005) noted that, “...*biodiversity exists on multiple scales biologically, spatially and temporally, and these scales are, to some extent, independent of one another.*” They related spatial scales of conservation planning to physical, temporal, and biological patterns and processes, to mapping scale as follows (Lourie and Vincent (2004, p. 1,007):

- (1) *global approximate map scale 1:100 million – ocean basin divisions, major currents, global climate, historical biogeography, highly migratory species, large marine ecosystems (LMEs);*
- (2) *regional, 1:10 million – regional currents,*

historical biogeography, genetic connectivity, widespread species, individual LMEs or ecoregion;

- (3) *provincial, 1:1 million – small scale currents, upwelling, genetic connectivity, major habitats with LME or ecoregion restricted-range species, bioregion;*
- (4) *local, 1:500,000 – local gyres and eddies, watershed runoff, coastal geomorphology, ecological connectivity, planning unit;*
- (5) *site, 1:10,000 – tides, watershed runoff, ecological connections, habitat specialists, habitats within planning unit, zoning for marine protected areas.*

The scales are germane because they give additional texture to how (unless otherwise specified) the concepts of realm and province should be understood and, generally, the geographic distinctions between “region” and “area” as used in this report. Typically, “region” is used to refer to large-scale patterns and process (for example, scale 3 in Lourie and Vincent [2004]) and “area” refers to local or site specific ecological conditions (for example, scales 4 and 5).

The use of other geographical or habitat terms, including inshore, coastal, nearshore, and offshore in this report are somewhat more ambiguous with respect to meaning or area involved. For example, in some instances “coastal” may have a legal meaning with respect to a state’s territorial waters, or meteorological and oceanographic meaning with respect to wave influence. Similarly, “nearshore” also may have multiple oceanographic meanings including reference to littoral zone components, photic zones, or waters extending to the shelf break. There can be considerable overlap in area with respect to how these terms are applied with respect to the notion of “close to shore.” In an attempt to reduce such ambiguity, some practical distinctions are made for these terms based on scientific knowledge of Arctic fish habitat characteristics (depth, temperature and salinity influences, and distance from shore) and realities of their sampling by proven fisheries techniques:

- Inshore reflects the area from shoreline to depths of 2 m. This reflects the shallow water areas where much of the historical fish baseline data were collected in the Chukchi and Beaufort Seas surveys with fyke net and gill net sampling techniques. Freshwater influences typically are important seasonally, especially in the Beaufort Sea.
- Coastal habitats can include lower reaches of rivers and streams, deltas, inshore, and deep waters adjacent to the coast. Lagoons and shallow waters adjacent to outer coasts of barrier islands are included in the category. Freshwater influences are seasonally important in coastal habitats.
- Nearshore, or nearshore marine, as used herein, generally refers to those waters located inside the 10-m isobath. This depth is often where large (class 1) oceanographic vessels cease to operate for safety reasons. Additionally, the presence of brackish water

can be a factor in describing the distance that nearshore waters occur from the coast. For example, during summer, brackish waters can extend more than 10 km offshore and often overlay cold more saline water masses deep in the water column. The nearshore includes inshore and coastal habitats, but tend to extend farther offshore.

- Offshore as used here describes shelf, slope, and deep-water habitats located beyond the nearshore.
- Nearshore-Marine refers to a descriptive adaptive model in this report as evidenced by those species having distribution patterns that are widespread over nearshore, shelf, and slope environments. An example would be the distribution of Arctic Cod in the United States Chukchi and Beaufort Seas.

A fish species can be distributed in one or more habitats in time and space. This report provides a comprehensive examination of how fish in Arctic environments have adapted, which depending on life strategy adaptations, represents a continuum of habitats on a gradient from freshwater to marine. For each species, patterns of habitat use are multi-dimensional with respect to areas and volumes occupied, space and time, and life cycle requirements for reproduction, growth and survival, dispersal, and other life functions. The distribution and abundance of life stages for each species throughout the water column are presented in [chapter 3](#) to capture these relationships in the context of life zones (Allen and Smith, 1988) that portray key aspects of reproductive ecology by depth and location. Depictions in this report are unique for this region because the shelf break is depicted at 75 m on the basis of the bathymetry of the Chukchi and western Beaufort Seas.

Organization of the Catalog

The BOEM requested that the USGS conduct a synthesis of available environmental information addressing Arctic marine fish biology and ecology in the following areas: environmental and biological constraints; oceanographic overview; adaptation and acclimation; life history strategies; fish assemblages; foraging and feeding behavior; bioenergetics; use of time and space; growth and reproduction; migration; predation, parasitism, competition, and mutualism; dynamics of population abundance and production; conservation; subsistence; climate change; and information needs. The resultant *Arctic Marine Fish Ecology Catalog* is organized in eight chapters, a glossary, and three appendixes.

[Chapters 1–3](#) provide detailed characterizations of the United States Arctic region’s environmental setting and marine fish biodiversity and establish much of the physical and biological background information supporting ecological synthesis and management objectives of this project. [Chapter 1](#) provides a broad overview of the Arctic marine environment

and scientific goals and methods of this synthesis as it pertains to BOEM information needs as well as other users. Additional purposes are to describe the meaning of commonly used oceanographic and zoogeographic terminologies to avoid possible ambiguity associated with their use herein. [Chapter 2](#) presents an inventory of the marine fish known from the United States Chukchi and Beaufort Seas including an analysis of changes resulting from new data and information acquired from the region since the early 2000s. [Chapter 3](#) includes more than 100 species accounts and describes current knowledge about the biology and ecology for each marine fish known from the United States Arctic region using information from studies in Alaska and elsewhere within the species ranges. The species accounts are quick references to some topics (for example, climate change) and are described in more detail in [chapters 5–6](#).

[Chapter 4](#) provides a synthesis of information that, in its entirety, addresses the ecological objectives requested by BOEM. The USGS approach to this synthesis was to evaluate data and information about the descriptive and interpretive components of biogeography as described by Nelson (2006). By necessity, much information is incorporated by reference in this description of historical and environmental influences on marine fish presence and patterns of distribution and abundance in the United States Arctic marine environment.

[Chapter 5](#) focuses on the modeling of climate change effects on the distribution of Arctic and Saffron cod in the Bering Sea. The Bering Sea was selected because of the extensive fishery data that are available from this region. Arctic and Saffron cod were selected because they are notably important in Arctic food webs and subsistence fisheries north of the Bering Strait. Our emphasis on modeling approach and distributional effects represent an important potential application to the Chukchi and Beaufort Seas as Arctic fishery data become more widely accessible in electronic formats. The results of modeling in the Bering Sea are considered in light of potential warming effects in the Chukchi and Beaufort Seas.

[Chapter 6](#) focuses on how scientific information about the Arctic marine fish can inform policy and the conservation and management of Arctic species. Information needs relate to environmental assessment for OCS oil and gas development, fisheries management, and understanding potential effects of climate change. A traits-based approach can be used to assist resource management until population-level information and dynamics are better known. The information needs for high-priority species identified in [chapter 3](#) also are evaluated with respect to future research and ecosystem-based management.

This report includes many descriptive and quantitative terms and complex concepts common in scientific literature. A “Glossary of Ecological Terms” is provided in [chapter 7](#) to reduce confusion about these terms and concepts as used in this report. [Chapter 8](#) provides a list of scientific references cited in narrative sections of the report. Each species account presented in [chapter 3](#) includes a listing of the scientific reports and articles used.

[Appendix A](#) describes age, weight, and size relationships for marine fish species where data are available. The information supports life history and population dynamic sections of the report in [chapters 4 and 6](#). [Appendix B](#) provides additional information about the availability of recent fishery investigations supported by BOEM as well ongoing studies, and topics where new information is anticipated. [Appendix C](#) provides summaries of the models developed to examine temperature effects on Arctic and Saffron cods in [chapter 5](#).

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assistance with final publication will be forever appreciated. Tony DeGange's (formerly USGS Alaska Science Center) literature review in support of USGS Circular 1370 provided important background on the regional setting of the Chukchi-Beaufort Sea study area. The authors are especially grateful for the efforts of the USGS Science Publishing Network, Tacoma Publishing Service Center for producing this report and specifically to acknowledge Debra Grillo for editorial assistance and William Gibbs for the cover design.

Summary

The need for reliable fishery information for National Environmental Policy Act analysis related to offshore oil and gas development in Chukchi and Beaufort Sea Planning Areas is described. The conduct of systematic surveys in these areas has been hampered by environmental and budgetary constraints and thus, in many respects, the existing data remain scattered and fragmented and are difficult to access. Lack of access to quantitative catch and observational data from ongoing research precluded our full use of modern geospatial technologies. Despite, this limitation, new information and visualization products were developed for each species of confirmed presence in the study area. The biological and ecological information presented in this report is regional in scale and, unless otherwise noted, local variations in seasonal fish habitat and abundance can be found in the literature cited. Given the spatial resolution of existing data, background descriptions of the physical and biological environments of the Chukchi and Beaufort Seas are presented at the landscape scale. All methods, terminologies, and operational definitions for this study are described. The organization of the report and linkages between chapters are described as they relate to the Bureau of Ocean Energy Management's information need for this synthesis.

Chapter 2. Alaska Arctic Marine Fish Inventory

By Lyman K. Thorsteinson¹

Abstract

Several other marine fishery investigations, including efforts for Arctic data recovery and regional analyses of range extensions, were ongoing concurrent to this study. These included Bureau of Ocean Energy Management-sponsored research in the Chukchi Sea and nearshore and transboundary surveys in the Beaufort Sea. New collections in the Chukchi Sea and Chukchi Borderland also were being obtained through National Oceanic and Atmospheric Administration's multidisciplinary Russian-American Long-term Census of the Arctic (RUSALCA) program. These were major exploratory efforts and represented potential sources of new marine species information. Building on the "*Fishes of Alaska*," an updated checklist was constructed of known and probable marine fishes with catch data obtained in these studies. There are 109 known species from 24 families of marine fish from the United States High Arctic, with 97 species reported from the Chukchi Sea and 83 from the Beaufort Sea. As this synthesis was being done, changes in the confirmation process, based on morphological and genetic analysis, were captured as information became available in scientific publications. The known species are reviewed with respect to taxonomic, geographic, and large-scale abundance considerations. Each species' zoogeographic pattern with respect to our understanding of broadly defined evolutionary origins is noted. Changes in species nomenclature are described as they relate to newly described standards.

¹U.S. Geological Survey.

Introduction

A large number of Arctic fisheries studies were started following the publication of the *Fishes of Alaska* (Mecklenburg and others, 2002). Although the results of many of these efforts are not yet available, those involving field sampling are important new sources of biodiversity information including voucher specimens and genetic confirmation of a species existence and phylogenetic relationships. The addition of new morphological data and genetic analyses is important because despite many efforts, systematic sampling in the Chukchi and Beaufort Seas has been logistically difficult due to ice, storms, and platform limitations. Further variations in research missions and sampling methods have hampered regional assessments of diversity, relative abundance, and habitat importance because the resulting database is sparse and fragmented in time and space. Quantitative evaluations of abundance based on catch data are difficult, although local variability and persistent hot spots are known to exist. This chapter builds on the species inventory established by the *Fishes of Alaska* by incorporating new species information obtained primarily in Bureau of Ocean Energy Management (BOEM)-sponsored ([appendix A](#)) and National Oceanic and Atmospheric Administration (NOAA) Russian-American Long-term Census of the Arctic (RUSALCA) surveys (Mecklenburg and Steinke, 2015). This information is complemented with a uniformly applied assessment of relative abundance and qualitative analysis of population viability based on present day understanding of endemism.

Checklist of Marine Fish

The updated checklist of confirmed occurrences is significant because it incorporates the new knowledge gained since the publication of the *Fishes of Alaska* (Mecklenburg and others, 2002). It includes the most recent information from the Pacific Arctic Region including the Chukchi and Beaufort Seas from Mecklenburg and Steinke (2015). Unlike Mecklenburg and Steinke (2015), this checklist includes diadromous species from the family Salmonidae as these species spend significant portions of their lives in the marine environment and have great importance in subsistence lifestyles. Even though this list represents a significant advance, many uncertainties remain about the true composition of the marine fish assemblage. For this reason, information about probable occurrences of marine fishes is included in this chapter. The uncertainties result in part because the taxonomy of Arctic fishes was still in its infancy at the turn of the 21st century, with many species misidentified in historical literature and others not recognized from the region due to sampling inadequacies (Mecklenburg and others, 2011). The scientific improvements in knowledge about the Arctic region's biodiversity reflect new data collection and, importantly, advances in taxonomic and zoogeographic understanding that have resulted from genetic resolution of issues that morphological studies failed to notice or resolve (for example, Mecklenburg and others, 2011; Lynghammar and others, 2012; Mecklenburg and Steinke, 2015). The Arctic marine fish inventory, presented in [table 2.1](#), is a major biodiversity achievement, which documents known (verified) marine fish species from the Chukchi and Beaufort Seas.

Although advances have been significant in recent years, the taxonomy, including naming of Arctic marine fishes remains a source of inconsistency and confusion between leading authorities such as the American Fisheries Society (AFS), California Academy of Sciences *Catalog of Fishes*, Integrated Taxonomic Information Systems, and World Register of Marine Fishes, for members of several families. This is especially true for common names associated with different languages (Mecklenburg and others, 2013). Changes in nomenclature are not uncommon in the classification process, especially for lesser-studied species, and can affect the regional use of scientific and common names in literature (Eschmeyer and others, 2010). Thus, in creating checklists, it is important to cite the authority used and rationale for inclusion or naming of a particular species where

disagreement occurs. In this report, the marine fish inventory presented in [table 2.1](#) reflects the editors' understanding of the classification and nomenclature of marine Arctic fishes. In most instances, the scientific and common names are those listed by Page and others (2013) and Eschmeyer and others (2015). However, in several instances where differences exist, we relied on the work of contemporary Arctic specialists and note areas of transitional change with respect to common names for species.

The nomenclature of a small number of fish species from four families (Squalidae, Gadidae, Liparidae, and Zoarcidae) are in transition and reflect areas where we disagree with the AFS nomenclature (Page and others, 2013). For purposes of this report, we decided to agree with the AFS nomenclature for *Boreogadus saida* due to the species' significance to the region's marine ecology. Although, we acknowledge that Polar Cod is emerging as the widely accepted common name for *B. saida*, we decided to use Arctic Cod (as recommended by Page and others [2013]) to avoid any confusion with new and historical Alaska literature. In contrast, we decided to use Ice Cod, not Polar Cod, as the common name for *Arctogadus glacialis*. This decision was made to avoid any potential ambiguity and confusion with *B. saida*. The use of Ice Cod is emerging nomenclature in scientific literature (for example, Arctic Council's Conservation of Arctic Flora and Fauna) and clarification of the vernacular name is supported by genetic analysis (Nelson and Bouchard, 2013). Regarding other families and species, we recognize (1) Spotted Spiny Dogfish instead of Pacific Spiny Dogfish as the common name for *Squalus suckleyi* (Squalidae, see Lynghammar and others [2012]); (2) Estuarine Eelpout, not Polar Eelpout as the common name for *L. turneri* (Mecklenburg and others, 2002); and (3) Arctic Sand Lance for *Ammodytes hexapterus* following Orr and others (2015) and Mecklenburg and others (2016). Other more recent changes (for example, Mecklenburg and others, 2016) include changes in the scientific names for Capelin (now *Mallotus catervarius*) and Arctic Flounder (now *Liopsetta glacialis*). In every case, the scientific name of a fish is conclusive for the species being described.

One hundred nine (109) species from 24 families are confirmed with 97 verified occurrences from the Chukchi Sea and 83 from the Beaufort Sea ([table 2.1](#)). Mecklenburg and others (2002) suggested other species (<20) also might be present and it remains likely that the total number will change with additional field sampling, examination of existing voucher specimens, and with shifts in range due to climate warming. Mecklenburg and others (2007, 2011, 2014, 2016)

and Mecklenburg and Steinke (2015) have recently confirmed the presence of at least 18 species in the Alaskan Chukchi and Beaufort Seas that were not previously verified to be present: *Somniosus pacificus*, *Amblyraja hyperborea*, *Bathyrāja parmifera*, *Myoxocephalus polyacanthocephalus*, *Triglops nybelini*, *Hypsogonus quadricornis*, *Careproctus reinhardtii*, *Liparis bathyartcticus*, *Paraliparis bathybius*, *Lycenchelys kolthoffi*, *Lycodes adolfi*, *L. frigidus*, *L. jugoricus*, *L. marisalbi*, *L. pallidus*, *L. reticulatus*, *Anarhichas denticulatus*, and *Zaprora silenus*. The status of three of these species was previously described as being of “probable” occurrence in the provisional checklist developed for this study:

- **Pacific Sleeper Shark** (*Somniosus pacificus*): Benz and others (2004) reported a new occurrence of the species from an animal found washed onshore at Point Hope, Alaska. The animal remains were highly decomposed; this occurrence was reviewed by Lynghammar and others (2012), who determined that the physical condition of the shark suggested its death from outside the Chukchi Sea. In 2014, a Pacific Sleeper Shark was taken alive by a seal hunter in a southeastern Chukchi Sea lagoon. Parts and photographs were archived in the University of Alaska Museum. This is a mesobenthopelagic shark species recorded as deep as 2,205 m. It is abundant in the southern Bering Sea and the Gulf of Alaska, and reaches 4.4 m TL or more (Mecklenburg and others (2016).
- **Alaska Skate** (*Bathyrāja parmifera*): Mecklenburg and others (2011 Online Resource 1) reported that two specimens were found washed ashore in the Chukchi Sea. Examination of one of the specimens indicated advanced deterioration and possible death elsewhere in the northern Bering Sea. Later, Mecklenburg and others (2016) reported that in 2012 an adult specimen was taken alive in the southern Chukchi Sea. Mecklenburg and others (2016) also reported the collection locations of other beachcast specimens and spent egg cases from the Chukchi and Beaufort Sea. The authors noted the species can reach a size of 135 cm TL. They also reported that the occurrences of the Alaska Skate in the Chukchi Sea could indicate a northerly shift in its distribution.

- **Pale Eelpout** (*Lycodes pallidus*): Mecklenburg and others (2016) identified this species in a collection made in 1971 in the Beaufort Sea and confirmed presence in the Beaufort Sea again in voucher collections from 2012 and 2013. Common at least in the Greenland, Barents, and Kara Seas, otherwise found nearly circumpolar. It is epi-meso-bathybenthic and lives on muddy substrate at depths of 11–1,750 m and temperatures of -1.8–3.7 °C. Maximum size is 28.9 cm SL or more (Mecklenburg and others, 2016).

The updated checklist was examined with respect to new species occurrences and differences in the geographic distributions reported in the *Fishes of Alaska* (Mecklenburg and others, 2002) for the Chukchi and Beaufort Seas (table 2.2). Our decision to include two species, *Artediellus ochotensis* and *Lumpenus sagitta*, on the checklist was made recognizing that uncertainty exists about their occurrence in the Chukchi Sea (Mecklenburg and others, 2016). As an example, Mecklenburg and others (2016) state “Many of the specimens that had been previously identified as “*A. ochotensis*” on further investigation have been found to be *A. scaber*.” However, not all of the identifications were refuted. In the case of *L. sagitta*, Mecklenburg and others (2011) described a range extension for this species into the Chukchi Sea based on a single specimen. Presently, Mecklenburg and others (2016) raise doubts “The provenance of a specimen reported to be a possible record of *L. sagitta* from the Chukchi Sea...is uncertain.” The uncertainty stems from conflicting issues in the 1960s field collection data and location of sampling (possibly not Chukchi Sea), and not with species identification. Until these issues can be resolved with species confirmations with new specimens, we chose to retain them on the checklist. As a final note, we recognize *Icelus spiniger* as a valid species from the Chukchi Sea noting that genetic similarities with *I. spatula* specimens from the region raise questions about relationships. Other technical and unresolved issues for the marine fishes in the Chukchi and Beaufort Seas are described in Mecklenburg and Steinke (2015) and Mecklenburg and others (2016).

Table 2.1. Inventory of confirmed species of Arctic marine fish in the United States Chukchi and Beaufort Seas, Alaska.

[Blank cells indicate that the species occurrence has not been confirmed in that sea. Marine waters out to the U.S. Exclusive Economic Zone (200-mile limit) are included]

Family	Scientific name	Common name	Confirmed occurrence	
			Chukchi Sea	Beaufort Sea
Petromyzontidae	<i>Entosphenus tridentatus</i>	Pacific Lamprey	X	
Petromyzontidae	<i>Lethenteron camtschaticum</i>	Arctic Lamprey	X	X
Squalidae	<i>Squalus suckleyi</i>	Spotted Spiny Dogfish	X	
Somniosidae	<i>Somniosus pacificus</i>	Pacific Sleeper Shark	X	
Rajidae	<i>Amblyraja hyperborea</i>	Arctic Skate		X
Rajidae	<i>Bathyraxa parmifera</i>	Alaska Skate	X	
Clupeidae	<i>Clupea pallasii</i>	Pacific Herring	X	X
Osmeridae	<i>Hypomesus olidus</i>	Pond Smelt	X	
Osmeridae	<i>Mallotus catervarius</i>	Pacific Capelin	X	X
Osmeridae	<i>Osmerus dentex</i>	Arctic Smelt	X	X
Salmonidae	<i>Coregonus autumnalis</i>	Arctic Cisco	X	X
Salmonidae	<i>Coregonus laurettae</i>	Bering Cisco	X	X
Salmonidae	<i>Coregonus nasus</i>	Broad Whitefish	X	X
Salmonidae	<i>Coregonus pidschian</i>	Humpback Whitefish	X	X
Salmonidae	<i>Coregonus sardinella</i>	Least Cisco	X	X
Salmonidae	<i>Oncorhynchus gorbuscha</i>	Pink Salmon	X	X
Salmonidae	<i>Oncorhynchus keta</i>	Chum Salmon	X	X
Salmonidae	<i>Oncorhynchus kisutch</i>	Coho Salmon	X	X
Salmonidae	<i>Oncorhynchus nerka</i>	Sockeye Salmon	X	X
Salmonidae	<i>Oncorhynchus tshawytscha</i>	Chinook Salmon	X	X
Salmonidae	<i>Salvelinus malma</i>	Dolly Varden	X	X
Salmonidae	<i>Stenodus leucichthys</i>	Inconnu	X	
Myctophidae	<i>Bentosema glaciale</i>	Glacier Lanternfish	X	
Gadidae	<i>Arctogadus glacialis</i>	Ice Cod	X	X
Gadidae	<i>Boreogadus saida</i>	Arctic Cod	X	X
Gadidae	<i>Eleginus gracilis</i>	Saffron Cod	X	X
Gadidae	<i>Gadus chalcogrammus</i>	Walleye Pollock	X	X
Gadidae	<i>Gadus macrocephalus</i>	Pacific Cod	X	X
Gasterosteidae	<i>Gasterosteus aculeatus</i>	Threespine Stickleback	X	X
Gasterosteidae	<i>Pungitius pungitius</i>	Ninespine Stickleback	X	X
Hexagrammidae	<i>Hexagrammos stelleri</i>	Whitespotted Greenling	X	X
Cottidae	<i>Artediellus ochotensis</i>	Okhotsk Hookear Sculpin	X	
Cottidae	<i>Artediellus scaber</i>	Hamecon	X	X
Cottidae	<i>Enophrys diceraus</i>	Antlered Sculpin	X	X
Cottidae	<i>Gymnocanthus tricuspis</i>	Arctic Staghorn Sculpin	X	X
Cottidae	<i>Hemilepidotus papilio</i>	Butterfly Sculpin	X	
Cottidae	<i>Icelus bicornis</i>	Twohorn Sculpin	X	X
Cottidae	<i>Icelus spatula</i>	Spatulate Sculpin	X	X
Cottidae	<i>Icelus spiniger</i>	Thorny Sculpin	X	
Cottidae	<i>Megalocottus platycephalus</i>	Belligerent Sculpin	X	X
Cottidae	<i>Microcottus sellaris</i>	Brightbelly Sculpin	X	
Cottidae	<i>Myoxocephalus jaok</i>	Plain Sculpin	X	X
Cottidae	<i>Myoxocephalus polyacanthocephalus</i>	Great Sculpin	X	
Cottidae	<i>Myoxocephalus quadricornis</i>	Fourhorn Sculpin	X	X
Cottidae	<i>Myoxocephalus scorpioides</i>	Arctic Sculpin	X	X
Cottidae	<i>Myoxocephalus scorpius</i>	Shorthorn Sculpin	X	X
Cottidae	<i>Trichocottus brashnikovi</i>	Hairhead Sculpin	X	X
Cottidae	<i>Triglops nybelini</i>	Bigeye Sculpin	X	X
Cottidae	<i>Triglops pingelii</i>	Ribbed Sculpin	X	X
Hemitriptidae	<i>Blepsias bilobus</i>	Crested Sculpin	X	
Hemitriptidae	<i>Nautichthys pribilovius</i>	Eyeshade Sculpin	X	X
Psychrolutidae	<i>Cottunculus microps</i>	Polar Sculpin		X
Psychrolutidae	<i>Eurymen gyrinus</i>	Smoothcheek Sculpin	X	
Agonidae	<i>Aspidophoroides monopterygius</i>	Alligatorfish	X	X
Agonidae	<i>Aspidophoroides olrikii</i>	Arctic Alligatorfish	X	X

Table 2.1. Inventory of confirmed species of Arctic marine fish in the United States Chukchi and Beaufort Seas, Alaska.—Continued

Family	Scientific name	Common name	Confirmed occurrence	
			Chukchi Sea	Beaufort Sea
Agonidae	<i>Hypsagonus quadricornis</i>	Fourhorn Poacher	X	
Agonidae	<i>Leptagonus decagonus</i>	Atlantic Poacher	X	X
Agonidae	<i>Occella dodecaedron</i>	Bering Poacher	X	
Agonidae	<i>Pallasina barbata</i>	Tubenose Poacher	X	
Agonidae	<i>Podothecus veterinus</i>	Veteran Poacher	X	X
Cyclopteridae	<i>Eumicrotremus andriashevi</i>	Pimpled Lumpsucker	X	
Cyclopteridae	<i>Eumicrotremus derjugini</i>	Leatherfin Lumpsucker	X	X
Liparidae	<i>Careproctus reinhardti</i>	Sea Tadpole	X	X
Liparidae	<i>Liparis bathyarticus</i>	Nebulous Snailfish	X	X
Liparidae	<i>Liparis fabricii</i>	Gelatinous Seasnail	X	X
Liparidae	<i>Liparis gibbus</i>	Variegated Snailfish	X	X
Liparidae	<i>Liparis tunicatus</i>	Kelp Snailfish	X	X
Liparidae	<i>Paraliparis bathybius</i>	Black Seasnail	X	X
Zoarcidae	<i>Gymnelus hemifasciatus</i>	Halfbarred Pout	X	X
Zoarcidae	<i>Gymnelus viridis</i>	Fish Doctor	X	X
Zoarcidae	<i>Lycenchelys kolthoffi</i>	Checked Wolf Eel		X
Zoarcidae	<i>Lycodes adolfi</i>	Adolf's Eelpout		X
Zoarcidae	<i>Lycodes eudipleurostictus</i>	Doubleline Eelpout		X
Zoarcidae	<i>Lycodes frigidus</i>	Glacial Eelpout	X	X
Zoarcidae	<i>Lycodes jugoricus</i>	Shulupaoluk		X
Zoarcidae	<i>Lycodes marisalbi</i>	White Sea Eelpout		X
Zoarcidae	<i>Lycodes mucosus</i>	Saddled Eelpout	X	X
Zoarcidae	<i>Lycodes palearis</i>	Wattled Eelpout	X	X
Zoarcidae	<i>Lycodes pallidus</i>	Pale Eelpout		X
Zoarcidae	<i>Lycodes polaris</i>	Polar Eelpout	X	X
Zoarcidae	<i>Lycodes raridens</i>	Marbled Eelpout	X	X
Zoarcidae	<i>Lycodes reticulatus</i>	Arctic Eelpout		X
Zoarcidae	<i>Lycodes rossi</i>	Threespot Eelpout		X
Zoarcidae	<i>Lycodes sagittarius</i>	Archer Eelpout		X
Zoarcidae	<i>Lycodes seminudus</i>	Longear Eelpout	X	X
Zoarcidae	<i>Lycodes squamiventer</i>	Scalebelly Eelpout		X
Zoarcidae	<i>Lycodes turneri</i>	Estuarine Eelpout	X	X
Stichaeidae	<i>Acantholumpenus mackayi</i>	Blackline Prickleback	X	
Stichaeidae	<i>Anisarchus medius</i>	Stout Eelblenny	X	X
Stichaeidae	<i>Chirolophis snyderi</i>	Bearded Warbonnet	X	
Stichaeidae	<i>Eumesogrammus praecisus</i>	Fourline Snakeblenny	X	X
Stichaeidae	<i>Leptoclinus maculatus</i>	Daubed Shanny	X	X
Stichaeidae	<i>Lumpenus fabricii</i>	Slender Eelblenny	X	X
Stichaeidae	<i>Lumpenus sagitta</i>	Snake Prickleback	X	
Stichaeidae	<i>Stichaeus punctatus</i>	Arctic Shanny	X	X
Pholidae	<i>Pholis fasciata</i>	Banded Gunnel	X	
Anarhichadidae	<i>Anarhichas denticulatus</i>	Northern Wolffish	X	X
Anarhichadidae	<i>Anarhichas orientalis</i>	Bering Wolffish	X	X
Zaproridae	<i>Zaprora silenus</i>	Prowfish	X	
Ammodytidae	<i>Ammodytes hexapterus</i>	Arctic Sand Lance	X	X
Pleuronectidae	<i>Hippoglossoides robustus</i>	Bering Flounder	X	X
Pleuronectidae	<i>Hippoglossus stenolepis</i>	Pacific Halibut	X	
Pleuronectidae	<i>Limanda aspera</i>	Yellowfin Sole	X	X
Pleuronectidae	<i>Limanda proboscidea</i>	Longhead Dab	X	X
Pleuronectidae	<i>Limanda sakhalinensis</i>	Sakhalin Sole	X	
Pleuronectidae	<i>Liopsetta glacialis</i>	Arctic Flounder	X	X
Pleuronectidae	<i>Platichthys stellatus</i>	Starry Flounder	X	X
Pleuronectidae	<i>Pleuronectes quadrituberculatus</i>	Alaska Plaice	X	
Pleuronectidae	<i>Reinhardtius hippoglossoides</i>	Greenland Halibut	X	X
Totals:		109	97	83

Table 2.2. Changes in occurrence and geographic distribution of Arctic marine fishes in the Chukchi and Beaufort Seas since 2002.

[Changes were made since publication of Mecklenburg and others (2002)]

Scientific name	Common name	New occurrence	Geographic distribution	
			Range change	No change
<i>Entosphenus tridentatus</i>	Pacific Lamprey			X
<i>Lethenteron camtschaticum</i>	Arctic Lamprey			X
<i>Squalus suckleyi</i>	Spotted Spiny Dogfish		X	
<i>Somniosus pacificus</i>	Pacific Sleeper Shark	X	X	
<i>Amblyraja hyperborea</i>	Arctic Skate	X	X	
<i>Bathyraja parmifera</i>	Alaska Skate	X	X	
<i>Clupea pallasii</i>	Pacific Herring			X
<i>Hypomesus olidus</i>	Pond Smelt		X	
<i>Mallotus catervarius</i>	Pacific Capelin			X
<i>Osmerus dentex</i>	Arctic Smelt			X
<i>Coregonus autumnalis</i>	Arctic Cisco		X	
<i>Coregonus laurettae</i>	Bering Cisco			X
<i>Coregonus nasus</i>	Broad Whitefish			X
<i>Coregonus pidschian</i>	Humpback Whitefish			X
<i>Coregonus sardinella</i>	Least Cisco			X
<i>Oncorhynchus gorbuscha</i>	Pink Salmon			X
<i>Oncorhynchus keta</i>	Chum Salmon			X
<i>Oncorhynchus kisutch</i>	Coho Salmon		X	
<i>Oncorhynchus nerka</i>	Sockeye Salmon		X	
<i>Oncorhynchus tshawytscha</i>	Chinook Salmon			X
<i>Salvelinus malma</i>	Dolly Varden			X
<i>Stenodus leucichthys</i>	Inconnu		X	
<i>Benthosea glaciale</i>	Glacier Lanternfish			X
<i>Arctogadus glacialis</i>	Ice Cod		X	
<i>Boreogadus saida</i>	Arctic Cod			X
<i>Eleginus gracilis</i>	Saffron Cod			X
<i>Gadus chalcogrammus</i>	Walleye Pollock		X	
<i>Gadus macrocephalus</i>	Pacific Cod		X	
<i>Gasterosteus aculeatus</i>	Threespine Stickleback			X
<i>Pungitius pungitius</i>	Ninespine Stickleback			X
<i>Hexagrammos stelleri</i>	Whitespotted Greenling			X
<i>Arctediellus ochotensis</i>	Okhotsk Hookear Sculpin			X
<i>Arctediellus scaber</i>	Hamecon			X
<i>Enophrys diceraus</i>	Antlered Sculpin			X
<i>Gymnocanthus tricuspis</i>	Arctic Staghorn Sculpin			X
<i>Hemilepidotus papilio</i>	Butterfly Sculpin		X	
<i>Icelus bicornis</i>	Twohorn Sculpin		X	
<i>Icelus spatula</i>	Spatulate Sculpin			X
<i>Icelus spiniger</i>	Thorny Sculpin	X	X	
<i>Megalocottus platycephalus</i>	Belligerent Sculpin			X
<i>Microcottus sellaris</i>	Brightbelly Sculpin		X	
<i>Myoxocephalus jaok</i>	Plain Sculpin		X	
<i>Myoxocephalus polyacanthocephalus</i>	Great Sculpin	X	X	
<i>Myoxocephalus quadricornis</i>	Fourhorn Sculpin			X
<i>Myoxocephalus scorpioides</i>	Arctic Sculpin			X
<i>Myoxocephalus scorpius</i>	Shorthorn Sculpin			X
<i>Trichocottus brashnikovii</i>	Hairhead Sculpin		X	
<i>Triglops nybelini</i>	Bigeye Sculpin	X	X	
<i>Triglops pingelii</i>	Ribbed Sculpin		X	
<i>Blepsias bilobus</i>	Crested Sculpin			X
<i>Nautichthys pribilovius</i>	Eyeshade Sculpin		X	
<i>Cottunculus microps</i>	Polar Sculpin		X	
<i>Eurymen gyrinus</i>	Smoothcheek Sculpin			X
<i>Aspidophoroides monopterygius</i>	Alligatorfish		X	
<i>Aspidophoroides olrikii</i>	Arctic Alligatorfish			X

Table 2.2. Changes in occurrence and geographic distribution of Arctic marine fishes in the Chukchi and Beaufort Seas since 2002.—Continued

Scientific name	Common name	New occurrence	Geographic distribution	
			Range change	No change
<i>Hypsagonus quadricornis</i>	Fourhorn Poacher	X	X	
<i>Leptagonus decagonus</i>	Atlantic Poacher		X	
<i>Occella dodecaedron</i>	Bering Poacher		X	
<i>Pallasina barbata</i>	Tubenose Poacher		X	
<i>Podothecus veterus</i>	Veteran Poacher		X	
<i>Eumicrotremus andriashevi</i>	Pimpled Lumpsucker			X
<i>Eumicrotremus derjugini</i>	Leatherfin Lumpsucker		X	
<i>Careproctus reinhardti</i>	Sea Tadpole	X	X	
<i>Liparis bathyarticus</i>	Nebulous Snailfish	X	X	
<i>Liparis fabricii</i>	Gelatinous Seasnail		X	
<i>Liparis gibbus</i>	Variegated Snailfish			X
<i>Liparis tunicatus</i>	Kelp Snailfish			X
<i>Paraliparis bathybius</i>	Black Seasnail	X	X	
<i>Gymnelus hemifasciatus</i>	Halfbarred Pout		X	
<i>Gymnelus viridis</i>	Fish Doctor		X	
<i>Lycenchelys kolthoffi</i>	Checked Wolf Eel	X	X	
<i>Lycodes adolfi</i>	Adolf's Eelpout	X	X	
<i>Lycodes eudipleurostictus</i>	Doubleline Eelpout			X
<i>Lycodes frigidus</i>	Glacial Eelpout	X	X	
<i>Lycodes jugoricus</i>	Shulupaoluk	X	X	
<i>Lycodes marisalbi</i>	White Sea Eelpout	X	X	
<i>Lycodes mucosus</i>	Saddled Eelpout			X
<i>Lycodes palearis</i>	Wattled Eelpout			X
<i>Lycodes pallidus</i>	Pale Eelpout	X	X	
<i>Lycodes polaris</i>	Polar Eelpout			X
<i>Lycodes ravidens</i>	Marbled Eelpout		X	
<i>Lycodes reticulatus</i>	Arctic Eelpout	X	X	
<i>Lycodes rossi</i>	Threespot Eelpout			X
<i>Lycodes sagittarius</i>	Archer Eelpout			X
<i>Lycodes seminudus</i>	Longear Eelpout		X	
<i>Lycodes squamiventer</i>	Scalebelly Eelpout		X	
<i>Lycodes turneri</i>	Estuarine Eelpout		X	
<i>Acantholumpenus mackayi</i>	Blackline Prickleback			X
<i>Anisarchus medius</i>	Stout Eelblenny			X
<i>Chirolophis snyderi</i>	Bearded Warbonnet			X
<i>Eumesogrammus praecisus</i>	Fourline Snakeblenny		X	
<i>Leptoclinus maculatus</i>	Daubed Shanny		X	
<i>Lumpenus fabricii</i>	Slender Eelblenny			X
<i>Lumpenus sagitta</i>	Snake Prickleback	X	X	
<i>Stichaeus punctatus</i>	Arctic Shanny		X	
<i>Pholis fasciata</i>	Banded Gunnel		X	
<i>Anarhichas denticulatus</i>	Northern Wolffish	X	X	
<i>Anarhichas orientalis</i>	Bering Wolffish			X
<i>Zaprora silenus</i>	Prowfish	X	X	
<i>Ammodytes hexapterus</i>	Arctic Sand Lance			X
<i>Hippoglossoides robustus</i>	Bering Flounder		X	
<i>Hippoglossus stenolepis</i>	Pacific Halibut		X	
<i>Limanda aspera</i>	Yellowfin Sole			X
<i>Limanda proboscidea</i>	Longhead Dab		X	
<i>Limanda sakhalinensis</i>	Sakhalin Sole		X	
<i>Liopsetta glacialis</i>	Arctic Flounder			X
<i>Platichthys stellatus</i>	Starry Flounder			X
<i>Pleuronectes quadrituberculatus</i>	Alaska Plaice		X	
<i>Reinhardtius hippoglossoides</i>	Greenland Halibut			X
Totals: 109		20	59	50

Species Range Extensions

Comparing Arctic marine fish distributions as described by recent studies to similar historical information reveals some significant changes. Some of the changes in distributional patterns relate to increased sampling and new discovery and others to changes in species classifications and nomenclature. Since 2002, 20 new species were confirmed from the Chukchi and Beaufort Seas. By family, the new Alaska records were reported from Somniosidae (1), Rajidae (2), Cottidae (3), Agonidae (1), Liparidae (3), Zoarcidae (7), Stichaeidae (1), Anarhichadidae (1), and Zapruidae (1). The new Alaskan records are valid range extensions resulting from BOEM-sponsored surveys by NOAA (Logerwell and others, 2009; Rand and Logerwell, 2011) and University of Alaska-Fairbanks (UAF) and NOAA's RUSALCA (Mecklenburg and others, 2014; Mecklenburg and Steinke, 2015) or changes in taxonomy and distribution reported by Mecklenburg and others (2011, 2015, 2016).

Extensions to the known ranges for five marine species were reported from trawl collections in the Beaufort Sea by Rand and Logerwell (2011): Walleye Pollock (*Gadus chalcogrammus*), Pacific Cod (*G. macrocephalus*), Festive Snailfish (*Liparis marmoratus*), Bigeye Sculpin (*Trigllops nybelini*), and Eyeshade Sculpin (*Nautichthys pribilovius*). Apparently, Rand and Logerwell (2011) did not notice that the Antlered Sculpin (*Enophrys diceraus*) listed in their tables also was an extension of this species' known range in the Beaufort Sea. This extension was confirmed by Maslenikov and others (2013).

Additional information about the Rand and Logerwell (2011) collection includes:

- **Walleye Pollock** (*Gadus chalcogrammus*): This probably was the first published record from the Beaufort Sea for *G. chalcogrammus*, since the previous record from Elson Lagoon (near Barrow, Alaska) was shown to pertain to *Boreogadus saida* (Mecklenburg and others, 2011, Online Resource 1, p. 15). Rand and Logerwell (2011, p. 484) reported this occurrence from Elson Lagoon incorrectly.
- **Pacific Cod** (*Gadus macrocephalus*): "Major changes in the composition of gadine genera in recent years mean patterns of species distribution are different" (Mecklenburg and others, 2011, Online Resource 1, p. 120). Historically, *G. macrocephalus* from the Beaufort Sea were identified as *G. ogac* (Mecklenburg and others, 2002). Owing to recent DNA studies and similarity in morphology, and the consequent synonymization of *G. ogac* in *G. macrocephalus*, this

species is now recognized to have a broad distribution from the Chukchi Sea and continuing eastward in the Arctic across Canada to Greenland and the White Sea (Mecklenburg and others, 2011, Online Resource 1, p. 120). Given this information, the range extension reported by Rand and Logerwell (2011) was not truly an extension of known range.

- **Bigeye Sculpin** (*Trigllops nybelini*): From Maslenikov and others, 2013, p. 12): "An Arctic species reported from northwest of Alaska in the international waters of the Chukchi Borderland (Mecklenburg et al., 2011), the Beaufort Sea off Alaska (eastward to 71.21836N, 149.90316W by benthic trawl in 2011; C.W. Mecklenburg, personnel [sic.] communication), and from western Canada in Mackenzie Bay and Amundsen Gulf eastward around the Arctic to the Laptev Sea (Pietsch, 1993). Captured in a midwater tow, the specimens reported here from the Beaufort Sea east of Point Barrow are vouchers for the 1st Alaskan records cited by Rand and Logerwell (2011)."
- **Eyesshade Sculpin** (*Nautichthys pribilovius*): From Maslenikov and others, 2013, p. 12) "Known from the Chukchi Sea off Wainwright south through the western and eastern Bering Sea, Sea of Okhotsk, and Sea of Japan, and the Aleutian and Commander Islands to southeastern Alaska, the record cited here provides a voucher for the northern range extension of *Nautichthys pribilovius* into the Beaufort Sea cited by Rand and Logerwell (2011)."

As an additional note, the single specimen reported by Rand and Logerwell (2011) from their 2008 cruise is the first record from the Beaufort Sea, as described by Mecklenburg and others (2011, Online Resource 1, p. 27). Others have been collected in the same area since then (Mecklenburg and others, 2016).

- **Festive Snailfish**: Reports of *L. marmoratus* in the Bering Sea and the Alaskan Arctic have been questioned because the voucher specimens are similar morphologically and genetically to *L. tunicatus* (Mecklenburg and others, 2011, 2016; Mecklenburg and Steinke, 2015). The DNA sequences from all specimens collected in the Bering and Chukchi Seas in recent years with the external appearance described for *L. marmoratus* (Mecklenburg and others, 2002), are identical to sequences from *L. tunicatus*. Mecklenburg and others (2011) did not count this species among those considered valid in their review and list of Arctic marine fishes. The specimens reported by Rand and Logerwell (2011), which would be the only records from the U.S. Arctic, look morphologically the same as the barcoded specimens².

²Mecklenburg and others (2011) questioned the validity of collection records for *L. marmoratus* from the Beaufort Sea. DNA barcoding indicate the species is not valid from the Chukchi or Beaufort Seas but may be found in the Sea of Okhotsk (Mecklenburg and Steinke, 2015).

- **Longear Eelpout** (*Lycodes seminudus*): from Maslenikov and others (2013): *L. seminudus* is an Arctic species known from the Beaufort Sea and the Chukchi slope north of Alaska (Mecklenburg and others, 2011), as well as the Norwegian and Kara Seas. The record cited here extends the range 200 km west in the Beaufort Sea and represents only the second Alaskan record.

Mecklenburg and others (2016, p. 197) reported a significant extension in the northern distribution of the Bearded Warbonnet in sampling conducted off Pt. Barrow:

- **Bearded Warbonnet** (*Chirolophis snyderi*): “The northernmost documented locality is Point Barrow, Alaska, at 71°23’N, 156°29’W, where juvenile specimens were taken in a beach seine in 2012 (e.g., CAS 237946, 2 specimens, each 31 mm). The previously reported northernmost record was from northwest of Point Franklin in the eastern Chukchi Sea (Mecklenburg et al., 2002, 2011; UAM 4582).”

These descriptions highlight the dynamic nature and taxonomic issues associated with documenting or confirming range extensions from the Arctic. In many instances, Alaska records seem to be new because there has been so little previous sampling. Researchers often are not able to review historical collections in light of new taxonomic knowledge. In fairness, the historical data are often difficult to access and interpret because of documented changes in taxonomy and geographical distribution. To illustrate, Rand and Logerwell (2011) noted that Bering Flounder (*Hippoglossoides robustus*) was not reported in Arctic fish sampling by Frost and Lowry (1983) in 1977, nor was it reported north of Point Barrow by Mecklenburg and others (2002). However, additional research by Mecklenburg and others (2011) discovered that this species was distributed eastward through the Beaufort Sea to Bathurst Inlet (Canadian Arctic) as early as 1965.

The Walleye Pollock catches reported by Logerwell and others (2011) were to the north of all larval, age-1, and adult pollock catches depicted by Wyllie Echeverria (1996) for the northeastern Chukchi Sea and the geographic distributions described by Mecklenburg and others (2002). The new Alaskan records, and size of fish captured, raise the possibility that this species, particularly juvenile pollock, may have been misidentified in earlier Beaufort Sea surveys as Polar Cod³. It also raises questions about their potential origins and dispersal into this part of the Arctic Ocean. Walleye Pollock are captured off Norway and thus their dispersal into the Beaufort Sea with possible genetic interchange along the upper slope is plausible. Cold temperatures are constraints to northerly movements and abundance of pollock; therefore, large expansions and swarms, such as those reported for Arctic Cod

(*Boreogadus saida*) by Crawford and others (2012), would not be expected under present environmental conditions.

Other range extensions are reported in Love and others (2005), Mecklenburg and others (2011), Maslenikov and others (2013), Mecklenburg and Steinke (2015), or evaluated more conventionally in the *Pacific Arctic Marine Fishes* guide (Mecklenburg and others, 2016). In addition to the species discussed from the Rand and Logerwell (2011) collection, an annotated list of range extensions provides new distributional information with supporting documentation as available, or appropriate, for citation at this time. The new information results from an increased Arctic research sampling emphasis in offshore marine habitats in the Chukchi and Beaufort Seas. The annotated list of extensions is represented by lesser-known marine fishes having no commercial value that researchers are aware of and are presented as they relate to the (1) Beaufort Sea, (2) Chukchi Sea, and (3) Chukchi and Beaufort Seas:

1. From the Beaufort Sea:

- **Arctic Skate** (*Amblyraja hyperborea*): Mecklenburg and others (2016) report this species to be circumpolar; found in polar basins southward to Beaufort Sea of Alaska and Western Canada at depths ranging from 92 to 2,925 m. Size information is reported in Wienerroither and others (2011).
- **Plain Sculpin** (*Myoxocephalus jaok*): New record identified from the Beaufort Sea in 2011 (Mecklenburg and others, 2016).
- **Alligatorfish** (*Aspidophoroides monopterygius*): Identified by Catherine W. Mecklenburg from a specimen voucher in the NOAA RACE groundfish surveys 2012 survey collections (Mecklenburg and others, 2016).
- **Black Seasnail** (*Paraliparis bathybius*): Previously reported from the western Arctic Canada Basin north of Alaska in 2005 (Mecklenburg and others, 2016). Alaskan collections were from slope and deep waters of the Beaufort Sea in 2011.
- **Checkered Wolf Eel** (*Lycenchelys kolthoffi*): One specimen was taken in the Alaskan Beaufort Sea near the U.S.–Canada border at 70°28’N, 141°09’W at a depth of 500 m (Mecklenburg and others, 2016). Otherwise, the species lives eastward from that point to Greenland and on to the Kara Sea. It is common at least around Greenland. It is mesobenthic, lives on sandy or muddy or mixed soft-stony sea floors, at depths of 202–930 m and temperatures of -0.9–4.1 °C. Maximum size is 29 cm TL.

³This is a common misidentification in museum collections (Mecklenburg and others, 2011; Mecklenburg and Steinke, 2015).

At least five new occurrences of eelpout species (table 2.2) from the Beaufort Sea sampling were confirmed in the processing of voucher specimens from University of Alaska Fairbanks fishery collections between 2010 and 2011 (Mecklenburg and Steinke, 2015; Mecklenburg and others, 2016). Specimens collected from the WEBSEC-71 survey in the Beaufort Sea (U.S. Coast Guard Cutter [USCGC] Glacier; Hufford, 1974) were evaluated in 2007 and new information gleaned from the specimens was reported by Mecklenburg and others (2016). Additional records and information on the following species may also be found in Mecklenburg and others (2016):

- **Adolf's Eelpout** (*Lycodes adolfi*): A voucher specimen collected in the Beaufort Sea in University of Alaska Fairbanks surveys conducted between 2010 and 2012 (Mecklenburg and others, 2016). This species was also sampled on Chukchi slope, outside the 200-mi limit, by 2009 RUSALCA (Russian-American Long-term Census of the Arctic, 2009); no other records near or in the Chukchi Sea; see Mecklenburg and others (2011, Online Reference 1).
 - **Glacial Eelpout** (*Lycodes frigidus*): From Mecklenburg and others (2011, Online Resource 1, p. 39): “Arctic; Makarov Basin northwest of Ellesmere Island, deep slopes and basins of Greenland and Norwegian Seas, Nansen to Canada basins off Laptev, East Siberian, Chukchi, and Beaufort Seas. Benthic, at depths of 475 m to 3,000 m, rare in depths less than 1,000 m. The first vouchered collection from north of Alaska (California Academy of Sciences, Department of Ichthyology, San Francisco, USA CAS 230372; 2 specimens, 53–76 mm) was made by remotely operated vehicle (ROV) and suction sampler in 2005 north-northwest of Point Barrow at a depth of about 2,500 m.”
 - **Shulupaoluk** (*Lycodes jugoricus*): The University of Alaska Fairbanks Beaufort Sea 2012 voucher specimen collection includes several *L. jugoricus*. (Mecklenburg and others, 2016).
 - **White Sea Eelpout** (*Lycodes marisalbi*): From Mecklenburg and others (2011, Online Resource 1), p. 40: “Arctic; White Sea and Beaufort Sea. Benthic, at depths of 6–335 m. Records from the Beaufort Sea off Alaska identified as *L. pallidus* (e.g., Mecklenburg et al. 2002) are *L. marisalbi* (Canadian Museum of Nature, Ottawa, Canada CMNFI 1974-279, 1974-285, 1974-287, 1978-302; CWM, 15 May 2008).”
 - **Arctic Eelpout** (*Lycodes reticulatus*): Mecklenburg and Steinke (2015) investigated the validity of species in the family Lycodes from the Pacific Arctic Region using morphological observations and DNA barcoding sequences (<http://dx.doi.org/10.5883/DS-LYCODES>). Their genetic analysis revealed that specimens identified as *L. rossi* always fell into the Beaufort Sea clade for *L. reticulatus*.
 - **Threespot Eelpout** (*Lycodes rossi*): The inclusion of this species is based on information presented in Mecklenburg and others (2016).
 - **Longear Eelpout** (*Lycodes seminudus*): Based on UAF's fishery surveys in the Beaufort Sea (2011–12 records), an offshore pattern reflects a geographic distribution along the shelf deeper than 200–300 m to about 1,400 m. The species occurs only in the offshore-most tracts in the Beaufort Sea lease area.
 - **Scalebelly Eelpout** (*Lycodes squamiventer*): Catherine W. Mecklenburg tentatively identified this species from specimens collected from the Beaufort Sea in 2012 (Mecklenburg and others, 2016).
2. From the Chukchi Sea:
- **Ice Cod** (*Arctogadus glacialis*): Identified from samples collected from the Chukchi Sea (Mecklenburg and others, 2016).
 - **Sea Tadpole** (*Careproctus reinhardti*): Geographic distribution from Baffin Bay and Davis Strait, off eastern Greenland, off northern Russia (Kara, and Laptev Seas), and Chukchi Sea slope and northern Bering Sea (Mecklenburg and others, 2016). Benthic, at depth of 100–1,840 m. Preliminary genetic data suggest the sea tadpole could be a species complex (Mecklenburg and others, 2016).
 - **Great Sculpin** (*Myoxocephalus polyacanthocephalus*): Okhotsk Sea and eastern Japan Sea to Commander–Aleutian Island chain to Chukchi Sea, 70°20'N, 163°06'W (Mecklenburg and others, 2016) to southern Puget Sound, Washington. Benthic; intertidal and to 825 m.
 - **Prowfish** (*Zaprora silenus*): Hokkaido, Japan, and Sea of Okhotsk to Bering Sea (Mecklenburg and others, 2002) and to southeastern Chukchi Sea (west of Kivalina, 67°32'N, 165°54'W) (Mecklenburg and others, 2011) and Aleutian Islands (Mecklenburg and others, 2002) to San Miguel Island, southern California (Allen and Smith, 1988). At depths of 10–801 m. Adults found near bottom, young fish often collected near surface (Mecklenburg and others, 2002).

3. From the Chukchi and Beaufort Seas:

- **Bigeye Sculpin** (*Triglops nybelini*): Arctic Ocean, practically circumpolar, Chukchi Sea north of Alaska, western Beaufort Sea slope between 152°W and 155°W (Mecklenburg and others, 2011). Benthic, at depths of 30–1,354 m, usually deeper than 200 m (Mecklenburg and others, 2016).
- **Nebulous Snailfish** (*Liparis bathyarticus*): Circumpolar, Beaufort and Chukchi Seas to southeastern Bering Sea (Mecklenburg and others, 2016). Benthic at depths of about 12–510 m (Mecklenburg and others, 2016).

Probable Occurrences in Alaska Arctic

More species are known to occur in the study area than are described in the species accounts in this catalog because the taxonomic examinations of these fish are in an early stage, and valid identifications are not possible without all results from the multi-faceted research (that is, meristic, morphological, and molecular genetic). The ongoing research approach will include formal descriptions of new species and documentation of significant distributional changes. For instance, Mecklenburg and others (2011) reported an unidentified sculpin, *Icelus* sp., from the Chukchi Sea (*editor's note*: recently confirmed by Mecklenburg and Steinke, 2015), and Rand and Logerwell (2011) reported an unidentified snailfish, *Careproctus* sp. cf. *rastrinus*, from the Beaufort Sea. For this study, we determined that the biological information available for these two species to be too scant and preliminary to permit construction of dependable species accounts. Species accounts were not developed for *Sominosus pacificus*, *Bathyrja parvifera*, or *Lycodes pallidus* due to their recent confirmation from the Chukchi Sea (December 2015); information about these species is available in the *Fishes of Alaska* and species accounts are presented in the *Pacific Arctic Marine Fishes* guide (Mecklenburg and others, 2016).

The additional species identified here are likely to be confirmed from Alaska waters. The information presented was primarily from an ongoing effort by several authors of this report to update Love and others (2005):

- **Atlantic Hookear Sculpin** (*Artediellus atlanticus*): From: Mecklenburg and others, (2011, Online Resource 1, p. 20): *Arctic–Boreal; to southern Baffin Island, northwest and northeast Greenland, Iceland, Jan Mayen, Faroe Islands, Norway, and Barents Sea, northern Kara Sea, and northwestern Laptev Sea; upper slope off the Chukchi Sea; south to Cape Cod, the Skagerrak, Irish Sea, and coasts of Ireland* (Fedorov, 1986, p. 1,245; Mecklenburg and

others, 2011, fig. 2; this study). Benthic, at depths of 11–1,366 m. Found on the Chukchi slope (Chukchi Sea Borderlands, outside U.S. EEZ) in 2009: two at 74°29'N, 165°58'W, depth 365–370 m (California Academy of Sciences, Department of Ichthyology, San Francisco, USA CAS 228530, fig. 3; Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia ZIN 54840); and five at 74°07'N, 166°00'W, depth 227–236 m (CAS 228533, University of Alaska Museum, University of Alaska Fairbanks 5534). This is the first record from the East Siberian–Chukchi–Beaufort region. The specimens fit the description of *A. a. corniger* (Andriashev, 1954) from the Kara and Laptev Seas, Russia, with large parietal spines, but the most recent review of the species in the western Atlantic (Van Guelpen, 1986) determined this character not to discriminate between taxonomic groups and did not recognize any subspecies of *A. atlanticus*. Parietal spine size resembled a cline, with the most strongly developed found in northern parts of the range. The large size fish length (Total Length) of specimens from the Chukchi Sea (as long as 153 mm) agrees with Van Guelpen's determination that the largest specimens are found in the north. The four Co-1 (Cytochrome C Oxidase 1) gene sequences from the Chukchi Sea slope specimens match those of three specimens from southern Baffin Bay (Canadian Museum of Nature, Ottawa, Canada CMNFI 2002-0028.3, 2002-0031.1, 2002-0033.1; 68°26'–69°37'N). The species was confirmed from the Chukchi Borderland by Mecklenburg and others (2014).

- **Spinyhook Sculpin** (*Artediellus gomojunovi*): From Mecklenburg and others (2011, Online Resource 1)—Boreal Pacific north to Gulf of Anadyr, Russia, and Bering Strait. Benthic, at depths of 37–380 m (Mecklenburg and others, 2002). Bering Sea records are no deeper than 90 m. A specimen collected in 1950 near Point Barrow (Smithsonian National Museum of Natural History, Washington, D.C., USNM 152901) and tentatively identified as *A. gomojunovi* (Andriashev, 1961 as cited by Mecklenburg and others, 2011 Online Resource 1) was misplaced (Mecklenburg and others, 2002), but was found in 2005, and subsequently identified as *A. scaber*. The current northernmost record of *A. gomojunovi* is a specimen caught in 1933 at Bering Strait (ZIN 33093).
- **Hookhorn Sculpin** (*Artediellus pacificus*): From Mecklenburg and others, (2011, Online Resource 1)—Boreal Pacific north to southern Gulf of Anadyr and northeast of St. Lawrence Island, Bering Sea. Benthic, at depths of 15–250 m (Mecklenburg and others, 2002). The northern records are not recent: Zoological

Institute of the Russian Academy of Sciences, St. Petersburg, Russia ZIN 33657, Gulf of Anadyr at 63°53'N, 178°48'W, depth 87 m, collected in 1952; and University of Washington Fish Collection at the Burke Museum, Seattle, WA UW 11740, at 63°40'N, 167°28'W, depth 22–40 m, in 1949.

- **Leister Sculpin** (*Enophrys lucasi*): Mecklenburg and others (2016, p. 55) described the distribution as “Southeastern Kamchatka, Commander Islands, Aleutian Islands, Gulf British Columbia, Bering Sea north to Bering Strait. The distribution is difficult to assess due to misidentifications in the literature and museum collections, and the distribution depicted on our map may not be accurate north of the Aleutian Islands and Gulf of Alaska.”
- **Threaded Sculpin** (*Gymnocanthus pistilliger*): Mecklenburg and others (2016) suggested this species to be common from Bering Strait. The northernmost record is CAS 230370, taken in 2006 west of Port Clarence at 65°21'N, 167°41'W. Records from Port Clarence include CAS 230369, CAS 230370, CMNFI 1958-0093, UAM 1201, and UW 41676). The several records from Port Clarence and nearby suggest it also occurs in the southeastern Chukchi Sea and there are reliable identifications northward to Kotzebue Sound, but distribution in the Chukchi Sea has not been documented with voucher specimens. Historical records from the Chukchi Sea remain unverified or have been reidentified (Mecklenburg and others, 2016).
- **Yellow Irish Lord** (*Hemilepidotus jordani*): From Mecklenburg and others, (2011, Online Resource 1)—Boreal Pacific north to Bering Strait, perhaps to southeastern Chukchi Sea. Benthic, at depths of 15–400 m or more, typically shallower than 150 m. Reported from Chukchi Sea (Allen and Smith, 1988), but voucher specimens are lacking. A specimen from the Chukchi Sea southwest of Kivalina identified as *H. jordani* (University of British Columbia, Vancouver, B.C., UBC 61-0064) is *H. papilio* (Mecklenburg and others, 2016). The northernmost verified record is CAS 230368, two juveniles (77–82 mm) caught in 2006 near eastern Bering Strait at 64°59'N, 168°30'W, by bottom trawl in 25 m of water.

- **Frog Sculpin** (*Myoxocephalus stelleri*): This species, once believed to possibly be present rarely in Alaskan waters (Mecklenburg and others, 2002), has been determined from evaluation of all pertinent literature and voucher records identified as this species to be absent from the eastern Pacific and Alaskan waters (Mecklenburg and others, 2011, 2016). See also Mecklenburg and Steinke (2015, p. 176).
- **Polar Sculpin** (*Cottunculus microps*): One record is from the Arctic Ocean on the slope north of the Chukchi Sea, outside the 200-mi limit. Taxonomic revision is in progress; confirmed from the Chukchi Borderland (Mecklenburg and others, 2014).
- **Threaded Sculpin** (*Gymnocanthus pistilliger*): Mecklenburg and others (2016) extended the range for this species into the southeastern Chukchi Sea based on “reliable” identifications but not confirmed specimen vouchers. Although this species is likely to occur in the region, our list includes only species whose presence is known from voucher specimens.
- **Northern Sand Lance** (*Ammodytes dubius*): Predominantly in boreal western Atlantic; Canadian Arctic from Beaufort Sea to Baffin Bay, and Davis Strait. Benthic, shallows to 108 m (Coad and Reist, 2004). These authors also listed Alaska but provided no specific locality.

Other Changes in Species Distributions

In addition to the new occurrences and range extensions in [table 2.2](#), mapping for this study ([chapter 3](#)) documents expansions in the known geographic distributions of another 45 species in this updating of information presented in the *Fishes of Alaska* (Mecklenburg and others, 2002). These shifts in range result from the new information and knowledge gained from recent field surveys and discoveries, improved identification techniques, evaluation of museum collections, and the wide-ranging search of data and literature for this study. In light of the recent field sampling, some changes in geographic, depth, or both, were realistic expectations. Marine ecosystems are dynamic and fish distributions may contract and expand due to various factors including, but not limited to, temperature changes, current patterns, changes in population size, and changes in predator and prey distribution.

Nomenclature and Previous Misidentifications

Genetic analysis, in concert with other species identification techniques, has greatly assisted ichthyological efforts to clarify and resolve existing taxonomic uncertainty surrounding many Arctic species. This work has resulted in several important changes in scientific and common names, which must be continually tracked for natural resource inventories to remain current. The changes in nomenclature

in table 2.3 relate to the greater resolution in phylogenetic understanding that presently exists than was available at the time when the *Fishes of Alaska* (Mecklenburg and others, 2002) was published.

Many species relationships require further study and additional changes in synonymy are expected. As an example, the relationship between *Hippoglossiodes robutus* (Bering Flounder) and *H. elassodon* (Flathead Sole) are currently being investigated (Kartavtsev and others, 2008; Mecklenburg and Steinke, 2015; Mecklenburg and others, 2016); preliminary results suggest the two species are the same.

Table 2.3. Changes in scientific and common names of Arctic marine fishes in the Chukchi and Beaufort Seas since 2002.

[Changes were made since publication of Mecklenburg and others (2002). **Reference:** Information is critical for users. In some instances, specialists may disagree (“not clearly distinguishable” as supporting genetic information may not be available; for example, *Liparis herchelini* not clearly distinguished from *L. tunicatus*), or species may be part of an evolving complex (for example, *Lycodes rossi* and *L. reticulatus*)]

Family	Common or scientific name	Change in common or scientific name		Reference
		From	To	
Squalidae	Spotted Spiny Dogfish	<i>Squalus acanthias</i>	<i>Squalus suckleyi</i>	Lynghammar and others, 2012
Osmeridae	Capelin	<i>Mallotus villosus</i>	<i>Mallotus catervarius</i>	Mecklenburg and Steinke, 2015
Osmeridae	<i>Mallotus catervarius</i>	Capelin	Pacific Capelin	Mecklenburg and Steinke, 2015
Osmeridae	Arctic Smelt	<i>Osmerus mordax</i>	<i>Osmerus dentex</i>	Mecklenburg and others, 2011
Gadidae	<i>Arctogadus glacialis</i>	Polar Cod	Ice Cod	Jørgen Schou Christiansen, oral commun, 2013 ¹
Gadidae	Walleye Pollock	<i>Theragra chalcogramma</i>	<i>Gadus chalcogrammus</i>	Mecklenburg and others, 2011; Page and others, 2013
Gadidae	Pacific Cod	<i>Gadus ogac</i>	<i>Gadus macrocephalus</i>	Mecklenburg and others, 2011; Page and others, 2013
Psychrolutidae	Polar Sculpin	<i>Cottunculus sadko</i>	<i>Cottunculus microps</i>	Byrkjedal and others, 2014
Agonidae	Arctic Alligatorfish	<i>Ulcina olrikii</i>	<i>Aspidophoroides olrikii</i>	Mecklenburg and others, 2011; Page and others, 2013
Ammodytidae	<i>Ammodytes hexapterus</i>	Pacific Sand Lance	Arctic Sand Lance	Orr and others, 2015
Pleuronectidae	Arctic Flounder	<i>Pleuronectes glacialis</i>	<i>Liopsetta glacialis</i>	Eschmeyer and others, 2015; Mecklenburg and others, 2016

¹From Jørgen Schou Christiansen, University of Tromsø, Norway, written commun., May 12, 2013, regarding common names for *A. glacialis* and *B. saida*: “The scientific name is conclusive and should follow the vernacular name at first mention for these species. Whenever vernacular names are used, we suggest ‘ice cod’ for *Arctogadus glacialis* (Latin: *glacialis* = ice; Russian: ледовая треска) and ‘polar cod’ for *Boreogadus saida*. Fish names lists representing the official stand of national and international organizations such as the American Fisheries Society and American Society of Ichthyologists and Herpetologists (Nelson et al. 2004) and the Fisheries Society of the British Isles (Wheeler 1992) differ and, thus, preclude establishment of universal common names. Fortunately, use of scientific names at first mention allows preferential use of vernacular names.” We acknowledge that our use of Ice Cod is different from other North American nomenclature (Page and others, 2013; Hoff and others, 2015; Mecklenburg and others, 2016). Mecklenburg and others (2013) list Ice Cod as one of the “English” names for *A. glacialis*.

Zoogeographic Patterns

Definitions of zoogeographic pattern are from Mecklenburg and others (2011, Online Resource 1) and relate to species endemism and ranges of their population viability:

- *Arctic*—Species that live and reproduce in Arctic waters and are not found, or only infrequently found, in adjacent boreal waters.
- *Predominantly Arctic*—Species that are usually found in Arctic waters.
- *Predominantly Boreal*—Species that are characteristic of boreal waters and common in the border regions of the Arctic (for example, eastern Barents Sea, Gulf of Anadyr [Russia], Norton Sound [Alaska]). Can be more specific, such as predominantly Boreal Pacific or predominantly Boreal eastern Atlantic.
- *Boreal*—Species that are characteristic of boreal waters and only rarely or temporarily found in the border regions of the Arctic. Can be more specific, such as Boreal Pacific or Boreal eastern Atlantic. Includes subtropical, southern boreal category of Andriashev and Chernova (1994).
- *Arctic-Boreal*—Species are distributed and spawn in both Arctic and Boreal waters.
- *Widely Distributed*—Species common in the temperate, boreal, and subtropical zones and in the warm waters of at least two oceans or known from the southern hemisphere, and occurring only rarely in the Arctic.

⁴The decision to use three abundance categories used by Miller and Lea (1976) relates to the lack of consistent, long-term data sets needed for more precise estimates.

⁵Marine fishes are not uniformly distributed in time or space. This analysis was unable to capture seasonal and locality differences but rather portrays regional patterns in abundance.

⁶“Acceptable,” as used here, refers to the precision of existing data with respect to the seasonal, geographic, and taxonomic qualities of data collection and how accurately they describe baseline conditions.

Abundance Terminology

Species distribution and abundance was determined from the reports of a large number of reconnaissance surveys and research expeditions. The wide variation in sampling times, areas, and collection methods reported raised issues of data comparability, which required reviewing existing abundance measures, defining appropriate relative abundance terms, and consistently applying operational definitions. Many methods and descriptors have been used to express fish abundance in Arctic studies. Relative abundance terms such as abundant, common, fairly common, present, occasional, uncommon, or rare are commonplace in the reported literature (for example, Coad and Reist, 2004). Existing baselines for Arctic marine fishes are not consistent for sampling in time, space, or methods to support a quantitative, multi-scaled classification that might be suggested by the definitions from Mecklenburg and others (2011) and Mecklenburg and Steinke, (2015). The challenge was to define a simple, but robust classification system that would have broad regional application. Four ecological principles guided the definition process: (1) abundance is a continuum between rare and abundant, (2) abundance is scale dependent, (3) sampling bias affects estimates of abundance, and (4) environmental influences on species abundance are taxon-specific.

“Rare,” “uncommon,” and “common” terms are defined in this report to classify relative abundance in the species accounts. These terms also were used by Miller and Lea (1976) to describe the coastal marine fishes of California⁴. For the Arctic ichthyofauna, abundance was classified using the same terms but with different operational definitions determined by species compositions and capture rates of marine fishes. These descriptive statistics are commonly used to characterize catch and, with respect to a regional classification scheme, meet pragmatic criteria related to acceptability (are ecologically sound and reliable), practicality (are applicable to existing records), and effectiveness (are realistic with broad-scale⁵ patterns). Species composition (percentage of occurrence of a species with respect to total number of individuals in the catch) provides a simple and scale dependent quantification of an assemblage on an acceptable⁶ continuum. Capture rates are a lower resolution measure of abundance based on the presence or absence of a species detected per sampling session and frequency of capture (or rate) over sampling period and survey area.

Detection rates allow a higher order, less precise comparison of abundance across gear-types and habitats and are a more subjective index. With respect to gear bias and comparability issues, the resultant abundance categories represent semi-quantitative composite metrics from descriptive analyses of catch and expert opinion about relative abundance across at the large-scales of distributional patterns (table 2.4).

Table 2.4. Relative abundance of Arctic marine fishes in the Chukchi and Beaufort Seas.

[Symbols: ≥, greater than or equal to; >, greater than; <, less than; ≤, less than or equal to]

Relative abundance term (ecological science)	Species composition (by geographic locale)	Frequency of capture (encounter rates in catch records)
Common	Regularly collected (comprise ≥10 to 50 percent of catch in terms of total numbers of individuals)	Constant rate of capture (>10 to 25 percent of records)
Uncommon	Infrequently observed or collected (<10 percent of catch in terms of total numbers of individuals)	Low rate of capture (≤10 percent of records)
Rare	Seldom reported	20 or fewer records in Arctic (or 1 to 2 captures per cruise)

Endemism and Relative Abundance

Mecklenburg and others, (2011) describe the zoogeographic pattern of 242 marine fish species from the Arctic zoogeographic province. This province includes the northern Bering Sea and North Atlantic Ocean at latitudes far south of this study area. These authors reported 41 percent of the zoogeographic patterns of the marine fauna were Arctic (that is, Arctic, Predominantly Arctic, and Arctic-Boreal zoogeographic patterns) and 59 percent were Boreal (that is, Predominantly Boreal, Boreal, and Widely Distributed zoogeographic patterns). Applying this approach to just the United States area of the Arctic Province, we determined that the Arctic pattern in 58 percent (n = 92) of the marine fishes was from the Chukchi Sea and 73 percent (n = 80) was from the Beaufort Sea. (Editors note: Analysis does not include newly confirmed species to the region—*Somniosus pacificus*, *Bathyraja parmifera*, *Icelus spiniger*, and *Lycodes pallidus*.) The Boreal pattern comprised 42 and 26 percent of the marine faunas, respectively. The ratio of Arctic to Boreal patterns for marine fish found in the U.S. Chukchi and Beaufort Seas is about 60:40 (table 2.5).

Table 2.5. Relative abundance and zoogeography of Arctic marine fishes in the Chukchi and Beaufort Seas.

[Zoogeographic pattern: Main references, Mecklenburg and others (2011) Online Resource 1, Mecklenburg and Steinke (2015), and Mecklenburg and others (2016). Blank cell indicates the species is unreported or unknown from the area]

Scientific name	Common name	Confirmed occurrence		Zoogeographic pattern
		Chukchi Sea	Beaufort Sea	
<i>Entosphenus tridentatus</i>	Pacific Lamprey	Rare		Boreal Pacific
<i>Lethenteron camtschaticum</i>	Arctic Lamprey	Common	Common	Arctic-Boreal
<i>Squalus suckleyi</i>	Spotted Spiny Dogfish	Rare		Boreal Pacific
<i>Somniosus pacificus</i>	Pacific Sleeper Shark	Rare		Boreal Pacific
<i>Amblyraja hyperborea</i>	Arctic Skate		Rare	Arctic
<i>Bathyraxia parvifera</i>	Alaska Skate	Rare		Boreal Pacific
<i>Clupea pallasii</i>	Pacific Herring	Common	Uncommon	Arctic-Boreal Pacific
<i>Hypomesus olidus</i>	Pond Smelt	Rare		Predominantly Boreal Pacific
<i>Mallotus catervarius</i>	Pacific Capelin	Common	Common	Arctic-Boreal
<i>Osmerus dentex</i>	Arctic Smelt	Common	Common	Arctic Boreal Pacific
<i>Coregonus autumnalis</i>	Arctic Cisco	Rare	Common	Arctic
<i>Coregonus laurettae</i>	Bering Cisco	Common	Common	Predominantly Arctic
<i>Coregonus nasus</i>	Broad Whitefish	Common	Common	Predominantly Arctic
<i>Coregonus pidschian</i>	Humpback Whitefish	Common	Common	Predominantly Arctic
<i>Coregonus sardinella</i>	Least Cisco	Common	Common	Predominantly Arctic
<i>Oncorhynchus gorbuscha</i>	Pink Salmon	Common	Uncommon	Predominantly Boreal Pacific
<i>Oncorhynchus keta</i>	Chum Salmon	Common	Uncommon	Predominantly Boreal Pacific
<i>Oncorhynchus kisutch</i>	Coho Salmon	Uncommon	Uncommon	Predominantly Boreal Pacific
<i>Oncorhynchus nerka</i>	Sockeye Salmon	Uncommon	Uncommon	Predominantly Boreal Pacific
<i>Oncorhynchus tshawytscha</i>	Chinook Salmon	Uncommon	Uncommon	Predominantly Boreal Pacific
<i>Salvelinus malma</i>	Dolly Varden	Common	Common	Arctic-Boreal Pacific
<i>Stenodus leucichthys</i>	Inconnu	Common		Arctic-Boreal ¹
<i>Benthosea glaciale</i>	Glacier Lanternfish	Rare		Arctic-Boreal Atlantic
<i>Arctogadus glacialis</i>	Ice Cod		Rare	Arctic
<i>Boreogadus saida</i>	Arctic Cod	Common	Common	Arctic
<i>Eleginus gracilis</i>	Saffron Cod	Common	Common	Arctic-Boreal Pacific
<i>Gadus chalcogrammus</i>	Walleye Pollock	Uncommon	Uncommon	Predominantly Boreal Pacific and Atlantic
<i>Gadus macrocephalus</i>	Pacific Cod	Uncommon	Uncommon	Arctic-Boreal Pacific and western Atlantic
<i>Gasterosteus aculeatus</i>	Threespine Stickleback	Common	Rare	Predominantly Boreal
<i>Pungitius pungitius</i>	Ninespine Stickleback	Common	Common	Predominantly Boreal
<i>Hexagrammos stelleri</i>	Whitespotted Greenling	Uncommon	Rare	Predominantly Boreal Pacific
<i>Arctodiellus ochotensis</i>	Okhotsk Hookear Sculpin	Rare		Boreal Pacific
<i>Arctodiellus scaber</i>	Hamecon	Common	Common	Arctic
<i>Enophrys diceratus</i>	Antlered Sculpin	Common	Uncommon	Predominantly Boreal Pacific
<i>Gymnocanthus tricuspidis</i>	Arctic Staghorn Sculpin	Common	Common	Arctic
<i>Hemilepidotus papilio</i>	Butterfly Sculpin	Common		Predominantly Boreal Pacific
<i>Icelus bicornis</i>	Twohorn Sculpin	Rare	Uncommon	Predominantly Arctic
<i>Icelus spatula</i>	Spatulate Sculpin	Common	Common	Arctic-Boreal
<i>Icelus spiniger</i>	Thorny Sculpin	Rare		Predominantly Boreal
<i>Megalocottus platycephalus</i>	Belligerent Sculpin	Common	Rare	Predominantly Boreal Pacific
<i>Microcottus sellaris</i>	Brightbelly Sculpin	Rare		Predominantly Boreal Pacific
<i>Myoxocephalus jaok</i>	Plain Sculpin	Rare	Rare	Predominantly Boreal Pacific
<i>Myoxocephalus polyacanthocephalus</i>	Great Sculpin	Rare		Boreal Pacific
<i>Myoxocephalus quadricornis</i>	Fourhorn Sculpin	Common	Common	Predominantly Arctic
<i>Myoxocephalus scorpioides</i>	Arctic Sculpin	Uncommon	Uncommon	Arctic
<i>Myoxocephalus scorpius</i>	Shorthorn Sculpin	Common	Common	Arctic-Boreal
<i>Trichocottus brashnikovi</i>	Hairhead Sculpin	Common	Uncommon	Predominantly Boreal Pacific
<i>Triglops nybelini</i>	Bigeye Sculpin	Uncommon	Uncommon	Arctic
<i>Triglops pingelii</i>	Ribbed Sculpin	Common	Uncommon	Arctic-Boreal
<i>Blepias bilobus</i>	Crested Sculpin	Uncommon		Boreal Pacific
<i>Nautichthys pribilovius</i>	Eyeshade Sculpin	Common	Rare	Predominantly Boreal Pacific
<i>Cottunculus microps</i>	Polar Sculpin		Rare	Arctic-Boreal Atlantic
<i>Euryomen gyrinus</i>	Smoothcheek Sculpin	Rare		Predominantly Boreal Pacific

Table 2.5. Relative abundance and zoogeography of Arctic marine fishes in the Chukchi and Beaufort Seas.—Continued

Scientific name	Common name	Confirmed occurrence		Zoogeographic pattern
		Chukchi Sea	Beaufort Sea	
<i>Aspidophoroides monopterygius</i>	Alligatorfish	Common	Common	Predominantly Arctic
<i>Aspidophoroides olrikii</i>	Arctic Alligatorfish	Common	Common	Predominantly Arctic
<i>Hypsagonus quadricornis</i>	Fourhorn Poacher	Rare		Boreal Pacific
<i>Leptagonus decagonus</i>	Atlantic Poacher	Uncommon	Uncommon	Arctic-Boreal
<i>Occella dodecaedron</i>	Bering Poacher	Rare		Boreal Pacific
<i>Pallasina barbata</i>	Tubenose Poacher	Rare		Predominantly Boreal Pacific
<i>Podothecus veterus</i>	Veteran Poacher	Common	Common	Arctic-Boreal Pacific
<i>Eumicrotremus andriashevi</i>	Pimpled Lump sucker	Rare		Arctic-Boreal Pacific
<i>Eumicrotremus derjugini</i>	Leatherfin Lump sucker	Rare	Uncommon	Arctic
<i>Careproctus reinhardtii</i>	Sea Tadpole	Rare	Rare	Arctic
<i>Liparis bathyartcticus</i>	Nebulous Snailfish	Common	Common	Predominantly Arctic
<i>Liparis fabricii</i>	Gelatinous Seasnail	Common	Common	Arctic
<i>Liparis gibbus</i>	Variiegated Snailfish	Common	Uncommon	Arctic-Boreal
<i>Liparis tunicatus</i>	Kelp Snailfish	Common	Common	Arctic
<i>Paraliparis bathybius</i>	Black Seasnail	Rare	Rare	Arctic
<i>Gymnelus hemifasciatus</i>	Halfbarred Pout	Common	Common	Arctic-Boreal
<i>Gymnelus viridis</i>	Fish Doctor	Common	Common	Predominantly Arctic
<i>Lycenchelys kolthoffi</i>	Checkered Wolf Eel		Rare	Arctic
<i>Lycodes adolfi</i>	Adolf's Eelpout		Rare	Arctic
<i>Lycodes eudipleurostictus</i>	Doubleline Eelpout		Uncommon	Arctic
<i>Lycodes frigidus</i>	Glacial Eelpout	Rare	Rare	Arctic
<i>Lycodes jugoricus</i>	Shulupaoluk		Rare	Arctic
<i>Lycodes marisalbi</i>	White Sea Eelpout		Rare	Arctic
<i>Lycodes mucosus</i>	Saddled Eelpout	Common	Uncommon	Arctic
<i>Lycodes palearis</i>	Wattled Eelpout	Common	Uncommon	Predominantly Boreal Pacific
<i>Lycodes pallidus</i>	Pale Eelpout		Rare	Arctic
<i>Lycodes polaris</i>	Polar Eelpout	Common	Common	Arctic
<i>Lycodes raridens</i>	Marbled Eelpout	Common	Common	Arctic-Boreal Pacific
<i>Lycodes reticulatus</i>	Arctic Eelpout		Common	Arctic
<i>Lycodes rossi</i>	Threespot Eelpout		Rare	Arctic
<i>Lycodes sagittarius</i>	Archer Eelpout		Common	Arctic
<i>Lycodes seminudus</i>	Longear Eelpout	Rare	Rare	Arctic
<i>Lycodes squamiventer</i>	Scalebelly Eelpout		Rare	Arctic
<i>Lycodes turneri</i>	Estuarine Eelpout	Uncommon	Uncommon	Predominantly Arctic Pacific
<i>Acantholumpenus mackayi</i>	Blackline Prickleback	Uncommon		Predominantly Boreal Pacific
<i>Anisarchus medius</i>	Stout Eelblenny	Common	Uncommon	Arctic-Boreal
<i>Chirolophis snyderi</i>	Bearded Warbonnet	Uncommon		Predominantly Boreal Pacific
<i>Eumesogrammus praecisus</i>	Fourline Snakeblenny	Uncommon	Uncommon	Arctic-Boreal Pacific and western Atlantic
<i>Leptoclinus maculatus</i>	Daubed Shanny	Common	Common	Arctic-Boreal Pacific and Atlantic
<i>Lumpenus fabricii</i>	Slender Eelblenny	Common	Common	Arctic-Boreal
<i>Lumpenus sagitta</i>	Snake Prickleback	Rare		Boreal Pacific
<i>Stichaeus punctatus</i>	Arctic Shanny	Common	Common	Arctic-Boreal Pacific and western Atlantic
<i>Pholis fasciata</i>	Banded Gunnel	Uncommon	Rare	Arctic-Boreal
<i>Anarhichas denticulatus</i>	Northern Wolffish	Rare	Rare	Arctic-Boreal
<i>Anarhichas orientalis</i>	Bering Wolffish	Uncommon	Uncommon	Predominantly Boreal Pacific
<i>Zaprora silenus</i>	Prowfish	Rare		Boreal Pacific
<i>Ammodytes hexapterus</i>	Arctic Sand Lance	Common	Common	Arctic-Boreal Pacific
<i>Hippoglossoides robustus</i>	Bering Flounder	Common	Common	Arctic-Boreal Pacific
<i>Hippoglossus stenolepis</i>	Pacific Halibut	Rare		Boreal Pacific
<i>Limanda aspera</i>	Yellowfin Sole	Common	Rare	Predominantly Boreal Pacific
<i>Limanda proboscidea</i>	Longhead Dab	Uncommon	Rare	Predominantly Boreal Pacific
<i>Limanda sakhalinensis</i>	Sakhalin Sole	Uncommon		Predominantly Boreal Pacific
<i>Liopsetta glacialis</i>	Arctic Flounder	Common	Common	Predominantly Arctic
<i>Platichthys stellatus</i>	Starry Flounder	Uncommon	Uncommon	Arctic-Boreal Pacific
<i>Pleuronectes quadrituberculatus</i>	Alaska Plaice	Uncommon		Predominantly Boreal Pacific
<i>Reinhardtius hippoglossoides</i>	Greenland Halibut	Uncommon	Uncommon	Arctic-Boreal Pacific and Atlantic

¹ Author determination.

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Summary

One hundred nine (109) marine fishes from 24 families are described and compared regarding their occurrence in the United States Chukchi and Beaufort seas. Ninety-seven (97) species are confirmed from the Chukchi Sea and 83 from the Beaufort Sea. Twenty species are newly confirmed to the U.S. Arctic since the publication of *Fishes of Alaska* in 2002. The taxonomy of Arctic marine fishes has improved since 2002, but issues in the naming and acceptance and validity of several species in the Liparidae and Zoarcidae require additional resolution. Many of the common species are benthic or demersal in their habitat orientation. Small-sized marine species such as those representing Cottidae, Liparidae, Stichaeidae, and Zoarcidae families, were common to both seas. The diversity of Salmonidae species reflects the plasticity of this group of fishes and its adaptive linkage to freshwaters. Our analysis supports high rates of Arctic endemism in both seas, especially in the Beaufort Sea. Numerous range extensions and their sources are noted. The estimates of species diversity can be expected to increase with new sampling, with greater reliance on genetic and molecular identification aids, and in response to large-scale effects of changing environmental conditions on present patterns of regional fish distribution and abundance. *Fishes of Alaska* remains an important reference for species taxonomy and identification of more than 600 species from the Gulf of Alaska and Bering Sea to the Arctic but is not complete with respect to species in the Chukchi and Beaufort Seas.

Chapter 3. Alaska Arctic Marine Fish Species Accounts

By Milton S. Love¹, Nancy Elder², Catherine W. Mecklenburg³, Lyman K. Thorsteinson², and T. Anthony Mecklenburg⁴

Abstract

Species accounts provide brief, but thorough descriptions about what is known, and not known, about the natural life histories and functional roles of marine fishes in the Arctic marine ecosystem. Information about human influences on traditional names and resource use and availability is limited, but what information is available provides important insights about marine ecosystem status and condition, seasonal patterns of fish habitat use, and community resilience. This linkage has received limited scientific attention and information is best for marine species occupying inshore and freshwater habitats. Some species, especially the salmonids and coregonids, are important in subsistence fisheries and have traditional values related to sustenance, kinship, and barter. Each account is an autonomous document providing concise information about a species zoogeography, western and Alaska Native taxonomy, life history, niches, and life requirements. Each account is fully referenced with the identification of the most critical literature for Alaska and a more comprehensive listing of referencing from which biological and ecological information was drawn. New-to-science narratives, distributional maps, and vertical profiles, provide quick, reliable sources of information about fish life history and habitat requirements for this segment of the Arctic fauna.

Purpose and Design of Species Accounts

Individual species accounts were prepared for 104 of the 109 confirmed marine fishes for which adequate biological information was available from the U.S. Chukchi and Beaufort Seas. These descriptions are an important source of documentation about Arctic Alaska's marine fish fauna.

Although tailored to address the specific needs of BOEM Alaska OCS Region NEPA analysts, the information presented in each species account also is meant to be useful to other users including state and Federal fisheries managers and scientists, commercial and subsistence resource communities, and Arctic residents. Readers interested in obtaining additional information about the taxonomy and identification of marine Arctic fishes are encouraged to consult the *Fishes of Alaska* (Mecklenburg and others, 2002) and *Pacific Arctic Marine Fishes* (Mecklenburg and others, 2016). By design, the species accounts enhance and complement information presented in the *Fishes of Alaska* with more detailed attention to biological and ecological aspects of each species' natural history and, as necessary, updated information on taxonomy and geographic distribution.

Each species account includes a concise summary of the natural history, population dynamics, functional roles, and traditional and economic values of the marine fish found off Alaska. An initial organizational task was to create a standard format for effective information delivery. The species descriptions by Ehrlich and others (1988) were provided to the USGS by BOEM as an example of a creative template for information transfer. Four pilot species accounts, representing well known to poorly known species, were developed, reviewed, and repeatedly revised for improvements, interagency approval, and selection of the final layout and design. Final decisions about content represented the priority needs of BOEM.

More than 1,200 individual scientific publications relevant to Arctic marine fishes were reviewed in preparation of the species accounts. In each species account, the most relevant literature for each species is cited. A shorter list (about 5–10 articles) identifies key Alaskan information sources that, in our opinion, have had the greatest scientific effect on understanding the species of the Arctic area of the United States.

¹University of California, Santa Barbara.

²U.S. Geological Survey.

³California Academy of Sciences, San Francisco, and Point Stephens Research, Auke Bay, Alaska.

⁴Point Stephens Research, Auke Bay, Alaska.

Limitations of Data

The species accounts reveal many gaps in the biological information needed to conduct vulnerability assessments of the marine fishes of the Beaufort and Chukchi Seas to human interventions. Part of this problem relates to the geographic coverage of existing research and surveys in Alaska as, in many instances, we were required to incorporate the results of investigations conducted outside the region. This raises an important caution because, even though the best available information was used in preparing the species accounts, our reliance on data and information from outside Alaska will introduce uncertainty to EIS expectations. Ideally, and with respect to oil and gas activities, baseline information for fishery resources should be collected from the potentially affected environment to appropriately evaluate the potential effects of oil spills or other possible industrial-related disturbances. However, as has been widely noted (for example, Bluhm and others, 2011), systematic and methodologically comparable data typically are not available from Arctic Alaska marine ecosystems. Evaluating change in populations and communities from natural and anthropogenic stressors is limited by the variable quality and lack of quantitative reports on abundance, distribution, community structure, and demographics for Arctic marine fishes.

In each species account, an attempt was made to incorporate the most reliable baseline information available and offer impressions of information needs. Important ongoing studies sponsored by BOEM, and others, may be addressing some of these needs. The needs assessments for this study considered these efforts to the extent that oral and (or) written communications and preliminary results allowed. The focus of this study was on impressions of the population parameters (Williams and others, 2002) and environmental measurements needed to detect changes in marine fish populations (Reist and others, 2006; Wassmann and others, 2011) and their resilience to a variable and rapidly changing environment (Holland-Bartels and Pierce, 2011). For key marine fish species, examples might include changes in range, community structure, abundance, phenology, behavior, and population growth and survival.

Each species account is designed as a self-contained article; therefore, no references to other accounts are included. Additionally, to reduce complexity in the presentations, only common names were used to identify the major predator and prey species for the marine fish described. Because this document was meant to be a companion document to the *Fishes of Alaska* (Mecklenburg and others, 2002), interested readers are encouraged to consult this book or Page and others (2013) and Mecklenburg and others (2016) for more complete information about the scientific authorities and literature citations associated with the original descriptions of each species. Readers are directed to the references cited in each species account for additional information on the species.

Operational Definitions

In [chapter 1](#), several concepts about the temporal and spatial habitat requirements for Arctic marine fish were introduced. More information is presented in this chapter to explain the vertical distribution and the location of shelf break, as used in this report.

Vertical Distribution

The conceptual design of the species depth profiles (vertical structure by life history stage) was patterned after the “coastal marine life zones” of Allen and Smith (1988). The goal of the profiles is to visualize what is known about a species occurrence and reproductive ecology by depth and location. An idealized characterization of Arctic shelves was designed to visualize these relationships. Additional detail about origins of data was included in the depth profiles to reflect Alaskan records or collections from other Arctic regions. This is important because actual field collections and observations are limited from this region. In many instances, the actual presence of a life stage remains unverified by field sampling. Thus, for many of species, the depth of a fish’s life cycle should be considered untested hypotheses in need of additional testing.

Location of Shelf Break

Early versions of the depth profiles were modified at the request of BOEM with respect to the depiction of the continental shelf break. As a special effect for the Arctic, the species depth profiles were redrawn to depict the change in bathymetry that typically occurs at depths of about 75 m throughout the Chukchi and western Beaufort Seas. This depiction is not an attempt to redefine the oceanographic definition of shelf break. Instead, it highlights the relatively sharp gradient in depths that often occurs near 70- to 80-m contours over much of the region. Although species depth profiles in this report depict an apparent “break” at 75-m, three factors were considered: (1) this is a generalization and the actual shelf break may be geographically close but at a slightly greater depth; (2) shelf edge effects on fish distribution at depths occurring between 75-, 150-, or 200-m are likely negligible due to the gradient and area involved; and (3) the conceptual depictions of depth distributions by life history stage are consistent with accepted oceanographic conventions for continental shelf and slope (despite the magnified view at 75-m) and thus are compatible to the import of biological data obtained elsewhere.

Keystone Species

The concept of keystone species describes the critical role certain organisms are perceived to have in maintaining the structure of biological communities and resilience of ecosystem dynamics (Paine, 1966). Arctic Cod (*Boreogadus saida*) are widely distributed in the Arctic Ocean and by virtue of their abundance and intermediate trophic position between invertebrates and higher-level predators are integral to the movement of nutrients in marine food webs. For this reason, Arctic Cod are considered a keystone species in the Arctic marine (Bradstreet and others, 1986; Walkusz and others, 2011). Arctic Cod are common in United States waters of the Beaufort and Chukchi Seas being considered for energy exploration and development and are an ecological focus of BOEM fishery studies to understand potential effects on the species (Maule and Thorsteinson, 2012).

Outline of Species Accounts

The species accounts are scientifically accurate descriptions of the life histories, populations, habitats, and community values of individual species in the Arctic marine ecosystem. The mix of quantitative and qualitative information presented reflects state-of-the-art knowledge, a faunal assessment of information gaps, and prioritization of priority needs for population and process understanding. Limited information for many Alaskan species required that relevant observations from other geographic locales be included. Each species account attempts to be clear about the geographic origins of data and information, through scientific referencing or special notations in graphics. As an example, *italics* are used in the species accounts to highlight data collections from the Alaska study area. In several instances, species information was so lacking that inferences from a closely related species were required.

The generic species account includes a comprehensive accounting of scientific and cultural information in a standard format. The scientific information addresses multiple disciplinary areas including taxonomy, life history and habitats, ecological relationships including predator-prey interactions and environmental preferences, and population ecology. The population information is critical to evaluations of population status and health, resilience, and vulnerability to natural and anthropogenic changes in the marine environment. Each species account includes a photograph of an adult specimen (or line drawing if an image was not available); distribution maps (horizontal and vertical); and concise descriptions of abundance, life history, and ecology (11 life history categories); major stressors; research needs; and key references. To assist users, a suite of easily recognized icons was developed to provide quick access to specific life history information. In addition, some species attributes

regarding life history, population dynamics, and biological interactions are defined in the Glossary ([chapter 7](#)).

Information presented in each species account is outlined and described as:

Taxonomic—Scientific and Common Names

The format of the species accounts was, by design, intended to link the biologic and ecologic information presented in this document directly to the species identification guides contained in the “*Fishes of Alaska*.” This connection was established by adherence to naming conventions as described by Mecklenburg and others, 2002 (p. 25 and 26). The common names of each marine fish are presented first, followed by scientific and family names. Each scientific name includes a reference to the name of the person (author) who formally described and named the species in the ichthyological literature. The bibliographic data for the authors and dates of publication of scientific names can be found in Eschmeyer’s Catalog of Fishes online (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>) and are not reported here. In some instances, a *Note* (italicized) has been included to describe exceptional details about existing biological data, morphology, nomenclature, taxonomic status, life history strategy, or occurrence of a species in the United States Chukchi and Beaufort Seas.

Iñupiat Name

The existence of colloquial Iñupiat (Iñupiaq) names for the Arctic’s marine fish fauna by indigenous peoples is an important component of traditional ecological knowledge. Relatively few marine fish species are abundant or susceptible enough to subsistence fisheries to have received special names. For those species having Iñupiat names, this information is reported to assure that a common vocabulary can facilitate future exchanges of ideas and knowledge across disciplinary boundaries. In this manner, colloquial names can provide a cultural link between local marine resources and science supporting sustainability of Arctic communities and ecosystems.

Ecological Role

Fishes play a pivotal role in marine ecosystems as secondary and higher-level consumers in many marine food webs. In many instances, information about predator-prey relationships is so limited that only preliminary, qualitative assessments of the relative role of each species are possible. The ecological niche describes how an organism or population responds to resources and competitors. Importance or significance descriptors do not diminish the fact that all organisms contribute in ways large or small to the provision

of ecosystem goods and services. These descriptors however, may provide useful information about the relative importance of a particular species as an indicator of ecosystem condition and trajectories of change associated with climate change, habitat fragmentation, ecosystem stress, effect of pollutants, or other anthropogenic effects.

Physical Description/Attributes

A brief physical description of the species is summarized from information presented by Mecklenburg and others, (2002) in the *Fishes of Alaska*; the relevant page number is included for quick referral to more comprehensive morphological information. An image of the adult form of each fish is presented with appropriate attribution. High-quality images were selected to highlight the key identifying features of a particular species.

Information about the presence of a swim bladder and antifreeze glycoproteins is included because of its relevance to geo-seismic oil and gas exploration, climate change issues, and evolutionary life history.

Range

The geographic occupancy of the species in United States sectors of Chukchi and Beaufort Seas and adjacent waters is presented in brief narratives and depicted on maps. Known occurrence in the Arctic OCS Planning Areas is highlighted by symbols indicating locations of valid species identifications from properly archived voucher specimens on each map. Although the symbols on the maps may suggest that some of the species are rare in the region, the study of historical collections from the United States and Canadian sectors of the Beaufort Sea, as well as the collections from BOEM surveys in the Beaufort in 2011 and 2012, is still in progress and may reveal that these species are more abundant in deep sectors of the study area than the maps suggest. Definitions of zoogeographic pattern are from the Online Resource 1 (electronic supplemental to Mecklenburg and others, 2011), Mecklenburg and Steinke (2015), and Mecklenburg and others (2016) and relate to ranges of population viability (see [chapter 2](#)).

Depth profiles in each species account graphically summarize existing information about the benthic and reproductive distributions of each marine fish. In both depth profiles, the width of areas depicted confers species information about horizontal (onshore-offshore) patterns of distribution. The italicized captions in the depth profiles highlight species information germane to the study area. Areas in the graphs denoted by the orange coloration represent understanding from data collection within the United States Chukchi and Beaufort Seas; olive colors represent data collection outside the study area. For benthic distributions,

solid lines in the depth profiles represent species for which no specific information is available about its preferred depth range. Solid lines represent a synthesis of understanding that includes information not necessarily specific to the study area. In some instances, only one record of a species occurrence by depth was available and coding in orange was not meaningful. In these cases, an explanatory comment, in italicized font, with a line pointing to the appropriate depth was included in the graph (for example, see the species account for *Megalocottus platycephalus*). Highlighted depths as indicated through “bolded” (dark black) and dashed segments, represent most common depths where the species has been detected, and depth distribution as has been reported throughout the species range, respectively. Areas denoted with diagonal cross-hatching represents depth distribution of juveniles (immature); adult distributions are not cross-hatched and age-related habitat overlaps, are informed by captioning in the figures.

For reproductive distribution, eggs and larvae (pre-juvenile life stages) of marine fishes are represented with respect to depth and distance from the coast. Orange areas in the reproductive distribution profiles represent data collection in the study area. In many instances, information about spawning habitats and egg and larval distributions is summarized from information reported from throughout a species range. In these cases, dark blue represents species distributions in spawning habitats; light blue represents the geographic distributions of eggs and larvae; and light green is used to highlight areas of substantial habitat overlap (for example, see the species account for *Hippoglossus stenolepis*). Distribution patterns of eggs and larvae are symbolized by “dots” and “horizontal dashes,” respectively, in the graphs. As for benthic distribution, solid lines represent species-specific information from data collections from throughout the species entire range. Highlighted (dark black lines) segments of solid lines indicate the most common depths where egg and larvae samples have been collected. Dashed lines represent areas of hypothesized distributions for species for which no information is available about egg or larval occurrence. In these instances the hypothesized distributions are based on known patterns for closely related species; the lack of data is stated in captions above the graph.

Relative Abundance

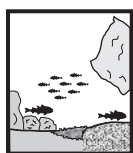
Relative abundance refers to the contribution a species makes to the total abundance of the fishery community. It is a measure that provides an index of the number of individuals present, but not the actual numbers. Relative abundance terms, such as “common,” “uncommon,” or “rare” often are used to express the general population status of a given species, but are most useful when they are defined by something that is measured or estimated in a manner that makes comparison meaningful.

Depth Range

Benthic distribution refers to the spatial arrangement of a particular species at different depths over continental shelf and slope waters. The life cycle of fishes occurs in multiple dimensions in time and space and generally reflects genetically determined life history or behavior that has evolved to maximize fitness (life time reproductive success, see Gross [1987]). Benthic distribution profiles for each species represent the location of important habitats as they are presently known for juvenile and marine fishes. Reproductive distributions depict important habitats for spawning and early life history development.

Life History, Population Dynamics, and Biological Interactions

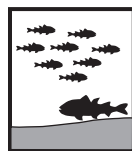
Life history theory holds that the schedule and duration of key events in a species' lifetime are shaped by natural selection to produce the largest possible number of surviving offspring. These events, notably juvenile development, age of sexual maturity, first reproduction, number of offspring and level of parental investment, senescence, and death, depend on the abiotic and biotic environment of the organism. Specific information about these traits informs understanding of a species' adaptive capacity including major influences on population abundance. A number of fisheries models use basic length-weight and age-at-size relationships to describe the growth and dynamics of fishery populations (for example, von Bertalanffy and Gompertz, growth models and derivatives [Ricker, 1975]). Ecological models estimate transfer of energy or matter along the trophic chain (Gamito, 1998). The parameters that are estimated in these models are individually important indicators of population condition and may be used with other indicators to derive quantitative information about compensatory responses and resilience. Much of this information, including population parameters, has been compiled in FishBase for the Arctic marine fish (Froese and Pauly, 2012).



Habitats and Life History—Basic information about the life history (for example, body size, reproductive ecology, growth) and ecology (for example, mobility, growth, habitat) of a species and the environmental area inhabited by that species is foundational to

effective resource management. Habitat is the natural environment that influences and is used by a species population. Information about abiotic (that is, temperature, salinity, other physiochemical factors, depth, and substrate types) and biotic (that is, type and abundance of food, presence of other biota) often are used to describe fish habitats and provide insights about a species environmental preferences and habitat associations (for example, water masses). Maximum body size often is reported and can be an

important surrogate of different life history traits (for example, age at maturity, growth, and reproductive output). In population dynamics studies, the relationships between length and weight and size and age form the basis for population growth and production models and quantitative analysis of environmental effects. Length measurements are reported as standard length (SL), total length (TL), and fork length (FL) in fisheries studies.



Behavior (see also Glossary [chapter 7]).—

Behavior is the manner in which a fish operates or functions within its environment (that is, home range, territoriality, and many others) to procure food, orient to specific locations, or relate to other organisms. Knowing how

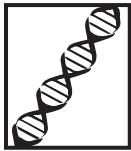
individuals respond to the environment (physical, chemical, and biological cues) is critical to understanding population processes such as distribution, survival, and reproduction and recruitment and for managing fisheries. Many behaviors are evolutionary adaptations to the physiological and reproductive requirements for a species' survival. For example, migration involves the regular movement of animals between different geographic locations. Migrations can be extensive in terms of time and distance involved (anadromous model) or seasonal (amphidromous and marine models). Each of these models reflects a life strategy adapted for age and growth at sea. Diel relates to daily changes in water column position due to changes in light, temperature, and food supply.

Migratory behaviors are rooted in physiological requirements for food, growth, reproductive, and survival ("scope for growth"). Movement behaviors are more tactical responses to local environmental conditions (for example, variable hydrographic conditions in the nearshore Beaufort Sea). Fish movement can be active or passive and involve large distances in search of suitable habitats and foods. The seasonal nature of migration and movement behaviors are typically related to life history stage, predator-prey distributions, or energetic requirements for growth.

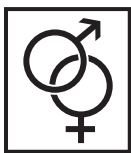
Schooling (that is, social structure of fish of the same species moving in more or less harmonious patterns in the sea) often is related to survival and reproduction. Schooling confers physical benefits to fish movement, safety against predators, search behaviors (for example, foods), population immunology, and reproduction.

The functional feeding morphology of a fish relates to its anatomical adaptations (for example, body size, gape sizes, shape, and body form) to environmental conditions especially food preferences. The adage "function determines morphology and morphology determines way of life" is an important evolutionary concept as it applies to fish feeding behavior, dietary preferences, habitat selection, and trophic stature. Trophic position (within categories of trophic levels) expresses the "tendency of larger (less abundant) fishes feeding on smaller (more abundant) fishes, which themselves feed on zooplankton and all these animals resting upon primary producers" (from Pauly and Watson, 2005). Categories of trophic levels are:

- Trophic level 1 (T1), plants and animals make their own food and are called primary producers;
- Trophic level 2 (T2), herbivores eat plants and are called primary consumers;
- Trophic level 3 (T3), carnivores eat herbivores and are called secondary consumers;
- Trophic level 4 (T4), carnivores eat other carnivores and are called tertiary consumers; and
- Trophic level 5 (T5), apex consumers, which have no predators, are at the top of the food chain.



Populations or Stocks—A population often is defined as a group of organisms of the same species occupying a particular space at a particular time with the potential to breed with each other (Williams and others, 2002). Stocks are subpopulations of a particular species of fish that result from reproductive isolation and subdivisions within the biological range. The current state of knowledge about local stocks and their genetic population structure is reported. Grossberg and Cunningham (2001) described the combined effects of demographic, behavioral, genetic, oceanographic, climate, and tectonic processes as major determinants of population structure. These mechanisms act across a range of temporal and spatial scales to determine the rates and patterns of dispersal of different life stages of marine fishes. Dispersal, combined with the successful reproduction and survival of immigrants, control the scale and rate of processes that build or erode structure within and among groups of individuals.

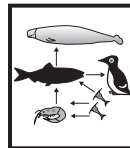


Reproduction Mode—Little information is available about the spawning times and locations, mating behaviors (breeders or nonbreeders), and genetic diversity of Arctic marine fishes. What is known is drawn largely from observations from populations studied outside the United States. For most Arctic marine fish species, there is no information about population or stock structure (for example, age structure, reproductive behavior, sex ratios, age-at-maturity, fecundity, and genetic). These are key population parameters needed for understanding reproductive ecology, population dynamics (for example, growth, survival, and mortality), and assessments of resiliency (response to disturbance).

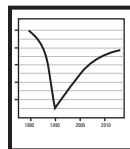


Food and Feeding—Dietary information is summarized from literature and, unless in italics, is reported from other regions. Fish communities can affect the ecological characteristics of marine ecosystems in

response to productivity and abundance patterns, the mobility and migratory behavior of species, and through food influences in different habitats (for example, Grebmeier and others, 2006b). Trophic Index (T) values are reported from FishBase (Froese and Pauly, 2012). The T values for Arctic marine fishes are largely derived from stomach contents analyses, which have correlated well with stable isotopes of nitrogen in tissues. The fractional values (between 1 and 5) realistically address complexities of consumer feeding behaviors (omnivory and feeding across multiple trophic levels) and predator-prey relationships. For example, the mean T value for Blackline Prickleback (*Acantholumpenus mackayi*) is 3.1 (± 0.31). This mid food web value is indicative of a primary carnivore that feeds across trophic levels, in this case on lower level herbivores.



Biological Interactions.—The effects organisms in a community have on one another. Competition and consumption (predation, herbivory, or cannibalism) are the best known of the major ecological processes affecting resource abundance, community composition, and ecosystem function. Competition involves interactions between individuals of the same species (intraspecific) or different species (interspecific) in which the fitness of one is lowered by the presence of another. Competition often is related to food and habitat requirements and reproductive behavior. Interspecific competition for foods is greatest for species occupying similar trophic positions in relatively short food chains and for animals living in regions of low biological productivity.



Resilience—In ecology, resilience traditionally refers to the ability of a population or biotic community to sustain or return to its former state after a disturbance. The rate of recovery is a measure of resilience determined by the population processes involved in restoring abundance to healthy, sustainable, or pre-disturbance levels. Four categories of productivity (high, medium, low, and very low) are used to classify reliance in marine fish populations (Musick, 1999). These categories are based on a combination of population parameters for intrinsic rate of growth, growth coefficient, fecundity, age at maturity, and maximum age. Because population parameters were unavailable, resiliency is defined here based on estimated population doubling time where high = <15 months, medium = 1.4–4.4 years, and low = 4.5–14 years.

Traditional, Cultural, and Economic Values

In August 2009, the U.S. Secretary of Commerce approved a Fishery Management Plan for the Arctic Management Area. The plan covers U.S. Arctic waters in the

Chukchi and Beaufort Seas, and acknowledges that changing climate may potentially favor the development of commercial fisheries. However, until adequate fisheries resource assessments are completed, the region remains closed to commercial fishing in federal waters. A small salmon fishery exists in Kotzebue Sound; in 2010, a small commercial fishery for Arctic Ciscoes in the Colville River was terminated.



Traditional and Cultural Importance.—

Several species of nearshore marine fishes are important in subsistence fisheries. The protection of traditional lifestyles and economies, including these subsistence fisheries, is a responsibility of the Federal government. Subsistence relates to resource use patterns (for example, seasonal round) and values (that is, sustenance, kinship, and barter) in coastal communities of northern Alaska.



Commercial Fisheries.—Currently (2016) there are no offshore marine fisheries in the U.S. Chukchi and Beaufort seas. Changing Arctic environmental conditions and shifting distributions of species in response to warming suggest that there may be fisheries in the

future. A precautionary approach by fishery managers has been adopted that requires the collection of reliable baseline information for decision-making and ecosystem management (North Pacific Fishery Management Council [North Pacific Fishery Management Council, 2009; Wilson and Ormseth, 2009]).

Climate Change

Alaska's climate is changing at more than twice the rate of the rest of the United States (Mellilo and others, 2014). Year-to-year and regional variability in air temperatures are evident and the warming trend currently is being moderated by large-scale cooling associated with the Pacific Decadal Oscillation. Even so, climate effects are pronounced and are being seen in changes in sea ice, timing of snowmelt, widespread glacier retreat, and changes in hydrology (runoff) and coastal processes, such as erosion (Markon and others, 2012). The effects of rising ocean temperatures and ocean acidification on marine food webs are of growing regional concern with respect to the condition and trends in marine ecosystems and human community resilience are of concern. Climate changes potentially can affect marine fish in numerous ways, leading to distributional changes, increased or decreased mortality rates, changes in growth rates, and by altering the timing in reproduction (Clow and others, 2011).

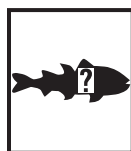


Potential Effects of Climate Change.—A pole-ward shift of many fish distributions is possible as is a reduction or extinction of species that are narrowly adapted to Arctic

environments. Generally, the species are expected to increase in abundance if they are currently present in the Bering Sea and decrease if they have very low tolerance for temperatures greater than 1.5–2.0 °C. However, it is hypothesized in current climate projections that temperatures near the ocean floor in the northern Bering Sea will remain cold (<2 °C) due to persistence of winter sea ice (Sigler and others, 2011). Cold-water conditions and other marine ecosystem effects related to seasonal sea ice extent and timing of retreat may effectively block northward migrations and production of exploitable quantities of species, such as pollock and cod, for several decades. Shifts in range and other possible climate-related effects, such as increased predation or competition for food, are identified in the species accounts. Only “loose qualitative generalizations” are presently possible (Reist and others, 2006).

Research Needs

The compilation and review of species information for species in U.S. Arctic waters revealed many gaps in life history understanding and environmental relations. These are evaluated on the basis of a species current fishery and community values and ecological significance in marine ecosystem structure and function. The needs reflect the researcher's perceptions and their understanding that new fishery information is becoming available for the Arctic region and that, although Arctic research is currently a national priority, some aspects of population ecology will take many years of data collection to accurately assess.



Areas for Future Research.—The preparation of individual accounts led to the identification of many information gaps in knowledge about the biology and ecology of marine species including life history, population dynamics, and community associations. Generally,

species life history and ecology gaps are most pronounced with respect to: (1) depth and location of pelagic larvae; (2) depth, location, and timing of young-of-the-year habitats; (3) preferred depth ranges for juveniles and adults; (4) spawning seasons; (5) seasonal and ontogenetic movements; (6) population genetics and dynamics; (7) prey–predator relationships and food web relationships; and (8) environmental health (multiple stressor effects on fitness). Behavioral studies for all life stages are virtually non-existent. New information is being developed and, for the lesser-known species, gaps may be slowly addressed over time. Priority needs, for species having special significance in subsistence fisheries and marine food webs or that may be indicator species are emphasized in the species accounts. One of two categories of identified research need is identified for each species. The meaning of the categories [A] and [B] is as follows:

- **[A]** Many gaps in our understanding of the species life history and ecology remain in Alaska (for example, research areas 1 through 8). These are high profile species in terms of ecological, subsistence, or potential fisheries values. Specific research priorities are briefly discussed.
- **[B]** Most aspects of the species life history and ecology are unknown for Alaska (for example, research areas 1 through 8). Species information will likely accumulate over time and focused studies are not warranted at this time.

References Cited and Bibliography

A thorough review of scientific literature was done in the preparation of the species account. A list of references (References Cited [[chapter 8](#)]) is provided for each species for readers seeking additional information. This list identifies key sources of information that make the greatest contributions to current knowledge (2014) and understanding. The Bibliography section provides a full accounting of all scientific literature cited in each species account. For a small number of species from the family Cottidae, only a Bibliography was possible to provide and this is indicative of the lack of information available. Citations are not always in numerical order in species accounts because new information became available during the production phase of this publication and were incorporated into the species accounts as appropriate.

Acknowledgments

We wish to acknowledge the technical assistance of other project personnel who contributed to the gathering of data and information and preparation of maps, graphs, and figures in this report. Among those from the U.S. Geological Survey's Western Fisheries Research Center, we thank Angela Lind-Null, Michael Hayes, and Steve Rubin for their early work in reviews of age-and-growth information. From University of California, Santa Barbara, we express our special gratitude to Rebecca Bloom and Eddy Peralta for their efforts in generating vertical distribution charts for the Arctic marine fish fauna. Many individuals are acknowledged for their reviews of early drafts of this report. Included in this group we appreciate the reviews and comments of Jim Reist (Department of Fisheries and Oceans, Canada), Robert Meyer (formerly USGS), Larry Moulton (MJM Research LLC), David Brown (U.S. Fish and Wildlife Service), Ben Gray (University of Alaska Fairbanks), Jefferson Childs (formerly BOEM), Nancy Deschu (BOEM), Catherine Coon (BOEM), Katherine Wedemeyer (BOEM), Louis Fortier (Université Laval, Quebec, Canada), and Alec Maule (formerly USGS).

Summary

The species accounts are a major biodiversity milestone confirming the presence of 109 marine fishes in 24 families in the U.S. Chukchi and Beaufort Seas. One hundred four (104) species accounts are presented. Full species accounts for the Alaska Skate, Pacific Sleeper Shark, Thorny Sculpin, Checkered Wolf Eel, and Pale Eelpout were not prepared due to their very recent confirmation and general lack of information from the region. Each account describes what is presently known about the biology and ecology of each species from observations from Alaska, adjacent seas, and other locations. A species account summarizes current information about geographic distribution, abundance, life history and habitats, community relationships and population ecology, and ecological roles. The listing of Iñupiaq names for some species, but not others, provides an important measure of traditional values of these fish. Each species account represents an autonomous review of relevant data and information; each is scientifically documented with key literature sources so that users will have easy access to additional detail from the studies reviewed. Collectively, this treatment is the most comprehensive inventory of species information undertaken for this segment of Alaska's marine fish fauna to date. The species accounts present thorough information, some of which reflects quantitative depictions of complex ecological concepts and population understanding. Information about life cycle requirements, trophic position, and population resilience are essential to National Environmental Policy Act assessments of potential effects from offshore energy development at population and ecosystem levels of biological organization.

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Chapter 4. Synthesis of Arctic Alaska Marine Fish Ecology

By Lyman K. Thorsteinson¹ and Milton S. Love²

Abstract

The compilation of data and information, its review, and the synthesis processes leading to the development of individual species accounts focused on descriptive elements of Arctic Alaska's marine fish fauna. The species accounts reflect the compilation and review of a large body scientific information about the marine fishes off Alaska in United States waters in the northern Bering Sea, north of the Bering Strait, and throughout the circumpolar Arctic. The purpose of this synthesis is to interpret the whole of this biological and ecological information in the context of the marine biogeography of the Chukchi and Beaufort Seas. This interpretive approach provides historical and contemporary perspectives to our descriptions of (1) patterns of species occurrence, habitat and population relationships, and (2) functional ecosystem processes that affect the distribution and abundance of marine fishes, and, with respect to the present, (3) conceptual understanding and information needed for resource management and conservation. The objectives of this synthesis focus on environmental relationships including physio-chemical factors (for example, temperature, salinity, dissolved oxygen, and turbidity), mechanisms (for example, currents, migrations, and movements), and biological processes (for example, competition, predation, colonization, and reproduction) that collectively have limited the distribution, abundance, and productivity of marine fish populations through adaptations to Arctic conditions.

Introduction—A Biogeographic Emphasis

Individual species accounts present a large amount of information about the biology, geography, and environmental factors affecting large-scale patterns of distribution and abundance. Collectively, this compilation of environmental information is foundational for an improved understanding of the descriptive and interpretive components of this region's biogeography (Nelson, 2006). Our focus on the

interpretive component (historical and ecological elements of biogeography) provides a meaningful approach for explaining the observed diversity relationships, synthesizing the information presented, and expressing our impressions about outstanding needs. Historical biogeography addresses the origins of distributional patterns as determined from systematic studies. The paleoceanographic record is not well-developed from this part of the Arctic and here we explore species origins in light of possible dispersal and vicariance events as suggested by paleontology and geologic records, climatic histories, and known phylogenetic relationships. Ecological biogeography addresses the environmental relationships including physiochemical factors (for example, temperature, salinity, dissolved oxygen, and turbidity), mechanisms (for example, currents, migrations, and movements), and biological processes (for example, competition, predation, colonization, and reproduction) that limit the distribution, relative abundance, and productivity of a species. Information about body size and trophic position also are reviewed because they are important parameters that correlate with metabolic processes and other life history traits (Romanuk and others, 2011).

The descriptive component of biogeography is addressed in project tasks leading to an updated checklist of marine fishes, presentation of information in the species accounts, and special analyses related to (1) new species occurrences and range extensions, (2) large-scale patterns of abundance from past and ongoing studies, and (3) identification of species likely to occur, but yet-to-be confirmed from the Chukchi and Beaufort Seas. The visualization of species information in new maps and depth profiles provides another dimension to evaluation of the status of baseline information than was previously available. This is especially relevant as it applies to availability of age- or stage-specific information and related habitat relationships. Quantitative relationships between age-and-length and size-at-length have been described for several dominant species, but this information is dated. For almost all species, information about stock structure and population dynamics (that is, differential mortalities between life stages or age classes) remains to be described. Although many science gaps exist, compiling and integrating descriptive and interpretive information-types allows a more detailed examination of linkages between geographic distributions, evolutionary processes (patterns of life history variations), ecological factors, genetic diversity, and population dynamics

¹U.S. Geological Survey.

²University of California, Santa Barbara.

for the fauna as an initial approach to estimating effects of environmental change (Winemiller, 2004; Benton and others, 2006). This approach illustrates why the information presented in the species accounts is relevant to decision making and, for potential indicators species, a rationale for research priorities.

Historical Biogeography

The Chukchi and Beaufort Seas occupy a relatively small region within the zoogeographic realm (Mecklenburg and others, 2011) that has been used by classical ichthyologists to describe the taxonomy and composition of the Arctic marine fishes (Briggs, 1974; Andriashev and Chernova 1994; Eastman, 1997; and Mecklenburg and others, 2011). In Alaska, the Arctic Realm includes the northern Bering Sea and marine environments beyond the EEZ³. As such, it does not directly correspond to conventional natural resource management areas in the Alaskan Arctic. The southern boundary of the province in the Bering Sea is ecologically significant because the area demarks a sharp gradient in diversity and abundance of Arctic and Boreal marine fishes that is defined by temperature (<2 °C). As such, a natural rather than administrative faunal separation is represented. For example, NOAA collected 86 species of marine fishes in the northern Bering Sea in 1981 (Thorsteinson and others, 1984) compared to the 300 species reported from the southeastern Bering Sea (Wilimovsky, 1974). The zonation is important to contemporary Arctic issues with respect to extralimital species and northerly shifts in distributions and range expansions associated with climate change and potential fisheries. The importance of the Bering Strait with respect to geologic and climatic history and origins and exchanges of fishes, especially during the late Pleistocene, has been shown to be critical to understanding Pacific influences on Arctic fauna (for example, Mecklenburg and others, 2011).

A systematic comparison of the marine fishes reported from the Arctic province, marginal seas of the Arctic Ocean, and Bering Sea provides clues and insights about the evolutionary processes (origins, rates of endemism) underlying current patterns of taxonomic representation (zoogeographic patterns, [chapter 2](#)). The comparison of marine fish faunas from adjacent waters also is instructive with respect to origins (distribution centers), expectation of probable occurrence, or in some instances, understanding founding sources of confirmed species from the U.S. Arctic ([table 4.1](#), additional Arctic seas in Christiansen and others, 2013).

The estimates of marine fish diversity (occurrence) in [table 4.1](#), was from published literature or acquired through reliable sources of written communications, and represent “working” totals from a field of ichthyology that is rapidly changing. These changes relate to new discoveries, increased sampling, and new genetic tools for identification and better understanding of evolutionary relationships. The presence of 15 new marine fishes from the U.S. Arctic not reported in the *Fishes of Alaska* (Mecklenburg and others, 2002) has been confirmed for this report ([table 2.2](#)). Many of the authors cited reported significant problems associated with species identifications (related these to unresolved taxonomic issues), deficiencies in geographic sampling coverage, or access to existing data and information. Despite these issues, the systematic comparisons help to begin to explain large-scale patterns of biodiversity including origins of species distributions.

Biogeographic research has shown that fish species in the Pacific and Atlantic Oceans have similar zoogeographic patterns with respect to latitudinal gradients, but not diversity (Christiansen and others, 2008; Christiansen and others, 2013). In each ocean, species richness peaks in the tropics with sharp gradients between tropical and temperate waters. There is leveling off in decline of richness toward the poles (Roy and others, 1998). Using marine gastropod diversity data, Roy and others (1998) examined latitudinal gradients in the Atlantic Ocean with respect to ecological traits (that is, range size, habitable area, and input of solar energy). The greatest correlation reported was between diversity and sea surface temperature (a proxy for solar input) suggesting that, if the relation was causal, it probably was linked through some aspect of production. Because the physical mechanisms of dispersal for marine invertebrates and fishes are similar (or the same), process effects—such as production cycles and events—would similarly influence geographic distribution and abundance patterns.

In areas where regional faunas are relatively well known, Briggs and Bowen (2012) described a high concordance between levels of endemism in fishes, molluscs, and other biota. However, Roy and others (1998) could not explain latitudinal gradients in the North Atlantic based on recent geologic history. By contrast, Vermeij (1991) and Briggs (1995, 2003) described the biogeographic consequences of the opening of the Bering Strait and the Great Trans-Arctic Biotic Exchange (3.5 million years ago [Ma]) on the dispersal of Arctic molluscs and marine fishes, respectively (see [table 4.2](#) for geologic periods). Prior to this opening, the marine barrier formed by Beringia had isolated Pacific and Atlantic faunas for millions of years. Vermeij (1991) determined that of the 295 mollusc species that participated in the interchange, almost 90 percent (n=261) had Pacific origins or were descended from taxa with Pacific origins. Briggs (2003) hypothesized an asymmetrical invasion of marine fishes from a North Pacific evolutionary center (“*centres of origin*” hypothesis) and that at least one species from

³The three provinces described in Sigler and others (2011) relate to Bering, Chukchi, and Beaufort Seas and relate more directly to smaller ecological units in a conservation context. For this discussion, the classical definition for a province is used based on endemism. In this case, the provincial boundaries correspond with the geography of shelf areas of the Arctic Region described by Briggs and Bowan (2012).

Table 4.1. Systematic comparisons of marine fishes occurring in the Arctic marine and adjacent seas or marine areas bordering the U.S. Chukchi and Beaufort Seas.

[Regions: Arctic Realm (as defined in this chapter), Arctic Zoogeographic Region described by Mecklenburg and others (2011). OCS, Outer Continental Shelf; ~, approximately; –, not applicable]

Regions	Geography relative to U.S. study area	Estimated total number of				References
		Orders	Families	Genera	Species	
Arctic Realm	Encompasses circumpolar Arctic including the northern Bering Sea	22	45	126	242	Mecklenburg and others (2011)
U.S. Beaufort Sea	Beaufort Sea OCS Planning Area	9	19	44	83	This report
U.S. Chukchi Sea	Chukchi Sea OCS Planning Area	11	22	56	97	This report
Chukchi Borderland	North U.S. Chukchi Sea	4	7	11	12	Mecklenburg and others (2014); Longshan and others (2014)
Canadian Beaufort Sea ¹	East of U.S. Beaufort Sea	21	48	115	189	Coad and Reist (2004)
Yukon	Adjacent to U.S. Beaufort Sea and north of Yukon Territory, Canada	9	14	28	44–46	Coad and Reist (2004)
Russian Chukchi Sea	West of U.S. Chukchi Sea	11	26	68	112	Parin (2004); Parin and others (2014); Datsky (2015)
East Siberian Sea	Northern Russia east of Chukchi Sea	9	14	33	65	Pauley and Swartz (2007)
U.S. Bering Sea	U.S. territorial marine waters south of Chukchi Sea	21	64	190	~375	Mecklenburg and others (2002); Mecklenburg and others (2011 OR1); Maslenikov and others (2013); Love and others, written commun. (2015) ²
Northern Bering Sea	Bering Sea from the Bering Strait to the south of St. Lawrence Island	–	–	–	(a) 128 (b) 136 (c) 165	(a) OBIS database (http://www.iobis.org/); (b) Chernova (2011); (c) Datsky and Andronov (2007)
Bering Sea	Entire Bering Sea south of Chukchi Sea	–	–	–	(a) 385 (b) 418	(a) Christiansen and others (2013); Mecklenburg and Steinke (2015) (b) Greenwald and others (2006)

¹This estimate does not include brackish water species.

²Love and others, written commun. (2015) refers to an ongoing updating of Love and others (2005).

Salmonidae, Osmeridae, Hexagrammidae, Cottidae, Agonidae, Liparidae, Stichaeidae, and Pholidae contributed to the Arctic-North Atlantic fauna. The Capelin (*Mallotus catervarius*) is an example of such a Trans-Arctic dispersal during the Pleistocene (Dodson and others, 2007). Similarly, the cod family, Gadidae, is thought to have developed in the North Atlantic and contributed two species to the North Pacific.

Large segments of an ancient fauna of boreal origins are believed to have gone extinct during the late Miocene (Mecklenburg and others, 2011). The opening of the Bering Strait, prevailing ocean conditions and currents probably favored the dispersal of new North Pacific species into habitable Arctic shelf areas during the Pliocene (Eastman, 1997; Briggs, 2003). Ocean connections to the Arctic during this period are hypothesized to have been primarily through the Fram (North Atlantic) and Bering (North Pacific) Straits.

The relatively small number of species in the Arctic suggests that widespread dispersal processes were constrained by the separation of basins and absence of a circumpolar current.

Christiansen and others (2013, p. 195) noted that (Arctic) freshwater and diadromous fishes were “*significantly molded by glaciation, deglaciation and geological events during the late Pleistocene and Holocene epochs (i.e. ~ 126,000 and 12,000 years ago, respectively)*” and that (citing Krylov and others, 2008 and Polyak and others, 2010) the evolutionary history of the marine fish fauna “*dates back to the Neogene period as the modern circulation in the Arctic Ocean began to form some 14–17 million years ago.*” The Great Exchange occurred during a period of ice-free, boreal conditions. The greater success of Pacific invaders was hypothesized by Briggs (1995) to be related to their “superior competitiveness” (for example, behavioral, reproductive rate, individual

Table 4.2. Geologic and climatic history of the Arctic.

Era(s)	Recent geologic history (millions of years ago)	Geologic and climatic significance
Late Cretaceous	80	Beringia (Bering Land Bridge) forms and separates North Pacific and Arctic-North Atlantic faunas.
Paleocene–Oligocene	66–23.03	The Arctic Region was in high latitude position and the climate was temperate with water temperatures of 10–15 °C. Water temperatures gradually cooled during the Eocene and Oligocene eras (56–23.03 million years [Ma] ago)
Miocene	23.03–5.3	Arctic land masses reached their present positions and water temperatures dropped below freezing (10–15 Ma). The Bering Strait may have opened during the Cenozoic (6–12 Ma) allowing for limited passage (Briggs, 2003). Additional cooling, ice sheet expansion, lower sea levels, and shallow Bering Strait, limit exchanges between Arctic and Pacific Oceans. Ocean circulation was latitudinal with limited Arctic-North Atlantic exchanges. The southward movement of the warm-temperate zone and its replacement by the cold-temperate zone are hypothesized to have caused mass extinctions of boreal families during the late Miocene.
Pliocene	3.5–3	The opening of Bering Strait allowed many Pacific species to invade the Arctic. Ocean circulation changed with the closure of the Isthmus of Panama (about 3.2 Ma), which strengthened the Gulf Stream, increased precipitation at high latitudes, and contributed to further glaciation in the northern hemisphere. The Atlantic and Pacific Oceans had oceanic connections to the Arctic during the late Pliocene and faunal interchange was possible.
Pleistocene	2.588–0.0117 (11,700 years ago)	The early Pleistocene was a time of glacial advances and retreats, periodic freshwater inputs into the Arctic Basin, and cooling leading to the formation of Arctic sea ice. Permanent ice cover has been present for at least 0.7 Ma and possibly intermittently as long as 2.0 Ma. Some components of the Arctic marine fauna may have persisted from the Miocene and Pliocene eras and exchanges with the Atlantic and Pacific were also possible as the Bering Strait remained open.

size, or vulnerability to predators or parasites) resulting from their evolution in a highly diverse marine ecosystem. Extended cooling between 2.9 and 2.4 Ma is postulated to have led to the extinction of the truly boreal species and given rise to the modern Arctic fauna (table 4.2; see Eastman, 1997; Mecklenburg and others, 2002, 2011; Briggs, 1974, 1995, 2003, 2004). This fauna is characterized by relatively few (numbers) endemic species when compared to the diversity of marine fish fauna from lower latitudes. The low amount of endemism has been hypothesized to be related to evolutionary effects of ocean continuity and lack of geographic isolation over recent time. Briggs (1995) indicated that the Arctic climate repeatedly warmed and cooled until about 3 Ma when present cold conditions stabilized.

In Alaska, the species richness of the marine fish fauna from the high Arctic (includes northern Bering Sea as used here) is similarly low when compared to lower latitudes (chapter 2). Interestingly, the number of endemic species relative to total number of marine fishes reported from the U.S. Chukchi and Beaufort Seas is relatively high. We propose that this relates to the geographic isolation of this region during the last glacial period resulting from a lack of connection between Pacific and Arctic oceans through the Bering Strait, and the absence of shelf environment between openings with the Nordic Seas.

Geographic Perspectives of Marine Fish Diversity

Mecklenburg and others (2011) examined the faunal composition of marine fishes in the Arctic region and confirmed earlier characterizations of the young phylogenetic age of dominant families (for example, Zoarcidae and Stichaeidae) and the apparent lack of successful invaders from the Atlantic (for example, Gadidae and Anarhichadidae). Data in this report support these findings as they extend to Alaska. As an example, the two largest families (Zoarcidae with 17 species and Cottidae with 17 species) were determined to contain almost one-third of the total number of species reported. They were followed, in order of decreasing species numbers, by Salmonidae (12), Pleuronectidae (9), Stichaeidae (8), Agonidae (7), and Liparidae (6). Collectively, seven (7) families accounted for nearly 68 percent of the region's confirmed marine fish diversity. In the western Chukchi Sea, Datsky (2015) noted a similar pattern (without Salmonidae), with members of the Cottidae, Zoarcidae, Pleuronectidae, Stichaeidae, and Agonidae accounting for 66 percent (73 species) of the total number of species identified.

Regional comparisons of the diversity of fishes reported from marine waters adjacent to the U.S. Arctic are qualitative⁴; however, the distributional patterns suggested by presence-absence data suggest dispersal processes. With respect to the U.S. Arctic, the Bering Sea, with more than 400 marine fishes, represents the largest regional source of potential colonizing species. The same is true of the North Atlantic for the Barents and Eastern Siberian Seas. When the species information is examined in the context of prevailing ocean currents and transport processes, a northerly dispersal of species in Pacific Waters, notably in Alaska Coastal Water, seems to be the most

probable (with respect to likelihood of success) historical and contemporary mechanism for large-scale colonization of the U.S. Chukchi and Beaufort Seas. The distribution of shared species in the Chukchi Sea (United States and Russian), Chukchi Borderlands, and southeastern Beaufort Sea (United States and Yukon) would seem to reinforce the Pacific transport hypothesis (table 4.2). However, Mecklenburg and others (2014) noted that all 12 species collected from the Chukchi Borderland occur, and many are common in northern Atlantic sectors of the Arctic. Their findings support an Atlantic transport hypothesis in subsurface currents associated with Atlantic water masses. Alternatively, as the authors suggest, the species could have been in the region for thousands of years but simply not discovered until recently because of the previous lack of sampling.

A regional comparison of the presence data indicates a high percentage of shared species between United States sectors of the Chukchi and Beaufort Seas (table 4.3). Although this could be an artifact of existing data collection, it supports a major dispersal pathway in Alaska Coastal Water. The regional data as a whole further support the existence of an inter-regional gradient of declining species richness with increasing latitude. This pattern was reported previously for the U.S. Arctic (Craig, 1984) and was related to the lack of expatriate species from the Bering Sea found in the Beaufort Sea (Crawford and others [2012] citing others). In this case, the transport of Alaska Coastal Water to the east and north of Point Barrow (fig. 1.1) may impede larval dispersal and colonization processes. Cold temperatures, availability of foods, and other physical and biotic prerequisites of the Beaufort Sea coastal habitats could be major constraints to successful colonization.

Table 4.3. Estimated numbers of common or shared species in the U.S Arctic and adjacent marine areas.

[**Russian Chukchi Sea:** Total estimate of 67 assumes Arctic Cod and Pacific Cod occur in the area, but were not reported by Pauly and Swartz (2007). **Arctic:** Includes Chukchi and Beaufort Seas in waters of the United States]

Regions	Chukchi Borderland	Russian Chukchi Sea	United States			Yukon
			Chukchi Sea	Beaufort Sea	Arctic	
Chukchi Borderland	12	4	7	9	7	3
Russian Chukchi Sea		67	46	42	39	22
U.S. Chukchi Sea			97	68	68	31
U.S. Beaufort Sea				83	68	34
U.S. Arctic					109	30
Yukon						44–46

⁴Comparisons are problematic due to differences in sampling, problems associated with field identifications and nomenclature, and taxonomic uncertainties.

Understanding the diversity of marine fishes in adjacent areas also provides information about extralimital occurrences and a basis for reasoned expectations about probable species occurrences (not yet recorded) and possible founding sources of new species into Alaska waters (table 4.3). Mecklenburg and others (2011) reported the presence of 242 species of marine fishes in a circumpolar Arctic study area that, for Alaska, extends into the northern Bering Sea. Mecklenburg and Steinke (2015) report 122 marine fishes from the Pacific Marine Region, a smaller region that includes northern Bering, Chukchi, Beaufort, and East Siberian Seas. They do not include amphidromous species in their tally of marine fishes. The Center of Biodiversity reports the occurrence of 418 species of marine fish in the Bering Sea (Greenwald and others, 2006) and although this number could not be verified, it is indicative of the high diversity of fishes found south of the Bering Strait. With respect to the U.S. EEZ in the Bering Sea, Mecklenburg and others (2002) reported about 350 species. As part an ongoing effort to update a checklist of marine and estuarine fishes in United States waters by Love and others (2005), the current estimate is between 375 and 400 species for this part of the Bering Sea.

An examination of regional oceanographic and zoogeographic patterns in light of known phylogenetic relations provides additional support for hypotheses regarding the ancestry of Arctic marine fishes. For the United States, the updated list of fishes is indicative of both widespread (Pacific and Atlantic) and endemic (Arctic Ocean) origins. The species derived from Atlantic and Pacific origins further suggest the role of ocean currents on dispersal and the hypothesized importance of the continuity of Arctic shelves to colonization (Eastman, 1997). To illustrate the concept, Carmack and Wassman (2006), estimated that the flow of Atlantic Water into the Arctic Ocean is, on average, more than five times larger than inflow of Pacific Water. This difference was considered to be responsible for the dominance of Atlantic-derived species over much of the northern Russian shelf.

The analysis herein of zoogeographic patterns revealed that Atlantic-derived species account for less than 10 percent of the diversity ($n=9$ species) of marine fishes confirmed from United States waters. This includes species from Stichaeidae (*Eumesogrammus praecisus*, *Leptoclinus maculatus*, and *Stichaeus punctatus*), Gadidae (*Gadus chalcogrammus* and *Gadus macrocephalus*), Psychrolutidae (*Cottunculus microps*), Osmeridae (*Hypomesus olidus*), Myctophidae (*Benthoema glaciale*) and Pleuronectidae (*Reinhardtius hippoglossoides*). Interestingly, only two stichaeids (*E. praecisus* and *S. punctatus*) are found in both Chukchi and Beaufort Seas suggesting a discontinuous dispersal for members of this family. A slightly broader examination of the distribution of Atlantic-derived species that included marine areas adjacent to Alaska revealed four species from four families in the Russian Chukchi Sea (*G. chalcogrammus*, *E. praecisus*, *L. maculatus*, and *R. hippoglossoides*); five species from five families in the Chukchi Borderland (*G. chalcogrammus*, *Artedellius*

atlanticus, *C. microps*, *L. maculatus*, and *R. hippoglossoides*); and one species from the Yukon (*Ammodytes dubius*) and the possibility of a longitudinal gradient along the shelf break.

Paleontological Connections

Knowledge of the paleoceanographic conditions and how these conditions affect the evolution of Arctic marine fishes is limited. It seems clear from the inventory of known marine fishes from U.S. Arctic waters that endemic species (that is, Arctic, predominantly Arctic and Arctic Boreal fauna) are significant components of Chukchi (58 percent) and Beaufort (>74 percent) assemblages. How the opening and closing of the Bering Strait, interglacials, and formation of shelf ecosystems affected dispersal and speciation processes and faunal distinctions must be related to observed differences in regional oceanography, dispersal corridors, and energy pathways (Barber and others, 1997; Carmack and Wassmann, 2006; Dunton and others, 2006; Cui and others, 2009; Norcross and others, 2010). For example, Pacific water influences on the Chukchi Sea shelf are more direct than advection of regional water masses onto the Beaufort Sea shelf. The hydrography of the Beaufort Sea shelf is affected by winds, upwelling, and river inputs, and presents a variable environment for its fishery occupants (Carmack and Wassman, 2006). Biogeographic data are indicative of Pacific influences on recent (<3 Ma) colonization processes. Regional differences in shelf environments (topographic, bathymetric, hydrographic, hydrologic, currents, and biologic) correspond to broad patterns of observed diversity in adaptive strategies between the Chukchi (greater than numbers/abundance of marine species) and Beaufort (greater than numbers/abundance of amphidromous species) Seas. The latitudinal gradient that forms the southern boundary of the Arctic province is evident in the data presented. A less pronounced subregional gradient is near Point Barrow (Chukchi Sea greater than numbers of Bering Sea species less than Beaufort Sea).

Adaptations in Marine Arctic Fishes

Environmental conditions in the Chukchi and Beaufort Seas pose numerous substantial challenges to their fish populations. As noted by Power (1997, p. 16), “Fish living in arctic marine waters have to adapt to low temperature, in most places below the usual freezing point of teleost blood; seasonally constrained low productivity; perpetual or long periods of darkness; and an ice-affected shoreline.” In contrast to waters of Antarctica, Arctic waters may also have substantial annual changes in salinity (Eastman, 1997). The Arctic challenges extend to how, where, and when research has been conducted, and the resulting ecological information is much better for coastally occurring species and for those taken in subsistence fishing, than for truly marine fishes. As a result,

Arctic marine fishes are a current emphasis of BOEM research including physiological studies in laboratory and field studies (appendix A) as sea ice retreats and technological advances allow greater access to offshore marine environments for scientists and industry alike.

Many investigations show how large-scale oceanographic processes over coastal, shelf, and slope environments of the Arctic Ocean and marginal seas relate to observed differences in regional productivity and transfer of energy to benthic and pelagic components of the marine ecosystem. These affect the form (anatomical and morphological, for example, Mecklenburg and others, 2002) and function (ecological niche) of individual species and, collectively, the suite of life strategies for marine fishes occupying these waters (chapter 3). Arctic shelves are shallow and often are characterized by the richness and biomass of their benthos. With respect to the U.S. Arctic, Carey and Ruff (1977) and Carey (1987) hypothesized the predominance of benthic- and pelagic-dominated ecosystems in the Chukchi and Beaufort Seas, respectfully, as suggested by the distribution and abundance of infaunal and epifaunal invertebrates. Subsequent research (for example, Grebmeier and others, 2006a) related observed patterns of distribution to ocean features and to the cropping efficiency of herbivorous zooplankton and transport of organic matter to the benthos. The tight coupling (low efficiency) between pelagic and benthic ecosystems reported by Grebmeier and others (2006a) support the Carey (1987) hypothesis for the Chukchi Sea shelf, but the effects of shelf-slope exchange in deeper waters and the Beaufort Sea (Forrest and others, 2007) are far less clear. The low diversity and biomass of benthic invertebrates reported in ongoing benthic surveys (Katherine Wedemeyer, BOEM Alaska OCS Region, Anchorage, Alaska, oral commun., 2015) may lend further support to the pelagic hypothesis especially in eastern sectors of the U.S. Beaufort Sea. Coastal processes and food webs in the nearshore marine (≤ 10 m depths) are affected by terrestrial, freshwater, and marine influences. Marine exposures and influences generally are relatively greater along the U.S. Chukchi Sea coast than the Alaska Beaufort Sea.

The role of sea ice as a substrate for algal production and marine food webs represents a specialized flow of energy in the Arctic marine environment (Alexander, 1992). The composition, low relative abundance, and low trophic position of the marine fish assemblage reported from the Chukchi Sea are indicative of an invertebrate-dominated benthic ecosystem over shelf waters. The suspected occurrence of large concentrations of Arctic cod in deep waters of the Chukchi and Beaufort Seas (Crawford and others, 2012) suggests more pelagic processes may be occurring over the slope. Nearer shore, the role of terrestrial peat in coastal food webs of the Alaska Beaufort Sea represents a conceptually different but important source of organic matter in coastal food webs and in the adaptation, and interactions of marine fish in ephemeral brackish waters that annually form along the coast (Dunton and others, 2006). As new data from BOEM studies on the

distribution and abundance of marine fish and invertebrates from offshore marine areas of the Chukchi and Beaufort Seas, including food habits and bioenergetics become available, greater insights into more specific Arctic adaptive strategies will be possible.

Descriptions of the survival strategies of cold-water fishes in the Arctic environment are provided herein along with considerations of adaptations gleaned from known information about marine fishes living in other polar regions and, to a lesser extent, more temperate waters. However, there is a shortage of research on the physiology and behavior of the fishes of the Chukchi and Beaufort Seas. Although some studies were conducted on taxa like Arctic Cod and Shorthorn Sculpin in other parts of their ranges, most physiological research has been on Antarctic species from a region quite different from the Arctic. At high latitudes particularly, Antarctic waters have been covered in an ice sheet for 10–15 million years. Its inshore waters have been isolated from lower latitudes for about 25 million years (leading to a suite of endemic and closely related species), and it has both temperatures and salinities that are quite stable over the course of a year (Eastman, 1997; DeVries and Steffensen, 2005; Verde and others, 2006). Additionally, the water beneath this ice sheet is super-cooled, leading to the formation of ice crystals to depths of more than 30 m. In contrast, a permanent ice cover has existed in the Arctic for only 0.7–3 million years, so there are no barriers to immigration into the region (leading to a relatively diverse fish assemblage). Water temperatures can vary as much as 15 °C during a year, and at least in some nearshore environments, the variability in salinity is significant (Eastman, 1997; DeVries and Steffensen, 2005; Whiteley and others, 2006). There is no super-cooled water in the Arctic. As an example, over the course of a year, conditions for the nearshore fish assemblage in Simpson Lagoon, Beaufort Sea, included temperatures from at least –2 to 14 °C, freshwater to marine conditions, and clear to extremely turbid waters (Craig and Haldorson, 1981).

Because most of the research on physiological and behavioral adaptations of fishes to polar conditions has been conducted on Antarctic fishes, some of the results of this research should be cautiously extrapolated to Arctic taxa. As noted by Wells (2005, p. 302), “*There is no a priori reason that their [Antarctic fishes] adaptations should parallel those seen in the Arctic fishes.*”

Physical and Sensory Adaptations

Particularly in comparison to fish physiology and biochemistry, physical adaptations to Arctic environments, if any, are poorly understood. Seasonal changes in light and sea ice effect in concert with cold temperatures, geographic vagaries in productivity and coupling of marine pelagic-benthic ecosystems, and the general low abundance of marine fishes are evident in their physical structure and

functional morphology. These adaptations relate to how fishes interact and navigate Arctic marine waters in search for prey, potential mates, and optimum habitats. Examples of physical adaptations have been described with respect to sensory organs such as eyes, lateral lines, and barbels; skeletal and musculature structures; egg and larval conditions; and patterns of coloration. The physical placement of eyes and mouth, shape and size of mouth, and arrangement of teeth, reflect examples of morphological adaptations to dietary requirements and evolved predator-prey relationships (for example, piscivores, planktivores, benthivores, and generalists). Collectively, the adaptations relate to various search, capture, and ingestion strategies related to life (that is, moving, feeding, growing, maturing, and reproducing) in the Arctic marine environment.

Little is known about the direct selective effects of cold on sensory organs, although there has been some research on adaptations of the nervous system to lower temperatures (see section, “**Physiological and Biochemical Adaptations**”). Some work has examined the role that low light levels (either seasonal or during summer under ice cover) might have on sensory system function. McAllister (1975) discussed a number of potential sensory adaptations to low light levels in Arctic fishes. He compared eye diameters between five pairs of closely related fishes—one pair from the genera *Eleginus*, *Gadus*, *Triglops*, *Aspidophoroides*, and *Liopsetta*). In each comparison, one species of the pair was taken from the Arctic; the other species were from boreal or subarctic waters. In each case, the northern representative had larger eyes. He also noted that Arctic-caught Pacific Cod (*Gadus microcephalus*; identified as Greenland Cod, *G. ogac*) and Arctic-caught Atlantic Cod (*G. morhua*) had barbels that were longer (when standardized against orbit length) than those of Atlantic Cod taken in boreal waters. Similarly, the barbels of the Arctic-dwelling Arctic Alligatorfish (*Aspidophoroides olrikii*) are prominent, whereas those of the congeneric and, arguably more boreal-dwelling Alligatorfish are small. McAllister also generalized that the lateral line systems of a number of Arctic gadids and sculpins are composed of exposed filaments rather than filaments inside of canals, a trait found in other members of these families that lived in more southerly waters.

Since McAllister’s (1975) review, no research has been done in Arctic waters that attempted to verify his hypothesis. Work on Antarctic fishes has shown that there are some, but not extreme, adaptations to low-light environments in visual, lateral line, chemosensory, and tactile systems. For instance, and apparently similar to some Arctic fishes, many nototheniids have relatively large numbers of free neuromasts, perhaps in response to feeding and avoiding predation at low light levels (Montgomery and Sutherland, 1997; Macdonald and Montgomery 2005). However, it may be difficult to assign the reason for the evolution of this trait. As an example, Coombs and Montgomery (1994) examined the frequent occurrence of free neuromasts on the ventral trunks of Antarctic notothenioid fishes. They argued that this may

not be a response to living in low light levels. Rather, it may be a non-adaptive, paedomorphic trait, essentially a holdover from larval structures. However, it is not clear whether a midwater lifestyle or a low-light environment selected for this morphology. McAllister also made the generalization that, with few exceptions, Arctic fishes tend to be drably colored and suggested that the relatively low light levels of that environment might favor species that blend in with that environment.

Numerous attempts have been made to link increasing vertebral number, and its possible ramifications, with adaptation to Arctic conditions. This was first presented by Jordan (1891) as “*in certain groups of fishes the northern or cold-water representatives have a larger number of vertebrae than those members which are found in tropical regions*” and is now called “Jordan’s Rule.” (McDowall, 2008, p. 502). Nikolsky (1963), McAllister (1975), and other subsequent authors have speculated that greater numbers of vertebrae would be selected for in cold-water species. They noted that the additional myomeres associated with those vertebrae would aid in swimming through more viscous cold waters and help overcome a putative lowered efficiency of colder muscles. However, McDowall (2008) questions whether “Jordan’s Rule,” as well as several other generalities (that is, “Bergmann’s Rule,” “Lindsey’s Rule,” and “Williston’s Rule”) regarding the interrelationships among water temperature, size of individuals, and number of vertebrae, have any evolutionary significance. McDowall’s (2008) position is that (1) there are many exceptions to these “rules,” (2) it remains unclear what drives these relationships in an adaptive sense, and (3) there is a lack of understanding regarding whether variation in vertebrae number is under genetic and (or) environmental control.

An additional generalization, summarized in varying degrees in Rass (1941, 1989) and Marshall (1953) is that species living in Arctic waters have larger and fewer eggs (with larger yolks) than do those living in boreal waters. Marshall (1953) suggests that larger and yolzier eggs may be most adaptive in polar waters, where prey may be available only over a short plankton season. The advantages of the larger larvae that emerge from these eggs are “*the smaller food requirements in relation to size combined with increased powers of swimming, leading to a widening of the range of search for suitable food...Hatching at an advanced stage with a shortening of the period leading to metamorphosis is likely to be advantageous in high arctic [sic] and Antarctic waters with a short seasonal plankton production...an increased supply of yolk leads to increased rates of growth of embryos and larvae, thus counteracting the retarding influence of low temperatures...*” (Marshall, 1953, p. 340). Since that time, only a few studies have examined this phenomenon. Miller and others (1991) determined that among 13 species of flatfishes in the Atlantic, the 3 species in Arctic waters had the largest eggs. The operative factor(s) selecting for this trend remain somewhat unclear. Rass (1941) considered water temperature

alone responsible, whereas Marshall (1953) considered both physical factors (such as temperature) and biological factors (such as a short planktonic production season) important. The results of several studies imply that, at least in some groups, larger eggs are attributable to differences in spawning seasons rather than directly to temperature clines (Chambers, 1997).

Lastly, we note the observations of Miller and Kendall (2009, p. 439): “*It’s interesting to note that on the Arctic and Antarctic shelves, fish eggs are mainly demersal. A review of maternal output in polar fishes (Christiansen et al. 1998) revealed that while there was a pattern of relatively few and large eggs in polar versus boreal fishes this difference did not exist in substrate spawning species with large yolk reserves and long incubation periods (e.g., Greenland cod [Gadus ogac] and arctic flounder [Liopsetta glacialis], whereas most other cods and right eye flounders [Pleuronectidae] have pelagic eggs. It’s possible that spawning demersal eggs may protect the eggs against the risk of freezing and/or also against the low salinity of the surface water (where osmoregulation is difficult) during the melting of the ice.*”

Physiological and Biochemical Adaptations

Adaptations related to living at low temperatures generally relate to the “scope for growth” bioenergetics processes that occur at molecular and cellular levels of fish physiology. Much of the available research has focused on antifreeze proteins (AFPs) in fishes from Polar regions. These proteins and other properties of blood chemistry are important adaptations to how Arctic marine fishes may avoid freezing or respond to below freezing conditions (for example, specializations in the nervous system).

Below freezing conditions represent a significant environmental threat to fish species living in polar regions, as the blood plasma of most marine teleosts freezes at about -0.7 to -0.9 °C (Holmes and Donaldson, 1969), well warmer than the freezing point of sea water (that is, -1.9 °C). In response, many fish species that inhabit Arctic waters have evolved the ability to lower the freezing point of their body fluids. Of particular importance to a fish living in subfreezing waters is the ability to prevent the ice crystals that occur in these waters from growing larger, either on that fish’s external surface or, after ingestion, within the body (DeVries and Cheng 2005; Cheng and others, 2006).

The freezing point of aqueous solutions, such as those in fishes, can be depressed through elevating the concentrations of dissolved solutes. These solutes include such plasma electrolytes as sodium (Na^+) and chloride (Cl^-) (O’Grady and DeVries, 1982). However, high concentrations of these ions can interfere with a range of biological processes, such as enzyme activity, protein subunit assembly, and protein solubility (Somero, 1992). Fishes also depress their freezing points with a number of organic compounds that have less disruptive effect on these processes (Raymond, 1997). These

compounds include glycerol (Raymond, 1992; Driedzic and Short, 2007), trimethylamine oxide (Raymond, 1994; Raymond and DeVries, 1998), urea (Raymond, 1994; Raymond and DeVries, 1998), and glucose (Benziger and Ummering, 1973). All of these ions and compounds depress the freezing point colligatively (acting through the number of ions or molecules in a given amount of solvent and not on their size or mass). Serum-ion concentrations in marine teleosts living in very cold waters generally are relatively high, typically, 40 percent higher than in fishes from more temperate waters (Raymond, 1997).

The concentrations of dissolved solutes in many cold-water dwelling marine fishes (that is, Shorthorn Sculpin, Hew and others [1980]; Sea Raven [*Hemitripterus americanus*], Fletcher and others [1984]; Atlantic Wolffish [*Anarhichas lupus*], Desjardins and others [2006]; see also O’Grady and DeVries [1982]) increase during the winter, probably in response to decreasing temperature and photoperiod (Driedzic and others, 2006). Dissolved solute concentrations may provide sufficient or near-sufficient antifreeze protection for only a few species (for example, Navaga [*Eleginus navaga*], Christiansen and others [1995] and Arctic Smelt, Raymond [1992]), whereas for all others the amount of freezing protection afforded is likely limited (Fletcher and others, 1985b).

All cold-water dwelling fish species exposed to ice protect themselves from freezing by synthesizing AFPs. There are five distinct molecular groups of antifreeze proteins (AFP Types I–IV and antifreeze glycoproteins (AFGPs) (Fletcher and others, 2001); for the purposes herein all antifreeze proteins are referred to as AFPs. The five AFP types (among only distantly related taxa) are sufficiently structurally different from each other as to have evolved independently (Davies and others, 1988; Fletcher and others, 2001). The evolution of AFPs in Northern Hemisphere Arctic teleost fishes (table 4.4) likely occurred within the last 3 million years. This was the first time that these waters were glaciated (ice crystals formed) since the last ice age about 280 million years ago before the rise of teleosts (see Kennett, 1982; Scott and others, 1986; Fletcher and others, 2001; Davies and others, 1988).

Each type of AFP likely is coded for by a gene family (Hew and others, 1988; Scott and others, 1988; Shears and others, 1993; Desjardins and others, 2006). For instance, the number of gene copies of Type III AFP in the Atlantic Wolffish and Ocean Pout (*Zoarces americanus*) is estimated to be 85 and 150, respectively (Desjardins and others, 2006). Although the adult fish ability to inhibit freezing in the presence of ice through the production of AFPs is well documented, there is growing evidence that this ability also is in embryos and larvae of some species (Murray and others, 2002, 2003; Robles and others, 2005; Desjardins and others, 2007) and perhaps in their eggs (Desjardins and others, 2007).

Table 4.4. Species known to have antifreeze-protein or antifreeze-glycoprotein activity in the U.S. Chukchi–Beaufort Sea region.

[All studies listed used fishes taken outside the U.S. Chukchi–Beaufort Sea region. Families are arranged in phylogenetic order (Nelson and others, 2004)]

Family	Common name	Source
Clupeidae	Pacific Herring ¹	Power (1997)
Gadidae	Arctic Cod	Denstad and others (1987); Enevoldsen and others (2003); Nahrgang and others (2010)
	Saffron Cod	Raymond and others (1975)
	Pacific Cod ²	Van Voorhies and others (1978); Enevoldsen and others (2003)
Osmeridae	Arctic Smelt	Raymond (1992)
Cottidae	Atlantic Hookear Sculpin ³	Enevoldsen and others (2003)
	Arctic Staghorn Sculpin	Enevoldsen and others (2003)
	Arctic Sculpin	Enevoldsen and others (2003)
	Shorthorn Sculpin ⁴	Raymond and others (1975); Hew and others (1980); Denstad and others (1987); Enevoldsen and others (2003)
Liparidae	Kelp Snailfish ¹	Enevoldsen and others (2003)
Stichaeidae	Arctic Shanny	Enevoldsen and others (2003)
Zoarcidae	Polar Eelpout ⁵	Davenport (1992)
Pholidae	Banded Gunnel	Enevoldsen and others (2003)
Pleuronectidae	Alaska Plaice ⁶	DeVries (1980)

¹Enevoldsen and others (2003) reported antifreeze proteins (AFPs) from “Pygmy Snailfish” now known as “Kelp Snailfish.”

²As Greenland Cod, *Gadus ogac*.

³Scientific name for Atlantic Hookear Sculpin is *Artediellus atlanticus*.

⁴Raymond and others (1975), reported AFPs from “*Myoxocephalus verrucosus*” from Saint Lawrence Island, Bering Sea. This is a synonym of *M. scorpius* (Mecklenburg and others, 2002).

⁵Enevoldsen and others (2003) reported AFPs from “Canadian Eelpout” now known as “Polar Eelpout.”

⁶DeVries (1980) reported AFPs from “Arctic Plaice” now known as “Alaska Plaice.”

AFPs may be produced in several parts of the body. In many species, AFPs are primarily (or solely) produced in the liver (Davies and others, 1988). However, in at least some species (for example, Shorthorn Sculpin, Longhorn Sculpin (*Myoxocephalus octodentatus*), Winter Flounder (*Pseudopleuronectes americanus*), and Ocean Pout) AFPs are produced in the liver and in the epidermis of structures such as the gills, skin, scales, and fins (Gong and others, 1992; Fletcher and others, 2001; Low and others, 2002; Murray and others, 2002, 2003). The exocrine pancreas appears to be the sole site of AFP production in all Antarctic notothenioid fishes (Cheng and others, 2006); such pancreatic production has not yet been detected in Arctic taxa. Praebel and Ramlov (2005) determined that, in some species, AFPs also are derived from food sources. They examined levels of AFPs in the gastrointestinal tracts of Arctic Cod (*Boreogadus saida*)

feeding either on AFP-containing Arctic Cod or on crustaceans that did not produce AFPs. They determined that Ice Cod (*Arctogadus glacialis*) that had fed on Arctic Cod contained significantly higher levels of AFPs in their digestive fluids. Praebel and Ramlev (2005) hypothesized that partly digested, but still functioning, AFPs could be absorbed into the bodies of Arctic Cod.

AFPs do not prevent the creation of ice crystals within the fish; rather they retard the growth of ice crystals that have entered the fish (Raymond and DeVries, 1977; Evans and others, 2011). Each AFP molecule binds preferentially (and likely permanently) to well-defined sites on newly formed ice crystals (rather than to the surrounding water), thus altering their structure and inhibiting their growth (Fletcher, 1977; Fletcher and others, 2001; Davies and others, 2002; Goddard and Fletcher, 2002; Howard and others, 2010). The different

types of AFP molecules bind to different surface planes on an ice crystal (Knight and others, 1991; Fletcher and others, 2001). In at least some species, “chaperone molecules,” such as glycerol, enhance AFP activity (Gong and others, 2011). Compared to dissolved solutes, AFP molecules act noncolligatively; that is they have little effect on the osmotic balance within a fish (because the action of AFP molecules is not proportional to the number of molecules present).

Preventing the buildup of ice crystals is a two-step process involving preventing ice crystals in the environment from entering the body through the skin and preventing those crystals that do enter the body from growing larger. For fishes encountering freezing temperatures and ice, the first barrier is through prevention of ice crystals entering the body through the epithelium. Fishes living in Antarctic waters (few studies have targeted Arctic fishes) have ice on their skin, gills, and in their gastrointestinal tract, but not in the body fluids, muscles, and most organ systems, except for the spleen (Praebel and others, 2009; Evans and others, 2011). Fish skin appears to be an effective barrier to ice crystal penetration into the fish, with gill epithelium perhaps less so (Valerio and others, 1992). How do fish prevent ice crystals that form on the mucous covering the skin (Praebel and others, 2009) from gaining access to the body interior? Although it is possible that larger ice crystals fall off through frictional forces as the fish moves through the water or as currents pass over the body, it is more likely that these ice crystals are prevented from growing by the AFPs in the mucous covering the skin. Ice crystals also have been found in the gastrointestinal tract, which were carried along with ingested food and as fishes drink seawater (to maintain osmotic balance). Here, these crystals are prevented from enlarging by AFPs in the esophagus and stomach as well as pancreatic secretion into the intestine where the fluid becomes hyposmotic to seawater (Cheng and others, 2006).

In some species, these mechanisms are not sufficient to completely prevent the entry of all ice crystals into the body. When this occurs at least some fish sequester these crystals in the spleen. Evans and others (2011) studied the process by which ice crystals are lodged in the spleen. Using nanoparticles as proxies for ice crystals, they found evidence that (1) AFP-coated ice crystals were removed from the circulatory system and stored by spleen phagocytes and that (2) these phagocytes were able to recognize the difference between AFP molecules alone (which they ignored) and those molecules attached to ice crystals (a process seen in crystallizable [Fc] receptor-mediated phagocytosis induced by immunoglobulin-bound foreign particles [Swanson and Hoppe, 2004]). Evans and others (2011) note that there remain several areas of uncertainty. First, it is unclear how high levels of AFP (all of which are first discharged into the intestinal tract) are maintained in the blood and lymph systems. Second, the fate of the stored splenic ice crystals is unknown. If fish find themselves in waters above freezing temperatures, as happens to some Antarctic species (Hunt and others, 2003), these crystals could be removed through passive melting.

Seasonal changes in AFPs in Arctic fishes are poorly understood and vary among species. For instance, although high AFP levels in Arctic Sculpin from the Canadian Arctic do not vary appreciably over the course of a year ([Fletcher and others, 1982], a pattern was observed in numerous Antarctic fishes [DeVries and Lin, 1977]). Arctic Cod taken off Svalbard, Norway (Nahrgang and others, 2010) and Shorthorn Sculpin (location unknown; DeVries, 1980) exhibited reduced AFP activity during summer and increased activity during winter. Generally, seasonal changes in AFP production seem to be widespread in fishes exposed to freezing winter temperatures and warmer summer waters (for example, Winter Flounder [Fletcher, 1981]; Atlantic Cod [Fletcher and others, 1987]; Ocean Pout [Fletcher and others, 1985b]; Eelpout [*Lycodes* spp.; Sorenson and Ramlov, 2001]; and Atlantic Wolffish and Spotted Wolffish [*Anarhichas minor*; Desjardins and others, 2006]), although there is considerable interspecific variation in the timing of this cycle (Fletcher and others, 2001). Given that Arctic waters, particularly relatively nearshore, exhibit considerable summer warming, it might be expected that many species will exhibit seasonal changes in AFP production. However, the degree of seasonal variation of AFP produced by skin cells is much less than that produced by liver cells (Low and others, 2002).

Two environmental parameters, photoperiod and water temperature (sometimes working together), help control annual cycles in AFP production, although the importance of each parameter may vary with species. Photoperiod (mediated through the hypothalamus), for instance, is likely a major controlling factor in Winter Flounder, although water temperatures must be less than 8 °C for a buildup of AFP mRNA in the liver and subsequent production of AFP (Fourney and others, 1984; Davies and others, 1988; Fletcher and others, 1989). However, even in Winter Flounder, water temperature does influence the maintenance of AFPs in the body through controlling its removal from the blood stream and controlling the levels of AFP mRNA in the liver (Davies and others, 1988). On the other hand, Fletcher and others (1987) determined that changes in water temperature alone were primarily responsible for boosting AFP production in Atlantic Cod, because manipulating day length did not affect antifreeze production, whereas lowering water temperature to 0 °C did. Finally, based on laboratory studies, it is likely that both seasonal changes in water temperature and photoperiod play a role in the timing of increases and decreases in AFP production in Atlantic and Spotted Wolffishes (Desjardins and others, 2006; Duncker and others, 2006). The timing of AFP production seems to be at least partially genetically fixed (Fletcher and others, 1985a), although these previously mentioned environmental cues, working through the central nervous system and the pituitary gland (particularly through the release of growth hormone), act to “fine tune” the precise timing of the onset and decrease of AFP production (Davies and others, 1988; Fletcher and others, 2001).

Within a species, concentrations of AFP may vary considerably, even among individuals living close together. As an example, juvenile Atlantic Wolffish hatched together from eggs collected in a single bay in Newfoundland, varied in their blood plasma AFP concentrations between a high of 18.1 mg/mL and a low of 8.5 mg/mL (Desjardins and others, 2007) and similar between-individual variability was observed in sympatric adults of that species (Dejardins and others, 2006). In these two wolffish studies, juveniles and adults harbored similar concentrations of AFPs.

Conspecifics taken from geographically separated areas commonly produce different amounts of AFP. For instance, Ocean Pout living off Newfoundland contained higher levels of AFP than did their conspecifics living off warmer-water New Brunswick, differences linked to the New Brunswick fish having only one-quarter the number of AFP genes than did those from Newfoundland (Hew and others, 1988). Similarly, in a comparison of plasma AFP from Ocean Pout from Denmark and Newfoundland, fish from both areas reportedly had high levels during the winter. However, the warmer-water Danish fish lost most of their plasma AFP during the summer, whereas levels in fish from Newfoundland remained relatively high (Fletcher and others, 1985b; Sorenson and Ramlov, 2001). Similar variability occurs in, among other species, Atlantic Cod and Winter Flounder (Fletcher and others, 1985a; Goddard and others, 1999).

There are differences in AFP production within closely related species. Desjardins and others (2006) compared AFP production in the Atlantic Wolffish and Spotted Wolffish. They determined that although both species produced AFPs only the Atlantic Wolffish produced sufficient AFP to protect an individual down to the freezing point of seawater. Likely of significance is that, although both species encounter subzero water temperatures, the more shallow-dwelling Atlantic Wolffish has more of a chance of encountering ice and freezing conditions.

Even at temperatures greater than freezing, AFPs may protect cells (including perhaps fish cells) against damage. As an example, cells require the ability to expel calcium ions through active transport (thus balancing the passive ion transport that is continually occurring). It is thought that low temperatures may damage a cell's ability to actively transport these ions out of the cell. Studies by Negulescu and others (1992) determined that AFPs "*inhibited passive Ca entry across the cell membranes*" without inhibiting such normal cell functions as active transport. Antifreeze proteins may also interact with various constituents of cell membranes to inhibit cell leakage and death (Rubinsky and others, 1990; Wu and Fletcher, 2000; Wu and others, 2001).

Lastly, the mechanism(s) of freezing protection in fish eggs are poorly understood. Davenport (1992) reported that the eggs of Capelin can survive as much as 6 hours at temperatures as low as -5.2 °C. He noted that the chorion of these eggs had a "sticky, thick extra outer layer, not found in other species, which appears to have the dual effect of slowing ice crystal penetration" thus implying that there is a

morphological component to fish egg protection. However, Goetz and others (2005) determined evidence of what they believed to be an antifreeze protein in the eggs of Atlantic Cod and significant amounts of AFPs exist (and significant resistance to ice propagation exists) in the newly spawned eggs of Antarctic notothenioids (for example, Ploughfish (*Gymnodraco acuticeps*, Cziko and others, 2006).

Cellular and Metabolic Adaptations

Evidence for one long-proposed adaptation, called Metabolic Cold Adaptation (MCA), has been effectively undercut by a relatively recent series of studies. MCA holds that fishes adapted to cold waters appear to have evolved a higher metabolic rate "*when corrected for differences in measurement temperature*" that is 2–4 times that of temperate species (Steffensen and others, 1994, p. 49). The hypothesis was based on fish respiration experiments by Ege and Krogh (1914) and Krogh (1916) and later followed by those of Scholander and others (1953) and Wohlschlag (1960). However, studies on a number of Arctic and Subarctic species (for example, Arctic Cod, Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), Spatulate Sculpin (*Icelus spatula*), Shorthorn Sculpin, Fish Doctor (*Gymnelus viridis*), Greenland Cod [now known to be Pacific Cod]) strongly imply that MCA is almost certainly an artifact caused by insufficient laboratory acclimation time for fishes in respiration experiments (Holeton, 1974; Mikhail and Welch, 1989; Steffensen and others, 1994; Hop and Graham, 1995; Steffensen, 2002; Karamushko and others, 2004).

Much of the experimental research on the cold-adapted performance of fishes has focused on the selective forces on energy production, particularly on how these forces have influenced mitochondria. Cold temperatures affect the aerobic capacity of mitochondria; the respiration rates of isolated mitochondria generally decrease with decreasing temperature (Johnston and others, 1998). In response, and to maintain sufficient aerobic activity, cold-water species harbor higher volumes and densities of mitochondrial clusters than do more temperate taxa; these may reach 50 percent of the muscle fiber volume in the Antarctic Icefish (*Champscephalus esox*] see Johnston and others, 1998; Pörtner and others, 2005). However, several factors limit the amount of mitochondria produced by Arctic fishes. First, there is a maximum limit to mitochondrial densities beyond which there is not space for myofibrils, thus muscle function suffers, and the greater volumes of mitochondria in cold-water fishes only partially compensate for the reduced oxidative capacity the mitochondria afforded at low temperatures (Johnston and others, 1998). Second, an increase in mitochondrial density causes an increase in oxygen demand even under resting conditions and, as noted by Pörtner and others (2001, p. 1,992) this particularly becomes "*detrimental during warming when [oxygen demand] can no longer be covered by oxygen uptake through ventilation and circulation.*" As an example,

an increase in ambient water temperatures of only 2.3 °C results in large increases in oxygen consumption in Arctic Cod (Hop and Graham, 1995). Additionally, a comparison of the mitochondrial enzyme capabilities (citrate synthase, cytochrome *c* oxidase, and the electron transport system) of Arctic and boreal populations of Atlantic Cod demonstrate that there also have been cold adaptations in these systems (Lannig and others, 2003).

With greater mitochondrial densities in Arctic fishes has come a shift from carbohydrate to lipid (fatty acid) catabolism by these mitochondria. Although the rationale for this shift and the process by which it occurs remains somewhat obscure, one possible reason is that fatty acids are transported across cell membranes composed of fatty acids at a lower energy cost than those with high levels of carbohydrates (Pörtner, 2002). As a consequence, lipid accumulations in Arctic fish tend to be higher than in many temperate taxa. Additionally, the mitochondrial membranes of Arctic fishes tend to have elevated levels of polyunsaturated fatty acid phospholipids, probably because this type of fat supports efficient energy release rates (proton leakage) through the inner mitochondrial membrane (Brand and others, 1992; Pörtner and others, 2005). This increase in polyunsaturates, combined with the aerobic generation of high-energy phosphates, increases the opportunity for damage by free radicals and, likely in response, Antarctic fishes have high levels of the antioxidants vitamin E and C (Ansaldi and others, 2000; Giese and others, 2000; Davison, 2005).

In cold-water fishes, mitochondrial proliferation and associated adaptations come with physiological tradeoffs, as energy demands for these adaptations can be relatively high and would be shifted away from growth and reproduction (Lannig and others, 2003). Pörtner and others (2001) gave an indication of what these tradeoffs might entail. Their work was conducted on Atlantic Cod and Ocean Pout at a number of sites ranging from the European Arctic through the more temperate Baltic and North seas. They determined that in both species growth rates and fecundity declined with increasing latitude (that is, decreasing ambient water temperatures).

Selection for greater metabolic efficiency at fluctuating lower temperatures also may have led to intraspecific polymorphisms in the hemoglobin molecule. Functional differences in polymorphic hemoglobin molecules are known from Arctic Cod (*Boreogadus saida*) and Ice Cod (*Arctogadus glacialis*) (Verde and others, 2006) as well as in Spotted Wolffish, Ocean Pout, and in several Antarctic taxa (Hjorth, 1974; Verde and others, 2002). As an example, some hemoglobin molecules of both *Boreogadus saida* and *Arctogadus glacialis* show a low oxygen affinity and a low Root effect, probably linked to the high concentrations of oxygen in cold marine waters (Verde and others, 2006). Polymorphic hemoglobins, labeled HbI(1) and HbI(2), have been most intensively studied in the Atlantic Cod. First described by Frydenberg and others (1965) and Sick (1965), the frequency of the two alleles shows a north-south cline

along the Norwegian and eastern North American coasts. In both instances, a greater proportion of fishes living in cold more northerly waters carry the HbI(2) alleles. Since that time, a range of studies has demonstrated that the two polymorphisms function most efficiently at different temperatures (Karpov and Novikov, 1981; Pörtner and others, 2001; Brix and others, 2004). For instance, HbI(2) is better fitted to cold temperatures through its ability to transport more oxygen to the tissues by superior oxygen binding capabilities at low temperatures. This, in turn, seems to be responsible for differences in a number of life history parameters. For instance, Atlantic Cod living off northern Norway and carrying the homozygotic HbI(2) allele exhibit faster growth, earlier maturation, and earlier spawning season than do fish carrying the homozygotic HbI(1) allele (Mork and others, 1983). Laboratory studies have also shown that Atlantic Cod held at low temperatures grew faster when carrying the HbI(2) gene (Immsland and others, 2004). Additionally, fish behavior also may be influenced by hemoglobin type as juvenile cod that carry the HbI(2) form seem to preferentially inhabit significantly lower temperatures than do fish carrying the HbI(1) variant (Petersen and Steffensen, 2003). Although few studies have examined the handful of cartilaginous species that inhabit polar waters, the hemoglobin of the Arctic Skate (*Amblyraja hyperborea*) and the Antarctic Eaton's Skate (*Bathyraja eatonii*) seem to be (1) similar to one another and (2) functionally different from those of temperate cartilaginous species (Verde and others, 2005).

Hibernation

Small to moderate levels of reduced activity, feeding, and growth in winter are widespread among fishes, largely because metabolism is directly coupled to environmental temperature. However, true hibernation among fishes has been perhaps best documented in the Antarctic species Black Rockcod (*[Notothenia coriiceps]*; Johnston and Battram, 1993; Coggan, 1996; Campbell and others, 2008). These studies determined that in natural habitats during winter (or in testing situations that simulated winter conditions) Black Rockcod had (1) greatly reduced feeding rates (even when additional food was available) and increased mobilization of lipid reserves, (2) a negative growth rate (the loss of body mass), (3) a 58 percent suppression in total metabolic rate and 29 percent in standard metabolic rate, and (4) a 20-fold reduction in activity and a 6-fold reduction in home range. Thus, despite living in a thermally stable environment where food was readily available throughout the year, *N. coriiceps* exhibits a number of the characteristics of terrestrial hibernators. It is likely that the trigger for hibernation in this fish species is decreasing light levels rather than decreasing temperatures. As Campbell and others (2008, p. 7) note: “*The winter dormancy we have documented...is distinct from the facultative dormancy observed in temperate fish species by the levels, and duration of the reduced physiological state...*”

Hibernation in fishes is likely a continuum (Campbell and others, 2008) ranging from small amounts of metabolic depression in some species to the extreme examples of physiological and behavioral adaptations noted in Black Rockcod. What evidence for hibernation is there in Arctic fishes? To date, no studies have directly addressed this issue in fishes living in the Chukchi and Beaufort Seas. However, results from other research imply that hibernation, or at least dormancy, is a likely strategy for many Arctic species. For example, in the Subarctic waters of Newfoundland Cunner (*Tautoglabrus adspersus*) display numerous attributes suggestive of dormancy (Green and Farwell, 1971; Green 1974; Valerio and others, 1990). At temperatures less than 5 °C, Cunner become extremely torpid and shelter in the rocks and boulders of shallow, nearshore waters (at water temperatures as low as -1 °C). Here they remain, without feeding, throughout winter and spring, until water temperatures increase in May or June. Additionally, Cunner produces a thick mucus coat that likely hinders contact between ice crystals and skin and that skin produces antifreeze. Unlike Antarctic fishes, however, these survival mechanisms are imperfect, as extremely stormy winter conditions can drive ice crystals with sufficient force against sheltering fishes that they freeze to death. In the cold waters of laboratory experiments, a North Atlantic species, Winter Flounder, burrow into soft bottom, perhaps to avoid ice crystals (Fletcher, 1975).

Hibernation has not been directly investigated in Arctic fishes. However, the winter behavior of young Arctic Cod in Franklin Bay, southeastern Beaufort Sea off Canada, led Benoit and others (2010) to speculate that these fish were hibernating. During this hibernation period, these fish form extremely dense midwater schools and make only occasional vertical excursions, likely for feeding. Noting the slow digestion rates in this species (about 17 days), Benoit and others (2010) speculated that fish remained for the most part in a torpid state, leaving that state only when sufficiently hungry. Amphidromous species, such as Arctic Cisco (*Coregonus autumnalis*) and Least Cisco (*C. sardinella*), overwintering in the Sagavanirktok River and Colville River deltas in Alaska may become torpid during winter, as feeding ceases or is much reduced (Schmidt and others, 1989). However, during winter these fishes will migrate upstream away from the more saline conditions that occur as winter progresses, so hibernation is not complete. On the other hand, the marine Fourhorn Sculpin (*Myoxocephalus quadricornis*), a dominant benthic species in the nearshore of the Beaufort and Chukchi Seas, shows no sign of hibernation, as it actively feeds throughout the year (Schmidt and others, 1989). Fishes including Arctic Cisco and Least Cisco, Humpback Whitefish (*C. pidschian*) and Broad Whitefish (*C. nasus*), Arctic Cod, Saffron Cod (*Eleginus gracilis*), Fourhorn Sculpin (*M. quadricornis*), and Arctic Smelt (*Osmerus dentex*) are all captured in winter fisheries, implying enough individual activity for them to become entangled in gillnets or to strike hooks (Craig, 1989b).

Other Functional Adaptations

As water temperatures decrease, blood viscosity increases in Antarctic fishes. For instance, blood viscosity in the Emerald Rockcod (*Trematomus bernacchii*) at 0 °C is about 40 percent higher than at 10 °C, thus increasing cardiac workload (Axelsson, 2005). To compensate for this added viscosity, a major adaptation in the circulatory system of Antarctic fishes in extremely cold water has been a reduction in haematocrit (packed red blood cell volume) and mean cell hemoglobin concentration (Egginton, 1996; Davison and others, 1997). Interestingly, there is no evidence for increased flexibility of red blood cells, although this would also reduce the effect of increased viscosity (Lecklin and others, 1995). Additionally, the gross anatomy of Antarctic fish hearts appears to be similar to those of more temperate-water taxa, although the diameter of Antarctic fish heart myocytes (muscle cells) are slightly larger, due to an increased number of mitochondria (Axelsson, 2005). There is no evidence for cold adaptation of vascular control as measured by branchial artery contractility in polar compared with temperate fishes (Hill and Egginton, 2010).

Most research addressing possible adaptations to the nervous system of Arctic fishes also has studied Antarctic species. These studies demonstrate that polar fishes have evolved a number of adaptations to this cold environment. Among these, alterations in the cell membrane to maintain fluidity is one of the most important and is accomplished through an increase in unsaturated fatty acids, thus lowering viscosity that would normally attend ambient lower temperatures (Morris and Schneider, 1969; Macdonald, 1981). Work on Shorthorn Sculpin from the northern Bering Sea demonstrates that at low temperatures this trend of increasing membrane fluidity declines or ceases (Cossins and Prosser, 1978). Conductivity within the axoplasm of nerve cells also has adapted to lower temperatures through an increase in ion concentrations within and around these cells (Dobbs and DeVries, 1975; MacDonald, 1981). The brain gangliosides (molecules in the cell plasma membrane that influence membrane fluidity and are involved in cell signal transduction) of Antarctic fishes seem to be cold adapted through an increase in their concentrations and polarity (Becker and others, 1995). However, this variety of adaptations leads to only a partial compensation for low temperatures. Overall, the nervous systems of Antarctic fishes transmit impulses at a slower rate than in fishes living in warmer environments (Macdonald, 1981; Pockett and Macdonald, 1986), a phenomena also found in the peripheral nerves of Arctic species such as Arctic Cod, Snakeblenny (*Lumpenus lampretaeformis*), and an unidentified eelpout (*Lycodes* sp.) (Moran and Melani, 2001).

Similar to the nervous system, the musculature of cold-water fishes has seen a series of adaptations to maximize function under Arctic conditions. These adaptations include (1) changes in myosin structure (Johnson and Johnston, 1991) and the abilities of cross bridges to generate force (Johnston,

1985; Johnston and Altringham, 1985), (2) increases in rates of Ca^{2+} accumulations in sarcoplasmic reticulum (McArdle and Johnston, 1980), (3) and changes in the activation enthalpies of the sarcoplasmic reticulum ATPase (McArdle and Johnston, 1980). All these adaptations have helped bolster the force generation, muscle contraction speed, and twitch duration of cold muscles beyond what might be expected. Within the Antarctic notothenioid fishes, there has also been a marked trend toward large white and red muscle fibers (Davison, 2005). However, this may represent an ancestral trait within the group, rather than an adaptation to cold water. As with the nervous system, these compensations (including the changes in aerobic capacity due to increases in mitochondrial densities) are relatively modest and muscle function of fishes living in Arctic conditions is significantly impaired compared to those of fishes living in warmer waters (Montgomery and Macdonald, 1984; Johnson and Johnston, 1991). For instance, power output for the Antarctic Icefish at -1°C is about 60 percent that of the Pacific Blue Marlin (*Makaira nigricans*) at 20°C (Johnston and Altringham, 1985). Together, this translates to generally lower maximum swimming speeds and low maximum tail-beat frequencies in polar fishes (Johnson and Johnston, 1991) and to relatively poor burst swimming performance in at least some of these species (Archer and Johnston, 1989).

Despite a range of compensatory adaptations, cold-water dwelling fishes remain incapable of maintaining the metabolic rates and active life styles of most temperate species (Macdonald and Montgomery, 1982; Johnson and Johnston, 1991; Lannig and others, 2003). This is true both for the Antarctic (Steffensen, 2005) and for northern Arctic and subarctic fishes, which have the additional burden of coping with significant annual changes in temperature (Lannig and others, 2003). Inevitably, many Arctic species have a relatively sluggish (that is, lowered mobility) lifestyle and shift a significant amount of their energy budgets away from growth and reproduction (summarized in Steffensen, 2005).

Life Strategy Adaptations

Arctic fishes have evolved numerous life strategies for coping with low temperatures, long periods of diminished light conditions, and brief periods of marine production that generally favor benthic-dwelling species (for example, Mecklenburg and Steinke, 2015). These strategies relate to a fish's environmental requirements for food, growth, and reproduction. These requirements involve multiple life history stages, habitats, and behaviors that optimize life processes and opportunities for successful reproduction. Diadromous (migratory) patterns that involve amphidromy or anadromy are common life strategies that link the fish to stable conditions in freshwater and marine environments and, at the species level, are characterized by species that vary widely in their tolerance to salinity, exhibit variable freshwater residencies in immature fish, older ages at first

reproduction, and widespread differences in their fidelity, or suspected fidelity, to known spawning and overwintering areas (for example, DeGraaf and Machniak, 1977; and Craig, 1989a). The amphidromous species (for example, charr and whitefishes) are iteroparous and generally long-lived, typically living 20 years or more. They tend to mature at 7–8 years and, after their first spawning event, tend to spawn every other year thereafter. Anadromous species (for example, Pacific salmon and lampreys) are semelparous, spending most of their lives at sea. The anadromous fishes tend to live between 2 and 7 years and die shortly after spawning. These species tend to be much larger and more fecund than the amphidromous fishes. Both are conspicuous members of the Chukchi and Beaufort Sea nearshore fish assemblages during summer months. Existing information for many marine fish species suggests shorter life cycles, earlier maturation, and greater relative investments of energy in the production of young (for example, large numbers of eggs). There are exceptions such as sharks, rays, and Pacific Halibut. The location of important seasonal habitats, reproductive ecologies, and life histories of most species from Arctic Alaska remain largely undescribed. It is known that many populations, or segments of populations have important life history linkages to coastal waters for food, reproduction, and migration between seasonal habitats. Examples include all of the amphidromous and anadromous species as well as other coastal dominants such as Arctic Cod, Arctic Flounder, Capelin, Arctic Smelt, and several sculpin species such as the Fourhorn Sculpin. Generally, onshore-offshore movements such as those related to ontological development of species like Pacific Herring and Arctic Smelt, or feeding or spawning of Arctic Cod remain to be described because winter surveys are lacking.

Reproductive Ecology

Although patterns of reproductive ecology (for example, timing of reproduction) vary considerably among species, the spawning seasons and incubation periods of some Arctic fishes, particularly anadromous or amphidromous species, are timed to take advantage of the late spring-early summer breakup of ice and the concomitant increases in photoperiod and temperatures and in primary and secondary production of prey. This synchrony is a “hedge betting” strategy that has evolved to increase the probability for early recruitment. For instance, although many amphidromous species (for example, charr, ciscoes, and other whitefishes) spawn under ice in autumn (Craig, 1989a), the eggs remain in gravel beds for 7–8 months and larvae emerge from April to July (McCart and others, 1972; Yoshihara, 1973; Craig and McCart, 1974; Griffiths and others, 1975; Burns, 1990). In the Beaufort and Chukchi Seas, both juvenile and adult Arctic Smelt overwinter under ice in brackish river deltas and coastal waters; many of the river mouths along the Beaufort and Chukchi Seas harbor overwintering populations (Bond, 1982; Schmidt and others, 1987; Bond and Erickson, 1989; Craig, 1989a;

Sekerak and others, 1992). As winter progresses, fish gather near spawning grounds (Haldorson and Craig, 1984) and spawning occurs in spring, just prior to ice break-up with most spawning occurring in the lowermost, but still fresh, parts of rivers (Belyanina, 1968; Burns, 1990). Compared to autumn-spawning fishes, however, Arctic Smelt eggs hatch quickly, in 10–30 days depending on water temperature (Belyanina, 1968; Morrow, 1980; Gritsenko and others, 1984; Burns 1990). Saffron Cod spawn under ice from December to at least May (Andriyashev, 1954; Stewart and others, 1993) and Arctic Flounder from March to June (Ratynski, 1983; Lawrence and others, 1984). However, the spawning seasons of other marine fishes appear to be less tightly linked to seasonal productivity and are perhaps tied to pelagic-benthic coupling of energy to benthic organisms that comprise the diets of the juveniles of some species. For instance, in the Chukchi and Beaufort Seas, Pacific Herring spawn from June to September (Ratynski, 1983; Gillman and Kristofferson, 1984; Lawrence and others, 1984; Stout and others, 2001), Capelin primarily in July and August (Kendel and others, 1975; Fechhelm and others, 1984; Stewart and others, 1993), and Polar Eelpout (*Lycodes polaris*) likely in autumn or early winter (Andriyashev, 1954; Frost and Lowry, 1983). In some instances, at least part of the adult population spawns during a season where few larvae survive. As an example, Fortier and others (2006) demonstrated that most of the Arctic Cod larvae produced during the relatively cold spring die soon after. However, early spawning persists in this species because the few larvae that survive are larger and better able to survive the following winter than the larvae produced later in the year.

Synchrony

The regional bathymetry of the Chukchi and Beaufort Seas indicates small-scale local variability in the physical location of the shelf break relative to average conditions across larger scales. In many areas, the gradient between 75- and 200-m is relatively sharp, occurs over a short distance, and the corresponding surface area and volume is relatively small. The effects of small-scale physical and biological features resulting from shelf-slope interactions along a shallower, but sharper gradient, especially in the northeastern Chukchi and western Beaufort Seas, could be seasonally important to many species having evolved life history and reproductive ecologies linked to, or concentrated in these environments (Crawford and others, 2012). For marine fishes occupying shelf and slope habitats, this is important because the ecological processes operating over short times and small spatial scales, such as food or prey concentrations, may be especially critical to early life history success (for example, match-mismatch survival of larval fish predators). For instance, *it is common that wind forcing at the shelf break of both seas frequently drives upwelling events that lift nutrient-rich water from the depths to the shelves* (from Crawford and others [2012, p. 180], citing Weingartner [1997] and Carmack and Kulikov [1998]). We hypothesize that shelf-slope processes in areas

of sharp gradients are important oceanographically to life history processes. However, from a practical view, the spatial extent of existing data relative to this narrow depth interval is coarse at best. For analytical purposes, this scale of resolution limits our predictive capability and, although we know from many studies (for example, Norcross and others, 2009) that temperature and depth are important determinants of fish distribution, only broad hypotheses are currently possible regarding the relative importance of habitats near shelf break and slope areas in the U.S. Arctic (for example, Crawford and others, 2012). At the population level (for example, reproduction, immigration, and emigration processes), the importance of shelf-slope processes are further suggested by newer biogeographic information presented herein.

Life History and Behavioral Adaptations

Unlike the small number of well-studied nototheniid species of Antarctica that live in a stable environmental regime, the behavioral adaptations of Chukchi and Beaufort Seas fishes to seasonally fluctuating temperature, salinity, turbidity, and variable food conditions are quite poorly understood. Much research, especially in the coastal waters of the Beaufort Sea indicates the existence of many adaptive responses to seasonally dynamic hydrographic and biological properties of nearshore ecosystems and coastal lagoons. Examples include fish migration (for example, bathymetric, between freshwater and marine), reduced activity and potential hibernation, and reproductive specialization (for example, Arctic Cod and sea ice). How reproduction and early life history in marine fishes (that is, timing, habitat locations, and spawning behaviors) have evolved with respect to being in synchrony with biological production events, sea ice, hydrological and meteorological conditions remains to be described. For most species, studies of genetic diversity and population structure are needed to understand the variability in patterns of age and growth that have been observed and genetic relationships in the regional fauna.

Migration is an evolved process that reflects the regular movement of fish populations between habitats important to the completion of their life cycle. Movement, although related, generally describes the immediate tactical responses of fish to environmental surroundings. During winter, ice covers the marine waters of the Chukchi and Beaufort Seas and in some coastal areas freezing occurs throughout the water column. In response, fishes move into unfrozen parts of rivers (that is, amphidromous and anadromous taxa), into river mouths (euryhaline species), into unfrozen, near-shore marine refuges, or perhaps into deeper, more-offshore marine waters. Arguably, seasonal-linked coastal migrations of many amphidromous species (whitefishes) are reasonably well understood. However, there have been few winter studies of Arctic nearshore or, particularly offshore, marine fish species. Thus, the behavior of the generally sluggish, benthic species that occupy these waters is little understood.

With that caveat, examples of life strategy models of known or inferred seasonal movement patterns of some of the most conspicuous or ecologically and traditionally important species inhabiting the Chukchi and Beaufort seas are presented. This focus, illustrated with several prominent species, or groups of species, serves to model key features of the life history strategies and regional variations in migratory patterns in order to explain the range of behaviors and habitat dependencies that have evolved. The models described reflect adaptive strategies for life processes that occur in Arctic marine fishes across the continuum of freshwater, estuarine, and marine habitats:

Amphidromous/Anadromous Model.—This segment of the nearshore fish community is important in subsistence fisheries throughout Arctic Alaska. Prior to the 1990s, most technical reports and publications did not distinguish between the two life strategies and referred only to anadromous species. Craig (1989a) examined the evolution of anadromy in the Arctic as an adaptation related to differences in food quality and availability and energetic benefits conferred by coastal migrations. Most young fish reside in fresh water for 1–3 years prior to their first coastal excursion, the exception being the Arctic Cisco in the Alaska Beaufort Sea. However, although the species undertakes a coastal migration during its first year of life, once re-entering freshwaters in and around the Colville River, they resume the variable residency strategy. Overwintering habitats in freshwaters may be limiting and, where studied, strong density dependence is evident in their population dynamics.

Amphidromy Example: Dolly Varden.—All Dolly Varden (*Salvelinus malma*) overwinter in fresh water habitats. Amphidromous Dolly Varden must return to rivers and streams during summer or early autumn and timing of return often varies with whether they will spawn that year (Craig and McCart, 1975; Griffiths and others, 1975). Except for the rare and small habitat areas kept free of ice by perennial springs (taliks), the upper parts of rivers draining into the Beaufort Sea and southeastern Chukchi Sea freeze solid during winter. Perennial springs are located in rivers and streams flowing from the eastern Brooks Range into the Beaufort Sea (Craig 1989a; Wiswar, 1994). Both spawning and overwintering occurs in those tributaries where perennial springs prevent freezing throughout the water column (Craig and McCart, 1974; Griffiths and others, 1988; Burns, 1990), whereas in rivers flowing to the Chukchi Sea, the lower parts of the waterways also may be partially ice-free (DeCicco, 1996; DeCicco, 1997). It is likely that spawning does not occur in low-lying coastal plain rivers of the southwestern Beaufort Sea west of the Colville River because they tend to be connected to lakes and lack the perennial springs that prevent freezing (Burns, 1990; Gallaway and Fechhelm, 1997). Thus, in some waterways, a large segment of a population may be found in a small stretch of water (Burns, 1990).

In Beaufort Sea drainages, most Dolly Varden are thought to overwinter in their natal drainages. For instance, in the Sagavanirktok River, one study determined that an estimated 86 percent of overwintering fish had originated in that river (Crane and others, 2005). In the rivers flowing into the southeastern Chukchi Sea, fish do not show overwintering fidelity to natal waterways and stocks from various rivers share ice-free zones (Armstrong and Morrow, 1980; DeCicco, 1997; Crane and others, 2005).

As they make their return migrations into fresh waters, the timing and behavior of Dolly Varden is quite complex and varies with location, reflective of variable water temperature regimes and states of maturity (DeCicco, 1997; Crane and others, 2005). Spawning occurs in autumn. During those years when a fish will spawn, some spawners will remain in freshwater; others will undertake an abbreviated coastal migration and return to their spawning habitats as early as late June (Armstrong and Morrow, 1980). The lack of, or short-term nature of, the coastal migration of an individual may be an adaptive strategy that allows these fish to occupy and defend premium spawning sites. Additionally, size and bright coloration helps them attract mates and, by remaining resident, or almost resident, allows them to spawn during most optimal times. However, although many Dolly Varden begin returning in July, in most instances most Dolly Varden are thought to return to freshwaters from mid-August and early-September. The environmental trigger for this migratory behavior is unknown but is thought to relate to changing light and hydrographic properties. A return migration may occur as late as October (after ocean freeze-up) before fish move into river systems (Yoshihara, 1973; Kendel and others, 1974; Bendock, 1977; Craig and Haldorson, 1981; Griffiths and others, 1988; Burns, 1990; Thorsteinson and others, 1990).

The migratory behaviors of fish in the southeastern Chukchi Sea drainages are more complex than in the Beaufort Sea drainages and regional differences in summer and autumn spawning populations may be related to differences in thermal regimes and summer durations of open water periods (DeCicco, 1997). There is apparently a greater incidence of summer spawning in Chukchi Sea drainages. Summer spawning fish do not seem to migrate to sea during the spawning year. Rather, in June and early July, they ascend rivers, spawn, and then descend to lower river over-wintering grounds. Summer spawning fish that have overwintered in non-natal rivers move into the Chukchi Sea in June, migrate directly to the spawning grounds, and descend to lower-river overwintering areas. In both instances, fish do not feed in the sea during the spawning year. Fish that spawn in autumn behave more like their Beaufort Sea congeners, migrating to sea in summer, feeding, and then returning to fresh waters in autumn. Recent satellite telemetry studies of Dolly Varden from the Wulik River reconfirm the extensive ocean migrations by adult fish (Courtney, 2014), whereas previous, limited tagging indicated transboundary movements between Alaska and Russia (DeCicco, 1992).

Amphidromy Example: Whitefishes.—The seasonal movements of all of the whitefishes of the U.S. Arctic (Arctic Cisco, Bering Cisco, and Least Cisco, Broad and Humpback Whitefish) have much in common. The degree of tolerance for salinity varies by species and affects the extent of intrusions into marine waters. The Least Cisco life cycle model is broadly representative of most whitefishes and generally illustrates the migratory pattern of this group.

Juvenile Least Cisco may remain in rivers for several years before entering the sea (variable residence). During feeding migrations in coastal waters, Least Cisco schools can maintain this integrity for months (Craig and Haldorson, 1981). Juvenile fishes do not migrate as far away from natal origins as larger adults and tend to remain in brackish habitats (5–10 °C, 10–25 practical salinity units [psu]). Older fishes are more tolerant of both colder temperatures and increased salinity (27–32 psu), and disperse farther along the coast. Most Least Cisco stay within the brackish water lens, although they have been found in river plumes as much as 20–30 km (12–19 mi) off shore (Kendel and others, 1975; Griffiths and others, 1988; Burns 1990, Schmidt and others, 1991; Philo and others, 1993a, 1993b). Most Least Cisco found along Alaska's south central Beaufort Sea are thought to originate from spawning and overwintering grounds in the Colville River (Griffiths and others, 1988). Generally, the extent of coastal migrations is affected by prevailing summer winds (for example, wind direction and speed). Least Cisco from the Colville River migrate farther east in years of persistent westerly winds. Similarly, fish from the Mackenzie River benefit from wind-aid migrations and move farther to the west in years of prevailing easterly winds (Griffiths and others, 1988; Fechhelm and others, 1996; Gallaway and Fechhelm, 1997).

Along Alaska's North Slope, larger fish can swim faster and reach distant feeding grounds before smaller individuals (Fechhelm and others, 1996). Given the short summer season, Least Cisco can travel substantial distances when conditions are favorable. For instance, a fish tagged in Simpson Lagoon was recaptured off Barrow, 300 km to the west (Craig and Haldorson 1981). However, fish leaving the Colville River generally migrate eastward along the coast of the Alaska National Wildlife Refuge because marine waters bathing the nearshore between Smith Bay and Cape Halkett appear to retard westward movement (Gallaway and Fechhelm, 1997; L. Moulton, MJM Research, oral commun., 2012). Most of the fish emigrating from the Mackenzie River travel westward perhaps as far as Phillips Bay (Kendel and others, 1975) and eastwards to the Tuktoyaktuk Peninsula (Percy, 1975).

Between July and September, Least Cisco begin to return to freshwater spawning and overwintering grounds (Jones and Den Beste, 1977; Craig and Haldorson, 1981; Griffiths and others, 1988; Fechhelm and others, 1996). At least in some areas (for example, Prudhoe Bay), the initiation of this migration may be linked to the onset and intensity of the coastal marine water intrusion or to food availability (Gallaway and Fechhelm, 1997). Several researchers have

noted that the fish that will spawn in a given year are the first to leave coastal waters, followed by non-spawning adults and juveniles (Mann, 1974; Kendel and others, 1975; Jones and Den Beste, 1977). Both juveniles and adults overwinter in the brackish waters of river deltas (the Colville and Mackenzie Rivers are the largest overwintering areas along the Beaufort Sea), open coast (for example, Tuktoyaktuk Harbor), and the freshwater lakes of the Tuktoyaktuk Peninsula, Canada (Percy, 1975; Bond, 1982; Fechhelm and others, 1996). Except for the Sagavanirktok River (where some overwintering occurs in delta waters), Least Cisco do not seem to either spawn or overwinter in any waterway between the Colville and Mackenzie Rivers (Fechhelm and others, 1996). Although water temperature and food availability likely trigger most of the movements in this species, Schmidt and others (1989) observed that during their under-ice sojourn in the Sagavanirktok River Delta these fish also moved upstream when saline waters increased over the course of the season.

Anadromy Example: Pacific Salmon.—Although all five species of Pacific salmon spawn in rivers entering the Chukchi Sea (Craig and Haldorson, 1986; Craig, 1989b; Healey, 1991; Mecklenburg and others 2002; Stephenson, 2006), currently only Pink Salmon and Chum Salmon are likely to spawn in significant numbers in the rivers of the Beaufort Sea (Stephenson, 2006; Irvine and others, 2009). All of the salmon species spend at least one winter at sea. Given the harsh conditions in the marine nearshore, the location of where Beaufort Sea salmon overwinter while at sea is of increasing interest. Irvine and others (2009) posit three options: (1) Bering Sea Refuge—during their marine sojourn, young salmon migrate westward and live in the Bering Sea and perhaps Gulf of Alaska; (2) Atlantic Layer Beaufort Refuge—salmon remain in the Beaufort Sea, but winter deep under the pack ice; (3) Freshwater Beaufort Refuge—salmon remain in the Beaufort Sea region, overwintering in river plumes. Irvine and others (2009) examined the strontium (Sr):calcium (Ca) microchemistry signatures of otoliths of Chum Salmon from the Colville River (emptying into the Beaufort Sea) and the Tanana River, a tributary of the Yukon River, which drains into the Bering Sea. Although the results were somewhat ambiguous, Irvine and others (2009) reported that “*the most parsimonious explanation is that Arctic chum salmon live in the North Pacific for most of their marine life...[but] may spend their first winter deep within the Beaufort Sea.*”

Nearshore—Marine Model

The movements of the vast majority of species inhabiting the waters of the U.S. Chukchi and Beaufort Seas are not known. However, seasonal data are available for a small number of species, especially those occurring in coastal waters during summer months. The brackish water conditions, especially along the Alaska Beaufort Sea, provide important nursery habitats for Arctic Cod, Capelin,

Pacific Herring, snailfish, and probably many other marine fishes that are not adequately represented in the sampling of existing research (Thorsteinson and others, 1991). The (1) roles of deltas, lagoons, and other nearshore habitats for reproduction, incubation, and rearing of early life stages; (2) relative importance of such coastal areas with respect to fish production; and (3) evolutionary significance of these sites with respect to freshwater inflows, substrate, or wind- and current-aided transport or retention of early life stages are expected to be the subject of future studies.

Linked Estuarine—Marine Example: Forage Species.—The spawning, overwintering, and migration patterns of Pacific Herring are highly variable. For example, Bond (1982) reported that many Pacific Herring remained in Tuktoyaktuk Harbor (Canadian Beaufort Sea) for most of the year, leaving the harbor only for a few months during the summer to feed. Of the 10 known wintering sites in the Tuktoyaktuk Peninsula region, 8 were in estuarine coastal habitats, 1 was in the lower Mackenzie River, and 1 in the saline waters of Tuktoyaktuk Harbor (Sekerak and others, 1992). At the other extreme, many herring in the eastern Bering Sea overwinter hundreds of kilometers offshore (at depths of 110–130 m [361–426 ft]) and move into nearshore waters in spring preparatory to summer spawning (Dudnik and Usol'tsev, 1964). It is not known if Pacific Herring use offshore waters in the U.S. Chukchi and Beaufort Seas.

Capelin and Arctic Sand Lance (*Ammodytes hexapterus*) are seasonal dominants of the Chukchi Sea nearshore and are important in the diets of some fish, seabirds, and mammals. Like the Pacific Herring, reproduction, especially in Capelin is linked to inshore and coastal waters. Their distribution over shelf waters and seasonal use of shelf habitats, including onshore-offshore linkages are not well understood. Arctic Sand Lance burrow into sandy substrates of the shelf and are known to spawn coastally. In the Beaufort Sea, Capelin reproduction occurs in the delta habitats of the larger rivers such as the Colville and Sagavanirktok Rivers near Prudhoe Bay. Thorsteinson and others (1990) hypothesized that the successful reproduction of Capelin in these areas was spatially and temporally linked to the first marine intrusion of the year. That is, the success of Capelin spawning, incubation, and offshore transport and recruitment of young fish to other nearshore habitats is related to strong westerly winds and oceanographic conditions that push inshore waters carrying larvae and early-age juveniles offshore along the central coast. The hypothesized wind-driven transport in relatively fresh surficial waters was further suggested to span a critical period for capelin growth and physiological development in which juvenile transformation from living in brackish to marine conditions occurs (Thorsteinson and others, 1990). These authors noted a strong association between young Capelin and Arctic Cod, a predator, in surface catches taken off the Sagavanirktok River, which suggests another adaptive mechanism linking, in this case, brackish and marine environments.

Nearshore—Marine Example: Demersal Species and Other Coastal Dominants.—If the water column does not completely freeze, some nearshore species remain in shallow waters throughout the year. An example of such residency is the Fourhorn Sculpin. In the Beaufort Sea, these fish overwinter along shallow-bottom coastlines (Kendel and others, 1975; Percy, 1975; Jones and Den Beste, 1977; Craig and Haldorson, 1981) and in river deltas (for example, Colville and Sagavanirktok River deltas, see Craig [1989a] and Schmidt and others [1987]). A few winter surveys have determined that at least some individuals of the following species also overwinter more-or-less where they reside during warmer months: Arctic Smelt, Saffron Cod, and unidentified snailfish (Craig and Haldorson 1981, Craig 1989b). The Arctic Flounder, another shallow-water species, however, is known to undertake a bathymetric migration and move slightly offshore in autumn. In the Beaufort and Chukchi Seas, the extent of this winter migration is not known and may not be extensive (Andriyashev, 1954, Craig and Haldorson, 1981). For instance, in Tuktoyaktuk Harbor, fish overwinter in the deep parts of the harbor, at depths of 12 m or less (Bond, 1982). As waters warm in spring, fish move into shallow waters in large numbers, where they remain until autumn (Bond, 1982). Spawning of at least some of these species (that is, Fourhorn Sculpin, Arctic Flounder) occurs in winter and spring under ice in shallow marine waters. Arctic Smelt spawn in fresh or brackish waters under ice in spring, just prior to breakup.

Marine Example: Arctic Cod.—The Arctic Cod is an excellent example of a truly marine, although euryhaline, species. Arguably, this is the most widespread and abundant fish species in the U.S. Arctic. However, although it is clear that these are highly mobile and migratory fish, their movements, particularly seasonal movements, throughout much of the Arctic are poorly understood (Ponomarenko, 1968; Craig and others, 1982; Benoit and others, 2008). Throughout their range, fish are abundant in nearshore waters in summer, the precise time varying between locations and between years at the same location. In the nearshore, schools may move quickly through an area (Craig and Haldorson, 1981; Craig and Schmidt, 1985) or may reside in the same location for weeks at a time (Welch and others, 1993). How much of the overall population migrates into shallow waters is not known, although many fish may not migrate to the shallowest waters (Fechhelm and others, 1984; Frost and Lowry, 1983; Hop and others, 1997). In the Alaskan Beaufort Sea, Arctic Cod tend to be relatively scarce immediately after ice-out, but move into shallow waters as the season progresses especially after the first marine intrusion that typically occurs in mid-July following a west windstorm (Craig and others, 1982; Palmer and Dugan, 1990; Wiswar and others, 1995). The high abundance of colonizing epibenthic invertebrates in lagoonal waters provides a rich prey base for cod and other marine fishes. The species also has been shown in recent studies to be abundant over shelf and slope environments.

Ecological Theory

Adaptations (anatomical, molecular, physiological, and behavioral) of marine fishes to life in Arctic waters are evidenced in strategies (genetically determined life history or behaviors [Gross, 1987]) and demographic characteristics of each population. The strategies relate to how resources are allocated to maximize fitness (in individuals and populations) and are tightly linked to life history parameters (Stearns, 1977). The primary life history traits—size at birth; growth pattern; age and size at maturity; number, size, and sex ratio of offspring; age- and size-specific reproductive investments; fecundity; age- and size-specific mortality schedules; and life span—are poorly known for Arctic fish species. These parameters inform the population dynamics (survival, recruitment, growth rate) of each species and vary in response to temporal variations in ecological traits (for example, habitat, diet, home range, and other ecological traits) and other environmental factors.

Population Theory (r-K Selection)

Life history information provides important insights about selective forces operating on fish populations and their evolution to niches in marine ecosystems. In the absence of reliable population parameters, general studies of environmental effects on species adaptations are possible within an r-K conceptual framework⁵. Considering the postulated recency of marine ecosystem stability and related phylogenetic age of the Arctic fish families, r and K selection models are instructive. At one evolutionary extreme, the amphidromous fish (that is, Salmonidae) are unambiguous K-strategists (for example, Craig, 1989a). Amphidromy, like anadromy, involves the alternate occupation of freshwater and sea habitats by fishes. It involves complex migratory behaviors that ensure population fitness through predictable migrations of populations, or segments of populations, between stable habitats in freshwater, brackish, and marine

⁵The r-K conceptual framework is useful for understanding adaptations to life in the Arctic marine environment. The underlying theory concerns population growth in stable and unstable environments and the respective roles of density-dependent and density-independent factors on population dynamics in each. Carrying capacity (K) is an attribute of the ecosystem (habitat) and the selection of K attributes (long-life spans, slow growth, large size, delayed maturity, iteroparity, few offspring, and stable mortality rate) reflects population growth near in stable environments. At the opposite end of the r-K continuum, r-selected species are adapted (short life expectancy, small size, early maturity, reproduces once, many offspring are produced, variable recruitment rate) to living in unstable, fluctuating environments and density-independent factors (abiotic factors) affect population processes such K values are low and the exponential growth rate (intrinsic rate of growth rate [r]) is characteristic of the population. Density-dependent factors seldom come into play in r-selected species. The r/K concept represents a continuum and many species display a mix of both traits.

environments. At the other end of the continuum, r-strategists, like the Pacific Herring and Capelin (for example, published values for instantaneous rate of natural mortality [M] and gonadosomal index [GI] from Gunderson [1980] and Rose [2005]) and Arctic Cod are adapted to seasonal periods of high food abundance followed by periods of relative scarcity. These small pelagic species allocate a greater proportion of their resources to reproduction, produce larger numbers of young, and have short life spans and wide niche widths (unspecialized). Although population sizes are unknown for Capelin and Arctic Cod, it is likely that they are prone to fluctuating stock abundance as is the pattern for similar forage species elsewhere. Life history information presented in the species accounts shows that the vast majority of Arctic species display mixes of r and K traits (for example, Cottidae and Agonidae). The mix of life history traits reported, although mostly incomplete, is thought to have adaptive significance with respect to ecological trade-offs (for example, production of young and longevity) and changes in M (Gunderson, 1980; Power, 1997).

Environmental Stability

The Arctic marine ecosystem is a relatively young system that is characterized by both stable (predictable) and variable (seasonal) environmental features in time and space. The small size and low densities of many species would suggest that many of the marine fishes are living at the abiotic and biotic extremes of their ranges (for example, temperatures between -2 and +2 °C). How body size and abundance co-varies with other traits (for example, temperature tolerance and foods) is an area of increasing interest given the rapidity and potential effects of changing Arctic ecosystems. The relative vulnerabilities (extinction selectivity, see McKinney, 1997) of marine species to climate effects or other large-scale perturbations is presently difficult to assess on the basis of life history and ecological traits not only because information is lacking (that is, environmental tolerances and preferences), but because non-linear threshold effects (population and ecosystem levels) are impossible to estimate. Linked biological and physical models are needed to inform research and assessment processes.

The biological mechanisms linking environment, through the life history, to the population dynamics are complex. As harsh as Arctic environmental conditions may seem, the Arctic marine fishes are adapted to life therein. The presence of sea ice and cold water temperatures are stable features in deep waters and the life histories of some species, such as the Arctic Cod, are intricately linked to sea ice habitats. How variations in environmental conditions (abiotic and biotic factors) influence population demographics is not known for most species and is an important topic for monitoring long-term change. Benton and others (2006) described the potential interplay of these factors in terms of differential mortality and

survival for different life stages and resulting effects on age structure and abundance of populations (that is, developing life cycle understanding). These authors note the importance of population structure for two primary and related reasons: (1) the life cycle takes time to complete and (2) different ages or stages may be affected differently by environmental effects (that is, potential for cascading effects).

Oceanographic influences on ecosystem conditions and productivity are critical determinants of the distribution and abundance of marine fishes. Marine production cycles in the Chukchi Sea lead to a tightly coupled benthopelagic system supporting a biotic community dominated by benthic invertebrates and small marine fishes (Grebmeier and others, 2006b). It is not known whether inefficient cropping of algal production produced beneath sea ice or in open water environments leads to a similar benthic pattern across the Beaufort Sea shelf and slope. The brackish habitat that forms along the north coast of Alaska (within 10–15 km of the shore) in early summer is often characterized as a wind-driven system subject to rapid changes in temperature and salinity. The brackish conditions are ephemeral and by late summer marine conditions are widespread nearshore. Terrestrial sources of organic matter can fuel invertebrate-driven (epibenthic crustaceans) food webs that are seasonally established along the Beaufort coast (Dunton and others, 2006; 2012). Winter ice, as deep as 2-m coastally, and hypersaline conditions in unfrozen waters, render nearshore and lagoon waters inhospitable to most marine fishes. The temporary conditions of many Arctic habitats makes them “ecological vacuums” for *r* strategists (Gunderson, 1980) and apparently many mixed-trait species (for example, those favoring a strategy of high investment in reproductive output, short generation times, etc.). The information presented about food habits, physical habitats, size, and reproductive ecology suggests that many species are non-specialists (opportunists), lacking competitive capacity (high dietary overlap in invertebrate foods), and expend large amounts of energy on gonadosomatic development at the expense of large body size.

The combinations of life history and abundance traits conceptually extend to fish assemblages associated with pioneer (developmental) and mature (climax) communities in Arctic marine ecosystems (Vadstein and others, 2004). Pioneer communities have low stability against perturbation and low biological control (that is, *r* strategists). Other characteristics include low diversity, wide niche width, and low specialization. Mature communities are typically dominated by *K*-strategists (for example, amphidromous species in Arctic rivers and lakes (for example, Johnson, 1997) in stable systems with high biological control and high resistance (below a specific threshold) to perturbation. The effect of high or low diversity, in the relative sense (that is, generally low across the Arctic) is not known. Other comparisons indicate niche width is wide and specialization is high in mature systems.

Ecological Biogeography

Correlative information about the relations between sea temperature, growth, life span, and marine fish diversity in Arctic conditions (generally -2 to > 6 °C) exists for many species. Much of this information was obtained for marine species studied outside the Chukchi and Beaufort Seas. Winter data regarding habitat requirements and fish behavior is generally lacking. Generalizing from the data presented in the species accounts (chapter 3) and section, “Adaptations in Marine Arctic Fishes” (this chapter), marine fish communities occurring in colder regimes have characteristic tendencies for slow growth (populations), small size, short food chains, and low diversity. Arctic conditions favor large species, populations, and predators in the marine invertebrates. Few species are considered apex predators (for example, sharks) and relatively few species are characterized by large populations. Arctic Cod is the most conspicuous exception and other commonly reported marine species (for example, Capelin, Arctic Sand Lance, and Fourhorn Sculpin) and amphidromous fishes (for example, Dolly Varden, Least Cisco, Arctic Cisco, and Broad Whitefish) also may have large population sizes. Large predators (for example, Pacific Halibut (*Hippoglossus stenolepis*), Pacific Salmon, Walleye Pollock (*Gadus chalcogrammus*), Inconnu (*Stenodus leucichthys*), and at least one shark species) are most abundant in the southeastern Chukchi Sea. Fewer species, such as Dolly Varden and possibly Arctic and Greenland flounders fit this description from the Beaufort Sea. No species from these high latitude seas is strictly piscivorous, which is indicative of the length of food chains and relative importance of invertebrate foods (including fish larvae in the zooplankton community) in energetic pathways.

Environmental Relations

Certain life history parameters (for example, growth rate, age at maturity, and fecundity) are sensitive to changes in temperature and food (that is, ecological conditions). This makes interpretation of field data difficult with respect to causal mechanisms and a requirement for laboratory work necessary (Stearns, 1977). Ongoing fieldwork on marine fish populations in the Chukchi and Beaufort Seas will develop much new information about population dynamics, structure, and community functions. New information about habitat associations will represent snap shots of ecosystem condition and laboratory experiments still will be needed to fill information gaps remaining about the physiological tolerances and environmental preferences of Arctic marine fish. Empirical data will be critical to evaluations of potential effects of climate change and human activities on this fauna (that is, natural and anthropogenic effects).

Temperature effects are especially important as they directly affect growth and survival of individuals and thereby recruitment at the population level. In many analyses of field data, thermal conditions often are used as a proxy for mechanisms affecting survival such as enhanced prey production or advection of young fishes in warmer water masses to nursery or feeding habitats. Because thermal relations are often indirect, temperature is not the only factor affecting recruitment, and correlations often break down. Well-designed experiments addressing the effects of multiple stressors may reduce the uncertainty associated with population forecasts.

Regarding environmental preferences, the species accounts support previous finding about marine fishes (excluding amphidromous and anadromous forms) and their apparent preferences for colder, more saline waters (for example, Logerwell and others, 2011). In the summer, this includes marine waters lying seaward, or underlying, nearshore brackish waters along the Alaskan Beaufort Sea. As summer wanes, the nearshore becomes more saline due to decreased freshwater input from rivers and streams and marine intrusions associated with summer storms. During this time, marine fishes often share nearshore brackish waters with diadromous fishes, primarily to feed on the abundant epibenthic fauna or possibly to spawn (for example, Capelin and Arctic Smelt). In autumn, after most amphidromous fishes have returned to freshwater systems to spawn and overwinter, the marine fishes remain in the nearshore area to feed. Onshore-offshore dimensions of their migratory or movement behaviors are generally unknown, but for important forage species like Capelin and Arctic Cod could be important to ecosystem function.

The use of coastal habitats by Arctic Cod in Simpson Lagoon (near Prudhoe Bay) follows a pattern of increased nearshore abundance with the first major marine intrusions (usually mid-July), seasonal residence through early winter months, followed by an occupation of offshore waters during winter months. How much of the Arctic Cod population undertakes such a bathymetric migration, how it relates to life history patterns (spawning times and locations), and locations of seasonal habitats remain largely unknown for both the Beaufort and Chukchi Seas. There are suggestions that large numbers of fish remain over shelf and slope habitats and, given their importance in regional food webs, there remain important questions to be addressed. Because of reports of nearshore spawning (for example, summaries by Thorsteinson and others [1990] and Pirtle and Mueter [2011]), important questions about reproductive ecology and stock structure remain for Arctic Cod and other dominant species of ecological or subsistence importance (for example, Saffron Cod).

Concern about the potential effects of North Slope oil and gas development on amphidromous species (ciscoes,

whitefish, and charr) and coastal habitats have a long-standing history. Because of their subsistence, and until recently commercial values, Arctic Cisco have received special research and monitoring attention. Coastal monitoring data from Prudhoe Bay and harvest records from the Colville Delta extend to the early 1980s. During the late 1980s and early 1990s, the effects of West Dock and Endicott gravel causeways in Prudhoe Bay on physical habitat conditions, especially temperature and salinity properties, and effects on the migrations and movements of amphidromous fishes, were a focus of many fishery studies. More than a decade later, in an innovative research approach, BOEM and its investigators worked with Nuiqsut residents (experts) in 2003 to identify new and continuing information needs relative to Arctic Cisco (Murphy and others, 2007). During the process of expert engagement, they identified issues and developed study hypotheses ($n = 27$). Within the constraints of existing information, each question was addressed and considered regarding future priorities. A summary of the issues identified from local observations included: fewer fish available to subsistence fishery; reduced size and (or) weight of fish; changes in distribution of fish in the Colville River; changes in the quality of fish (taste, texture, color); deformed fish; food chain effects; and energetics stress. These changes were thought to be related to changes in habitat associated with local industrial developments such as seismic noise, causeways and coastal siltation, ice roads, contaminants, and dredging, or larger scale processes such as ocean and climate changes. The possibility of over harvesting also was considered. Although causeway effects were still of concern, the study was done after a period of oil and gas development in the Colville Delta, and this explains the expanded list of local concerns.

The Murphy and others (2007) study was unique in its comprehensive evaluation of environmental influences on Arctic Cisco and the participation of Nuiqsut residents from beginning to end. Environmental influences were geographically partitioned into three regions including the MacKenzie River Region, Coastal Beaufort Region, and Colville-Prudhoe Bay Region to investigate population effects on immature ciscoes (age 0–5 and 5–7). Environmental factors analyzed included: MacKenzie River—river discharge, air temperatures, regional sea surface temperatures (SSTs), spring ice concentration, and a combined climate index (temperature, ice, discharge); Coastal Beaufort Region—winds, regional SSTs, and ice concentrations; and Colville-Prudhoe Bay Region—air temperature, river discharge, SSTs, sea surface salinities, autumn salinities (delta), ice concentration, Arctic Oscillation (AO), flow through the Bering Strait, and the combined climate index.

The results of the analysis reconfirmed, in part, the importance of east wind conditions on the recruitment of young-of-the-year Arctic Cisco to the Colville Delta.

Murphy and others (2007) reported that 80 percent of the natural variation in recruitment could be explained by these winds. Regional changes in sea ice conditions, winds, coastal circulation, and upwelling are known to affect the geographic extent and duration band and the quality and possibly coastal access to habitat by amphidromous fish; these relationships were examined by Murphy and others (2007). A weak correlation was established between survival rates (age 0–5) and the AO, possibly related to changes in regional circulation. Warming influences on the timing of breakup and river discharges were studied in the Colville-Prudhoe Bay Region and a relation between increased discharge and decreased survival in age 5–7 ciscoes was described. Changes in hydrology and changes in regional upwelling and nearshore prey conditions and competition were suggested as causes of the increased mortality and decreased fish condition. Insufficient information was available to evaluate the effects of siltation effects in coastal habitats in the West Dock area, effects of contaminants (for example, heavy metals), effects of autumn salinities on cisco distributions in delta habitats, or effects of seismic activities (noise and vibration) on fish distribution and abundance. A key finding for Arctic Cisco, and other marine fishes, is the demonstration of how physical drivers interact to affect coastal habitats at different time and spatial scales with differential effects to species throughout their life cycles.

With respect to Arctic Cisco, Murphy and others (2007) noted the lack of population information for this species from the MacKenzie River and need for greater resolution of the age structure of the population in the Colville River. Murphy and others (2007) also noted the need for increased understanding about AO effects on regional marine ecosystems. In response, the BOEM and USGS began researching the genetics and age of fishes in the Colville Delta and a broader study on the influences of AO on recruitment processes in young-of-the-year fish (von Biela and others, 2011; Zimmerman and others, 2013). The genetics research confirmed the MacKenzie River origins of Colville River ciscoes and the aging studies indicated the presence of small numbers of older-aged fishes than previously reported (that is, the presence of fishes to age 11). Large-scale effects of AO on the MacKenzie River focused on annual variability in coastal discharge and interannual effects of marine ecosystem conditions on the abundance and condition of euphausiid prey in coastal plumes. With respect to the latter, von Biela and others (2011) hypothesized that prior year conditions (to the arrival of age-0 migrants), are critical to the growth and condition of euphausiids and prey concentrations in the next year. The temporal connection between euphausiid ecology and early marine survival and growth in Arctic Cisco adds significant new information about another source of natural variation in the recruitment of these fish into Alaskan waters.

Fish Assemblages

DeGange and Thorsteinson (2011) used an earlier classification scheme (Mecklenburg and others, 2008; Minerals Management Service, 2008) to describe primary and secondary marine fish assemblages in the Chukchi and Beaufort Seas. The DeGange and Thorsteinson (2011) classification scheme is consistent with the life history profiles presented herein (for example, vertical distributions) and with respect to partitioning the primary assemblage (all species) into ecological categories. The ecological categories broadly define fish assemblages based on existing knowledge of fish behavior and ecology and associations with prominent oceanographic features (for example, seafloor, shelf break, pack ice, and other features). In this analysis, the ecological categories used by DeGange and Thorsteinson (2011) were re-defined to include regional distinctions in habitat and dominant fauna associated with nearshore (<5 m) and offshore areas (>5 m) of the continental shelf. This separation of inshore and offshore communities is more consistent with hydrographic properties (water mass distributions) of the Chukchi (for example, Norcross and others, 2009) and Beaufort Seas (for example, Craig, 1984; Logerwell and others, 2011). A nearshore assemblage was added to the classification and subdivided into three subregions to capture faunal differences in Kotzebue Sound, in the Barrow area, and in brackish coastal waters along the Alaska North Slope to the east of and including Harrison Bay.

The definitions of regional assemblages now includes: (1) *nearshore assemblages* (in shallow bays and lagoons and along open exposed coastlines); (2) *neritic-demersal assemblage* (at or near the seafloor of the continental shelf); (3) *neritic-pelagic assemblage* (in the water column over the continental shelf); (4) *oceanic-demersal assemblage* (living on or close to the bottom beyond the continental shelf break at 200 m); (5) *oceanic-pelagic assemblage* (inhabiting the water column of oceanic waters seaward of the continental shelf break); and (6) *cryopelagic assemblage* (inhabiting neritic or oceanic waters, but during their life cycle, are associated with sea ice). The dominant species associated with these assemblages are listed in [table 4.5](#).

A *cryopelagic assemblage* was not included in [table 4.5](#) and is considered separately due to the special role of Arctic Cod in sea-ice community dynamics. The cryopelagic assemblage and role of the Arctic Cod in the marine ecosystems are unique to the Arctic (Bradstreet, 1982). The term “cryopelagic” describes fishes that actively swim in neritic or oceanic waters but, during their life cycle, are associated with drifting or fast ice. Both young and adult fishes can be associated with ice or water immediately beneath the ice. These relationships can be trophic in nature or related to refuge and possibly reproduction and nursery for young.

Table 4.5. Marine fish assemblages in the Chukchi and Beaufort Seas.

[**Marine fish assemblages:** Cyropelagic assemblage is described in text. **Neritic-pelagic:** Salmon, Pacific Herring, and Yellowfin Sole from southeastern Chukchi Sea]

Community dominants (family/species)	Marine fish assemblages						
	Nearshore			Neritic-Demersal		Neritic-pelagic	Oceanic-demersal
	Southeast	Northwest	North Slope	Chukchi	Beaufort		
Petromyzontidae	Arctic Lamprey						
Squalidae				Spiny Spotted Dogfish			
Rajidae				Arctic Skate	Arctic Skate ¹		
Clupeidae	Pacific Herring					Pacific Herring	
Osmeridae	Arctic Smelt, Pacific Capelin	Arctic Smelt, Pacific Capelin	Arctic Smelt, Pacific Capelin		Pacific Capelin, Arctic Smelt	Pacific Capelin	
Salmonidae	Chum Salmon, Pink Salmon, Least Cisco, Inconnu, Dolly Varden	Pink Salmon, Least Cisco, Dolly Varden	Dolly Varden, Arctic Cisco, Least Cisco, Bering Cisco, Broad Whitefish, Humpback Whitefish			Chum Salmon, Pink Salmon	
Gadidae	Arctic Cod, Saffron Cod, Walleye Pollock	Arctic Cod	Arctic Cod	Arctic Cod, Saffron Cod, Walleye Pollock	Arctic Cod, Saffron Cod, Ice Cod, Walleye Pollock	Arctic Cod, Saffron Cod, Ice Cod	Arctic Cod, Ice Cod
Gasterosteidae			Ninespine Stickleback				
Hexagrammidae	Whitepotted Greenling						
Cottidae	Hamecon, Arctic Staghorn Sculpin, Fourhorn Sculpin, Ribbed Sculpin	Antlered Sculpin, Fourhorn Sculpin	Fourhorn Sculpin, Twohorn Sculpin	Hamecon, Arctic Staghorn Sculpin, Arctic Sculpin, Shorthorn Sculpin, Ribbed Sculpin, Eyeshade Sculpin	Hamecon, Arctic Staghorn Sculpin, Spatulate Sculpin, Ribbed Sculpin, Eyeshade Sculpin, Fourhorn Sculpin		Polar Sculpin, Bigeye Sculpin, Atlantic Hookear Sculpin ¹
Agonidae	Arctic Alligatorfish	Veteran Poacher		Arctic Alligatorfish	Arctic Alligatorfish		
Liparidae				Nebulous Snailfish, Variegated Snailfish, Kelp Snailfish	Gelatinous Snailfish, Variegated Snailfish, Kelp Snailfish, Nebulous Snailfish	Gelatinous Snailfish, Variegated Snailfish	Slender Eelblenny, Sea Tadpole

Table 4.5. Marine fish assemblages in the Chukchi and Beaufort Seas.—Continued

[Marine fish assemblages: Cyropelagic assemblage is described in text. **Neritic-pelagic:** Salmon, Pacific Herring, and Yellowfin Sole from southeastern Chukchi Sea]

Community dominants (family/species)	Marine fish assemblages						
	Nearshore			Neritic-Demersal		Neritic-pelagic	Oceanic-demersal
	Southeast	Northwest	North Slope	Chukchi	Beaufort		
Zoarcidae				Marbled Eelpout, Saddled Eelpout, Polar Eelpout, Fish Doctor	Marbled Eelpout, Polar Eelpout, Fish Doctor		Adolf's Eelpout, Longear Eelpout
Stichaeidae			Slender Eelblenny	Arctic Shanny, Slender Eelblenny, Stout Eelblenny, Fourline Snakeblenny	Arctic Shanny, Fourline Snakeblenny		Daubed Shanny
Ammodytidae	Arctic Sand Lance	Arctic Sand Lance		Arctic Sand Lance	Arctic Sand Lance	Arctic Sand Lance	
Pleuronectidae	Yellowfin Sole, Starry Flounder	Longhead Dab	Arctic Flounder	Bering Flounder, Yellowfin Sole, Alaska Plaice	Bering Flounder, Greenland Halibut, Arctic Flounder	Bering Flounder, Yellowfin Sole	Greenland Halibut

¹Fishery data suggest occurrence in assemblage.

Andriyashev (1970) was among the early investigators to find Arctic Cod in abundance in marine habitats associated with broken ice or near the ice edge. In spring, as ice thaws and breaks up, phytoplankton blooms and zooplankton colonize these habitats and provide food for Arctic Cod. The substrate formed by the underside of sea ice supports an amphipod-diatom ice community that is believed to provide an important source of food for cod. Other species, such as Capelin and Pacific Herring have been mentioned in this assemblage, and this relates to limited observations in broken-sea ice conditions or near the ice edge. Ecological linkages for these fish species with sea ice, and others, and the importance of polynyas (biological hotspots), are not known.

Diadromous fishes (migratory fishes), especially salmonids, are prominent members of nearshore fish assemblages and represent an important source of traditional foods for Arctic villagers. Diadromy involves regular occupation of fresh, brackish (5–10 °C, <15 psu), and marine waters. Fish migrations to, or movements between, reflect the response of a population (or segment of the population) to various biological stimuli, such as feeding or reproduction, or ecological factors, such as temperature, oxygen level, or specific spawning-habitat need. Diadromous fishes display a wide range of migration behaviors including once-in-a-lifetime events, repetitive multiyear events, spawning migrations, feeding migrations, and seasonal movements

between environments. Diadromous fishes inhabit various habitats including many of the lakes, rivers, streams, interconnecting channels, and coastal waters of the North Slope. Common amphidromous species include Arctic, Least, and Bering Ciscos; Arctic Smelt; Humpback and Broad whitefishes; Dolly Varden; and Inconnu. Common anadromous species include Pink and Chum salmon, Ninespine Stickleback, and Arctic Lamprey.

The highest densities and diversity of amphidromous fishes occurs in river-deltas, such as the Colville and the Sagavanirktok Rivers along Alaska's North Slope. Pacific Salmon and Arctic Lamprey are in greatest abundance south of Point Lay and in Kotzebue Sound in the southeastern Chukchi Sea. Lakes that are accessible to the sea typically are inhabited by diadromous fishes and many species have evolved resident forms (for example, Dolly Varden and Arctic Lamprey). The Least Cisco is the most abundant species in sea-connected Arctic lakes. With the exception of the Arctic Cisco, the amphidromous species are characterized by a variable freshwater residence for juvenile fishes that lasts 1–3 years before they undertake their first migration to sea. Fish and invertebrate prey are seasonally more abundant in coastal waters than in freshwater habitats; therefore, amphidromy represents a physiological adaptation to food availability (Craig, 1989a).

The primary marine fish assemblage found over the continental shelf is composed of relatively few species of small size and biomass when compared to similar ecosystem attributes of lower latitudes (Irvine and Meyer, 1989). As an example, most species are less than 15 cm (FL). Small schooling species such as the Arctic Cod can be abundant over shelf waters and near the shelf break (Crawford and others, 2012). Ecological processes (for example, Smetacek and Nicol, 2005; Grebmeier and others, 2006a, 2006b; Jay and others, 2011) and associations of fishes in Alaska coastal water, Pacific summer water, and Pacific winter waters (for example, Crawford and others, 2012) provide stable habitat conditions for shelf-affiliated assemblages, especially adult fishes, in the Chukchi Sea. The intermingling of these water masses with Atlantic water along the shelf break, slope, and deep waters of the Chukchi and Beaufort Seas results in conditions that are more inhospitable and fewer fish. The use and importance of fish habitats in river deltas and coastal lagoons have received the most research attention. The relative importance of other habitats such as those along exposed coastlines, near the ice edge and in polynyas, or located at special features, such as the Hannah Shoal, for feeding, reproduction, and other life activities have been postulated, but in most instances, remains to be described.

Trophic Relations

The available food habits data (stomach contents, fatty acids, isotopes) from across all habitats reviewed in [chapter 3](#) suggest that most Arctic marine fishes are primary carnivores that feed across trophic levels T2 and T3. Invertebrates are significant in their diets with pelagic species feeding on zooplankton herbivores compared to demersal species preying more frequently on early life history stages of benthic detritivores. Freshwater invertebrates swept downstream can be an important source of food for anadromous and amphidromous species as they move downstream into the coastal sea.

Trophic level status is an important indicator of diversity or ecosystem change (that is, changes in community, animal size, and consumption in pelagic and benthic environments) and has been used to study fishing and other effects on species abundance in the northeast Pacific Ocean. More than 90 percent of Arctic marine fauna are secondary consumers. Secondary consumers feed on various fish and invertebrate prey by feeding across trophic levels. The trophic position thus occurs at intermediate levels of the marine ecosystem.

⁶According to Romanuk and others (2011) omnivores, which consume plants or detritus as well as animals, have trophic levels between 2.2 and 2.79 and carnivores have trophic levels greater than 2.8. Secondary consumers (carnivores) have trophic levels between 2.8 and 4.0 and tertiary consumer levels are greater than 4.0.

The average trophic level position for all Arctic marine fishes (juveniles and adults combined) is 3.27 (range: 2.99–4.6)⁶. Of the tertiary consumers, only two species—Arctic Lamprey and Pink Salmon—are common in their occurrence in the southeastern Chukchi Sea.

The trophic positions of each species were estimated in FishBase (Froes and Pauly, 2012) and many assumptions relative to availability and recency of data are involved. Despite these limitations, the mid-level positions indicated are considered to be reasonably accurate. This determination is based on the widespread consumption of small invertebrate prey, benthic and pelagic species, almost universally reported in most species diets. The stomach contents indicate significant dietary overlaps in co-habiting species in marine and nearshore habitats. The abundance of invertebrate foods in each habitat type is related to carbon cycling associated with the delivery of marine-derived organic matter (primary production) to benthic systems offshore and transport of terrestrially derived carbon to nearshore systems. Of interest, the different life strategies that have evolved in the Arctic for marine fishes (anadromy, amphidromy, and marine) are adapted to an invertebrate food base and many species seem to lack specialization with respect to feeding behavior and diet. The generalist strategy may be an effective adaptation of marine fishes living in the invertebrate-dominated shelf systems of the Chukchi and Beaufort Seas. Although most marine fishes are lower-order carnivores, some of the larger, especially pelagic, predators are highly piscivorous during adult stage phases of their lives (for example, Pacific salmon and Inconnu). The absence of exclusive tertiary consumers and relatively few secondary consumers that cross over the T4 level (feed upward) are indicative of the pelagic-benthic coupling and energy pathways characteristic of invertebrate-dominated shelf environments.

Most Arctic marine fishes appear to feed at similar trophic levels and on similar prey comprising the trophic spectrum of available food and prey items available to them in near- and off-shore habitats. It is hypothesized that competition for food resources with invertebrate competitors on the shelf may, in concert with environmental temperature, contribute to observed abundance patterns and the hypothesized ecological redundancy of many cryptic species. In brackish marine environments, such as the open and pulsing lagoons along the North Slope, epibenthic foods (for example, amphipods and mysids) are seasonally abundant, tend to drive coastal food webs, and are not considered to be limiting. Competition between fish competitors in the nearshore marine such as between Arctic and Saffron cods may be significant in some locales and intensified in others through shifts in distribution or changes in ecosystem function brought forth by climate change. Predation pressures on the slope by marine fish, especially on benthos, were not historically considered great (for example, Carey and Ruff, 1977). However, recent data suggesting large standing stocks of Arctic Cod on the slope suggest a need for a re-examination of this hypothesis.

Relative Abundance

Spatial patterns of relative abundance for nearshore and shelf fish assemblages can be generalized from a compilation of regional fishery data and related to the diversity estimates (table 4.1), characterization of marine fish assemblages (table 4.5), and advection model developed by Grebmeier and others (2015, presented in chapter 1 of this report) (table 4.6). The species composition of the nearshore was historically known from fish catches in passive gear collections (that is, fyke nets and gill nets) from inshore habitats and expressed in indices of catch-per-unit-effort (CPUE). Sampling over the shelf has involved active sampling methods including bottom trawling (near the bottom), seining, and plankton tows (surface and water column). The fish catches reported from active sampling gears is expressed in densities of fish (in numbers or biomass) per area trawled or volume sampled. The various sampling and enumeration methodologies required development of a simple, unifying classification of abundance (rare, uncommon, and common) to describe regional patterns in the marine fish assemblage (chapters 2 and 3).

The diversity of Salmonidae species throughout the Pacific Arctic Region (table 4.6) reflects the plasticity of this group and its adaptive linkage to freshwaters. All five species of Pacific salmon are abundant in the northern Bering Sea having important spawning grounds in the Yukon and Anadyr Rivers. In the west, sockeye salmon are more abundant than in Norton Sound, USA in the east relating to spawning habitats in the Anadyr River, Russia, and its tributaries. North of the Bering Strait, Pink and Chum salmon are the abundant salmon species although successful colonization has not demonstrated in Alaskan habitats north of Kotzebue Sound. Coho Salmon are present in Kotzebue Sound drainages and along the Chukotka coast.

Many of the common species, or functional groups of species, are benthic, or demersal, in their habitat orientation (table 4.6). Densities are low and small-sized fishes such as snailfish, poachers, and pricklebacks predominant over shelves. The small size and low densities of many species suggests that they may be living at the abiotic and biotic extremes of their ranges (for example, temperatures between -2 and $+2$ °C). How body size and abundance co-varies with other traits (for example, temperature tolerance and foods) is of increasing interest given the rapidity and potential effects of changing Arctic ecosystems. The relative vulnerabilities (extinction selectivity, see McKinney, 1997) of marine species to effects of climate or other large-scale perturbations are presently difficult to assess on the basis of life history and ecological traits not only because information is lacking (that is, environmental tolerances and preferences), but because non-linear threshold effects (population and ecosystem levels) are not possible to describe.

These abundance patterns, and the classification used, are consistent with published literature and, the high number of rare and uncommon species reported raises questions

about their functional roles in the marine ecosystem.

Biodiverse environments were described by Mouillot and others (2013) as having large numbers of rare species whose functional importance in ecosystems is largely unknown. When the diversity of marine invertebrates is considered, the U.S. Arctic waters can be characterized as biodiverse. The occurrence of roughly 30 percent of the marine fishes from catches in the Beaufort Sea and 20 percent from the Chukchi Sea is described as rare. Even greater numbers are considered uncommon. Only 41 percent of the marine fishes found in the Beaufort Sea, and 53 percent in the Chukchi Sea, are described as common. According to Mouillot and others (2013), rare species in species-rich areas are generally considered to have little influence on ecosystem functioning and may fulfill the same ecological roles as common species. Because of their low abundance, they have less effect, a phenomenon known as functional redundancy (Mouillot and others, 2013). The redundancy hypothesis suggests that rare species serve as an insurance policy for the ecosystem in the event of severe disruption or regime shift and ecological loss. Thus, the ecological role of the individual species, especially in benthic ecosystems in the Arctic where invertebrates predominate and many marine fish are rare or uncommon, is probably best assessed for the demersal assemblage as a whole, rather than single species contributions to food webs and energy flows. Disruptions, such as the cascading effects of ecosystem change reported by Grebmeier and others (2006a; 2006b) related to climate change, would tend to favor pelagic species (for example, salmonids and cods) and potential switch from an invertebrate-dominated system to a gadid-dominated system. In this scenario, the pelagic community would be enriched through increased productivity and immigration at the potential expense of abundant invertebrates such as snow crabs. The potential effect on rare and uncommon fishes could be positive (reduced competition for foods) or negative (less food available). If the hypothesized effects of the cold water pool in the Bering Sea are true, this thermal barrier may protect many of the low density, benthic fishes living in the Arctic from extinction or northward shifts in the decades ahead.

The disruption of the marine food chain could lead to reduced growth rates, lower abundance of some marine fish populations, and restructuring of the fish assemblages. Regime shift effects on pelagic and benthic ecosystems, as hypothesized by Grebmeier and others (2006a; 2015), are driven by decoupling mechanisms (for example, influx of heat in Pacific waters, changing sea ice conditions, reduced transport of organic matter to the benthos, and remineralization), which result in the destabilizing of shelf environments (for example, increased use of pelagic habitats by salmon, reduced benthic productivity and abundance of invertebrate foods, changes in animal distribution relative to prey conditions) from current conditions. In an analysis of potential effects of climate change, Mueter and others (2009, p. 108) concluded that

Table 4.6. Most abundant species of Arctic marine fish in northern Bering Sea, Chukchi Sea, East Siberian Sea, and Beaufort Sea regions of the Pacific Arctic Region.

[Pacific Arctic Region is as described by Grebmeier and others (2015). **Habitat/shelf region:** Pelagic refers to species occurrence in water column; demersal refers to species occurrence at or near the seafloor]

Northern Bering and Chukchi Seas					
Arctic Sea	Habitat/shelf region		Fish abundance		
			East ←	Community dominants and species groups	→ West
			Nearshore	Offshore	Nearshore
Northern Bering	Pelagic		Pacific Salmon, Dolly Varden, Pacific Herring, Arctic Smelt, Capelin	Pacific Salmon, Pollock, Pacific Herring	Pacific Salmon, Dolly Varden, Pollock, Arctic Smelt
	Demersal		Arctic Lamprey; Starry Flounder and other flounders; Pollock, Arctic and Saffron Cods; pricklebacks	Pollock; Pacific Cod; Pacific Halibut; Bering Flounder, Yellowfin Sole, Alaska Plaice and Northern Rock Sole; Capelin; Pacific Herring; eelpouts; snailfish	Pollock, Pacific Cod, Saffron Cod, flounder, sculpins
Chukchi	South	Pelagic	Chum and Pink Salmon; Pacific Herring; Capelin, Arctic Smelt; Least Cisco; Inconnu	Chum and Pink Salmon; Dolly Varden; Pacific Herring	Chum and Pink Salmon, charr, Least Cisco
		Demersal	Arctic Lamprey; Arctic Cod; Saffron Cod; Pollock; Hamecon, Arctic Staghorn and other sculpins; Arctic Sand Lance; Yellowfin Sole; Starry Flounder; Whitespotted Greenling	Spiny Dogfish; Arctic Skate; Arctic and Saffron Cods; Arctic Sand Lance; Bering Flounder; Yellowfin Sole, Alaska Plaice and other flounders; numerous species of eelpouts, pricklebacks, poachers, and snailfish	Chum and Pink Salmon, charr, Least Cisco
	North	Pelagic	Pacific Herring, Capelin	Arctic and Saffron Cods	
		Demersal	Arctic Cod, Four Horn Sculpin, Veteran Poacher, Arctic Sand Lance, Arctic Flounder	Arctic Skate; Arctic and Saffron Cods; Arctic Sand Lance; Bering Flounder; Yellowfin Sole, Alaska Plaice and other flounders; numerous species of eelpouts, pricklebacks, poachers, and snailfish	Chum and Pink Salmon, charr, Least Cisco

Table 4.6. Most abundant species of Arctic marine fish in northern Bering Sea, Chukchi Sea, East Siberian Sea, and Beaufort Sea regions of the Pacific Arctic Region.—Continued

[Pacific Arctic Region is as described by Grebmeier and others (2015). **Habitat/Shelf region:** Pelagic refers to species occurrence in water column; demersal refers to species occurrence at or near the seafloor]

East Siberian and Beaufort Seas			
Arctic Sea	Habitat/shelf region	Fish abundance	
		East ←	Community dominants and species groups → West
		Nearshore	Offshore
Beaufort	Pelagic	Dolly Varden; Arctic and Least Ciscoes, Broad Whitefish; Pacific Capelin; Arctic Smelt; Ninespine Stickleback; Pacific Herring	Arctic Cod; larval and juvenile forms of demersal fish species
	Demersal	Arctic Cod; Fourhorn and Twohorn Sculpins; Arctic Flounder; Slender Eelblenny; snailfish	Arctic Skate; Pacific Capelin; Arctic Smelt; Arctic Cod; Saffron Cod; Arctic Sand Lance; Greenland Halibut; Arctic Flounder; Hamecon, Fourhorn, Arctic Staghorn, and other sculpins; snailfish, eelpouts, blennies
East Siberian Sea	Pelagic	Char, Arctic and least ciscoes, broad whitefishes, Arctic smelt	Meroplankton (fish larvae)
	Demersal	Saffron and Arctic Cods, Arctic Flounder, sculpins	Bering Flounder and other founders, sculpins, eelpouts, snailfish

“...further shifts in spatial distribution and northward range extensions are inevitable and that the species composition of the plankton and fish communities will continue to change under a warming climate. While overall productivity is likely to increase in the northernmost systems as the region changes from Arctic to subarctic conditions, some (primarily subarctic) species will increase, while other (primarily Arctic) species will decrease or retreat northward.” These analyses demonstrate linkages between climate and species distributions and, when considered in light of sea-ice retreat and marine ecosystem effects toward the poles (for example, Doney and others, 2012), suggested a heightened vulnerability of the pelagic fish community over the Chukchi shelf to widespread environmental change.

The life cycles of marine fishes (eggs, larvae, juveniles, and adults) variously link pelagic and benthic systems and nearshore and offshore through evolved life strategies and behavioral patterns. Many shelf species have a benthic life history stage and depend on the benthic environment for some part, or all of their lives. Cascading effects from pelagic to benthic ecosystems, without immediate additions of demersal fishes from the Bering Sea, are possible, and already may be occurring. Changes in productivity, competition, and predation as noted by Mueter and others, (2009) would accompany changes in habitat and affect population processes including growth and survival. The different species (for example, salmonids, forage fishes, flatfishes, and cods) will be affected differently by changes in the pelagic community. For instance, flatfishes live on the ocean bottom and typically release eggs into the plankton drift. Most eelpouts and sculpins dwell on

the bottom and their eggs, larvae, and juveniles develop on the bottom. Saffron Cod adults occur at various depths; however, they lay their eggs on the bottom and the eggs develop there. Key information gaps about the abundance, life history, migrations, and reproductive ecology (for example, spawning times and locations) of Arctic Cod, Capelin, and other forage species will be needed to inform assessments of trophic cascades and effects of ecosystem change.

The fish assemblages of nearshore and shelf waters of the Chukchi and Beaufort Seas are under current fishery investigation ([appendix A](#)). Previous research has shown that, although many marine species such as Capelin and Arctic Sand Lance commonly are detected in nearshore and offshore habitats, Arctic Cod are by far the most common marine species in the U.S. Chukchi and Beaufort Seas. In reviewing the life history and ecology of Arctic Cod, Crawford and others (2012) reported temperature preferences of early life history stages to be the same as those associated with cold marine waters (that is, larvae and fry development between 1.5 and 3.0 °C with highest survival rates between 0.5 and 3.0 °C). Juveniles and adults were tolerant of a wider range in temperatures conditions. Adults have been sampled in abundance in coastal waters >13 °C and in marine habitats typically no warmer than 6–7 °C. Although specific physical and biological information about migratory behaviors, reproductive ecology, and importance of offshore habitats for this species is lacking, its keystone role is supported by its widespread occurrence, dominance in fish assemblages, and importance in regional food webs.

Population Dynamics

Estimating how marine fish populations respond to changing environments requires an understanding of the mechanisms by which the environment (its mean and variability) creates changes in population dynamics. A life cycle approach that includes a numerical assessment of differential effects at different ages or stages enhances predictive capability and understanding of the contribution of individual effects to the population level (Benton and others, 2006). Environmental effects are mediated through changes in demographic rates and population size, which may result from functional responses at molecular and genetic levels of organization. In population ecology, the most important environmental factors are those that have the greatest effect on mortality, growth, and spawning and recruitment rates (Reist and others, 2006; Allen and Hightower, 2010). In the U.S. Arctic, research has addressed environmental effects on *physiology* (food and growth)⁷, *dispersal* (active and passive transport mechanisms), and *predation mortality* (predator-prey). How physical influences (for example, sea ice, light, temperature, salinity, currents, pH, and dissolved oxygen [DO]) affect these processes (directly or indirectly) and ultimately the distribution and abundance of fishes is an increasingly important part of ecosystem-based management and a focus of integrated science. The role of disease and parasitism in Arctic marine fish population dynamics, although thought to be significant, are unknown and baseline information has not been included. At present, the effects of fishing mortality on Arctic marine fishes are of negligible effect to their population dynamics.

Population Parameters and Models

Population size, the number of individuals within a geographic range, is a fundamental demographic parameter. In surveys of marine fishes, it is not possible to count all individuals in a census and therefore a number of techniques have been developed to estimate abundance and monitor change. These methods commonly include estimates of population density, the size of the population in relation to the space it occupies. Population density is affected by density-dependent factors (competition, predation, migration, and disease) and density-independent factors (for example, weather, storms, currents, temperature). The structure of populations often is studied with respect to age- or

size-related cohorts (for example, juveniles or adults) and related distributions of gender (sex ratios) to describe the reproductive potential of the population and its current and future growth. Genetic information is commonly obtained to further characterize population structures and elucidate evolutionary relationships. Age- and stage-structured analyses show how some individuals will have a greater effect on population-level processes. In this context, fecundity is an important parameter that describes the numbers of offspring an individual or population is able to produce in a given amount of time. In marine fishes, fecundity (number of eggs) varies by species and age/size of fish with younger smaller fish typically producing fewer eggs, and larger, older fish producing more eggs. Environmental conditions often affect the physiological condition of a fish and the number and quality of eggs produced, and for some species whether or not spawning occurs. Another individual trait that affects population growth is mortality, the measure of deaths per unit of time. Life tables are regularly used to display age-specific statistical patterns of a population's survival patterns.

Many different kinds of models (for example, exponential and logistic) have been developed to study growth in fish population to aid fisheries management, environmental impact assessment, or restoration of stocks that have been exploited or somehow reduced. Stock models range from surplus production models (for example, Schaefer, Fox, and Pella and Thomlinson models) to more detailed and age-structured demographic models (for example, yield-per-recruit, delay difference, and Beverton and Holt stock-recruitment models). The most common uses of population models have been to estimate recruitment (young fish entering the population) and yield (harvestable amount) in managed fisheries. The greatest challenge in these model systems is in their ability to realistically capture the “*complex causation driving population dynamics*”; the greatest value may be in the identification of the general mechanisms, which map the environment, through the life history, to the dynamics (from Benton and others, 2006, p. 1,173). In most instances, the scattered and fragmented nature of the existing Arctic data sets and lack of time series does not allow quantitative approaches to population modeling.

The ideal is to have the capability to estimate (1) long-term fluctuations in abundance and biomass production due to human perturbations or environmental variations, and (2) temporal-spatial responses of fish populations to change (Monterio, 2002). Surplus production models generally require much less biological information than age-structured models. In data-rich regions, like the southeastern Bering Sea, the role of the physical environment in predictions of resource availability is increasingly the focus of ecological (coupled physical and biological processes) models (for example, Miller, 2007).

⁷The studies stop short of linking bioenergetics (energy expenditures) and population dynamics (mortality, survival, and population growth).

Measures of growth, such as age-length and length-weight relationships are often used in stock assessments, in models that estimate habitat or ecosystem productivity, and in assessments of the health of individuals. However, it is not presently possible to model the population dynamics of most Arctic marine fishes with actual data collected from the Chukchi and Beaufort Seas. Regional-scale resource assessment surveys have been recently designed to collect data for the purpose of parameter estimations (that is, BOEM-sponsored NOAA and UAF surveys). Earlier baseline surveys produced information about species occurrences, relative abundance, and habitats. The collection of population data has, in the whole, been somewhat limited to length-weight and in some instances, age-length (size-at-age) relationships. In [appendix B](#), age-length and length-weight relationships are presented for 19 nearshore species of Arctic fishes. In fishes, both growth rates and length-weight relationships are highly variable reflecting differential changes in population responses to environmental parameters such as water temperature, prey quality, population density, and direct human interaction, such as fishing (Courcelles, 2011; Loher, 2012). Species specific and interspecific differences in population growth rates and age and weight relationships are evident within and across years and by geography from various locations in Chukchi and Beaufort Sea study areas ([appendix B](#)). These differences demonstrate the plasticity in age and growth noted by Courcelles (2011) and Loher (2012) in Arctic marine fishes. The sources of age-length data and regression analysis are appended to this report ([appendix B](#)) and the species and locations of data collection from outside the U.S. Chukchi and Beaufort Seas are listed in [table 4.7](#).

The length-weight regressions are dated, but at the time of their collection, allowed the estimation of fish condition and growth rates at scattered locations around the Arctic coast. Their historical value will be in comparison with contemporary estimates of these parameters and a potential benchmark to evaluate the effects of changing climate and environmental conditions (for example, Chen and Sakurai, 1993 for Saffron Cod). Given the status of existing information, a structured information management process, such as the Bayesian modeling approach used by Jay and others (2011) for Pacific walrus, could be used to evaluate needs and priorities for population dynamics modeling relative to offshore oil and gas development, climate change, and ecosystem-based management.

⁸Population information obtained through NOAA and MMS sponsored studies for the Alaska OCS Region; British Petroleum (Alaska), Inc. and the North Slope Borough fish monitoring in Prudhoe Bay; and U.S. Fish and Wildlife coastal resource inventories of the Arctic National Wildlife Refuge.

Current Understanding of Population Dynamics

There are typically four reasons to study population dynamics. First, population effects are often considered the most relevant response to environmental (ecosystem) perturbation. Second, population viability analyses (time to extinction) are used to manage endangered species. Third, they are critical determinants of sustainable yields in fishery management. Fourth, population processes are critical to understanding ecosystem dynamics and ecological processes (for example, regime shifts and trophic cascades). The first and fourth reasons are the most germane to the present Arctic management need and qualitative approaches to each are possible. Considerable research attention is being applied to developing quantitative understanding of population dynamics in light of changing Arctic conditions and potential fisheries.

Knowing how fish respond to variable environmental conditions and demographic changes in their populations is central to effective environmental assessments, potential fishery management, and informed Arctic policy. Knowledge about the demographics of marine fish population in the U.S. Arctic, while sparse, varies by season and distance from shore. More population data and information are available from nearshore areas during ice-free months simply because this is where the most research has been conducted. Offshore data collection has been of a reconnaissance nature and has allowed useful descriptions of the distribution and abundance of species for given areas and times. In the nearshore, the greatest amount of population information is available from inshore waters (<2 m) of the Alaska Beaufort Sea. This relates to the seasonal habitats for iconic species (Arctic Cisco and Least Cisco, Broad Whitefish, and Dolly Varden), logistical constraints of sampling, and coastal locations of industrial developments. Age-and-growth and size-at-age relationships, sex ratio, age- and size-at-maturity, fecundity, and other life history traits (for example, gonadosomal indices) have been described for Dolly Varden, Arctic and Least Ciscos, Broad and Humpback Whitefish, Arctic Cod, Arctic Flounder, and Fourhorn Sculpin with most data collections occurring between the mid-1980s and early-2000s⁸. Life history characteristics of Arctic Smelt sampled in the Colville River delta were summarized by Haldorson and Craig (1984).

The nearshore emphasis noted for the Beaufort Sea also extends to the amount of process-oriented research in Simpson Lagoon and Prudhoe Bay. For fishery components of the ecosystem, process studies have examined population movements and migrations with respect to prey availability, trophodynamic relationships, and coastal hydrodynamics.

Table 4.7. Age-length and length-weight relationships of fishes in the U.S. Arctic, with available data only from outside the U.S. Chukchi and Beaufort Seas.

Age-length relationships		
Species	Location	Source
<i>Acantholumpenus mackayi</i>	Tuktoyatuk Harbour, Yukon Territory, Canada	Hopky and Ratynski (1983)
<i>Ammodytes hexapterus</i>	Lower Cook Inlet, Alaska, USA	Robards and others (2002)
<i>Gadus chalcogrammus</i>	Eastern Bering Sea, Alaska, USA	J. Ianelli, oral commun. (2010)
<i>Gadus macrocephalus</i>	Bering Sea, Alaska, USA Gulf of Alaska, Alaska, USA	Stark (2007)
<i>Gymnelus viridis</i>	Northwest Territories, Canada	Green and Mitchell (1997)
<i>Hippoglossus stenolepis</i>	Northeast Pacific	Forsberg (2011)
<i>Limanda aspera</i>	Eastern Bering Sea, Alaska USA	Wilderbuer and others (1992)
<i>Lumpenus fabricii</i>	Tuktoyatuk Harbour, Yukon Territory, Canada	Hopky and Ratynski (1983)
<i>Pleuronectes quadrituberculatus</i>	Eastern Bering Sea, Alaska, USA	Zhang and others (1998)
<i>Squalus suckleyi</i>	Hecate Strait, British Columbia, Canada Georgia Strait, British Columbia, Canada Georgia Strait, British Columbia, Canada	Ketchen (1975) Ketchen (1975) Saunders and McFarlane (1993)
<i>Triglops pingelii</i>	Kamchatka, Russia	Tokranov (1995)
<i>Reinhardtius pingeli</i>	Eastern Bering Sea, Alaska, USA	Ianelli and others (2007)
<i>Zapraa silenus</i>	Kuril Islands/Kamchatka, Russia Northeast Pacific, Alaska, USA	Tokranov (1999) Smith and others (2004)
Weight-length relationships		
Species	Location	Source
<i>Acantholumpenus mackayi</i>	Tuktoyatuk Harbor, Yukon Territory, Canada	Hopky and Ratynski (1983)
<i>Ammodytes hexapterus</i>	Lower Cook Inlet, Alaska, USA	Robards and others (2002)
<i>Gadus chalcogrammus</i>	Eastern Bering Sea, Alaska, USA	J. Ianelli, oral commun. (2010)
<i>Gadus macrocephalus</i>	Eastern Bering Sea, Alaska, USA	Thompson and others (2007)
<i>Gymnelus viridis</i>	Northwest Territories, Canada	Green and Mitchell (1997)
<i>Hippoglossus stenolepis</i>	Northeast Pacific, Alaska, USA	Sadorus and others (2012)
<i>Limanda aspera</i>	Eastern Bering Sea, Alaska, USA	Wilderbuer and others (1992)
<i>Lumpenus fabricii</i>	Tuktoyatuk Harbor, Yukon Territory, Canada	Hopky and Ratynski (1983)
<i>Pleuronectes quadrituberculatus</i>	Eastern Bering Sea, Alaska, USA	Zhang and others (1998)
<i>Reinhardtius pingeli</i>	Eastern Bering Sea, Alaska, USA	Ianelli and others (2007)
<i>Squalus suckleyi</i>	Washington, USA	Wildermuth (1983)
<i>Triglops pingelii</i>	Kamchatka, Russia	Tokranov (1995)
<i>Zapraa silenus</i>	Northeast Pacific, Alaska, USA	Smith and others (2004)

Field and laboratory experiments have focused on physiological responses to natural variability in the physical conditions of habitats in bays, lagoons, and exposed coastlines as well as changes in conditions resulting from coastal construction. Years of research and monitoring in the vicinity of Prudhoe Bay has yielded a wealth of information about the life histories, habitats, and harvests of the coastal fishes and increasingly in the area around Point Barrow. Information about genetic relationships (diversity and structure) is more limited with respect to population dynamics. Genetic studies have been conducted on Arctic Cisco, Dolly Varden, Arctic Cod, and there is growing interest in Saffron Cod. The importance of these species in subsistence fisheries, possible effects of offshore oil and gas development, and possible effects of changing climate conditions, have, or currently are, responsible for these studies.

Salmon, charr, and whitefishes are regionally significant as traditional use species in subsistence fisheries and are of increasing value as recreational resources in Arctic watersheds. However, among these species, especially for those stocks occurring in North Slope drainages, harvest rates have not historically warranted management concerns about fishery effects on population sustainability. As an example, Arvey (1991) estimated sport fishery harvests to be 1,000–3,000 fish annually, and subsistence catches to be two to six times this amount. Freshwater habitats, especially overwintering sites, are thought to be most limiting to this species, and thus the possible effects of climate change have raised concerns about their management and conservation (Viavant, 2001; Crane and others, 2005; Greiner, 2009). These concerns have translated into efforts to identify and map overwintering locations and feasibility studies for enumeration of Dolly Varden at major overwintering sites including evaluation of the genetic stock composition at key index areas (for example, Hulahula River, Saganavirktok River, and tributaries). Population monitoring methods include aerial counts of overwintering abundance with possible validation by mark-recapture studies (that is, Ivishak, Anaktuvuk, Canning, and Hulahula Rivers, see Viavant, 2009; Rat River, see Harwood and others, 2009) and use of Dual Frequency Identification Sonar (DIDSON) technology and various species validation techniques (for example, underwater camera and hook and line sampling) in the Hulahula River (Greiner, 2009).

Information about the demographic traits for most marine fish populations in the Chukchi Sea is lacking largely due to the absence of large-scale fisheries operating in the region and corresponding lack of resource assessments and demographic data. Some population information is available from surveys sponsored by BOEM during the early 1990s. As an example,

demographic information was developed for Bering Flounder and Arctic Staghorn Sculpin in the northwestern Chukchi Sea by Barber and others (1994). New research being conducted and planned by NOAA and the University of Alaska is expected to address many of the gaps in life history and demographic traits for marine fishes in the Chukchi and Beaufort Sea shelf habitats.

Modeling Environmental Effects on Population Dynamics

The quantitative approaches to population ecology studies of Arctic fish, although limited, are most appropriately considered in light of traditional research associated with physiological responses, dispersal processes, and food web relations.

Physiological research in the nearshore Alaska Beaufort Sea has focused on seasonal growth rates (VBGM growth parameters), body condition (Anderson and Gutreuter, 1983), as part of long-term monitoring of coastal habitats (<2 m) most affected by oil and gas development⁹. The monitoring was designed to obtain biological information about key indicators (notably Arctic Cisco and Broad Whitefish), their use of habitats (generally in the area between the Colville and Saganavirktok Rivers), and population responses to variable hydrographic conditions. Shallow coastal waters are responsive to wind-driven circulation, regional upwelling, and, in the Prudhoe Bay area, localized changes in temperature and salinity associated causeway construction (for example, breaching and wake eddy effects at West Dock and Endicott projects). The long-term monitoring provided seasonal indices of fish abundance and samples for age and growth analysis and trophic studies for indicator species across a large segment of the coast. Physical data collections included observations about wind and weather conditions and hydrographic profiles associated with fish collection efforts. Fish catch records from the Colville River delta are another source of long-term population data. Genetic samples (mtDNA) were obtained for Broad Whitefish from freshwater habitats in the Colville and Saganavirktok Rivers to determine if they were distinct populations (Patton and others, 1997).

The monitoring in Prudhoe Bay was designed to evaluate potential causeway effects on coastal habitats and amphidromous fish populations and related effects to subsistence and commercial fisheries. In a 5-year study, Griffiths and others (1992) studied growth patterns in young (age-1 and age-2) Arctic Ciscos and Broad Whitefish collected around the causeways (Fechhelm and others, 1995a; 1995b). Growth (increase in length) in each species was positively correlated with temperature and body conditions. Negative correlations between condition and salinity were reported for larger Broad Whitefish and Griffiths and others (1992) suggested that the availability of prey and food benefits associated with marine waters moved inshore, outweighed

⁹A listing of scientific publications associated with long-term monitoring studies in the Prudhoe Bay area, Alaska, is available from LGL Limited (2014).

negative effects on their growth due to temporary exposures to colder-higher salinity conditions. Reduced growth in about 4–6 percent of each was attributed to causeway effects (for example, thermal barriers and wake eddies).

Numerous ichthyoplankton surveys have been done in the Chukchi and Beaufort Seas. The studies were designed as reconnaissance surveys rather than dispersal studies although the results, as reviewed in this report, shed considerable light on diversity patterns and processes. Research directly focused on *dispersal processes* was used to study population trends and origins of Arctic Cisco in northern Alaska. A delay-difference population model (Deriso, 1980) was used by Gallaway and others (1983) to estimate biomass production of Arctic Ciscos targeted in a local fishery in the Colville River¹⁰. Harvest records for the autumn gillnet fishery have been available since they were first collected in 1967 (Fechhelm and others, 2007; Moulton and others, 2010). The Deriso model, classified as a partially age-structured model, was used to investigate annual abundance patterns in the fishery relying on data obtained from (1) 15 years of catch records, (2) CPUE obtained in coastal surveys, and (3) population information acquired from tagging studies associated with those surveys. The model was parameterized with biological information about estimated growth, recruitment, survival and age structure, of fish captured in the Colville River fishery. In this case, the modeling allowed for time lags in the dynamics of the stock for Arctic Cisco (stocks are known for their slow growth and late age of entry to the fishery) and accounted for observed fluctuations in annual abundance as reflected in the catch. Importantly, the model generated a hypothesis about Mackenzie River origins for this Alaskan stock and annual transport of young-of-the-year ciscos (Gallaway and others, 1983). A dispersal mechanism in wind-aided currents was described by Fechhelm and Fissel (1988) and its effects on recruitment processes in the Colville River fishery by Fechhelm and Griffiths (1990). The interaction of fish, winds,

and currents on young-of-the-year (YOY) migration patterns was numerically modeled by Colonell and Gallaway (1997) and results considered in light of interannual fluctuations in abundance of fish in coastal monitoring in Prudhoe Bay and catch rates in the fishery¹¹. A simulation model was developed to investigate wind effects on interannual variations in summer dispersal patterns of juvenile Least Cisco in the Prudhoe Bay area (Fechhelm and others, 1995a). The study of age structure in Colville River harvested Arctic Cisco (Zimmerman and others, 2013) may result in the improved population modeling recommended by Murphy and others (2007).

Predator-prey studies, mostly in the form of stomach content analyses and more recently using stable isotope and fatty acids (for example, Pirtle and Mueter 2011) are important components of habitat and community analyses including understanding ecological relations with respect to the maintenance of important populations or evaluations of potential cascading effects of regime shifts (for example, Suryan and others 2009; Carey and others, 2013). Many investigations in the Chukchi and Beaufort Seas have indicated the critical role that Arctic Cod have in Arctic marine food webs (for example, Bradstreet and others, 1986; Springer and others, 1986; Pirtle and Mueter, 2011) and their intermediate position in top-down and bottom-up energy pathways (Hunt and McKinnell, 2006). The results of marine fishery surveys invariably list this species, regardless of depth, season, or year, as the most abundant; usually far exceeding all other species reported in survey catches (Pirtle and Mueter, 2011¹²). Given this abundance and its central role in energy pathways, Arctic Cod must be viewed as a keystone species. This does not detract from the ecological significance of lipid-rich Capelin (Carscadden and Vilhjálmsson, 2002; Rose, 2005) and Arctic Sand Lance (for example, Bluhm and Gradinger, 2008) and, to a lesser extent Pacific Herring (for example, Mueter and others, University of Alaska-Fairbanks, oral commun., 2013) and Arctic Smelt (Craig and others, 1984a). These populations are subject to greater interannual changes in abundance, but have been shown to be locally abundant at various coastal locations and to be important in regional food webs.

The role of invertebrate prey in carbon cycling in Arctic marine ecosystems (Dunton and others, 2006) and in the diets of marine fishes and many higher-level consumers is significant (Craig and others, 1984b). In the Beaufort Sea, especially, the annual colonization of coastal waters by epibenthic amphipods and mysids, pelagic copepods, and other species (Craig and others, 1984b) forms the basis of the nearshore food web. Craig (1989a) and Craig and others, (1984b) discussed the availability of food in coastal habitats to standing crops of macroinvertebrate prey in freshwater habitats as being a significant factor in the evolution of anadromy (amphidromy) in the Arctic. The role of the epibenthic invertebrate food base is a key premise of time-tested conceptual models of fish habitat use in the Beaufort

¹⁰Arctic Cisco are harvested between October and November each year. The availability of fish varies annually and Gallaway and others (1983) reported total catches ranging between 9,268 (1979) and 71,575 (1973) fish per year. The size of individuals captured in the fishery ranged from 240 to 380 mm (FL). From 1985 to 2004 about 38,600 Arctic Cisco have been harvested annually in commercial and subsistence fisheries (Least Ciscos averaged about 18,600 annually during the same period). The average annual removal rate for Arctic Cisco was 8.9 percent of the available fish; the average annual removal rate for Least Cisco was 6.8 percent

¹¹Zimmerman and others (2013) re-examined the Mackenzie River hypothesis in light of new genetics data, otolith microchemistry, and potential climate change effects on the coastal migration of YOY fish. Their analysis did not refute Mackenzie River origins for Arctic Cisco found in the Colville River.

¹²Pirtle and Mueter (2011) report peak densities of adult Arctic Cod at 150,000 fish per ha⁻¹ at bottom depths of 100–350 m, and peak densities of YOY Arctic Cod at 160,000 fish per ha⁻¹ at bottom depths of 20–75 m in the U.S. Beaufort Sea.

Sea (Craig and others, 1982; Craig, 1984) and bioenergetics of coastal fishes in Prudhoe Bay (Fechhelm and others, 1995a; 1995b). Marine food webs for fishery resources in the offshore Beaufort Sea are less studied, but likely are similar to shelf and slope areas of the Chukchi Sea. Planktonic species and under-ice fauna (phytoplankton, amphipods, copepods, euphausiids, and larval fish) are important food resources for marine fishes in pelagic systems (for example, Gadidae, Salmonidae, and others). Invertebrate species associated with the seafloor (for example, shrimp, amphipods, polychaetes, and benthic fauna) for marine species occupying benthic systems (for example, Pleuronectidae, Liparidae, Sticheaidae, and others).

In both nearshore and offshore environments of the U.S. Beaufort and Chukchi Seas, a broad generalization can be made that fish are also important in the diets of many fish species (for example, Gadidae, Salmonidae, Pleuronectidae, and others), particularly older, larger-sized individuals. Like other gadids, the Arctic Cod is cannibalistic. Thorsteinson and others (1990) hypothesized that the observed differences in coastal habitat used by YOY Arctic Cod and older cod in Camden Bay, Alaska, were an adaptive response to cannibalism. Similarly, some species, such as the Dolly Varden, are much more piscivorous than other dominant members of the coastal assemblage, but like most other species are opportunistic in their selection of foods. Although the food habits of some marine fishes are better known than others, the application of bioenergetics approaches to population dynamics modeling suffers from a (1) quantitative data about predator-prey relationships; (2) lack of seasonal information (spring and winter months especially); and (3) lack of long-term population data for most species of interest. For a small number of species in which appropriate data are available (for example, Broad Whitefish and Arctic and Least Ciscoes), bioenergetics applications to population ecology studies in coupled models may be possible. In the absence of data, other approaches to reduce uncertainties associated with selecting population models to evaluate responses to environmental influences (Katsanevakis, 2006), such as changes in recruitment and growth, have been done for Arctic Cisco (for example, von Bielea and others, 2011). In the latter instance, YOY recruitment into the Colville River was used to examine the long-term response (1978–2004) of the population to climate change using multi-model inferences to study relations between trends in abundance and YOY growth and various environmental parameters (AO Index, air temperature, east wind speed, sea-ice concentration, and MacKenzie River discharge) and their influences of primary production and life stages of important cisco foods.

Biological Interactions

Estimation of ecosystem functions (for example, primary, secondary, and tertiary productivity; nutrient fluxes; carbon fixation; and organic matter mineralization and suspension removal) are feasible measures of biodiversity importance (Weslawski and others, 2006). The ecological effects of marine production cycles on the distribution and abundance of the Arctic marine fishes has received relatively little attention in the United States Arctic. In a large-scale analysis, Smetacek and Nicol (2005) compared the biological productivity reported in the Barents (Russia) and Chukchi Seas to the Siberian and Canadian shelf seas. The much higher productivity in the Barents and Chukchi Seas—gateways to the Arctic—were related to the advection and retention of nutrients in these systems. With respect to the Chukchi Sea, currents flowing through Bering Strait are rich in nutrients which, when mixed with iron (Fe) in shelf water and melting ice, fuels the high primary productivity of the region. Because of the Chukchi Sea's shallow depth and lack of a well-developed pelagic community, much of the bloom biomass (organic matter) settles out on the sediments and supports a rich, especially invertebrate, benthic fauna (Jay and others, 2011). The carbon sink and intense nutrient recycling occurring near the seafloor are critical processes supporting the region's benthic communities. In contrast, the Barents Sea is deeper and a greater proportion of phytoplankton production is retained in the water column. *"The exceptionally high copepod biomass of the western Barents Sea, largely attributable to advection from the adjoining Norwegian Sea, supports, or has supported, huge stocks of planktivorous fish including capelin and herring and their predators, particularly Atlantic cod"* (from Smetacek and Nicol, 2005, p. 364).

Trophic Linkages

Knowledge about ecosystem functions is foundational to understanding biological interactions of marine fishes. Fishes and zooplankton not only are important prey, but also are critical conduits of energy in regional food webs (for example, Chukchi Sea—Piatt and others, 1989). The large-scale animal distribution patterns (fishes, birds, and mammals) are driven by food availability, not the absence of predators (Hunt and McKinnell, 2006). These authors noted that at regional scales, current predation or past predation events likely have shaped local distributions, at least in marine birds and pinnipeds. Wasp-waist control occurs when one of the intermediate trophic levels is dominated by a single species, which may be the case with Arctic Cod in the Chukchi and Beaufort Seas.

Considerable research underscores the critical function of Arctic Cod in Arctic marine ecosystems because no alternate food source of equivalent trophic value exists. Processes in these ecosystems may have features that result in a switch from bottom-up to top-down control (Hunt and McKinnell, 2006) given the variable abundance of small pelagic species in response to changing environmental conditions. A moderating influence of sea ice in the population dynamics of Arctic Cod is hypothesized; however, loss of sea ice due to climate warming and unknown associated effects on the ecology of this species is of environmental concern¹³. Similarly, the potential effects of large oil spills and related clean-up activities on Arctic Cod could affect marine ecosystem functions.

The Arctic Cod is a key prey of many marine mammals and seabirds as evidenced by their occurrence in the diets of belugas and ringed and bearded seals, Pacific walrus (occasionally), Thick-billed (*Uria lomvia*) and Common Murres (*U. aalge*), Black Guillemots (*Cepphus grylle*), Black-legged Kittiwakes (*Rissa tridactyla*), Northern Fulmars (*Fulmarus glacialis*), Arctic Terns (*Sterna paradisaea*), and Glaucous (*Larus hyperboreus*), Sabine's (*Xema sabini*), Ivory (*Pagophila eburnea*), and Ross's Gulls (*Rhodostethia rosea*) (Hunt and McKinnell, 2006). Arctic Cod also are of indirect importance to Polar bears (*Ursus maritimus*) and Arctic foxes (*Vulpes lagopus*), because their primary marine food, the ringed seal, also relies on them as food.

Other fishes are important in regional food webs. Pirtle and Mueter (2011) summarized the known trophic linkages for seven species of marine fish (Arctic Cod, Capelin, Arctic Sand Lance, Pacific Herring, and Saffron Cod, and Arctic and Least Ciscoes) in the U.S. Beaufort Sea. Some aspects about trophic linkages between marine fish and invertebrate communities are described in detail in the species accounts (chapter 3). Depending on season and location, many of

the marine species are major food resources for regional populations of seabirds, marine mammals, other fishes, and humans. As an example, the largest seabird colony in the North American Arctic is located at Capes Lisburne and Thompson in northwestern Alaska. Arctic Sand Lance, Capelin, and Arctic Cod are important prey for kittiwakes and murres at the colony during the breeding season (including pre-breeding and post-fledging periods). Pacific Herring and Arctic Cod are important foods of other fish (Inconnu, Chum and Pink Salmon, Dolly Varden), birds, and marine mammals in the Bering Strait and southeastern Chukchi Sea. Least Cisco is an important summer food of the Red-throated Loon in coastal habitats along the Chukchi Sea. Arctic Cod and Saffron Cod are notably important in the diets of most marine animals common to the Chukchi and Beaufort Seas including many seabirds, cetaceans, seals, polar bears, and Arctic foxes. The amphidromous fishes (whitefishes and charr) in the nearshore Beaufort Sea are preyed upon by Beluga whales (*Delphinapterus leucas*) and Ringed Seals (*Pusa hispida*).

Marine Fish Disease Ecology

In spite of obvious effects to humans and captive animals, fisheries managers often ignore disease as a significant factor affecting the abundance of wild populations because the effects are difficult to observe and quantify. Historically, most fish-health research has been directed toward identification, treatment, and prevention of diseases of hatchery fishes; however, recent studies (for example, Hershberger and others, 2013) from marine, freshwater, and terrestrial environments indicate that infectious and parasitic diseases can be responsible for population oscillations, extinction of endangered species, reduced host fitness, and increased susceptibility to predation as well as an important component of natural mortality. The recognition of disease as a population-limiting factor for wild fish is partly the result of the emergence of high profile pathogens and changes in environmental conditions that shift the host-pathogen balance in favor of disease. Among such environmental changes, global warming associated with climate change is seen to be a particularly important threat for poikilothermic vertebrates, such as fish, for which environmental temperature is a controlling factor in their physiology and immune response. The emergence of *Ichthyophonus* infections¹⁴ in adult Yukon River Chinook Salmon, Pacific Halibut in the northeast Pacific, and Atlantic herring (*Clupea harengus*) off Iceland, are examples of disease conditions with links to global warming and possible transmission through trophic linkages (Woodson and others, 2011; Dykstra and others, 2012; Jim Winton, U.S. Geological Survey, oral commun., 2013). The disease is associated with adverse flesh quality and possible pre-spawning losses.

¹³Arctic Cod are the most abundant forage fish and play a central role in the transfer of energy from plankton to higher-level consumers like ringed seals and polar bears (Hunt and McKinnell, 2006). As warming alters sea ice conditions, northward shifts in the distribution of marine fishes are expected. Such food-web impacts would propagate through the ecosystem, from sea-floor organisms to their predators, and, ultimately, to the subsistence users whose livelihoods largely depend on having reliable access to marine mammals, fish, and other wildlife. Shifts in marine biodiversity will partly depend on whether species are associated with the open ocean or with seasonal sea ice (Hunt and others, 2013).

¹⁴Phenotypic (Hershberger and others, 2008) and genotypic (Criscione and others, 2002; Rasmussen and others, 2010) differences have been identified among isolations of *Ichthyophonus hoferi* from the northeastern Pacific, suggesting that there are multiple sympatric species in the region. Due to this taxonomic uncertainty, the parasite is referred herein by its generic name.

Human Interactions

Subsistence Fisheries

Generally, subsistence is considered hunting, fishing, and gathering for the primary purpose of acquiring, sharing, or bartering traditional foods. Craig (1987; 1989b), Braund and Kruse (2009), and DeGange and Thorsteinson (2011) summarized the relative importance of marine fishes in the traditional economies of 11 Arctic communities using data obtained from the Alaska Department of Fish and Game¹⁵ and others. Depending on village location, Pacific salmon, Dolly Varden, Arctic and Least Ciscoes, Broad and Humpback whitefishes, and Inconnu were the major fish species harvested. Arctic Cod, Saffron Cod, flounders (for example, Arctic Flounder), and sculpins (for example, Fourhorn Sculpin) and other marine fishes, such as Capelin and Pacific Herring, that occur in inshore waters, are of more limited, but still important usage. The subsistence survey data summarized by DeGange and Thorsteinson (2011) that Alaska Native Arctic residents are actively engaged in subsistence fishing and that fish are important foods (5–10 percent or more of traditional diet); fish is consumed on a daily basis in many villages, and in some cases provides more of a dietary contribution than any other food source. In the Kotzebue Sound area, fully one-third to one-half of the total subsistence harvest by weight consists of fishes. Although the inhabitants of the North Slope often depend much less on fishing and more on marine mammal and caribou (*Rangifer tarandus*) hunting, significant fish harvests are still made. The fact that fishes comprise more than 10 percent of the total subsistence harvest of Point Barrow is remarkable, considering the number and biomass of bowhead whales (*Balaena mysticetus*) harvested there annually (DeGange and Thorsteinson, 2011). At a larger scale, communities north of Bering Strait harvested 23 bowhead whales (about 750 tons) in 2008; the subsistence catch of marine fishes for the same area in Alaska was estimated at 60–70 percent of this amount. At Nuiqsut (Colville River), fish are the largest single contributors to the subsistence economy at nearly 40 percent of the total harvest.

According to an Alaskan catch reconstruction study (Booth and others, 2008), the total yearly subsistence harvest of fishes from Wales to Kaktovik in 1950 was approximately the same as in 2006 (450–500 tons). Changes in subsistence use at Wainwright, Barrow, Nuiqsut, and Kaktovik pre- and post-2000 were reported by Braund and Kruse (2009) and, within the constraints of existing data, show consistency over time for most species, and increasing catches of Pacific salmon (Carothers and others, 2013). Fish landings in the Chukchi

Sea are primarily for local consumption (North Pacific Fishery Management Council, 2009). The most important species are salmonids, especially Chum Salmon and Inconnu, although 15 species of marine fishes are used. In Kotzebue Sound, Dolly Varden, Pacific Herring, and several species of flounder also are regularly harvested. About 90,000 fish are harvested annually and, in recent years, about 25,000 salmon were captured (Magdanz and others, 2011). Small numbers of five Pacific salmon found in Arctic Alaska are occasionally caught as far to the east as Amundsen Gulf, Canada. Generally, the closer a community's proximity to the more temperate and productive Bering Sea, the greater the number of salmon species caught and the greater the contribution of salmon to the local population's diet. This corresponds directly to the distribution of spawning populations of various salmon species. In the U.S. Arctic, Chum and Pink Salmon have the widest range and subsistence values.

The whitefish species are significant subsistence fishery resources in the 11 coastal villages where data are available (DeGange and Thorsteinson, 2011). Georgette and Sheidt (2005) documented their importance in Kotzebue Sound including the seasonality and methods of catch and complexity of Inupiaq taxonomy. Farther north and east of Kotzebue Sound, various whitefish and cisco species and Dolly Varden comprise the marine basis of regional subsistence fisheries. Inconnu are important in the area of the central Kotzebue Sound and in the Mackenzie River Delta, Canada, but nowhere between. Least Cisco are important in local fisheries east of the Saganavirktok River, Alaska, but are little used by villagers at Kaktovik. Capelin, Arctic Smelt, Arctic Cod, other gadids, and some sculpins are eaten at Point Barrow. A small commercial and subsistence fishery for Least and Arctic ciscoes occurred until recently in the Colville River Delta, near Prudhoe Bay. In 2010, the Helmerick family terminated the commercial fishery for Arctic Cisco, but subsistence fishing continues by villagers from Nuiqsut. The Arctic Ciscoes captured in this fishery originate in the MacKenzie River, Canada; the Colville River, by virtue of its size, is the major overwintering site for Arctic Cisco in Arctic Alaska. The subsistence gill net fishery is size selective for 5- and 6-year-old fish, which are used by residents of Nuiqsut and Barrow, Alaska. Long-term fishery monitoring in Prudhoe Bay indicates increasing abundance of some marine fishes, such as Arctic Smelt and Arctic Flounder (Fechhelm and others, 2006), and suggests the possibility of their increased use by coastal residents in Nuiqsut and Barrow.

Dolly Varden is an important subsistence resource throughout the coastal Chukchi-Beaufort Sea region from the Seward Peninsula east to Kaktovik. Reliance on this species by humans is greatest in the villages of Wainwright and Kaktovik and in Kotzebue Sound. Located in the eastern Alaska Beaufort Sea, Kaktovik is situated near Dolly Varden spawning grounds in the Brooks Range (Craig, 1989a).

¹⁵See <http://www.subsistence.adfg.state.ak.us/CSIS/>.

The timing and location of subsistence fisheries are intimately linked to the life cycle and habitats of targeted fishes. Environmental conditions, such as temperatures for drying and freezing of the fish flesh also are important. Marine and estuarine species are vulnerable to coastal fishing and the amphidromous/anadromous species are captured in both freshwater and coastal sites. Overwintering species, such as Arctic and Least ciscoes are targeted in autumn and winter fisheries with gillnets fished under ice. Coastally, during summer months, many species are captured in hook-and-line fisheries. Other species, such as Dolly Varden and Pacific Salmon can be captured in these fisheries. The marine connections of some lagoons, such as those in Kotzebue Sound, often are blocked by storm-induced gravel barriers near the end of summer, forming natural traps, or ditching, for desired species, such as Least Cisco (Georgette and Shiedt, 2005). Under certain conditions, gill nets are seined and fish weirs (traps) are used in Kotzebue Sound.

Commercial Fisheries

Commercial fishing in the U.S. Arctic is currently prohibited by Federal and international regulations (for example, National Pollution Funds Center (NPFC) and International Halibut Commission) because most fish stocks in the Chukchi and Beaufort Seas cannot support commercial harvesting (Wilson and Ormseth 2009). Three stocks (snow crab [*Chionoecetes opilio*], Arctic Cod; and Saffron Cod) were identified as sufficiently abundant to support potential fisheries. However, additional research (life history, interactions, and population dynamics) and resource assessments (monitor abundance and productivity) are needed to design sustainable harvest strategies (Levin and others, 2009; Fluharty, 2012). The current knowledge and understanding of fishery managers is that Arctic Cod and Saffron Cod are too important in regional food webs (for example, marine mammal and seabird predators) to be the targets of new, offshore commercial fisheries. Ongoing research by BOEM, NOAA, and NPRB involves ecological baseline surveys that may provide the basis for age- or length-based stock assessments for management of marine

fish and shellfish resources in the Arctic. Oceanographic measurements and data on abundance, stock structure, growth, food habits, and energetics data, are being collected to develop quantitative information about the populations and responses to environmental changes including those resulting from human interventions.

Policy Interface—Ecological and Biologically Sensitive Areas

The Convention of Biological Diversity considered the ecological significance of Arctic marine fishes in defining Ecological and Biologically Sensitive Areas (EBSAs; Speer and Laughlin, 2011). Seasonally important habitats for many fishes, birds and mammals were identified along the ice edge, in polynyas, in coastal lagoons and on barrier islands, and in bays and river deltas. In the U.S. Pacific Region (Arctic Monitoring and Assessment Programme [AMAP]), the EBSAs include St. Lawrence Island, Bering Strait, Chukchi Beaufort Coast, Wrangell Island and polar pack ice. The global significance of these EBSAs is based on ecosystem functioning and with respect to marine fishes in the U.S. Chukchi and Beaufort Seas includes the Bering Strait, Chukchi Beaufort Coast, and Polar ice pack.

Bering Strait

The Bering Strait¹⁶ exhibits the highest levels of fish and wildlife productivity and diversity in the Arctic and is the only connection between the Pacific and Arctic Oceans. Arctic Cod and other species of forage fishes are abundant and important to many marine predators, and the region supports populations of whitefishes and charr, which are important seasonally for native community subsistence.

Chukchi Beaufort Coast

The Chukchi Sea has massive phytoplankton blooms, which along with annual sea ice algae production, cannot be fully exploited by the zooplankton communities resulting in an impressively high biomass of benthic infauna and epifauna. Capelin occurs along the sandy seaward beaches of barrier islands in the area of Points Lay and Barrow. Coastal waters provide whitefish nursery areas and migration corridors for whitefish, ciscoes and Dolly Varden. The spring lead and Hanna Shoal (Chukchi Sea) retain sea ice, making it an important area for seabirds in spring and pinnipeds in late summer when sea ice is absent over the rest of the continental shelf.

¹⁶ The importance of the Bering Strait, as a gateway to the Arctic is widely recognized in national science policy (Speer and Laughlin, 2011; Wilson and Ormseth, 2011; Clement and others, 2013; National Ocean Policy Implementation Plan, 2013; U.S. Arctic Research Commission, 2013) and marine research associated with the Northern Bering Research Area (NPFMC) and Distributed Biological Observatories (National Science Foundation [NSF] and Alaska Ocean Observing System [AOOS]) and other large-scale ecosystem initiatives (that is, NRPB, BOEM, and NSF).

Polar Pack Ice

The multiyear pack ice provides habitat for distinctive fauna and flora. The extent of the multi-year ice is extremely variable inter-annually and is not a static geographic area, but rather an ever-changing feature that provides critical habitat for many animals. Arctic Cod is a key species in short food chains leading to seal and polar bear consumers.

Arctic Climate Change

Non-linear responses of marine ecosystems and populations to atmospheric forcing and warming are major sources of scientific uncertainty as they pertain to estimating probable outcomes of climate scenarios and describing the vulnerability of key biotic resources. The major sources of variation can be characterized as short-term effects on physical (for example, wind, waves, currents, temperature, stratification, nutrients, precipitation, and freshwater input) and biological (for example, phenology, primary production, food availability, and recruitment) environments, and long-term ecological changes (for example, temperature regimes, distributional shifts, and trophic cascades). Because warming effects are occurring more quickly toward the poles, both short- and long-term effects of these changes will be amplified in the Arctic. At the Arctic basin scale, marine ecosystems are affected by the interactions of physical and biological processes occurring at multiple scales of spatial and temporal resolution (for example, global—warming, regional—regime change, local—predation and survival). At a geographic scale, atmospheric forcing—related to the geography, persistence, and teleconnections of continental pressure systems—affects ecosystem function and structure at different spatial and temporal scales (Grebmeier and others, 2006a; 2006b). At smaller scales (centimeters to meters), recruitment processes can be affected by the dispersal and survival of larval fishes.

Ocean Connections

In association with atmospheric influences, Arctic marine ecosystems are also connected through ocean circulation and the long distance transport and mixing of north Atlantic and northeast Pacific waters. Marine waters over the Chukchi Sea shelf tend to be colder and more nutrient rich than water in the Beaufort Sea because of upwelling processes in the northern Bering Sea and transport of marine nutrients of deep northeast Pacific origins. Hydrographic conditions on the shelf indicate the presence of three main water masses that move to the north along the Alaska coast, across the Bering Sea from the northeast Pacific, and to the south along the Russia coast (Crawford and others, 2012). Farther north, the offshore Beaufort Sea is influenced by a mixing of Chukchi Sea water masses and north Atlantic-derived waters (transported to the

east) and circulation of other Arctic waters in the Beaufort Gyre (transported to the west). An ephemeral band of brackish water forms along the coast of the North Slope during summer months. As summer advances, the frequency of west winds along the North Slope increases, resulting in marine intrusions and colder, higher salinity water nearshore.

Marine Ecosystem Effects

Extensive and rapid losses of sea ice in the Arctic are already affecting marine ecosystems and raising conservation concerns for ice-dependent fishes, birds, and mammals (Marz, 2010; Jay and others, 2011; Wiese and others, 2015). Sea ice melt and break-up during spring strongly drive phytoplankton production by enhancing light and stratification and stabilization of the water column. The intensity and magnitude of the events is therefore determined in large part due to temperature and salinity, light conditions, and nutrient availability as well as composition and fate of the plankton community. Generally, the annual production event, including algal growth under sea ice, forms the base of the marine food web, which in turn supports higher trophic level consumers including zooplankton, fishes, birds, and mammals. The consumption of phytoplankton by the herbivorous zooplankton in the Chukchi Sea tends to be inefficient (incomplete grazing) leading to a tight coupling between pelagic and benthic ecosystems and deposition of significant amounts of organic debris (decaying phytoplankton) to the benthos. In areas of high deposition, sea floor habitats have a diverse and abundant benthos that provides important feeding grounds for a rich invertebrate community and benthic feeding animals such as walrus and bearded seals. Biological hotspots have been identified in the Barrow Canyon and Hannah Shoal in the northeastern Chukchi Sea near Barrow, Alaska.

Climate-induced changes in growth conditions for primary producers could affect the timing, productivity, and spatial extent of biological hot spots—areas of elevated food web activity (Leong and others, 2005). As an example, Frey and others (2011) reported a 20 percent increase in production throughout the Arctic Ocean during 1998–2009; an estimate that included a 48 percent increase in primary production for the Chukchi Sea. The increases were thought to reflect increased bloom durations in open water in time and space. Zooplankton communities may be particularly sensitive to such changes as their seasonal life cycles are in synchrony with the timing of ice-breakup and phytoplankton blooms (Smith and Schnack-Schiel, 1990; Deibel and Daly, 2007). With warming and changing sea ice conditions, northerly shifts in the distribution of marine fish have been projected. Although commercial concentrations of marine fish are not anticipated in the near term (probably decades due to temperature constraints), conditions that are more favorable for energy use by pelagic species (gadids, salmonids, and other marine fishes) in the Chukchi Sea may result from ecological

changes associated with regime shift (Grebmeier and others, 2006b). In this instance, changes in the food web, such as reduced standing stocks of benthic invertebrate foods, could potentially affect the distribution and abundance of predators. Such changes in distributional patterns already are being observed in Pacific walrus (David Douglas, U.S. Geological Survey, Juneau, Alaska, oral commun., 2013).

In a study of possible responses of the Atlantic Cod to climate change, Pörtner and others (2008) examined functional interactions of ecological and physiological processes and effects on this species at various levels of biological organization. The potential effects associated to exposures beyond optimal temperatures can be broadly generalized to other Arctic marine fish species. At the ecosystem level, the thermal disturbance (warming) could result in changing biogeography, biodiversity, seasonal timing, species interactions (mismatch), food web relationships, and overall ecosystem (including social interactions) function (Harley and others, 2006). At the population level, reduced densities might be expected as a result of changes in growth, reproduction, recruitment, and mortality. Changes in fish behaviors and demographic traits altered the physiological scope for growth in individual fish with cumulative effects on population processes. The physiological mechanisms operate at cellular and molecular levels and can change metabolic processes, and alter an organism's functional integration, condition and health, and susceptibility to disease. Within this conceptual framework, it is also possible to envision more positive effects if warming enhances thermal conditions for a particular species life functions and behaviors resulting in possible population growth and expansion.

Ocean Acidification

Changes in ocean chemistry, known as ocean acidification, are an expected outcome of global warming. Ocean acidification (OA) occurs when increases in atmospheric carbon dioxide (CO_2) cause an increase in the oceanic uptake of CO_2 . This in turn leads to an increase in marine production of carbonic acid, reducing the pH of marine waters—ocean acidification. Ocean acidification changes ocean chemistry by reducing calcification rates and lowering calcium carbonate saturation (Mathis and Questel, 2013). Calcium carbonate is a key mineral used in calcareous shell production and other biological processes (Doney and others, 2009). The changes in ocean chemistry from ocean acidification are expected to be amplified in the Arctic Ocean¹⁷ with potential biological effects to food

webs (that is, shell forming organisms such euphausiids) and marine fish populations (development and survival of early life stages of marine fish and foods) could be significant. In the U.S. Arctic, the ecological effects from amplification of potential acidification in freshwater discharges from the Yukon ($195 \text{ km}^3/\text{yr}$) and Mackenzie ($306 \text{ km}^3/\text{yr}$) Rivers (Milliman and Meade, 1983), including nutrients, organic matter, and sediments into Chukchi and Beaufort Seas are not known. For comparison, the freshwater discharge from the Mississippi River into the Gulf of Mexico is $580 \text{ km}^3/\text{yr}$.

Shifts in Distribution of Marine Fish Populations

Climate change effects in the Arctic marine environment include loss of sea ice in summer, increased stratification, and shifts in the timing and intensity of the seasonal production cycle (Slagstad and others, 2011; Wassmann and others, 2011). Several authors have attempted to project how these changes will affect marine fish populations (Reist and others, 2006; Huse and Ellingsen, 2008; Mueter and Litzow, 2008; Pörtner and others, 2008; Cheung and others, 2009; Bluhm and others, 2011; Mueter and others, 2011; Sigler and others, 2011; Hunt and others, 2013) and suggest potential effects on biogeography (for example, shifts in distributional), physiology (reproductive timing) and behavior (diet; Hollowed and others, 2013). Cheung and others (2009) projected that expanding bioclimatic windows would result in increased biodiversity in the Arctic. In contrast, Sigler and others (2011), projected that the shallow sill separating the northern Bering Sea and the Chukchi Sea, and the persistent presence of the cold water over the northern Bering Sea shelf (Stabeno and others, 2012a), would serve as a barrier to invasions of fish species into the region. Fishery baselines are changing rapidly throughout the Arctic; the possibility of new fisheries has increased the urgency for scientific attention to biodiversity and stock assessments (Christiansen and others, 2014).

Mueter and Litzow (2008) described the southern edge of the *cold water pool* as defining the ecotone between Arctic and subarctic communities in the northern Bering Sea. The ecotonal boundary reportedly moved 230 km northward since the early 1980s, and Mueter and Litzow (2008) reported that community-wide shifts in distributions and related increases in biomass, species richness, and average trophic level occurred as subarctic species colonized new habitats. The warming temperatures were indicated as the primary cause of changing community distribution and function although other factors were implicated. Importantly, specific responses of individual populations to temperature changes were more difficult to estimate. The range extensions reported in this report are not indicative of significant new additions of subarctic fish species to the Arctic fauna. The effects of winter sea ice and thermal effects of the Earth's inclination at high latitudes suggest cold water temperatures will persist in the Arctic and act to impede successful widespread expansions of many harvestable stocks

¹⁷Global warming trends have been amplified in the Arctic region relative to the global mean, and increased vulnerability of the Arctic, is due to the effects of increased freshwater input from melting snow and ice, temperature, and from increased CO_2 uptake by the sea as a result of ice retreat (Fabry and others, 2009).

from the Bering Sea. Given the ecological significance of Arctic Cod in Arctic marine food webs and energy cycling, a special analysis was done to describe climate change effects on Arctic and Saffron Cod in the northern Bering Sea (see [chapter 5](#)).

In an Arctic-wide climate-change assessment, Hollowed and others (2013) examined the vulnerability of 17 commercially exploited species in the Bering, Barents, and Norwegian Seas to move farther into the Arctic. The vulnerability assessment was based on exposure (to variations in the environment resulting from climate change), sensitivity (degree to which a species responds to variations in the marine environment that will be affected by climate change), potential affect (probable combined effects of exposure and sensitivity), and adaptive capacity (a species physiological or behavioral abilities to mitigate the effect). The potential for movement of the stocks was evaluated on climate change projections and expert opinion relative to life history (for example, reproductive ecology, feeding, and migratory behavior) and environmental preferences for temperature. Several of the Bering Sea species considered (that is, Walleye Pollock, Pacific Cod, Arctic Cod, Capelin, Arctic Skate, Greenland Halibut, Yellowfin Sole, and Bering Flounder) already occur in the Chukchi (all species listed) and Beaufort (Walleye Pollock, Arctic Cod, Arctic Skate, Capelin, and Greenland Halibut) Seas. Pacific Ocean Perch (*Sebastes alutus*) and Northern Rock Sole (*Lepidopsetta polyxystra*) were considered as having a low potential to move into the Arctic. Neither species has been collected from the U.S. Beaufort and Chukchi Sea. The potential for expansion of Walleye Pollock and Pacific Cod was determined to be low due to temperature and spawning site fidelity, respectively. Greenland Halibut and Capelin potentially could expand in the Arctic if temperature and conditions for larval transport and survival, or prey concentrations, respectively, were sufficient to sustain increased populations. Three stocks (Arctic Cod, Bering Flounder, and Arctic Skate) were determined to have a high potential to expand or move into the Arctic. Arctic Cod spawning occurs under ice and spawning areas will likely change if winter ice cover is lacking in the traditional spawning areas.

For many of the species identified by Hollowed and others (2013), the issue may not be the potential likelihood for northward movements, but climatic and habitat conditions (temperature, foods, substrates, and other conditions) for all life stages that increase the viability and relative abundance and expansion of small populations already present in the Arctic. Our analysis of marine fish diversity indicates that Pacific Cod and Greenland Halibut are uncommon in the Chukchi and Beaufort Seas. Alaska Plaice has been confirmed from the Chukchi Sea but not the Beaufort Sea. Yellowfin Sole is common in the Chukchi Sea but is rare in the Beaufort Sea.

Available data support a hypothesis that natural selection favors individuals that maximize growth and energy efficiency at the expense of ranges of thermal tolerance (Pörtner, and others, 2008). Capelin is a cold water, circum-Arctic species (temperature preferences from -1 to 6 °C; Rose, 2005). In the U.S. Arctic, this species is locally abundant at various locations along the coast as spawning occurs in nearshore deltaic areas. The vulnerability of the species, or stocks adapted to Arctic conditions, to warming and their sensitivity to exposures exceeding a narrow range of temperature optima, is probably great. Under warming conditions, physiologically-motivated shifts in distribution and seasonal abundance could result in cascading effects on regional food webs and changes in foraging behaviors. The disappearance of Capelin in the Gulf of Alaska during the temperature regime shift beginning in the mid-1970s was hypothesized to be in response to elevated temperatures (Anderson and Piatt, 1999; National Research Council, 1996). Generally, other marine species evaluated by Hollowed and others (2013) that are already occurring in the northern Bering Sea or southern Chukchi Sea (with the possible exception of Pacific Cod because of the species fidelity to spawning areas in the Bering Sea) increased abundances of species in the Chukchi Sea and further expansions onto the Beaufort Sea shelf and slope are considered a highly probable response to climate change.

Effects on Salmon Colonization

Pink and Chum Salmon are the most commonly reported species in the Alaska Arctic north of Point Hope (Nielsen and others, 2012). Small commercial fisheries operate in Kotzebue Sound and subsistence fishing occurs farther north. Small numbers of spawning Chum and Pink Salmon have been observed in rivers as far east as Prudhoe Bay in the southeastern Beaufort Sea (Craig and Haldorson, 1986). Whether the spawning observations to the north of Point Hope represented putative populations or straying continues to be unclear. Lack of suitable spawning habitats and extremely cold temperatures have been cited as reasons why this salmon straying has not led to sustainable populations (Irvine and others, 2009; Nielsen and others, 2012). However, each year increasing numbers of Chinook Salmon are being captured at Point Barrow and other sites along the coast. Over the next 30 years, as thermal barriers to migration and successful reproduction break down and, as freshwater, coastal, and marine habitats improve for salmon (for example, extended growing seasons, increased productivity, and other improvements) range expansions for chum, pink, and Chinook Salmon in Alaskan Arctic rivers seems certain. The successful colonization of these habitats by salmon is more difficult to estimate (Nielsen and others, 2012).

Salmon Disease Ecology

Ichthyophonus in adult Chinook Salmon in the Yukon River has been linked to global warming and, because it is prevalent in marine fishes elsewhere in the northeast Pacific (for example, Pacific Halibut in the Gulf of Alaska), represents a potential threat to Arctic marine fishes (James Winton, U.S. Geological Survey, oral commun., 2013). Other diseases of fish, notably viruses of the Rhadoviridae family (for example, viral hemorrhagic septicemia and infectious hematopoietic necrosis virus) would be novel pathogens in the Arctic marine fauna and potentially threaten members of the Salmonidae. Some ways that global warming can affect the severity and distribution of infectious diseases of fish include changes in the growth rate of pathogens, the types or strains of pathogens present, the distribution or biological carriers and reservoirs, the density or distribution of susceptible species, the diets that can alter resistance to disease, and the physical habitat that can affect disease ecology (Woodson and others, 2011). Although disease information is generally lacking, the anticipated effects of climate change, especially global warming, on fish diseases will include warmer temperatures and, in freshwater, lower flows that will exacerbate diseases caused by endemic parasites and pathogens, increase growth rates of pathogens, favor pathogens or strains that replicate at higher temperatures, and alter the strength and speed of host immune response disease (Hershberger and others, 2013). Additionally, altered freshwater and ocean conditions could change the distribution or density of hosts as well as the overlap with vectors, carriers, or reservoirs of infection. These altered habitats can produce biotic and abiotic stressors that will decrease the resistance to disease, and finally, a greater disease burden and associated fitness losses will increase the disease component of natural mortality among populations of fish.

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Summary

Historical biogeography objectives of this synthesis describe the probable origins of distributional patterns as determined from systematic studies. The description of origins is complicated and largely hypothetical because the paleoceanographic record is not well-developed from the U.S. Arctic. Despite this, species origins were examined in light of possible dispersal and vicariance events as suggested by paleontologic and geologic records, climatic histories, and known phylogenetic relations. Information is limited, but when the known histories are compared with the phylogenetic record, preliminary results suggest that most marine fish species currently in the U.S. Chukchi and Beaufort Seas evolved from a Pacific ancestor. Ecological biogeography objectives addressed the environmental relations including physiochemical factors (for example, temperature, salinity, dissolved oxygen, and turbidity), mechanisms (currents, migrations, and movements), and biological processes (competition, predation, colonization, and reproduction) that limit the distribution, relative abundance, and productivity of a species. Global warming effects on this part of the Arctic are occurring at twice the rate of change in lower latitudes. Changes in regional sea ice coverage, physical and chemical oceanography, and hydrology are expected to have profound effects on coastal and marine ecosystems. Northerly shifts in the distributions of many migratory marine fishes, such as Pacific salmon, are expected with physical changes in temperature and process changes associated with benthic-pelagic coupling over shelf waters.

Chapter 5. Arctic Climate Change—A Tale of Two Cods

By Deborah A. Reusser¹, Melanie L. Frazier², Rebecca A. Loiselle¹, Henry Lee II², and Lyman K. Thorsteinson¹

Abstract

Climate effects on the ecology of the Arctic marine environments are of local, regional, national, and circumpolar interest and concern. Habitats are changing at the species level and there will be winners and losers with population limiting factors and the related temperature effects. In this chapter, the potential effects of warming temperatures on Arctic Cod and Saffron Cod in the eastern Bering Sea are evaluated. A Bering Sea study area was selected because, in contrast to the Chukchi and Beaufort Seas, a large volume of long-term fishery data was available for 1982–2006. A generalized additive modeling (GAM) approach was used to explore the effects of depth, bottom temperature, and surface temperature on the distribution and abundance of the cod species as well as each species' response to warming conditions. The GAMs estimate significant contraction and expansion in the marine distributions and abundances of Arctic Cod and Saffron Cod, respectfully, as simulated bottom temperatures increase in 0.2 °C increments over shelf and slope habitats to a maximum of 2 °C. In the vernacular of “winners and losers,” the GAMs suggest that Saffron Cod will be a winner and Arctic Cod a loser in warming habitat conditions. The model simulation results were examined with respect to their application to species interactions and other ecosystem functions in the Chukchi and Beaufort Seas where each cod is more abundant and of greater ecological importance.

Introduction

Global climate change is an increasingly important ecological driver for oceanic and nearshore ecosystems, potentially affecting economically important fisheries stocks and ecosystem structure and function. Arctic systems are estimated to be especially vulnerable because of projected air and sea temperature increases (Anisimov and others, 2007). Summer sea ice extent in the Arctic has been decreasing at a rapid rate with some estimations indicating it will completely

disappear by 2050 (Wang and Overland, 2009; Overland and Wang, 2013). Additionally, Arctic systems are changing almost twice as fast as anywhere on Earth from warming temperatures and melting ice (National Aeronautics and Space Administration, 2012); United Nations Environment Programme, 2013). Climate conditions in the eastern Bering Sea (EBS) have been highly variable over recent decades (Mueter and Litzow, 2008). In the EBS, winter sea-ice cover is the dominant factor creating a cold pool where bottom temperatures persist through the summer at less than 2 °C (Litzow, 2007; Stabeno and others, 2012b). Since 1954, this sea-ice cover in the EBS has decreased significantly coincident with an increase in summer bottom temperatures (Mueter and Litzow, 2008). The southernmost edge of the cold pool in the EBS has shifted about 230 km northward since 1982 (Litzow, 2007). Benthic community shifts in the center of distributions northward also have been associated with these changing climate conditions in the EBS (Mueter and Litzow, 2008).

A major challenge becomes how to estimate the effects of these climate alterations on Arctic biota. Given the complexity of projecting future effects, numerous approaches are being used in terrestrial and aquatic environments. These approaches range from laboratory tolerance experiments (Wernberg and others, 2012) to trait-based analyses (for example, Moyle and others, 2013; Lee and others, U.S. Environmental Protection Agency, written commun., 2014) to more mechanistically based food webs (for example, Aydin and others, 2007) and individual-based models (Chang and others, 2010). Each approach has strengths and limitations, as well as drastically different data requirements.

This chapter resulted from cooperative research between the U.S. Geological Survey and U.S. Environmental Protection Agency focusing on potential climate effects on Arctic Cod and common interests in the species because of its human and ecological values. The research was implemented as a demonstration project to feature the application of a modeling approach to assess distributional shifts in important fish populations in response to potential climate change effects in the northern Bering Sea.

¹U.S. Geological Survey.

²U.S. Environmental Protection Agency.

Species Distribution Models

One approach that has gained considerable attention in projecting species responses to climate change is the use of statistically based species distribution models (SDMs, also known as niche or bioclimatic envelope models [Olden and others, 2008; Elith and Leathwick, 2009]). These models establish statistical relations between a species' extant distribution and (or) abundance and a corresponding suite of environmental factors. This relation then can be used to project species' responses to climate-induced environmental changes. A major advantage of SDMs is that they can use data from existing field surveys. Additionally, as pointed out by Heikkinen and others (2006), they are a "particularly valuable" tool for providing insights into effects of climate warming for species where the range-limiting physiological factors are poorly known. However, SDMs have a number of limitations (Heikkinen and others, 2006; Robinson and others, 2011). They require a moderately large dataset, and if effects of warming temperatures in northern latitudes are being investigated, it is important that the dataset include the southern range of the species. If abundance is being modeled, directly comparable sampling techniques are also essential. One concern of many ecologists is that most SDMs do not incorporate life history attributes or biological interactions and, accordingly, the simulated responses may not result from the direct effects of the environmental factors in the model, but rather result from indirect effects on productivity, predator-prey interactions, or other biotic interactions. Given this final limitation, it is perhaps best to view SDMs as statistical "idiot savants" and interpret the results through an ecological lens.

Species Selection and Climate Change

With these caveats in mind, SDMs were generated for two Arctic fish, Arctic Cod (*Boreogadus saida*) and Saffron Cod (*Eleginus gracilis*) in the EBS using sea bottom temperature, sea surface temperature, and bottom depths as key environmental drivers. The Arctic Cod and Saffron Cod were selected as target species, partly because of their importance to higher trophic levels and because they have different biogeographic distributions; therefore, they potentially display different responses to climate warming. After the models were generated, various climate change scenarios were applied to explore how increases in temperature are likely to alter their distributions and abundances in the EBS. Besides projecting potential changes in the EBS, changes that occur in the EBS are likely to be an early harbinger of changes in more northerly environments especially as they pertain to the potential for expanding commercial fisheries. To generate these models, the extensive bottom-trawl survey data from the National Oceanic and Atmospheric Administration (NOAA) Resource Assessment and Conservation Engineering (RACE) Division program (National Oceanic and Atmospheric Administration, 2013)

were used. The RACE surveys in the EBS, Aleutian Islands (AI), and Gulf of Alaska (GOA) over the past three decades provide a large sample set for modeling and meet the criteria of having data from the southern part of the range for Arctic Cod and Saffron Cod. The circumpolar distribution of Arctic Cod and its intermediate position and importance in regional food webs makes this species a strong candidate as an indicator of environmental change and, in this regard, its interactions with congeners are of special interest.

Life History Considerations

The geographic range of Arctic Cod is circumpolar including the Chukchi Sea southward into the EBS. They are found from the surface to 1,390 m deep, although they were only captured from 30–150 m in the NOAA RACE surveys. Adaptations, such as anti-freeze proteins, allow this species to live in very cold waters and to use sea ice habitats to hide from predators, spawn, and forage for food. Spawning occurs in the late autumn–early winter. Eggs and larvae are pelagic, and larvae generally hatch in spring. Young Arctic Cod mostly feed on plankton in the upper water column, graduating to a diet of marine worms, adult copepods, and shrimps. Adult Arctic Cod grow to a maximum of 46 cm (Wienerroither and others, 2011) with an average length about 25 cm (Cohen and others, 1990) and are critical to marine food webs, providing food for other fishes such as Dolly Varden (*Salvelinus malma*), seabirds, and marine mammals. Although Arctic Cod are not fished commercially in North America, they are harvested in Russia and are considered an excellent table fish (Hebert and Wearing-Wilde, 2002).

Saffron Cod also are in Arctic and subarctic seas and, off Alaska coasts, have been sampled as far south as the GOA. They typically are in nearshore waters less than 50 m deep. Physiological adaptations such as the antifreeze proteins in Arctic Cod also allow this species to survive in cold waters. In winter, they live under the ice in nearshore habitats and probably move slightly offshore in summer. Saffron Cod grow to a maximum length of 55 cm, live much longer, and are more likely to spawn on multiple occasions than Arctic Cod. Spawning occurs in winter and eggs are demersal. In early spring, eggs hatch and pelagic larvae are transported beneath the ice into tidally influenced bays/inlets of 2–10 m depths. Saffron Cod are epibenthic feeders and juveniles may associate with jellyfish. Like Arctic Cod, Saffron Cod are important in nearshore food webs and are consumed by other marine fishes, birds, and mammals. They are seasonally important in some coastal subsistence fisheries.

Species Interactions

Interactions between adult Arctic Cod and Saffron Cod, such as competition and predation, are not well known even though each species niche is similar with respect to trophic level and position (chapters 2 and 4). Neither species is

especially abundant in the EBS especially when compared to other cod and flatfish species. Under current environmental conditions, therefore, the existing information would at least tentatively indicate reduced competition between the species including limited predation by one species on the other. How differences in spawning season affect interspecific competition and predation are not known, nor are effects of cannibalism (an intraspecific interaction common in gadids) on population dynamics. The differences in vertical distribution and the apparent absence of biotic interactions are significant with respect to climate change modeling. If interactions exist, they could reduce the accuracy of model simulations.

Methods

Data Source

Data were obtained from the NOAA Alaska Fisheries Science Center's RACE Division (<http://www.afsc.noaa.gov/RACE/groundfish/default.php>). The RACE resource assessment program was implemented in 1971 to monitor the condition of demersal fish and crab stocks on shelf regions off the coast of Alaska. This historical dataset for the Pacific Ocean and EBS includes trawl sampling by NOAA within the

benthic zone of the United States continental shelf and slope areas of the U.S. Exclusive Economic Zone.

The distribution of NOAA sampling varies by region and year, but fish monitoring protocols are consistent across the regions (Stauffer, 2004). In the EBS region, monitoring sites are located in the center of a regional grid of evenly distributed cells (37×37 km cells), with occasional samples collected at other sites in support of other research and management needs (fig. 5.1). In the EBS, monitoring stations were typically sampled every year (1982–2006), although Norton Sound in the northern Bering Sea was sampled only in 1985 and 1991.

For the AI and GOA regions, sampling stations were randomly selected from within grid cells (fig. 5.1) that were identified through management and ecological strata allocations. Sampling was biennial and took place between 1984 and 2006 in AI and 1983 and 2007 in GOA.

For the NOAA monitoring, physical attributes of each station were measured at the same time as all biological sampling and included bottom depth, bottom-water temperature, surface-water temperature, species composition, weight (all species), and number (fish only). Latitudes and longitudes at the start of the haul were used to describe sampling station locations. Only trawls with good performance (catch > 0) were included in analyses (Stauffer, 2004).

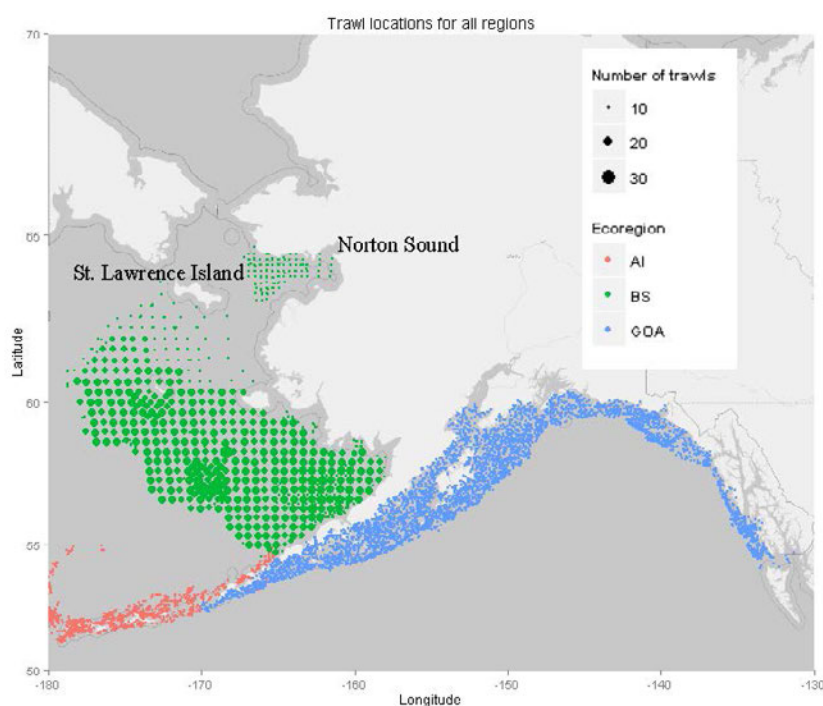


Figure 5.1. NOAA fishery-resource-assessment survey areas in the Eastern Bering Sea, Aleutian Islands, and Gulf of Alaska from NOAA RACE data collected between 1981 and 2006.

Trawls with haul depths inconsistent with reported station depths were excluded from analyses ($n=6$). Fish abundance is expressed in terms of catch (C in total numbers of individuals caught per station), relative abundance (numbers per kilometer), and density (numbers per kilometer and kilograms per hectare) in the RACE database. Initial examination of the trawl data revealed that the distributions of Arctic Cod and Saffron Cod were almost exclusively in the EBS (table 5.1). Therefore, species models were developed using only EBS station data (fig. 5.1).

Statistical and Modeling Approaches

Frequency histograms of bottom depths, bottom temperatures, and surface temperatures were created from data collected at all stations sampled in the EBS, AI, and GOA. The histograms were compared to similar summaries from all stations where Arctic Cod and Saffron Cod were collected, to describe the niche spaces sampled for each environmental variable. The initial histograms including data from all survey stations sampled compared with similar presentations for each species, allowed comparisons of the total marine environmental space sampled and the niche space of each species. Generalized additive models (GAMs) were used to more rigorously quantify the effects of depth and temperature on cod occurrences (presence/absence) and abundances. GAMs are smoothing models used to fit non-linear data using thin plate regression splines. All analyses were done in R 2.15.1 (R Core Team, 2012). The mixed GAM computation vehicle (*mgcv*) 1.7-18 package was used for the GAM analyses (Wood, 2003; 2006; 2011). A simultaneous confidence interval of 95 percent was used to delimit the credible regions (Wood, 2006) of each species simulated response to depth and temperature variables.

Only data collected from the EBS were used in the GAMs because Arctic Cod and Saffron Cod were rarely sampled in AI and GOA resource assessment areas. The observed effects of bottom temperatures ($^{\circ}\text{C}$), surface temperatures ($^{\circ}\text{C}$), bottom depths (m), and their interactions on abundance (C) as $[\ln(\text{abundance} + 1)]$ and distribution (presence/absence frequency of occurrence) were evaluated in the GAMs. Restricted maximum likelihood techniques were used to determine optimal smoothing functions in the regression analyses. The binomial family was used to estimate occurrence by depth and temperature relations. To select the best predictive model, we compared candidate GAM models with combinations of the three environmental variables including model runs with only one or two variables. Different smoothing functions also were evaluated. The best model for

each fish species (occurrence and abundance) was selected from the candidate models using Akaike Information Criterion (AIC; Akaike, 1973). In addition to AIC, environmental-response curves were developed to select among models with similar AIC scores. Environmental response curves are a way of displaying model simulations. To generate these plots, the model was used to simulate a species probability of occurrence or abundance in relation to a single environmental variable while holding the other environmental variables constant.

Spatial Interpolation of Environmental Data

Data from the World Ocean Database (National Oceanic and Atmospheric Administration, 2009) were downloaded and analyzed to examine the content and structure of bottom and surface temperatures to potentially increase the spatial extent of model simulations. Various interpolation schemes were applied to these data and tested for compatibility with the environmental values in the NOAA RACE data. Paired t-tests indicated that these data were not sufficiently compatible with the NOAA RACE data to expand the spatial extent of model simulations with any reliability; therefore, for this research, model simulations were limited to coverage within a smaller spatial extent that could be reliably interpolated with the NOAA RACE environmental data.

The three environmental variables (bottom depth, bottom temperature, and surface temperature) from the NOAA RACE program were spatially interpolated to create continuous coverage raster grids describing these variables across the EBS. An Inverse Distance Weighted (IDW) interpolation was completed in ArcGIS 10. The physical data for spatial interpolation were collected from a network of circular sample areas (37 km radius) in accordance with a random sampling plan that included greater than or equal to 12 sample points per area. The size of the circular area for spatial data collection was selected to approximate the grid size used in the NOAA RACE fish monitoring design. The resolution of all layers was set to 4.7 km. The data were then clipped to a buffer around the edge of the regular set of sampling stations to reduce extraneous information. The clipped region does not include Norton Sound because this area was sampled only during 2 years and the temperature varied significantly between 1985 and 1991. Consequently, although all EBS trawls were used in model development and analysis, data in Norton Sound were determined to be too sparse to create an interpolated average for each of the environmental surfaces. The clipped region is the spatial extent of estimated distributions and abundances of the cod species.

Simulated Effects of Climate Warming

To compare the accuracy of the model simulations to the measured data, the best GAMs for each fish species were used to simulate cod distributions and abundances based on the spatial interpolations of the environmental data. To evaluate the potential effects of climate change on each species, $+0.2^{\circ}\text{C}$ was incrementally added to every cell of the spatially interpolated bottom-water temperature layer until the total change measured a $+2^{\circ}\text{C}$ increase. Bottom temperature was varied because this variable had the greatest influence on the distributions and abundances of each species in GAMs. At each increment, GAMs were applied to established frequency baselines to predict changes in distributions (probability of occurrence) and abundances [$\ln(\text{abundance} + 1)$] of the Arctic Cod and Saffron Cod. The predicted changes described are for total habitat and estimated numbers of fish. Total probability is calculated as the cumulative sum of individual probabilities of occurrence estimated for each species in all the grid cells in the EBS. Because the GAMs underestimate abundance, the predicted effects of bottom temperatures are best considered as indicators of relative change. The predicted changes also are shown as habitat maps for each species.

Results and Discussion

Catch Characteristics of the RACE Surveys, 1982–2006

Physical and biological data from 18,470 trawl samples from NOAA surveys off Alaska were used to evaluate climate-warming effects on the distribution and abundance of Arctic Cod and Saffron Cod in the EBS. Trawl depths ranged from 0 to 1,000 m with most fish sampling occurring at stations located between 0 and 200 m. Bottom temperatures in the Bering Sea surveys ranged from 2°C to about 14°C with most measurements between 0 and 8°C . Surface temperatures ranged from 0 to 16°C with a few measurements indicating warmer temperatures.

Of the 9,423 trawls completed in the EBS between 1982 and 2006, about 10.5 percent or 901 trawls contained Arctic Cod (table 5.1). Arctic Cod were widely distributed across the shelf and were sampled in Norton Sound and southeast of St. Lawrence Island (fig. 5.2). Highest abundance was associated with the coldest bottom temperatures in northern parts of the study area.

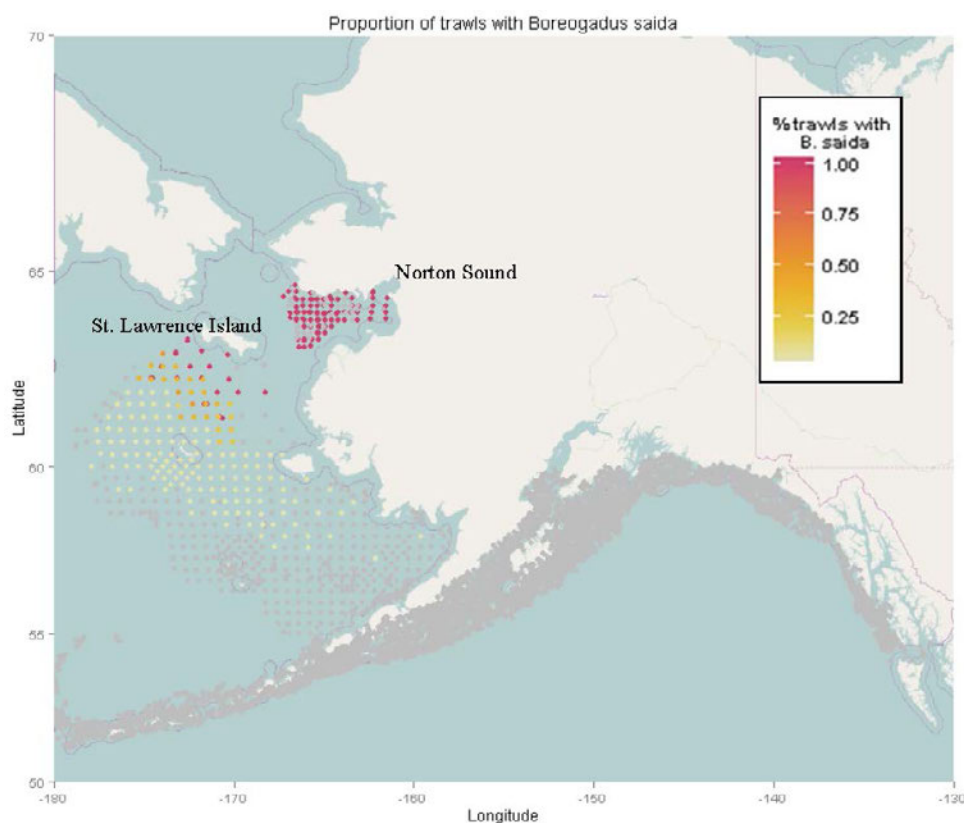


Figure 5.2. Locations where Arctic Cod (*Boreogadus saida*) samples were collected by NOAA in the eastern Bering Sea (source: NOAA RACE database, 1981–2006) (National Oceanic and Atmospheric Administration, 2013). The colors of the dots indicate the percentage of trawls in which Arctic Cod were captured. This analysis of presence-absence is possible because the same station locations are consistently sampled in the NOAA RACE resource assessment surveys. The NOAA RACE database includes samples collected in Norton Sound in 1985 ($n=74$) and 1991 ($n=47$).

In contrast, the highest abundance of Saffron Cod outside of Norton Sound was in Kuskokwim Bay and to the north and west of Nunivak Island (fig. 5.3). Saffron Cod were not collected in samples farther offshore (fig. 5.3). Of the 9,423 trawls completed by NOAA in the EBS, 5.7 percent or 531 trawls contained Saffron Cod (table 5.1). Both cod species were captured together in only about 1 percent or 109 trawls. About 81 percent or 89 of the 109 trawls that captured both cod species was in Norton Sound.

Table 5.1. Number of trawls completed by National Oceanic and Atmospheric Administration’s marine fishery resource assessment completed where Arctic Cod and Saffron Cod were collected in the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska.

Trawls	Eastern Bering Sea	Aleutian Islands	Gulf of Alaska
Total	9,423	3,202	5,845
Arctic Cod	901	0	0
Saffron Cod	531	0	7

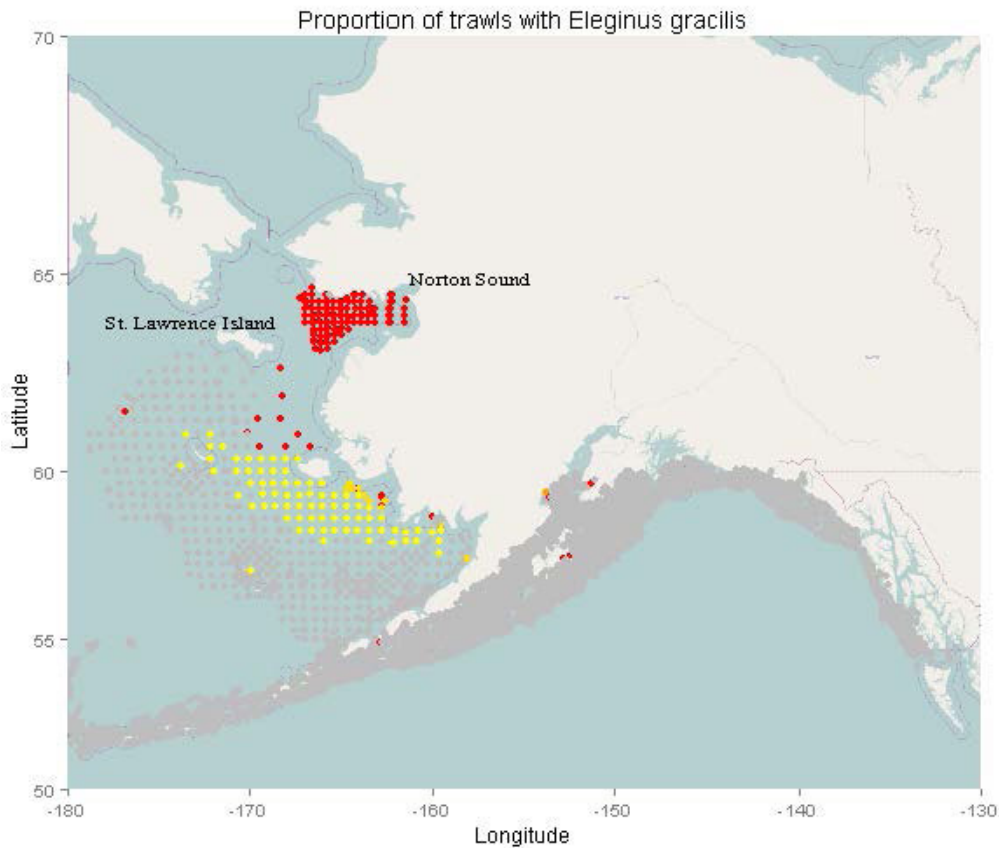


Figure 5.3. Locations where Saffron Cod (*Eleginus gracilis*) samples were collected by NOAA in the eastern Bering Sea (source: NOAA RACE database, 1981–2006) (National Oceanic and Atmospheric Administration, 2013). The colors of the dots indicate the percentage of trawls in which Saffron Cod were captured. This analysis of presence-absence is possible because the same station locations are consistently sampled in the NOAA RACE resource assessment surveys. The NOAA RACE database includes samples collected in Norton Sound in 1985 (n = 74) and 1991 (n = 47).

Environmental Variables and Models

The physical and biological variables reported in the NOAA surveys and used in this study are summarized in [figure 5.4](#). The histograms present frequency data for selected measurements made throughout the three Alaska regions sampled ([figs. 5.4a, d, g](#)) and for capture sites of Arctic Cod ([figs. 5.4b, e, h](#)) and Saffron Cod ([figs. 5.4c, f, i](#)).

The catch data indicate some overlap in species distributions in shallow waters ([figs. 5.4b and c](#)), but distinct differences in their response to bottom temperatures ([figs. 5.4e and f](#)). Arctic Cod were most frequently found at trawl stations having bottom temperatures of less than about 3 °C ([fig. 5.4e](#)) and Saffron Cod were more frequently detected in warmer waters ([fig. 5.4f](#)). These distributional relations were further supported in the GAM analyses ([appendix C](#)). Overall,

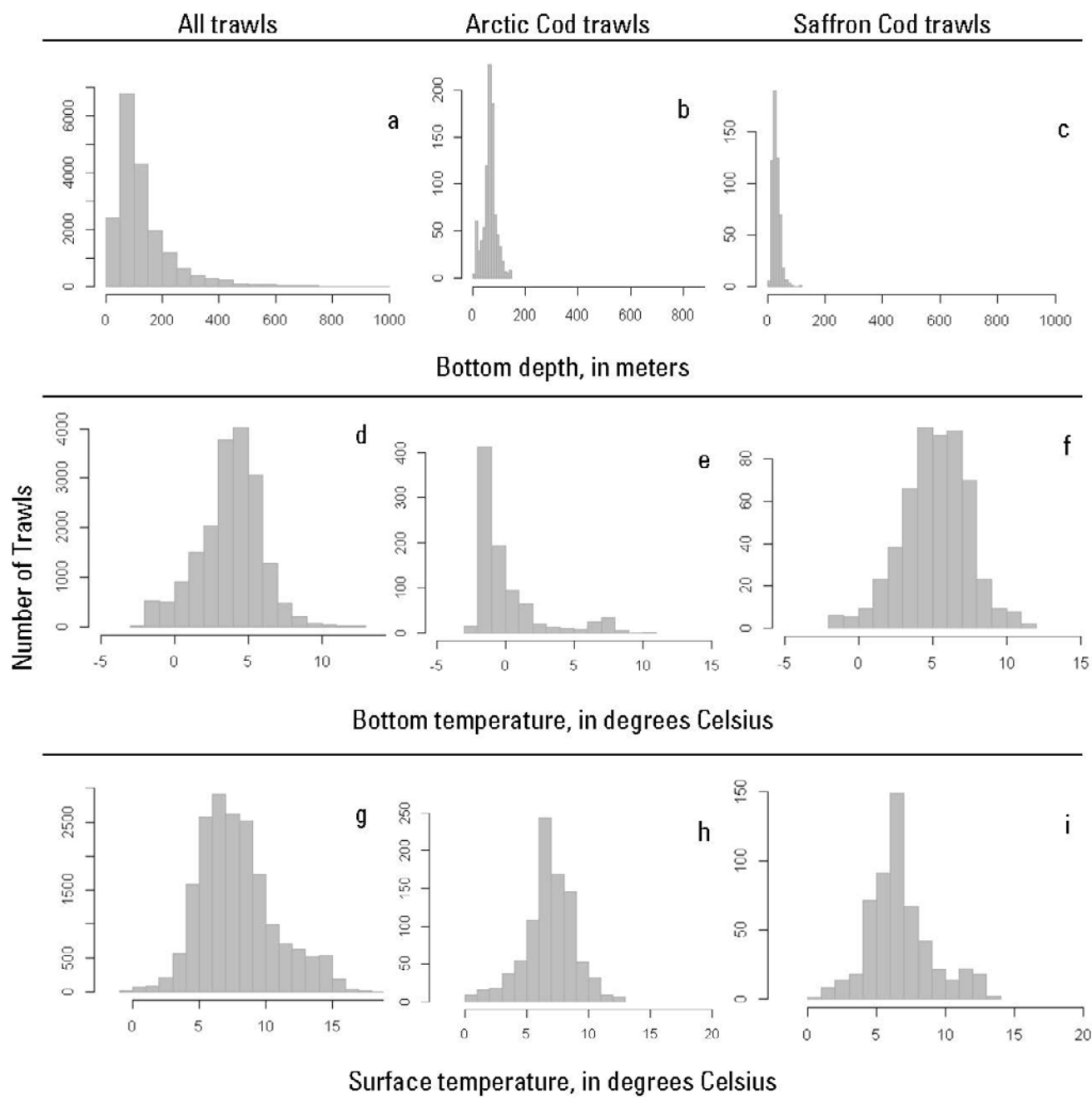


Figure 5.4. Histograms showing bottom depth, bottom temperature, and surface temperature for all trawl samples collected in eastern Bering Sea, Aleutian Islands, and Gulf of Alaska. Trawl samples include 901 Arctic Cod and 538 Saffron Cod. Total samples, 18,470.

the models that performed best (lowest AIC scores) for distribution and abundance of both species contained all three environmental variables. These models are highlighted in the tables included in [appendix C](#). When individual physical variables were modeled as a predictor of abundance in the EBS, bottom temperature was the strongest single predictor with an $r^2 = 0.46$ for Arctic Cod, and $r^2 = 0.35$ for Saffron Cod. In comparison, surface temperature was the weakest single predictor with an $r^2 = 0.006$ and $r^2 = 0.11$ for Arctic Cod and Saffron Cod, respectively.

The southernmost edge of Arctic Cod distribution is coincident with the southern boundary of the cold pool and does not extend beyond the 2 °C isotherm in the EBS. The location of this isotherm and geography of the cold pool varies from year to year ([fig. 5.5](#)). The Arctic Cod distributional pattern relative to the cold pool is consistent with the results of our predictive distribution (occurrence by presence/absence) and abundance modeling ([appendix tables C1, C4, and fig. 5.6](#)), which indicates the species is not likely to occur at locations where bottom temperatures are much warmer than 2 °C ([fig. 5.6c](#)). Catch and model simulations indicate that Arctic Cod are most common on the inner shelf and that their abundance generally decreases from 0 to 200 m, with few fish predicted to occur at depths greater than 200 m ([figs. 5.6a and b](#)). A similar pattern of decreasing abundance with increasing bottom temperatures is evident in [figure 5.6d](#). An interesting exception to this regional pattern occurred in the northern Bering Sea where the model predicted a slight increase in Arctic Cod abundance at bottom temperatures ranging between 2 and 4 °C, declining abundance as temperatures warmed to 7–8 °C, and a return to an increasing abundance pattern at temperatures higher than this. However, the uncertainty (dashed lines in [fig. 5.6d](#))

associated with estimated abundance at bottom temperatures greater than 4 °C is great and these results are questionable. The underlying statistical anomalies supporting abundance patterns in the northern Bering Sea may relate to interannual variations in hydrographic conditions across the northern Bering Sea shelf (Stabeno and others, 2012a; 2012b) and the associated interannual changes in the geographic extent of the cold pool. During warm years, the distribution of Arctic Cod would be geographically constricted in southern parts of its range providing at least a partial explanation for simulated abundance patterns in the northern Bering Sea. Arctic Cod responded to surface temperature with an optimal temperature of about 8 °C; however, this variable was less important than bottom temperature ([figs. 5.6e and f](#)).

The presence/absence model selected to develop environmental response curves for Saffron Cod was not determined to be the best fit as indicated by AIC score, but it seemed to perform better than others based on the environmental response curves ([appendix table C5](#)). The model performed well enough to predict the probability of occurrence ($r^2 = 0.42$), and overall, demonstrated that depth, surface temperature, and bottom temperature are major determinants of this species patterns of distribution and abundance ([fig. 5.7](#)). The model simulation results indicated that Saffron Cod prefer a warm, shallow habitat and that although bottom temperature is not a strong predictor of distribution ([fig. 5.7](#)), it is for abundance ([fig. 5.7d](#)).

The selected models were used to predict the probability of species' distribution and abundance in response to depth and temperature using the inverse distance weighted methods in ArcGIS 10 ([fig. 5.8](#)). The darkest area in [figure 5.8b](#) indicates the location of the cold pool.

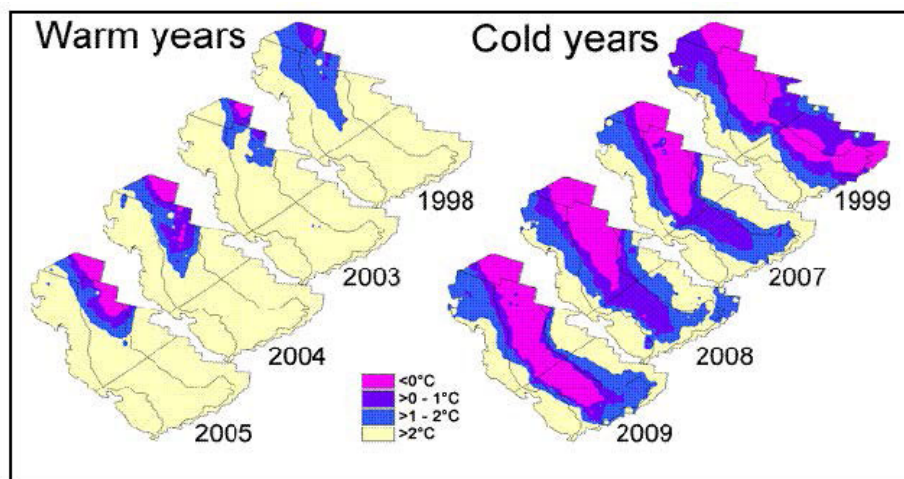


Figure 5.5. Average bottom temperatures from the bottom trawl survey comparing the extent of the cold pool (<2 °C) during years warmer and colder than the 1982–2008 grand mean, eastern Bering Sea shelf (National Oceanic and Atmospheric Administration, 2014).

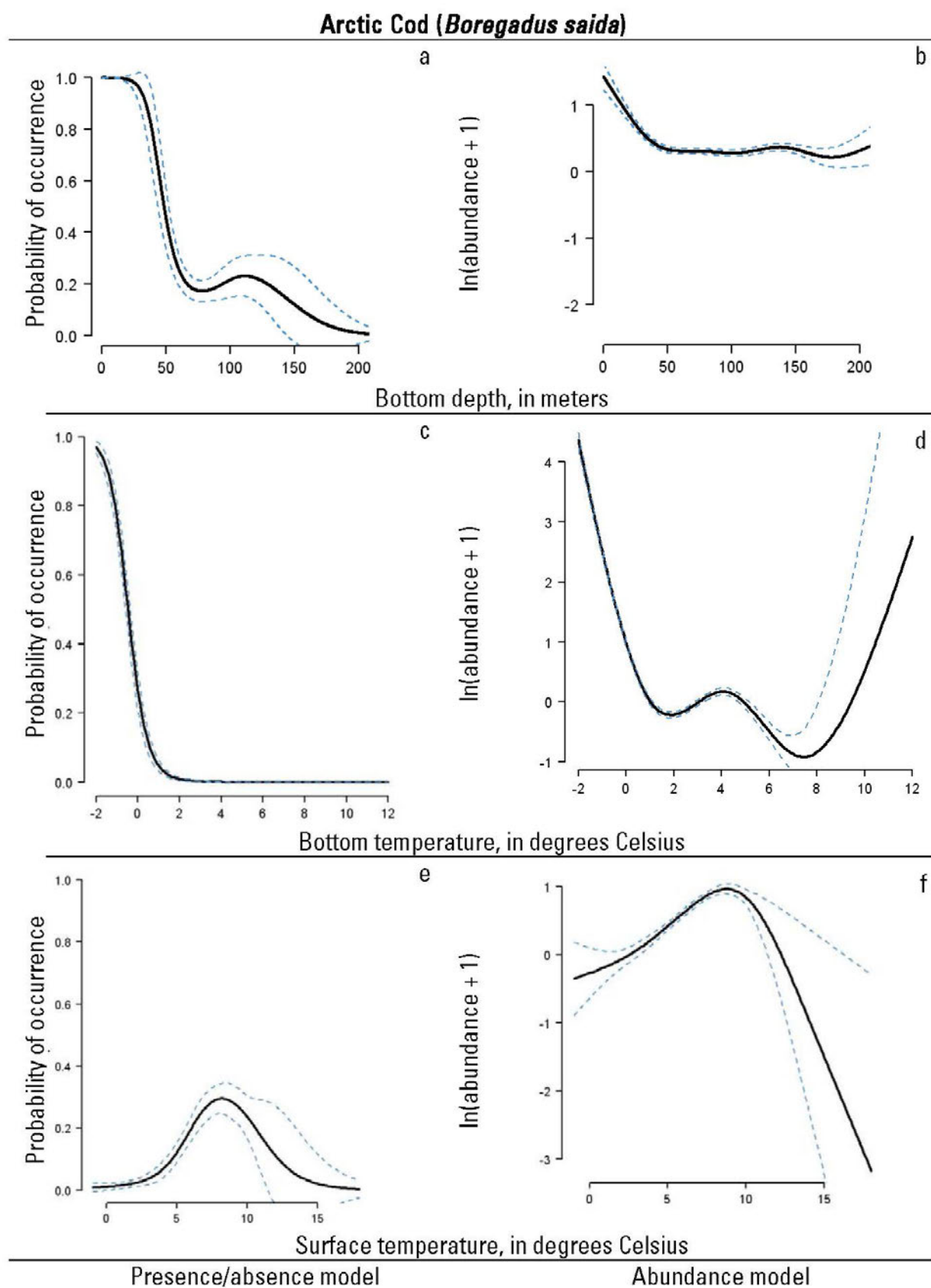


Figure 5.6. Environmental response curves for the selected presence/absence and abundance models for Arctic Cod in the eastern Bering Sea. Solid curves are the function estimates and dashed curves delimit the 95 percent confidence regions for each function.

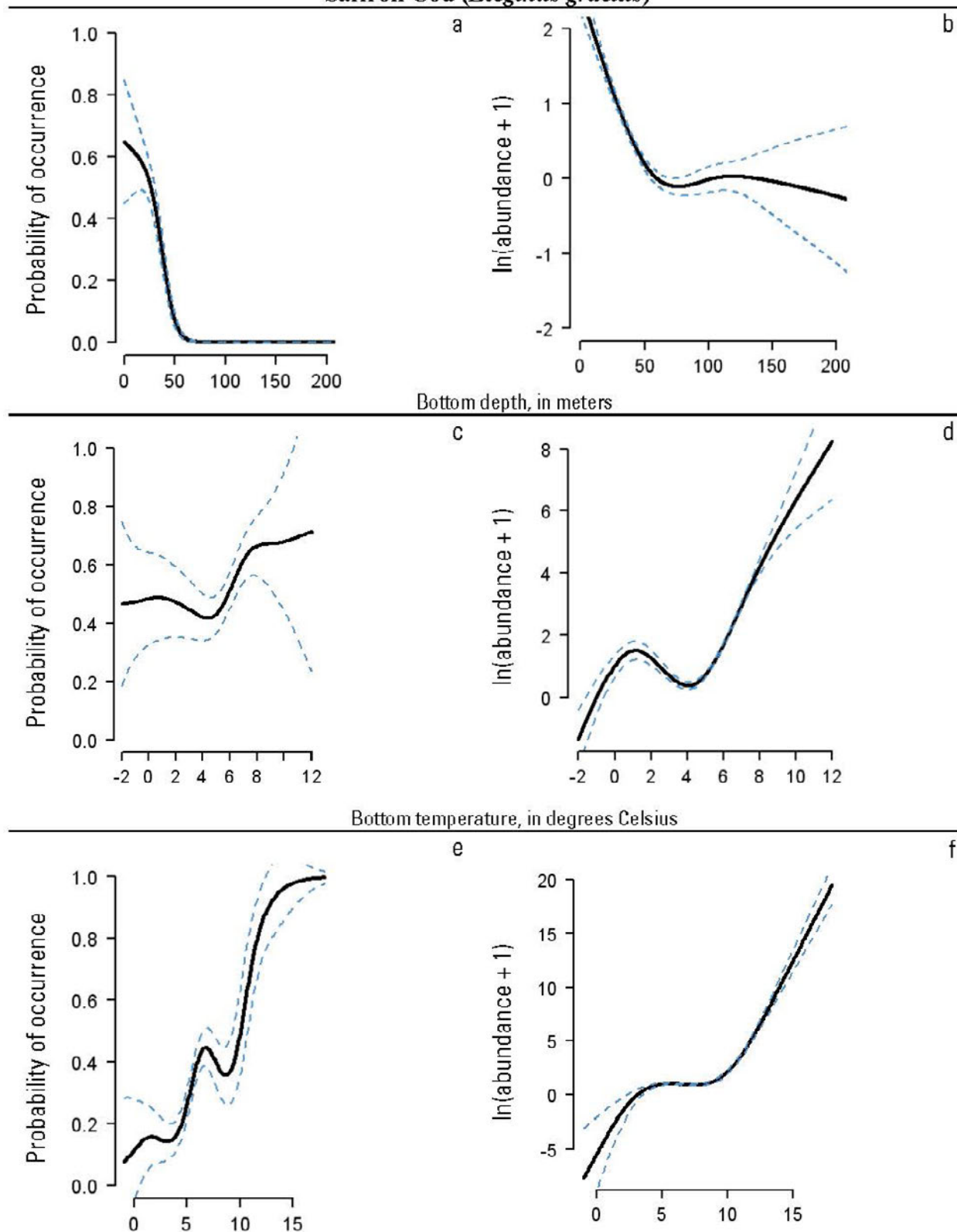
Saffron Cod (*Eleginus gracilis*)

Figure 5.7. Environmental response curves for the selected presence/absence and abundance models for Saffron Cod in the eastern Bering Sea. Solid curves are the function estimates and dashed curves delimit the 95 percent confidence regions for each function.

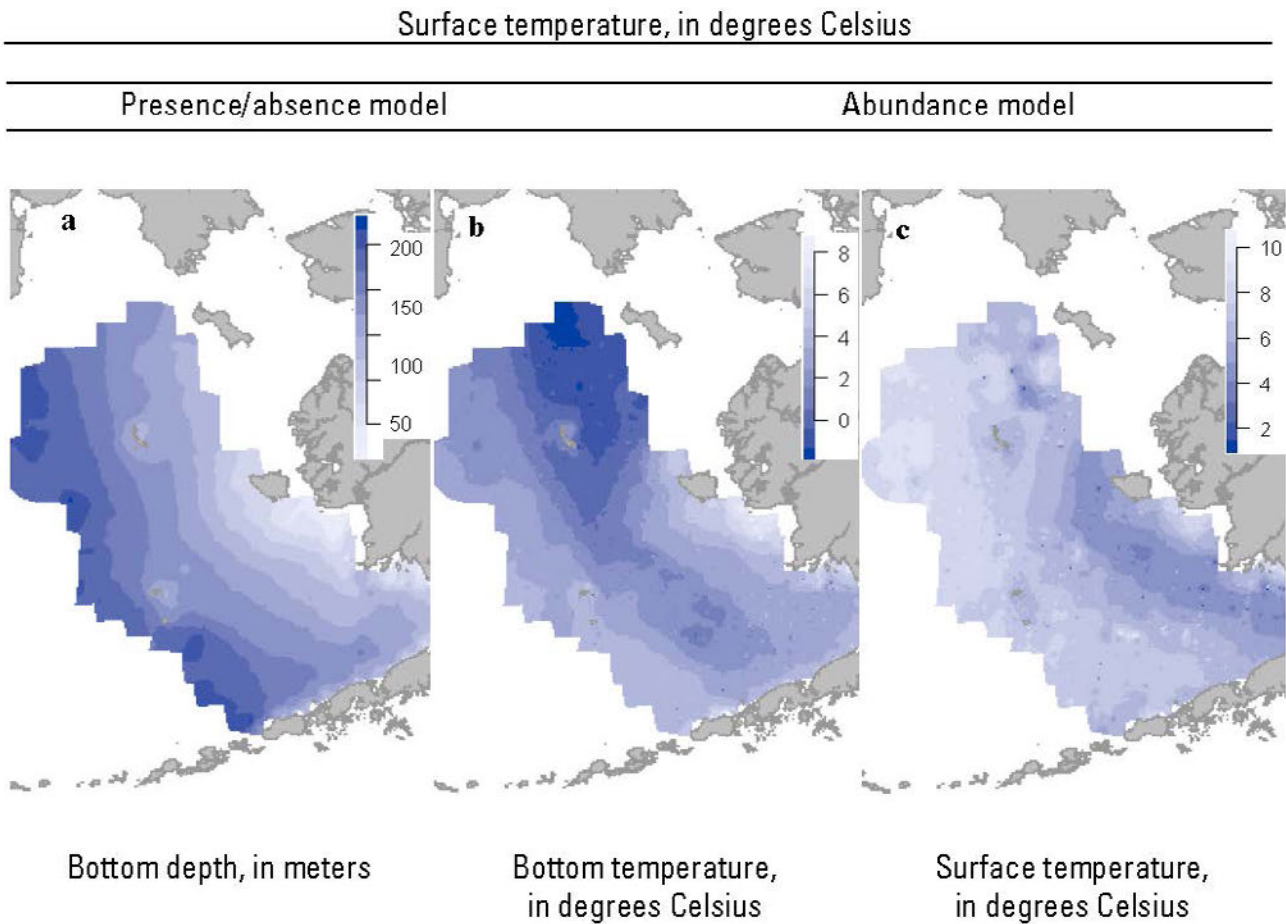


Figure 5.8. Physical description of the marine environment by (a) depth, and mean distributions of (b) bottom temperature, and (c) surface temperatures of the eastern Bering Sea (source: National Oceanic and Atmospheric Administration, 2012). Data from 1982–2006 interpolated using inverse distance weighted methods in ArcGIS 10.

Model performance was evaluated by making comparisons of the observed and simulated patterns of Arctic Cod distribution and abundance over shelf and slope habitats as determined by depth and temperature attributes (fig. 5.9). Generally, the models performed reasonably well with respect to regional spatial patterns although they tended to underestimate the observed distribution and abundance associated with NOAA’s survey data. For example, the distribution of Arctic Cod presented in figure 5.9a closely approximates the model-predicted occurrence in figure 5.8b. The same relation holds true for abundance (figs. 5.9c and d).

The analysis of temperature effects on the distribution (fig. 5.10) and abundance (fig. 5.11, table 5.2) of Arctic Cod shows a gradual reduction in the species range in the EBS with warming bottom temperatures. As bottom temperatures increase, the model also showed how the cold pool contracts northward and predicted that Arctic Cod distributions will similarly shift northward in association with the disappearance of cold water habitats. The main concentration of Arctic Cod to the southwest of St. Lawrence Island almost completely

disappears with an overall increase of 2 °C. There is great uncertainty associated with predictions of increasing abundance in the more southern areas of the species range, which reflects the difficulties of quantitative analysis with sparse datasets due to low detection rates of Arctic Cod in warmer environments.

The GAM models underestimated reported distribution and abundance patterns of Saffron Cod developed from NOAA catch data (fig. 5.12, table 5.3). For instance, the difference between observed and modeled patterns is especially evident in this species distribution in figures 5.12a and b. The reason for the difference may relate to the Saffron Cod’s apparent restricted distribution near the Yukon Kuskokwim Delta and the limited sampling in the RACE surveys in nearshore environments of the inner shelf compared to offshore areas where commercial fisheries occur. The low frequency of Saffron Cod occurrence in trawl catches in deeper and colder parts of the EBS is probably responsible for the model’s performance. It is important to remember that the value of the models is as a tool for simulating relative changes in response to changing environmental conditions (figs. 5.13 and 5.14).

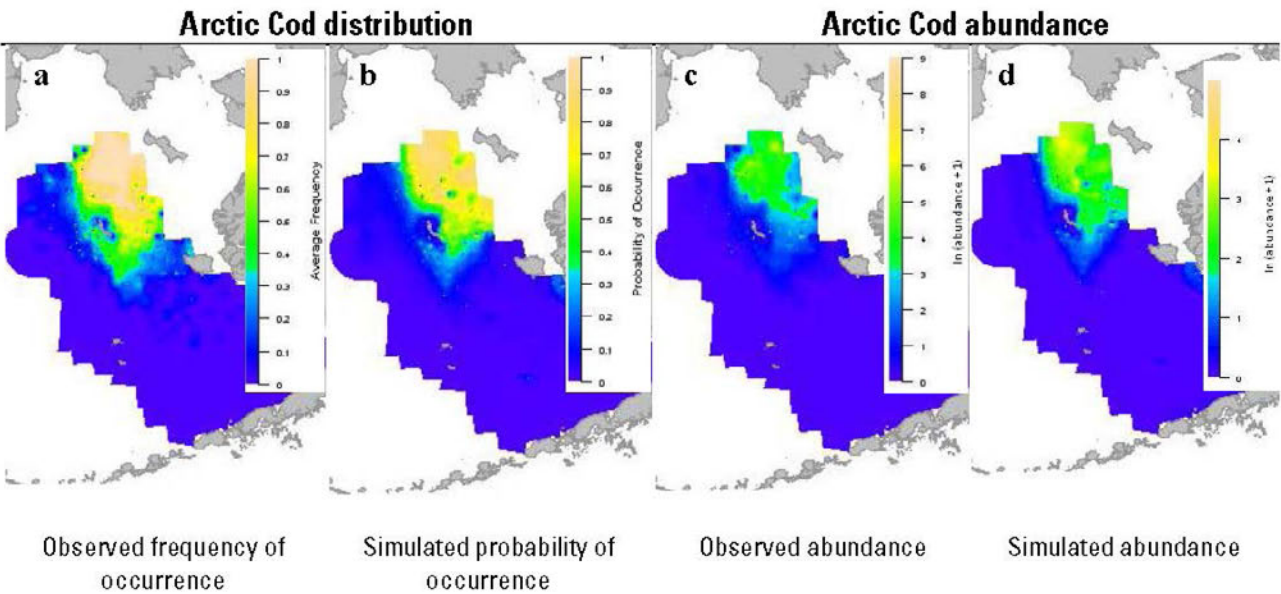


Figure 5.9. Observed and simulated distribution and abundance of Arctic Cod in the eastern Bering Sea (source: National Oceanic and Atmospheric Administration, 2012) . Simulations were generated using best performing Generalized Additive Models and fishery resource data from 1982 to 2006 (see [appendix C](#)).

Table 5.2. Changes in Arctic Cod habitat and relative abundance simulated with incremental warming of bottom temperature (+ 0.2 °C increments) and where surface temperature and depth are constant in the eastern Bering Sea.

[°C, degrees Celsius]

Simulated change in total Arctic Cod habitat			Simulated change in Arctic Cod abundance	
Temperature increase (°C)	Total probability	Total area (percent)	Total abundance (number of fish)	Relative abundance compared to time zero (percent)
Time Zero	3,274	12.12	39,416	100
0.2	2,825	10.45	27,884	71
0.4	2,397	8.87	19,950	51
0.6	2,002	7.41	14,525	37
0.8	1,654	6.12	10,857	28
1.0	1,363	5.05	8,434	21
1.2	1,137	4.21	6,922	18
1.4	974	3.61	6,083	15
1.6	869	3.22	5,757	15
1.8	811	3.00	5,833	15
2.0	790	2.92	6,212	16

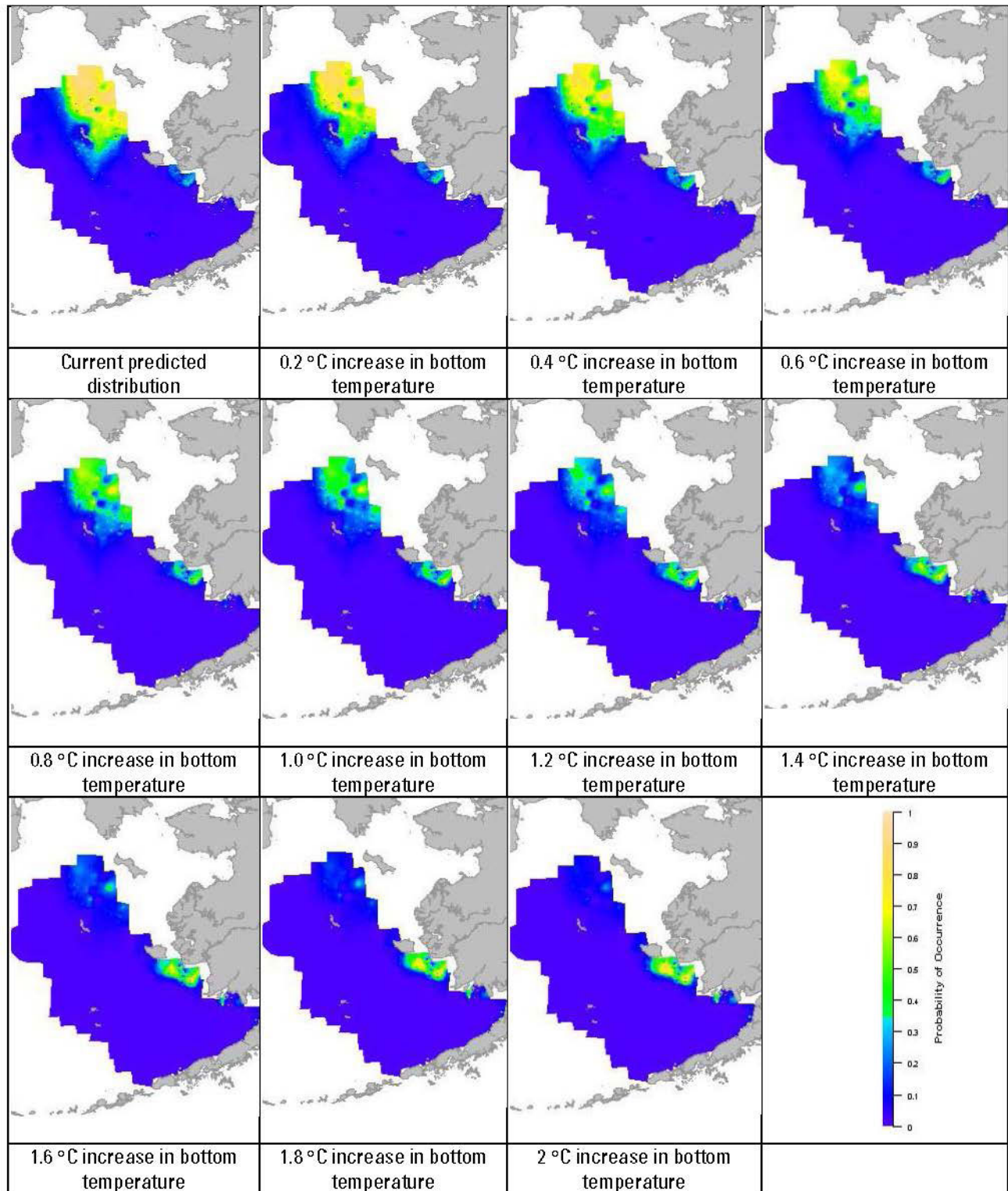


Figure 5.10. Changes in the distribution of Arctic Cod (probability of occurrence) in the eastern Bering Sea as simulated bottom temperatures increase in 0.2 °C increments.

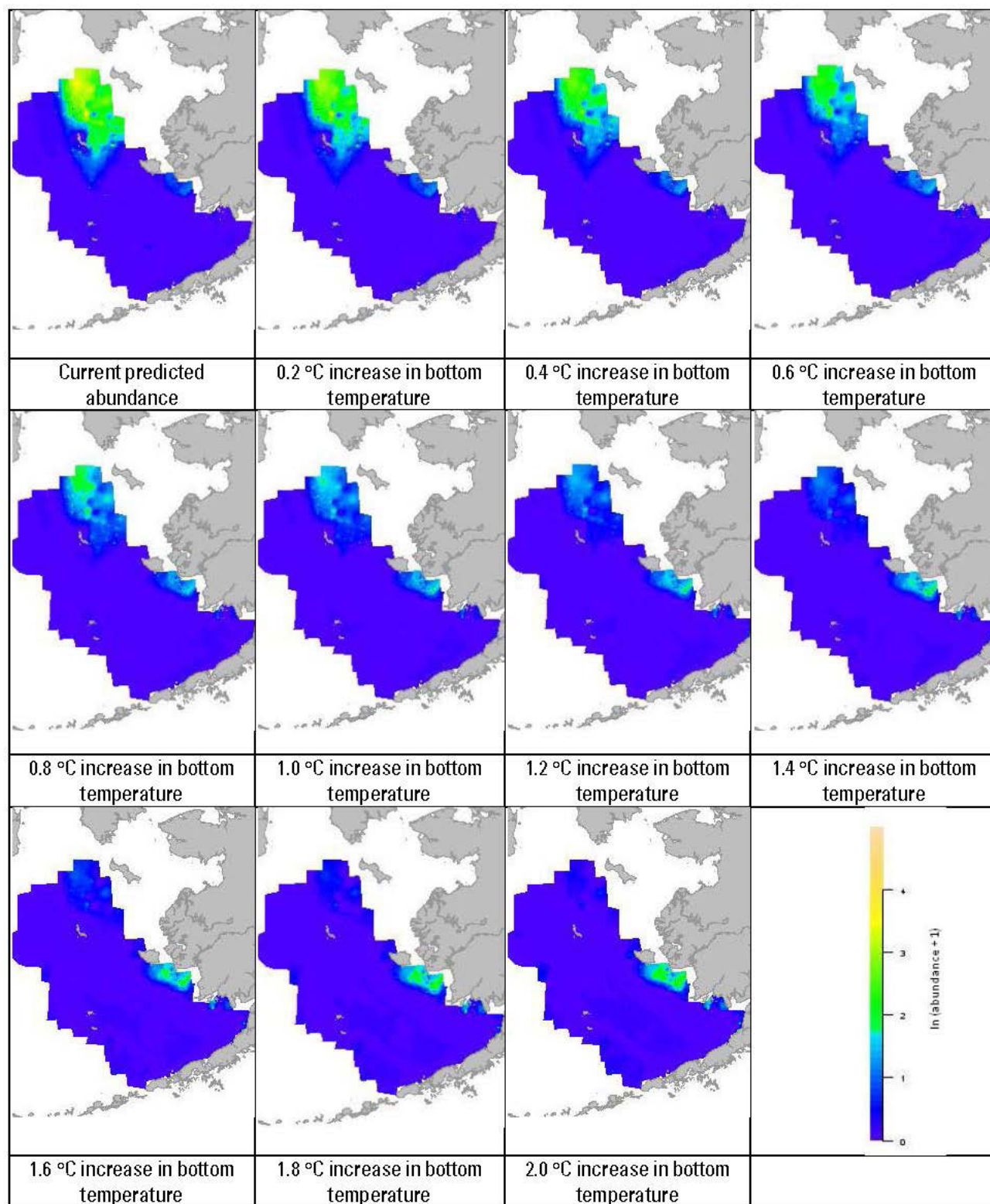


Figure 5.11. Changes in the abundance of Arctic Cod in the eastern Bering Sea as simulated bottom temperatures increase in 0.2 °C increments.

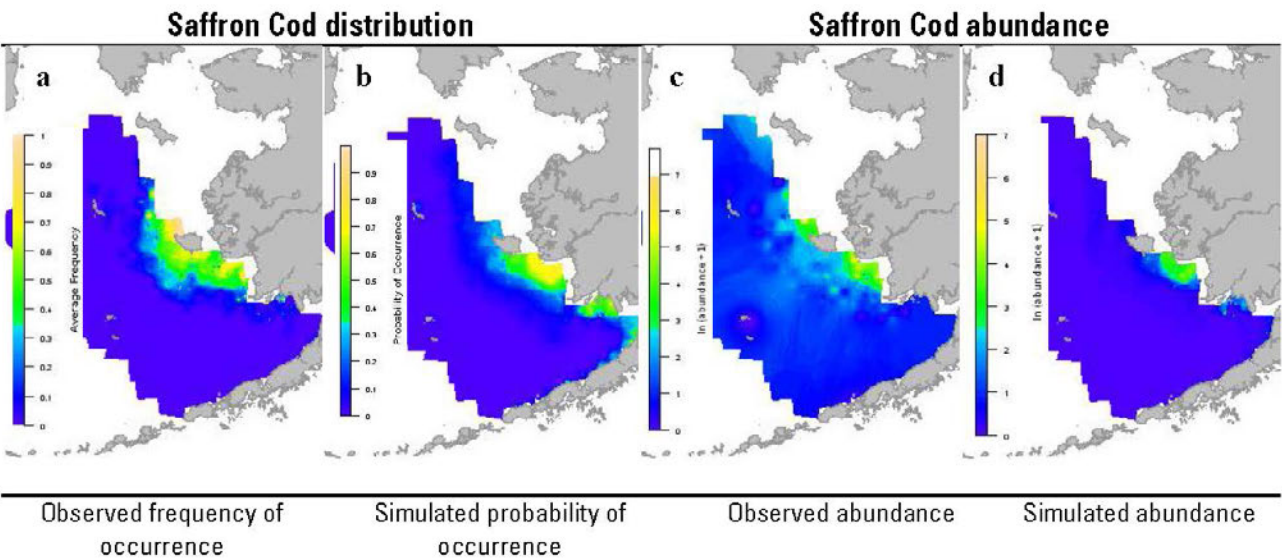


Figure 5.12. Observed and simulated distribution and abundance of Saffron Cod in the eastern Bering Sea (source: National Oceanic and Atmospheric Administration, 2012; fishery resource data from 1982–2006). Simulations were generated using best performing GAM models (see [appendix C](#)).

Table 5.3. Changes in Saffron Cod habitat and relative abundance simulated with incremental warming of bottom temperature (+0.2 °C increments) and where surface temperature and depth are constant in the eastern Bering Sea.

[°C, degrees Celsius]

Simulated change in total Saffron Cod habitat			Simulated change in Saffron Cod abundance	
Temperature increase (°C)	Total probability	Total area (percent)	Total abundance (number of fish)	Relative abundance compared to time zero (percent)
Time Zero	1,487	2.83	14,139	100
0.2	1,499	3.08	18,493	131
0.4	1,516	3.29	24,362	172
0.6	1,537	3.49	32,216	228
0.8	1,562	3.69	42,649	302
1.0	1,593	3.89	56,400	399
1.2	1,628	4.08	74,371	526
1.4	1,667	4.26	97,638	691
1.6	1,710	4.48	127,454	901
1.8	1,757	4.74	165,274	1,169
2.0	1,806	3.92	212,793	1,505

The models for Saffron Cod and Arctic Cod predict increases in the range and abundance in and around Kuskokwim Bay as bottom temperatures increase. This is probably a modeling artifact for Arctic Cod but not for Saffron Cod. The model simulation results shown in [figures 5.12](#) and [5.13](#) suggest that habitats more suitable for Saffron Cod than for Arctic Cod would be created with warming bottom temperatures. The models predicted an increase in Saffron

Cod distribution to the north, south, and offshore ([fig. 5.12](#)) to and potentially at depths greater than 50 m beyond the outer boundary of the coastal domain described for EBS (Kinder and Schumacher, 1981). Similarly, as bottom temperatures increase, Saffron Cod abundance shows a gradual increase in Kuskokwim Bay northward beyond Nunivak Island, south to Bristol Bay and farther offshore ([fig. 5.13](#)).

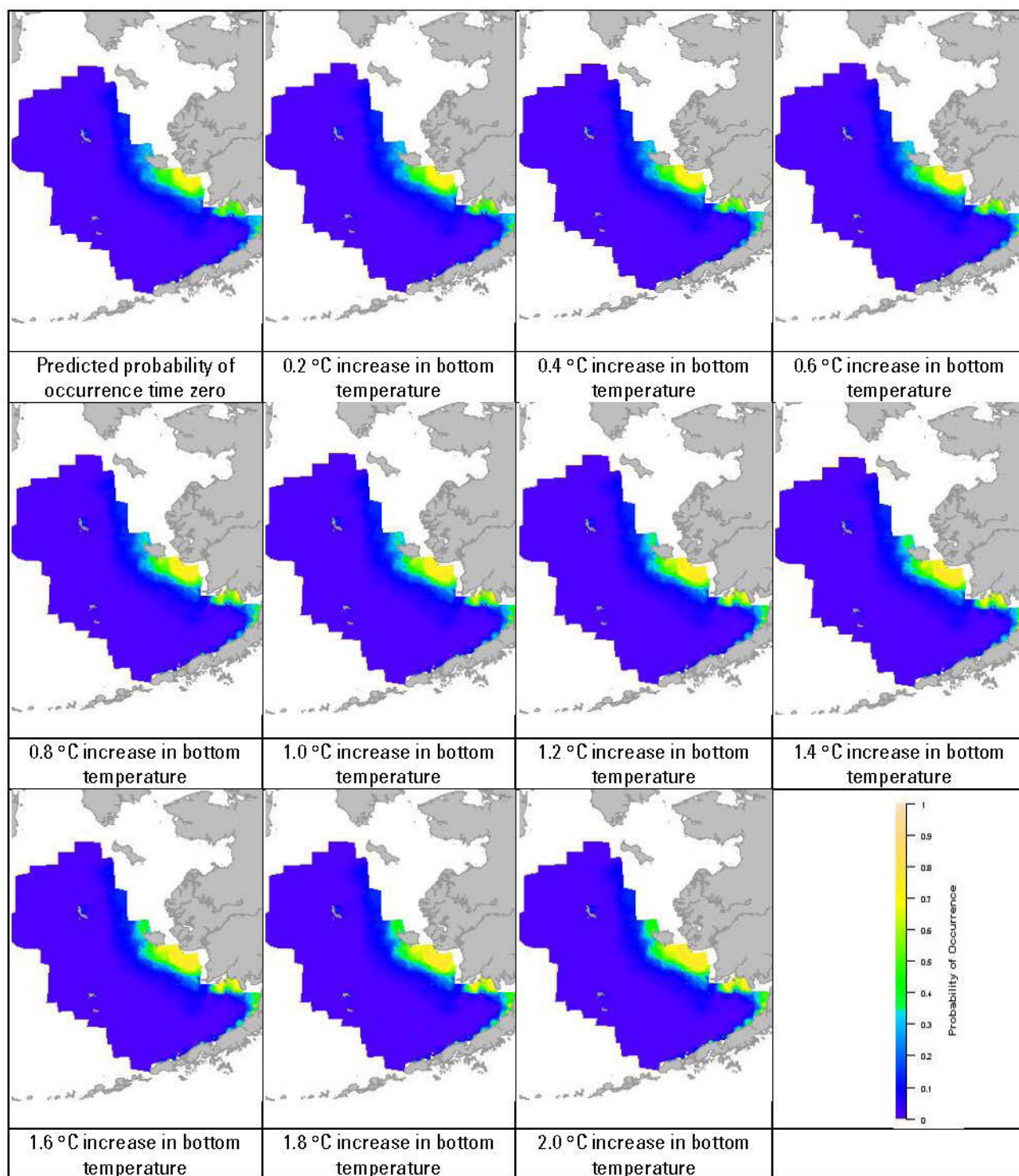


Figure 5.13. Changes in the distribution of Arctic Cod (probability of occurrence) in the eastern Bering Sea simulated as bottom temperatures increase in 0.2 °C increments.

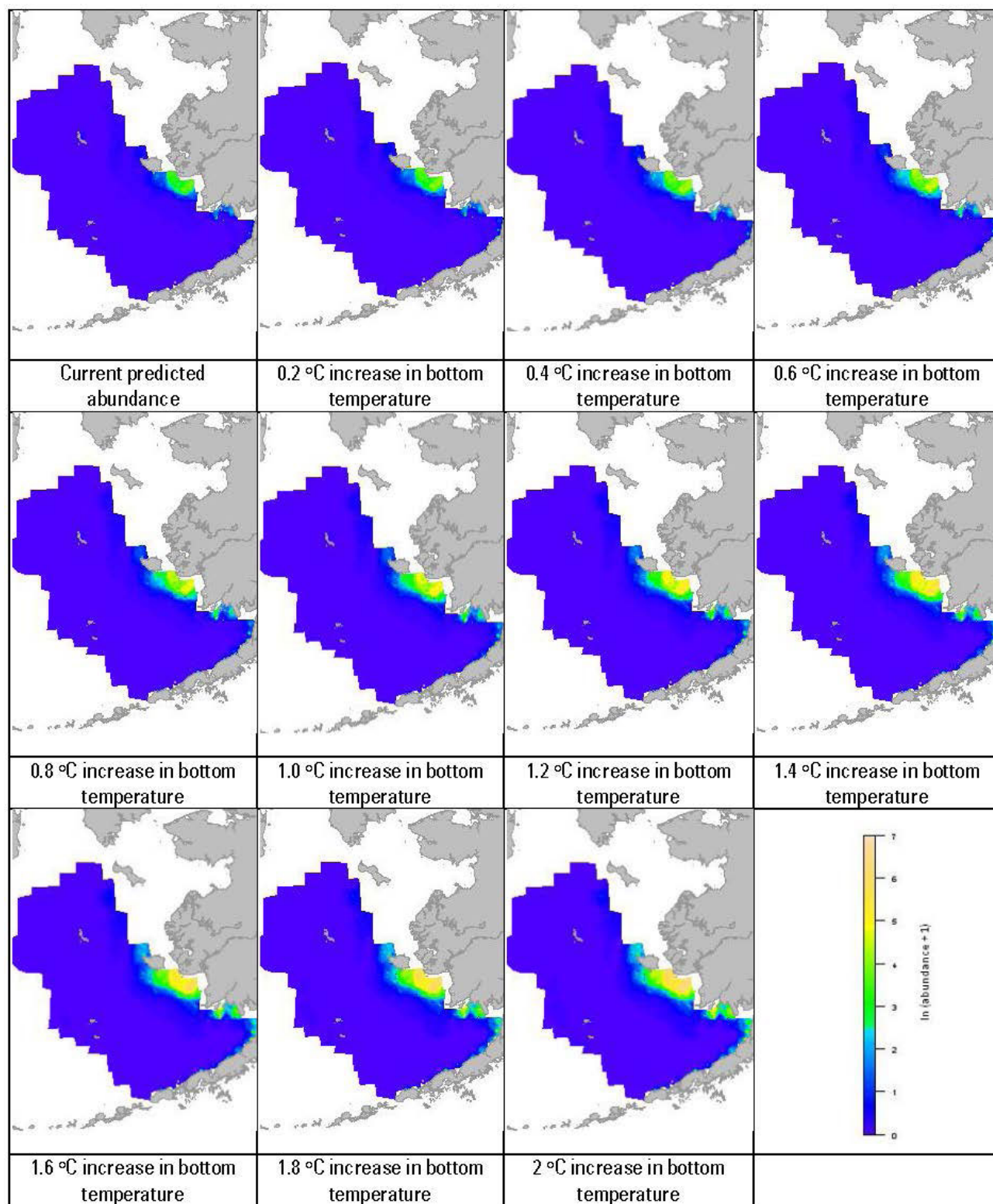


Figure 5.14. Changes in the abundance of Saffron Cod in the eastern Bering Sea simulated as bottom temperatures increase in 0.2 °C increments.

Norton Sound

The NOAA RACE database accessed herein included 2 years (1985 and 1991) of data collected from Norton Sound. Although Arctic Cod were frequently caught in the trawl catches, the thermal environmental conditions seem to be different to the preferred ranges suggested in [figure 5.4](#). Mean bottom temperatures in the Norton Sound trawls were relatively warm in both years (7 °C in 1985 and 6.1 °C in 1991) and, on first inspection, seem to approach or exceed the upper limits of thermal preferentia for this species. Perhaps this result reflects greater thermal tolerance for this species than described by the RACE data set. The occurrence of Arctic Cod also could be indicative of bathymetric migrations, habitat differences by life cycle stages, or other kinds of ecological benefits conferred by warmer waters. An example of the latter could be physiological (for example, growth) or related to increased prey abundance that overrides optimal temperature preferences.

The model outputs would also suggest that, because the mean bottom temperature decreased from 7 °C in 1985 to 6.1 °C in 1991, the distribution and abundance of Arctic Cod should have increased. However, although mean bottom temperatures showed a 0.85 °C decrease between 1985 and 1991, the presence and abundance of Arctic Cod also decreased from 65 of 74 trawls in 1985 to 24 of 47 trawls in 1991. Likewise, the average number of Arctic Cod per trawl in Norton Sound in 1985 was 82.7 compared to 6.9 in 1991. Corresponding changes in surface temperatures, however, showed an opposite trend with a mean temperature of 6.6 °C in 1985 and 11.7 °C in 1991.

Although Arctic Cod in Norton Sound generally respond negatively to increases in bottom temperatures, other factor(s), such as food abundance, may be involved. The large volumes of freshwater discharged by the Yukon and Kuskokwim Rivers creates hydrographic conditions in Norton Sound that may be similar to conditions in the nearshore Alaska Beaufort Sea in summer. The regional comparison is significant in that Arctic Cod are a common, if not dominant species, in nearshore waters farther north. Their occurrence in marine and brackish habitats of the Beaufort Sea has been related to invertebrate-driven food webs that are also important in Norton Sound (Thorsteinson and others, 1989). In comparison, the mean abundance and distribution of Saffron Cod remained about the same in 1985 and 1991 despite the observed environmental changes. A potential future project could include improving the models as more data become available in this area and farther north.

Arctic Applications

The overlap in habitats of Arctic Cod and Saffron Cod is much greater in the Chukchi and Beaufort Seas ([chapter 3](#)) than has been described for the EBS. However, because of the incomplete nature of fishery data from the high Arctic, it is difficult to describe how changing distribution patterns might affect interactions between these species. It is known that Arctic Cod play a keystone role in the bioenergetics of Arctic food webs as a consumer of primary and higher levels of biological production and are a significant prey resource for many marine fishes, birds, and mammals. The potential for large-scale changes in the forage base of the Chukchi and Beaufort Seas suggests the possibility for cascading ecosystem effects and corresponding needs for long-term and multivariate approaches to data collection and greater attention to scientific goals for population and functional understanding. A broadening of the ecological lens in climate change modeling is needed to understand the adaptive capacity and resilience of these species and their interaction with others. Although Arctic and Saffron cods are not currently of commercial importance in North America, their ecological and subsistence values are considerable and worthy of marine indicator status. Environmental changes that affect their distribution and abundance could alter the structure and function of the marine ecosystem and change the traditional and economic uses of these and other organisms in Arctic food webs.

The SDM results suggest that based on warming temperatures, without viewing climate effects more broadly, similar distributional changes as predicted for the EBS might be projected for the Chukchi and Beaufort Seas. These changes include a constriction in range to the north in Arctic Cod and a similar expansion in range to the north by Saffron Cod. Warming of bottom temperatures in the northern Bering Sea can be expected to result in other large-scale shifts in distributions of other marine fishes including Walleye Pollock, a species that, although presently known from the Chukchi and western Beaufort Seas, seems to be limited in numbers and biological condition in cold-water environments. Pollock are extremely abundant in the EBS and the comparatively low relative abundances of Arctic Cod and Saffron Cod relates to the zoogeographic boundary in the northern Bering Sea discussed in [chapters 2 and 4](#). The observed distribution and abundance data from the EBS suggests that deeper shelf and upper slope habitats are not occupied by Arctic Cod, in contrast to distribution and abundance in the Chukchi and Beaufort Seas, which suggests predation and other competitive processes with Pollock and other species, in addition to temperature, may be occurring.

Favorable environmental temperatures associated with possible large-scale changes toward more pelagic regimes over the Chukchi Sea shelf could result in difficult to estimate changes in predator-prey dynamics and species composition of regional fish assemblages (Grebmeier and others, 2006a). Questions about the stock composition in Arctic Cod and Saffron Cod populations and areas of life history importance (for example, spawning locations) are currently outstanding and thus expansions to the north would not necessarily translate to the Arctic Cod's extirpation from the Chukchi Sea. Movements to deeper, colder and more stable marine environments might remove these species from easily accessible coastal fishing areas, or at least make harvest more difficult, for subsistence users.

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Summary

The GAMs generated using NOAA's RACE survey data appear to be sufficiently dynamic to simulate the general response of Arctic Cod and Saffron Cod to climate-related changes in deeper shelf waters of the EBS. The modeling results suggest that both species likely will be affected by global warming trends, but in different ways. Analysis of fish catch and bottom water temperature data from the NOAA surveys further suggest that the southern boundaries of the cold pool in EBS vary annually in spatial extent and generally correspond to the southern range limit of Arctic Cod, an endemic Arctic species. It is hypothesized that Arctic Cod distribution in the northern Bering Sea will shift (contract) to the north with warming bottom temperatures. The presence of sea ice in the Bering Sea during winter and persistent cold bottom temperatures to the south of St. Lawrence Island will likely dampen this warming effect for the foreseeable future.

The model simulations presented in this chapter support this premise and indicate that Arctic Cod are sensitive to changes in bottom temperature and depth. For example, the model simulations indicate that small increases in bottom temperature will dramatically reduce their distribution and abundance. Significantly, a 2 °C increase in bottom temperatures is expected to reduce Arctic Cod distribution in the EBS by approximately 80 percent and its relative abundance by 90 percent. By comparison, the model simulations indicate a nearly opposite effect on Saffron Cod. Their distribution, with a 2 °C increase in bottom temperatures, would be expected to expand by approximately 28 percent with a corresponding increase in abundance of 92 percent. As data become available, the application of GAMs in the Chukchi and Beaufort Seas would enhance assessments of effects of climate change on marine ecosystems and subsistence in regions where Arctic Cod, and to a lesser extent Saffron Cod, are more important in food web dynamics.

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Chapter 6. Conservation of Arctic Alaska's Marine Fish Resources

By Lyman K. Thorsteinson¹

Abstract

Limitations in data and scientific uncertainties in our understanding of Arctic marine fish ecology are pronounced and indicative of the science that will be needed for effective resource management, environmental regulation, and conservation. The existing datasets are not conducive to quantitative evaluations of population dynamics or determinations of species abundance, and in most instances, it is not possible to estimate vital demographic parameters such as age and size structure, instantaneous growth rates, or mortality and survival rates. Cost and logistical constraints associated with Arctic research will likely focus future efforts on monitoring of trends in these key population parameters rather than actual changes in fish population sizes. Physiological data are lacking especially with respect to our understanding of key environmental effects on rates of growth, reproduction, and survival. Field and laboratory experiments will be needed to develop bioenergetics models to assess climate change effects or disturbances, such as possible Arctic oil spills. For now, in the absence of population understanding, information about species life history and ecological traits can be used to classify Arctic marine fish species into strategic groups based on the r-K theory to assist resource management and environmental decision-making including two previously undescribed groups we call Amphidromic and Cryophilic Strategists. Knowledge about the seasonal diets and food habits of dominant Arctic fishes are primarily known from stomach samples collected during ice-free months. Similarly, descriptions of predator-prey relationships and biological interactions tend to be limited to prominent species in food webs leading to apex predators. Integrated and interdisciplinary science approaches are priorities for long-term data collection that will be needed for the Arctic fishery-based ecosystem management recommended by the U.S. Department of Commerce. The information needs for 21 priority marine species identified in [chapter 3](#) are considered in light of integrated research and monitoring in the Chukchi and Beaufort Seas.

¹U.S. Geological Survey.

General Understanding of Marine Fish Life History

Much new biological information about marine Arctic fishes and their environmental relationships was acquired, reviewed, and synthesized in this study. It is an important synthesis because it expands the nature of information presented in the *Fishes of Alaska* (Mecklenburg and others, 2002) and along with biodiversity baseline presented in Mecklenburg and Steinke (2015) and Mecklenburg and others (2016) significantly updates the inventory represented for the Arctic in that monograph. The update of this information was timely because the user community is increasingly large and it requires accurate resource inventories and access to data and information. The need extends beyond a listing of species (Cook and Bundy, 2012) and, given the wide variety of uses for resource information, requires a consistent and reliable source of scientific information for each species (geographic distribution, abundance, and habitats). Although life history information is lacking for most species, it is generally true that, within a life cycle context, the most information is available for adult stages and much less is known about juvenile marine fish and younger stages ([chapter 3](#)). The ichthyoplankton sampling that has been done is an important source of information about the biodiversity of the region.

This synthesis is therefore timely for purposes of assessing potential climate effects and informing decision making about regional fisheries, offshore energy development, and other human uses (for example, increased marine shipping and tourism, and port developments). It is an encyclopedic effort with respect to content (biodiversity, life history, population ecology, and regional ecosystems), visualization of data, and scientific information presented and reviewed. The narratives, maps, and literature references provided in individual species accounts are meant to serve as trailheads or guides to more detailed information about the zoogeography, taxonomy, life histories, species niches, and life requirements in sectors of the Arctic marine ecosystem of the United States. We have attempted to present scientific information and concepts in language that will be understood and useful not only to professional scientists and resource managers but the broader swath of user communities involved in environmental research, community planning and development, and Arctic policy making.

Applications for Arctic Outer Continental Shelf Energy Development

The Chukchi and Beaufort Seas differ with respect to geographic setting, expanse of continental shelves, regional oceanography, and freshwater-marine interactions (rivers and streams). The differences (for example, topography of the shelf and slope habitats) affect patterns of species occurrence in Arctic marine habitats. The Chukchi Sea shelf is broad and generally less than 200 m deep. In contrast, the Beaufort Sea shelf is narrow and slope waters are deep (>1,000 m). The presence of sea ice is an important feature in both seas as it relates to environmental temperatures, light penetration, habitat for species such as the Arctic Cod (food, shelter, and potential nursery for early life stages), and processes affecting production cycles.

This report documents the confirmed occurrence of 109 species of known marine fishes in 24 families and 63 genera in the U.S. Chukchi and Beaufort Seas. The occurrences were based on published literature, specimens examined in museum collections, and species confirmed from expert identifications in ongoing field research. Of these, our review of Alaskan records indicates 97 species are found in the Chukchi Sea and 83 in the Beaufort Sea. Sixty-eight fishes are common to both seas. Since the latest publication covering all known Alaskan fishes (Mecklenburg and others, 2002), 18 new species to the region have been confirmed. In time, other species will be confirmed from this region. For example, at least three other species whose taxonomic identification is in progress are known, as well as several others marine fishes that are likely, but have not been observed in sampling. Given the intensity of sampling in nearshore areas, new species and range extensions are expected from these waters.

The NEPA process requires that BOEM analysts use the best resource information available in their assessments of environmental effects associated with offshore oil and gas development in Arctic OCS Planning Areas. Through review and synthesis, our summaries provide current information about which fishes are present, when and where they are present, and the physical and biological processes that affect their distribution and abundance. This information is valuable because in reporting what is known about the Arctic marine fish fauna and its traditional, cultural, and economic values, this study also indicates where further study is needed. The immediate applications of this work extend beyond the BOEM's purposes and are of immediate value to other Federal and state research and management agencies to Alaska Native and other Arctic residents interested in Arctic marine ecosystems, potential Arctic fisheries, and the conservation of Arctic marine fishery resources. At the same time, the format and information presented, especially in the species accounts, are intended to be useful to a public audience.

Theoretical Applications to Resource Management

Information about species-specific and interspecific life history and ecological traits informs not only theoretical ecology (such as r-K adaptations), but has implications for resource management (Hardie, 2003). The relationship between multiple traits is addressed in the fast-slow continuum hypothesis, which “*explains life history traits as reflecting the causal influence of mortality patterns in interaction with trade-offs among traits, particularly more reproductive effort at a cost of shorter lives*” (Paemelaere and Dobson, 2011). Bjørkvoll and others (2012) recently examined this hypothesis with respect to the population dynamics of nine species of marine fishes from the Barents Sea. A major finding was that mean natural mortality rates, annual recruitment, and population growth rates were lower in long-lived species (slow end of the continuum) than in short-lived species (fast end). Interspecific characteristics also were associated with ecological traits where it was determined that species at the fast end were mainly pelagic with short generation times and high natural mortality, annual recruitment, population growth rates, and high temporal variability in these demographic traits. In contrast, species at the slow end of the continuum were long-lived, demersal species with low rates and reduced temporal variability in the same demographic traits.

Life History and Ecological Traits

The relations between basic life history characteristics and population dynamics have implications for managing marine fish resources where population data are limited or non-existent, like the Arctic. To illustrate, in a conceptually similar analysis, Winemiller (2005) used a triangular model (Kawasaki, 1980; Winemiller and Rose, 1992) to classify the life history traits of mature individuals of marine fishes into life history strategist groups (based on position within the fast-slow continuum) to investigate their predictive capacity and management applications. King and McFarlane (2003) completed a much larger analysis ($n = 42$ species) and identified 5 strategist groups represented by species common to pelagic, benthic, and nearshore habitats in the western Gulf of Alaska. Two of the strategic groups had been previously described by Winemiller and Rose (1992) including opportunistic and periodic strategists. Three additional distinct groupings, equilibrium strategists, salmonic strategists, and intermediate strategists were described by King and McFarlane (2003). King and McFarlane (2003) described each group as:

Opportunistic Strategists.—Opportunistic strategists are short-lived with a small body size at maturation, low fecundity, high growth rates, and small eggs. They are surface and midwater pelagic species that exhibit little if any parental investment and are planktivores or lower-order carnivores. They occupy habitats that have a high degree of environmental variability but potentially large resources of energy. As such, their population responses tend to be large in amplitude and species in this group display highly variable, fluctuating population patterns. Species include clupeids (for example, Pacific Sardine, Pacific Herring), smelts (for example, Eulachons), and other forage fishes (for example, Northern Lampfish and Arctic Sand Lance). Because abundance is dynamic and survival rates are variable, the opportunistic strategists are susceptible to rapid depletion augmented by fisheries.

Periodic Strategists.—Periodic strategists are long-lived and slow growing with a high fecundity, but are medium in size, have a midrange for size at maturity, and have medium sized-eggs. These fishes are higher-order carnivores that inhabit shelf or slope benthic habitat and exhibit some parental investment. In the eastern Pacific, rockfishes and flatfishes are good examples of periodic strategists. These species were classified as having a steady-state population pattern. The period between strong year classes can be relatively long (as much as several decades), and these species can exhibit decadal scale patterns in recruitment coincident with climate–ocean regimes. Annual recruitment is only a fraction of the spawning stock biomass, and maintaining an appropriate age-structure in the spawning stock biomass should be a paramount management goal for these relatively long-lived, late maturing species.

Equilibrium Strategists.—Equilibrium strategists are dominated by elasmobranchs (skates and sharks), which are slow growing, have low fecundity, are large in size, and have large eggs (K selection traits). These species exhibit modest to great degrees of parental investment, are higher order carnivores and piscivores, and inhabit a range of habitats. Equilibrium strategists have a low fecundity and late maturation, and therefore, not able to recover as quickly as other fishes after population reduction.

Salmonic Strategists.—Salmonic strategists, *Oncorhynchus spp.*, are relatively short-lived, but fast growing and large sized. Compared with other marine species, they are not extremely fecund, but have large eggs. The life history traits of the Pacific salmon differ from opportunistic strategists with their semelparous nature and the higher degree of parental investment. Large-scale changes in ocean condition affect salmon productivity. Ocean survival, notably during the first marine summer conditions, may be especially critical in the salmon strategist population dynamics. Improved

estimation of freshwater (egg-smolt production) and marine (smolt-adult production) survival in population models will aid management forecasts.

Intermediate Strategists.—Intermediate strategists, cods and scombrids, have life history traits that are mid-range when compared to opportunistic and periodic strategists. They have a longer life span than the opportunistic strategists, with maximum ages typically 10–20 years, but exhibit the same population dynamics as this group. Gadids are considered typical groundfish species (that is, benthic or bathypelagic), but are different from the other groundfish species (for example, rockfish, flatfish, and sablefish) grouped with periodic strategists. For example, gadids are not as long-lived and scombrids are highly migratory surface pelagics, but differ from the other surface pelagics because of their larger size and longevity. Populations of intermediate strategists can withstand periods of unfavorable environmental conditions for recruitment better than the opportunistic strategists, but they do not exhibit the more stable populations as in periodic strategists. Their shorter generation time makes them more vulnerable to fluctuations in biomass through fluctuations in recruitment. Intermediate strategists are large-sized, highly migratory pelagic species that are able to move from areas of poor conditions to areas of better conditions as reflected in large distributional changes.

The study by King and McFarlane (2003) included species from the Gulf of Alaska where fish life histories and population dynamics and trends are relatively well known from long-term research. The species accounts demonstrate that, although in many instances, life history and ecological trait information is not available from United States waters, the general information that is available is of sufficient quality to identify the relative positions of certain species on the fast-slow continuum. Additionally, the similarities between Arctic and subarctic traits allow an initial classification of Arctic marine fishes using the strategist grouping of King and McFarlane (2003) as an initial screen.

The assignments are a first-order projection and, as such, are preliminary in nature; however, as noted by King and McFarlane (2003), in the absence of information on absolute or relative biomass (Arctic case) this conceptual framework can guide management options. Although a comprehensive analysis of the entire fauna is not feasible, initial decisions about (1) what species to include were based on abundance (that is, selected species were common in both Chukchi and Beaufort Seas), and (2) assignment to strategic groupings were based on life history knowledge including resiliency (that is, estimates of population doubling time). The Arctic marine fish strategic groupings for selected dominant species are shown in [table 6.1](#) following criteria described by King and McFarland (2003).

Table 6.1. Life history strategy groupings of common Arctic marine fishes in the Chukchi and Beaufort Seas.

[**Resiliency:** Based on estimates of population doubling time: low (4.5–15 years); medium (1.4–4.4 years); and high (<15 months) turnover. **Life history:** Information is based on King and McFarland (2003). <, less than]

Taxonomic family	Resiliency	Life history strategic grouping				
		Opportunistic	Periodic	Equilibrium	Salmonic	Intermediate
		Common fish species				
Petromyzontidae	Low				Arctic Lamprey	
Squalidae	Low			Spotted Spiny Dogfish		
Rajidae	Low			Arctic Skate		
Clupeidae	Medium	Pacific Herring				
Osmeridae	Medium	Arctic Smelt, Capelin				
Salmonidae	High				Chum Salmon	
Myctophidae ¹						
Gadidae	Medium					Walleye Pollock, Saffron Cod
Gasterosteidae	Medium	Ninespine Stickleback				
Cottidae	Low to high					Hamecon, Fourhorn Sculpin, Shorthorn Sculpin
Agonidae	Medium					Alligatorfish, Arctic Alligatorfish, Veteran Poacher
Liparidae	Medium					Gelatinous Snailfish, Kelp Snailfish
Zoarcidae	Low to medium					Fish Doctor, Marbled Eelpout, Polar Eelpout
Stichaeidae	Low to medium					Fourline Snakeblenny, Slender Eelbenny, Arctic Shanny
Ammodytidae	Medium		Arctic Sand Lance			
Pleuronectidae	Low to medium					Bering Flounder, Arctic Flounder

¹Not commonly found in Chukchi or Beaufort Seas.

Two additional strategic groupings are described to capture other adaptation strategies known to the Arctic marine fish fauna:

Amphidromic Strategists.—The amphidromous life history strategy is significantly different from the strategies of other Arctic and subarctic marine fishes. For this reason, we created a new life history strategy grouping, *amphidromic strategists*. Amphidromous strategists (that is, Dolly Varden char; Least Cisco, and Bering Cisco; Broad and Humpback Whitefish; and Inconnu) strongly exhibit K selection traits (Craig, 1984) and are similar to salmonic strategists with respect to migratory behavior, occupation of multiple habitats, and parental investment in young. Unlike the salmonic strategists they are iterperous and long-lived (>20 years). Density-dependent factors operating in freshwater overwintering sites result in a relatively steady state. The Arctic Cisco life cycle in the Alaska Beaufort Sea involves a long-distance migration of young-of-the-year (YOY) juveniles between the McKenzie River, Canada and Colville River, United States. Overwintering of immature ciscoes (generally <7–8 year old fish) in Alaskan waters occurs in salinity-influenced areas of the delta and thus the species shares some anadromous characteristics with the salmonic strategists. The abundance of migrant YOY ciscoes is variable and survival rates, at least during early life phases, are similar to the opportunistic strategists.

The amphidromic strategists include key, iconic species of Arctic marine fishes. Long-term harvest records for Arctic Cisco from a small fishery in the Colville River provide information about trends in population abundance for the species in Alaskan habitats. Upon reaching age 7–8 (average age of maturity), the ciscoes return to Canada to spawn. Information about Arctic Cisco from the McKenzie River is extremely limited. Dolly Varden stocks spawn and overwinter in rivers and streams originating in the Brooks Range, Alaska (with perennial springs) in the eastern sector of the Alaska Beaufort Sea. Arctic Cisco, Least Cisco, and Broad Whitefish freshwater habitats are farther west in the Sagavanirktok River and westward of Prudhoe Bay. For the latter two species, habitats are located in low-lying rivers that are usually connected to lakes. Maintaining the connectivity and quality of freshwater and coastal habitats is critical for these species long-term sustainability. The combination of delayed reproduction, low reproductive effort, and increased longevity adapts the organism to fluctuations in recruitment and management concepts described for periodic strategists apply.

Cryophilic Strategists.—The Arctic Cod and Ice Cod have strong ice affiliations in their life histories although the latter species is rarely encountered in U.S. waters. The Arctic Cod is a keystone species and its association with cold temperatures and sea ice presents a special case referred to herein as the *cryophilic strategist*. King and McFarlane (2003) classified the gadids with the intermediate strategists. Like its congeners in the south, Arctic Cod are widespread and abundant; however, unlike the other cods, the Arctic

Cod is a small and short-lived species. They are the most important forage species in the Chukchi and Beaufort Seas and share many of the life traits of opportunistic strategists including a medium resiliency with respect to its population dynamics (table 6.1). The relative importance of the ice edge ecosystem (Alexander, 1992) in the life cycle of this species is ecologically different enough that we classified them in a unique Arctic grouping. The life cycle association beneath the sea surface ice may provide refuge habitat and special food web dynamics that can dampen the effects of density-independent factors on population and possibly stock abundance. Genetic stock information is not yet available and, although ongoing research suggests the presence of large schools over slope waters (Crawford and others, 2012), the species is also a coastal dominant nearer to shore. The role of ice in the reproductive ecology of Arctic Cod is not known.

Most of our understanding about Arctic Cod in United States waters is from data and information collected from nearshore environments. The abundance of Arctic Cod in coastal waters of the Alaska Beaufort Sea varies greatly from year to year and even between adjacent sites within a year (Craig and others, 1982; Palmer and Dugan 1990; Wiswar and Fruge 2006) although in the Canadian Arctic, large schools move into some discrete areas with some predictability (Welch and others, 1993). This often-large influx makes Arctic Cod by far the most abundant fish in nearshore waters (Crawford and Jorgenson, 1996; Fechhelm and others, 1996; Gillispie and others, 1997). In a recent acoustic survey, Crawford and others (2012) observed large schools of unconfirmed Arctic Cod over shelf break and slope waters of the Chukchi and Beaufort Seas. Estimates of summer cod abundances have been as high as 12–27 million fish in Simpson Lagoon, Alaska (Craig and Haldorson, 1981), and 900 million fish in a small area off Cornwallis Island in the Canadian Arctic (Crawford and Jorgenson, 1996). Interannual variations in patterns of abundance of Arctic Cod in coastal waters may be related to the timing, frequency, and magnitude of westerly storm events relative to the location of water masses and currents relative and spatial distributions and sizes of schooling cod over shelf and slope waters (for example, passive transport inshore). In contrast, some segment of the Arctic Cod population may actively migrate inshore in response to the abundance of invertebrate prey in coastal waters.

Although there has been considerable speculation regarding the environmental parameters that drive inshore migrations, the data often are contradictory. For instance, in the Chukchi Sea, Fechhelm and others (1984) determined that catches increased when water temperatures increased and salinities decreased, but the opposite was noted by Griffiths and others (1998) in the Sagavanirktok River Delta. In Prudhoe Bay, Moulton and Tarbox (1987) noted highest densities in frontal areas bordering low salinity and high temperature surface waters and high salinity and low temperature bottom waters, perhaps an area of high productivity. In another Chukchi Sea study, Gillispie

and others (1997) determined there was no association between abundance and any environmental parameter and they hypothesized that food availability may underlay fish movements. Thorsteinson (1996) reported the presence of high numbers of YOY Arctic Cod in surface waters of Camden Bay, Alaska, and hypothesized their vertical distribution and separation from older cod as an avoidance mechanism from cannibalism noted in other gadids.

The autumn and winter behavior of Arctic Cod throughout the Arctic, but particularly in the U.S. Chukchi and western Beaufort Seas, is poorly understood. In the Beaufort and Chukchi Seas, at least some fish spend winters under nearshore ice (presumably spawning) (Lowry and others, 1980; Craig and Haldorson 1981; Fechhelm and others, 1984; Schmidt and others, 1987; Craig 1989b; and Thorsteinson and others, 1990). However, whether the bulk of the population overwinters and spawns in shallow waters is not known (Craig and others, 1982). For instance, Craig and others (1982) reported spawned-out cod both near the coast and 175 km (109 mi) off Prudhoe Bay. Arctic Cod have been reported to spawn near the bottom along the ice edge (Ponomarenko, 1968) and underneath ice (Andriyashev, 1954). Ponomarenko (1968) reported that in the autumn and winter, large, spawning-oriented migrations occurred in the Russian Arctic and that spawning in the Barents Sea may have occurred from nearshore to hundreds of kilometers off the coast. Thus far, the most complete study of winter behavior off North America was completed by Benoit and others (2008; 2010) in Franklin Bay, eastern Beaufort Sea. They determined that after spawning during the early winter (perhaps over deep waters in the Amundsen Gulf [D. Benoit, Université Laval, Quebec, Canada, oral. commun., 2013]), large numbers of fish either migrated to, or were passively carried into, waters primarily deeper than 180 m in Franklin Bay. Migration out of these waters coincided with spring phytoplankton blooms and the beginning of feeding. Whether cod in the western Beaufort Sea or Chukchi Sea perform similar migrations is not known, although fish that apparently spawned in winter in Simpson Lagoon had departed by February (Craig and others, 1982; Craig and Haldorson, 1986).

In other research in the Northeast Water Polynya (Greenland Sea), Fortier and others (2006) tested a hypothesis that the survival of Arctic Cod larvae is limited at sea ice cover greater than 50 percent and sea-surface temperature less than 0 °C. The authors described variable recruitment rates in a spring and summer cohort of cods. Although only a low percentage (12 percent) of the spring cohort survived to winter, their larger size was described as having evolutionary significance with respect to the survival and persistence of this cohort. The existence of multiple cohorts in Arctic Cod from the Chukchi and Beaufort Seas is suggested in the length frequency distributions of many coastal surveys.

Resiliency

Many environmental factors affect the population dynamics of any particular species. Stock assessments for Arctic marine fish have not been done and the population dynamics for the species listed in this report are not known. For the present, the qualitative evaluation of population resilience based on life history traits ([table 6.1](#)) suggests the time requirements for recovery of dominant species from a large-scale mortality event such as an oil spill. Quantitative approaches to evaluate the magnitude of population effects and recoveries of hypothetical oil spills on well-studied fishery species in the southeastern Bering Sea have considered the cumulative effects of natural and anthropogenic changes in mortality rates over the species life cycle in space and time (Laevastu and others, 1985). The many information gaps ([chapter 3](#)) in understanding of distribution and abundance of life history stages, population processes, and effects (positive and negative) of climate change, sea ice, and ocean acidification preclude a defensible quantitative approach. Long-term data and integrative science approaches are needed and may be an area where traditional ecological knowledge and Bayesian analysis could guide resilience thinking and science planning with respect to managing and protecting this component of marine ecosystem goods and services.

Marine Fishery Science in Support of Ecosystem-Based Management

Fishery research in the Arctic is challenging given the rough weather conditions, presence of sea ice, short open-water season, irregular seafloor topography, and great depths off the continental shelf. Despite these challenges, important Arctic fish studies have been accomplished since 2002. Notable is an earlier Arctic expedition in 2004 by the Russian American Long-Term Census of the Arctic, which was sponsored by NOAA and the Russian Academy of Sciences. BOEM, in cooperation with other agencies and several universities (including University of Alaska, University of Washington, University of Maryland, and University of Texas), has been investigating fish use and ecological process in the Chukchi and Beaufort Seas. The results of recent (2008–12) and ongoing marine fish studies (2013), when available, are expected to make important new contributions to our understanding of Arctic marine fish diversity, population dynamics, and community interactions. These contributions will be significant in their role in ushering a new era of fishery ecosystem-based management by the United States and its circum-arctic partners.

An important step in this synthesis process was the identification of general research needs and their priority in near- and long-term science activities. In many instances these complement or address similar needs that were previously identified for systematics of Arctic fishes (for example, Collette and Vecchione, 1995; Mecklenburg and others, 2011); life history and environmental relations (for example, Reist and others, 2006; Mueter and others, 2009; DeGange and Thorsteinson, 2011; von Biela and others, 2011; Hollowed and others, 2013) or quantitative population ecology (for example, Monterio, 2002; Katsanevakis, 2006; Wilson and Orsmeth, 2009). A Structured Information Management process (Bayesian analysis) involving expert opinions is recommended for priority setting and addressing the most relevant Arctic issues in an ecosystem-based structure (for example, Holland-Bartels and Pierce, 2011; Jay and others, 2011). Although a broad list of science themes for further consideration is provided, it should be noted that, if implemented, many of the specific needs identified in the species accounts would be addressed over the long-term.

The Chukchi and Beaufort Seas differ with respect to geographic setting, expanse of continental shelves, regional oceanography, and freshwater-marine interactions. The differences affect ecological processes and the patterns of species occurrence in shelf and slope habitats. The presence of sea ice is an important feature in both seas as it relates to environmental temperatures, light penetration, habitat for species, and more than 100 marine fish, including the Pacific salmon that are known from the region. Life history information is lacking for most, is best for adult stages, and is best known for species occurring nearest to the shore. Major limitations of existing information relate to the absence of large-scale fisheries and lack of related resource assessment surveys. This lack is beginning to be addressed in light of changing Arctic conditions, but needs much greater scientific attention to abundance patterns and dispersal processes, population dynamics, physiological requirements, and community relationships.

A commitment to long-term data collection within an integrated science framework is needed to develop quantitative population understanding (similar to current fisheries research and assessment surveys in the Bering Sea). Logistical, technological, and cost considerations have limited the practicality of early spring and winter surveys. As a result, under-ice resource information is inadequate for evaluation of effects such as those that might be related to an oil spill in winter months.

A combination of laboratory, field, and modeling approaches is needed to estimate the effects of climate effects and ocean variability on production cycles and the distribution, abundance, and movement behaviors of Arctic marine fishes.

As appropriate, these approaches should incorporate local and traditional ecological knowledge. Research and monitoring should focus on key species in Chukchi and Beaufort Seas fish assemblages in strategic locations (for example, Distributed Biological Observatories (long-term monitoring sites and biological hotspots) and include studies of human interactions. Human interactions extend beyond subsistence activities and may include changes associated with increases in marine transportation and OCS oil and gas activities on important biological habitats and ecosystems.

Crosscutting technology-analytical themes for integrated research are needed to make best use of historical and new data collection. Modern geospatial tools are needed to effectively and efficiently investigate distribution and abundance patterns of marine fishes in time and space. Greater reliance on modern scientific technologies and their fishery applications, such as gliders, remote sensing, telemetry, genetics, cellular and molecular biology, and quantitative ecology (for example, predictive models) is needed to establish species environmental relationships, address existing gaps about relative importance of habitats, understand natural variation in fluctuating stocks, and accurately assess anthropogenic effects.

Chukchi and Beaufort Seas Marine Ecosystem Studies

The Interagency Arctic Research Policy Commission (IARPC) published a conceptual model for the U.S. Arctic marine ecosystem as part of its planning for integrated, process-oriented research in the Chukchi and Beaufort Seas (Wiese and others, 2013). An IARPC team is using this framework to develop priority needs for future ecosystem research. The team has highlighted the importance of winds, currents, and advection on nutrient dynamics and consequent plankton distribution and production (Wiese and others, 2015). Additionally, the effects of changes in sea ice and other drivers in the ecosystem on energy pathways (benthic and pelagic systems), ecosystem structure and function, and the phenology and location of key elements of the food web (hot-spots, hot-times, biodiversity), including access for subsistence activities are seen as research priorities. In coastal waters, nearshore changes caused by ice, winds, currents, and freshwater runoff and their implications for biota and communities, especially changes in the habitats of fish, seabirds, and marine mammals and subsequent implications for subsistence use and culture are included in the planning process. The role of humans within the marine ecosystem as predators, as a source of perturbation, and as receivers of ecosystem services, will be an objective of future Arctic marine ecosystem research.

In Arctic Alaska important subsistence fisheries are located in seas projected to experience rapid transitions in temperature, pH, and other chemical parameters caused by global change, especially ocean acidification (Mathis and Questel, 2013). Many of the marine organisms that are most intensely affected by OA contribute substantially to Alaska's local traditional economies and subsistence way of life. Management concerns about OA effects on marine organisms and ecosystems relate to food web and community interactions, are interdisciplinary in nature, and are far reaching with respect to their potential consequences: reduced calcification rates; significant shifts in key nutrient and trace element speciation; shifts in phytoplankton diversity; reduced growth, production and life span of adults, juveniles, and larvae; reduced tolerance to other environmental fluctuations; changes to fitness and survival; changes to species biogeography; changes to key biogeochemical cycles; changes to food webs; reduced sound absorption; reduced homing ability; reduced recruitment and settlement; changes to ecosystem goods and services; and changes to behavior responses. The rate and extent of change in pH in the northeastern Chukchi Sea suggests the importance of the region as a bellwether for other coastal seas (Mathis and Questel, 2013).

Information Gaps: Priority Marine Fishes

Twenty-one or about 20 percent of marine fish species are identified as high priority [A] in [chapter 3 \(table 6.2\)](#). These species are important in Arctic food webs and human economies or are of potential commercial interest or indicator status in long-term monitoring. The species comprise a mix of marine ecosystem goods (7 being of subsistence importance) and services (8 having food web values). Six species may support viable commercial fisheries someday. The most conspicuous members of the nearshore fish assemblage (charr, ciscoes, and whitefish) are the best known of the Arctic fish fauna, but fishery information is dated and population understanding is non-existent. Additionally, Pacific salmon already are becoming important in recreational fisheries and in some villages (for example, Nuiqsut) the increasing abundance and potential interaction with traditional food species is of concern. Most species identified are common to both seas (13 species) or to the Chukchi Sea only. As new data become available in BOEM studies, it is possible that the true relative abundance of species such as Greenland Halibut especially on shelf and slope habitats across the Beaufort Sea will become better known. Its potential as a marine dominant in these habitats is an intriguing gap in our understanding of this ecosystem.

Walleye Pollock has the greatest potential to be a target of large-scale industrial fisheries in the Chukchi Sea. In

[chapters 4 and 5](#), potential changing ecosystem conditions and distributional shifts are discussed in light of warming effects. Currently, cold water temperatures in the Chukchi and Beaufort Seas are limiting to Pollock and it has been hypothesized that the persistence of low temperatures in the northern Bering Sea will for the foreseeable future, inhibit large-scale shifts in fishable biomass to the north. If, in the future, warming favors a northward shift, this species effects on the Arctic marine fish assemblage would be significant. The effects on other congeners, especially Arctic and Saffron cods, is hypothesized here to result in a rearrangement of dominance structure through competition and predation in a warmer, pelagic ecosystem through changes in top-down and bottom-up processes, respectively.

Arctic Cod, Capelin, and Dolly Varden have circumpolar distributions and for reasons related to ecological significance and food security make them of interest in monitoring programs like the Arctic Council's Arctic Monitoring and Assessment Programme. The colonizing potential of many other priority species from the Bering Sea lends similar support to the candidacy as indicators of climate change. Such selections must be based on a fuller suite of ecological indicators in an interdisciplinary monitoring design. That design should include pelagic and benthic marine ecosystem components, nearshore and offshore components of the survey region, and species whose values are representative of local concerns, information needed by resource managers, and species such as Arctic Cod, that are key to ecosystem function. The 21 species and collective fishery component of the Arctic marine ecosystem identified herein, would strategically contribute to the matrix of habitats, food webs, life history adaptations, Arctic and other zoogeographic patterns, and human uses that should be considered in a comprehensive experimental design. The composition of species is varied enough that processes important to the distribution and abundance of all marine fish and higher level consumers will be highlighted and strengthened by their inclusion in an integrated approach.

The information gaps identified for each of these species are similar to those of all other species. The needs were categorized in the species accounts ([chapter 3](#)) into eight life history, habitat, population, and ecological areas that are of importance for baseline development, environmental assessment, and fisheries management. The priority species identified inhabit all of the marine habitats and represent the major adaptive strategies discussed in this report ([table 6.2](#)). The significance of these features in future research and monitoring is, that lower priority species ([B] in [chapter 3](#)) may not be emphasized in field collections; they will be sampled and important information about them will more slowly accrue. In this way, new information about their life histories and ecological roles will emerge.

Table 6.2. Characteristics of high priority [A] species in the Chukchi and Beaufort Seas.

[Priority determinations and high-priority species are described in [chapters 2](#) and [3](#), respectively. **Status:** Fisheries reflects commercial potential as hypothesized by colonization potential, or for Pacific Salmon, existing fisheries in the southeastern Chukchi Sea, as well as potential expansions. For Pacific Herring, there is longstanding interest in Port Clarence, Kotzebue Sound, Alaska. **Abundance:** X, indicates “common” occurrence in Chukchi and Beaufort Seas. If common in one sea but not the other, the sea is indicated. Pollock is “uncommon,” but listed for the Chukchi Sea because of its colonizing potential. **Adaptive strategy:** Incorporates information about major habitats in life-cycle context]

Common name	Species characteristics				
	Status	Abundance	Adaptive strategy	Food web position	Habitat orientation
Pacific Herring	Fisheries	Chukchi	Linked Marine-Estuarine	Intermediate	Pelagic
Capelin	Ecological	X	Linked Marine-Estuarine	Intermediate	Pelagic
Arctic Smelt	Ecological	X	Nearshore Marine	High	Pelagic
Arctic Cisco	Subsistence	Beaufort	Amphidromy	Intermediate	Pelagic
Broad Whitefish	Subsistence	X	Amphidromy	Intermediate	Pelagic
Humpback Whitefish	Subsistence	X	Amphidromy	Intermediate	Pelagic
Least Cisco	Subsistence	X	Amphidromy	Intermediate	Pelagic
Pink Salmon	Fisheries	Chukchi	Anadromy	High	Pelagic
Chum Salmon	Fisheries	Chukchi	Anadromy	Intermediate	Pelagic
Dolly Varden	Subsistence	X	Amphidromy	High	Pelagic
Inconnu	Subsistence	Chukchi	Amphidromy	High	Pelagic
Arctic Cod	Ecological	X	Marine	Intermediate	Demersal
Saffron Cod	Subsistence	X	Nearshore Marine	Intermediate	Demersal
Walleye Pollock	Fisheries	Chukchi	Marine	High	Demersal
Arctic Staghorn Sculpin	Ecological	X	Marine	Intermediate	Benthic
Fourhorn Sculpin	Ecological	X	Marine	Intermediate	Benthic
Arctic Sand Lance	Ecological	X	Marine	Intermediate	Pelagic-Demersal
Bering Flounder	Fisheries	X	Marine	Intermediate	Benthic
Yellowfin Sole	Fisheries	Chukchi	Marine	Intermediate	Benthic
Arctic Flounder	Ecological	X	Nearshore Marine	Intermediate	Benthic
Greenland Halibut	Ecological	Uncommon	Marine	High	Benthic

Fishery Objectives for Ecosystem-Based Management

It is within an ecosystem context and interdisciplinary science approach that the long-term and most outstanding fishery research and resource assessment needs for the Chukchi and Beaufort Seas will be addressed most appropriately. This is particularly true because, with respect to continued offshore oil and gas development in the Chukchi and Beaufort Sea Planning Areas, the science needs for NEPA requirements, oil-spill damage assessment, ecological restoration, and assessment of climate change effects, are not the same (Holland-Bartels and Pierce, 2011). Thus, within the context of current national policy for the United States Chukchi and Beaufort Seas (for example, White House, 2013) and planning for interagency marine ecosystem framework (for example, North Pacific Research Board [Chukchi Sea], Bureau of Ocean Energy Management [Beaufort Sea], and Interagency Arctic Research Policy Committee [IARPC] [Chukchi and Beaufort Seas]), five science areas are identified having fishery objectives for possible address:

- Evaluate biological responses of populations and communities to natural and anthropogenic stressors with improved seasonal and geographic information on the distribution and abundance, life histories, habitats, community structure, and demographics for Arctic marine fishes.
- Determine how variability in environmental conditions (for example, temperature, salinity, light penetration, pH, water masses, and currents) influences ecological processes (advection of nutrients, zooplankton prey, and early life stages; recruitment; competition; feeding; reproduction; population growth and survival) and the abundance, and distribution of fish species, including the potential for Bering Sea species to move into high Arctic waters.
- Describe onshore-offshore linkages (physical and biological) for key species in a life history context focusing on seasonal habitats, food webs, and biological interactions.

- Determine physiological requirements of Arctic fish condition and health with emphasis on (1) effects of environmental factors responsible for changes in demographic rates, (2) environmental tolerances and preferences, and (3) effects of hydrocarbon contaminants and dispersants.
- Investigate the diversity and biogeography of Arctic marine fish through improved understanding of systematic, taxonomic, and phylogenetic relationships.

Fishery Research Priorities for United States Chukchi and Beaufort Seas

These broad fishery objectives are interconnected and would best be addressed in an integrated science approach as envisioned by the IARPC. Regular synthesis efforts are part of the planned process and, with the amount of ongoing BOEM research on Alaska Arctic fishes nearing completion, such activity should be supported. Within the objectives described in section, “[Fishery Objectives for Ecosystem-Based Management](#),” several recommendations that step-down for priority consideration are offered here. These recommendations specifically relate to the major information gaps identified in the marine fish species accounts and synthesis goals of this study.

Marine Fish Systematics, Taxonomy, and Phylogenetics

Systematists study the diverse forms of life and determine the evolutionary relations among them. There is a continuing need to support the collection, analysis, and archive of specimen vouchers in fisheries investigations. Concurrently, continued, or expanded, museum studies are needed to resolve systematic problems and update fish diversity evaluations. New fishery surveys collect large amounts of materials; voucher specimens should be retained to confirm field identifications. Field data and existing historical records should continue to be evaluated in light of new taxonomic and phylogenetic understanding to update regional resource inventories. Reliable comparisons of fauna across international boundaries are difficult due to widespread problems with taxonomic identifications, nomenclatural issues, and lack of attention to standard systematic conventions. For the harmonization and congruency goals of the Arctic Council to be effectively realized, considerable attention to the evaluation of historical ichthyological data (through education and coordination) by many countries (for example, Russia) will be needed for effective marine conservation across the Arctic Basin. Finally, it has been more than a decade since the first edition of the *Fishes of Alaska*

(Mecklenburg and others, 2002) was published. There have been many scientific advances in taxonomic knowledge and understanding since 2002. The recently published baseline assessment (Mecklenburg and Steinke, 2015) and atlas and guide to *Pacific Arctic Marine Fishes* (Mecklenburg and others, 2016) fill the need for an update of the taxonomy, diagnostic characteristics, geographic distribution, and basic habitat of the marine fishes of the Alaskan Arctic region. The same authors, with additional collaborators from around the Arctic region and with funding primarily from the Norwegian Ministry of Foreign Affairs, are building on the Pacific Arctic atlas and guide to produce a reference covering the entire Arctic region which also includes summary information on life history and diet. The primary objective of the Pacific Arctic and pan-Arctic works is to provide baseline references for identifying marine fish species of the Arctic region and evaluating changes in diversity and distribution. A critical component of the ongoing research is completion of a pan-Arctic DNA barcode reference library. These works are critical to help prevent errors and inform future research.

Enhance Species Accounts

A more complete understanding of the multi-dimensional temporal and spatial aspects of population maintenance is achievable by incorporating age-specific food habits information (included in the species accounts) in the life zone schemata developed for vertical distribution. This application would allow a novel visualization of life history stage, habitat, and trophic linkages and would especially be valuable for environmental assessments including those associated with National Oceanic and Atmospheric Administration needs for evaluating Essential Fish Habitat (for example, Rosenberg and others, 2000; National Oceanic and Atmospheric Administration, 2013).

Advanced Geospatial Technology for Biodiversity Assessments

Modern geospatial tools are urgently needed to most effectively and efficiently investigate distribution and abundance patterns of marine fishes in time and space. The application of existing fishery data within a Geographic Information System environment would allow users to (1) explore fishery environmental relationships, and (2) determine population responses to changing ocean at multiple scales of resolution. Advanced geospatial analysis tools are needed for NEPA and climate change assessments, marine spatial planning, fisheries management applications, and emergency response in the unforeseen event of an Arctic oil spill. Research applications of modern technologies would focus attention on (1) geographic coverage of sampling, and (2) reporting of data (standards and automations) such that more dynamic, quantitative geospatial analyses are possible.

Advance Scientific Technologies in Fisheries Applications

Greater reliance on modern scientific technologies and their applications, such as remote sensing, telemetry, genetics, cellular and molecular biology, and quantitative ecology (for example, predictive models) is needed to establish species environmental relationships, address existing gaps about relative importance of habitats, understand natural variation in fluctuating stocks, and to more accurately assess effects of proposed offshore oil and gas activities. As an example, the validation and use of environmental DNA (eDNA) approaches to rapid biodiversity assessments should be explored for through-the-ice sampling applications.

Life History and Ecological Traits

Information about status and trends, habitat requirements, relative distribution and abundance, and knowledge of life history stages of marine fish is incomplete and unavailable for large expanses of Arctic nearshore, shelf, and slope waters and should be developed for indicator species (that is, species that are broadly distributed, of subsistence or ecological significance, readily available for vulnerability assessments, and deemed sensitive to offshore oil and gas development and climate changes, see, for example, Parrish and others, 2003; Roessig and others, 2004; and Logerwell and others, 2015). Onshore-offshore linkages (physical and biological) associated with life history requirements (for example, seasonal movements and migrations and ontogenetic shifts in prey preference) have not been described. Many well studied marine fishes show shifts in diet over time with increasing size moving from low to higher trophic levels (and from smaller to larger prey sizes).

Quantitative Ecology

A commitment to long-term data collections is needed to develop population understanding. The new research that is currently underway will improve scientific understanding of abundance patterns, habitat relations, life history parameters, trophic relations and bioenergetics (including predators, for example, Brown and others, 2002), and genetic diversity and structure, for some species. Logistical, technological, and cost considerations have limited the practicality of early spring and winter surveys. As a result, under-ice resource information is limited and inadequate for evaluation of effects such as those that might be related to an oil spill in winter months. As of 2016, Arctic fieldwork is expected to continue in late summer sampling periods and significant information gaps will remain with respect to spatial and temporal coverage and life stage coverage. The data requirements for estimating population parameters are substantial and an initial focus on fewer

indicator species (common species in Chukchi and Beaufort Seas) may be a useful short-term approach to understanding change in representative marine habitats. The inclusion of bioenergetics components in coupled population models should be explored as part of efforts to evaluate population effects of climate change.

Empirical Data in Support of Field Work and Population Models

Laboratory studies are needed to investigate the causal mechanisms responsible for shifts in distribution or changes in population rates (growth, recruitment, and survival) and to determine the environmental preferences (for example, temperature and temperature-salinity relationships) of key Arctic species. Inferences drawn from correlations established in the field do not directly address mechanisms and their effects with respect to single or multiple stressors. Mueter and others (2009, p. 108) recognized the need for an analysis of biodiversity shifts of marine fishes in the northern Bering Sea: *“Although biological responses to past temperature changes provide some basis for predicting future changes, such predictions are fraught with danger because extrapolating observed relationships beyond the historical range of temperatures cannot account for potential thresholds or non-linearities. To be able to predict where the fish is going one has to gather biological and ecological field data and the results of experiments that provide an estimate of the fish environmental preferences.”*

Laboratory experiments are needed to understand the effects of variable environmental conditions on physiological processes and animal health. Processes of special concern include feeding and digestion, assimilation and growth, fish behavior (responses to stimuli such as orientation and swimming speed), and reproduction. Collectively, these processes are integral to an overall assessment of fish condition and health. They are dependent on key water properties, including temperature, salinity, light penetration, and oxygen concentration. Animal health also is affected by the presence of toxic substances, infectious pathogens, and parasites. Experiments are needed to examine the effects of ocean acidification on the development, behaviors, and productivity of key species, their food supplies, and natural predators.

The relation between field (including genetics) and laboratory data are critical to improved population dynamics and modeling. How marine fish populations (and metapopulations) respond to changing ocean conditions, which are variable in space and time, creates spatial distributions and abundance patterns (Mueter and others, 2013). Fish movements in these systems impose gradients in growth and survival through the effects of temperature, food concentration, sensory capabilities, predator density, and detection risk (Monterio, 2002; Carey and others, 2012).

Many marine fish stocks undertake seasonal horizontal migrations and the extent of these varies with age, size, and environmental conditions. Although field studies may reveal patterns at a given time and place, laboratory investigations may isolate causal effects. Using field and laboratory results, quantitative models can be used to study the effects of multiple environmental influences on population dynamics in continuous space and time (Fordham and others, 2013).

A combination of laboratory, field, and modeling approaches is needed to explore the potential effects of ocean variability on production cycles and the distribution behavior, movement, and abundance of Arctic marine fishes. Research and monitoring should focus on selected fishery resources in strategic locations to include effects of human interactions, which extend beyond subsistence use and may include effects associated with increased tankering, vessel support, and offshore construction activities on important biological habitats and ecosystems. The effects of invasive species also are an area of concern.

Participate in Regional Research and Monitoring Networks

Reference sites in biological hotspots should be estimated to support and contribute to existing long-term research and monitoring of coastal and marine ecosystems, including human interactions. Potential sites and ecological topics include: Bering Strait (marine ecosystem processes and fish distribution); Kasegaluk, Simpson, and Beaufort Lagoons (population dynamics of nearshore fish assemblages); Barrow Canyon-Hannah Shoal (benthic productivity and marine fish interactions); Capes Lisburne and Thompson (seabird colony and fishery oceanography dynamics); Point Barrow (dynamics of this transitional biogeographic zone); Boulder Patch (kelp bottom ecosystem processes); Stefansson Sound-Camden Bay (Arctic Cod ecology); Mackenzie, Colville, and Canning River deltas (onshore-offshore linkages); ice edge and polynyas (biological significance to marine fish and higher level consumers). Local residents are often the first to notice changes in fish and wildlife populations. Mechanisms should be developed to better solicit and integrate local and traditional ecological knowledge as a basic source of information.

Participate in Additional Investigations of Iñupiaq Taxonomy

Research in Kotzebue Sound (Georgette and Shiedt, 2005) demonstrated the complexities and subtleties of the Iñupiaq classification system. Additional investigations are needed in concert with subsistence resource surveys to fully incorporate traditional ecological knowledge into biological research on fishery populations and their habitats.

Summary

In many respects, present day understanding of Arctic Alaska's marine fishes is similar to what was known about the Bering Sea in the 1970s. Quantitative data are lacking or dated, but new information is slowly developing. The relationships between basic life history characteristics and population dynamics have implications for managing marine fish resources where population data are limited or non-existent. These relationships previously were used to describe strategic groups in the Northeast Pacific as an aid to fishery management. Taking a qualitative approach, we applied the criterion for these groupings to the Arctic marine fish fauna and added two new groups. One group, the amphidromic strategists, includes those Arctic fishes displaying an amphidromous life strategy. Arctic Cod, unlike other gadids, are similar to the opportunistic strategists, but because of their dependence on sea ice habitats, life history, and central role in Arctic marine ecosystems, they are considered independently as a cryophilic strategist. Long-term fishery research objectives for the Chukchi and Beaufort Seas are described in relation to information gaps and they are addressed in planned marine ecosystem research in the U.S. Arctic. Some suggestions for more immediately needed studies relate to access of existing information, description of environmental preferences for key marine species, participation in regional monitoring networks and cooperative research, and continued biodiversity assessments through field, laboratory, and museum studies.

Chapter 7. Glossary of Ecological Terms

Information Sources

The terminology used in [chapters 1](#) through [6](#) is common in fishery science and quantitative ecology. The list of science terms identified in this glossary focuses not only on the common vocabulary used but also the uncommon and specialized terminology used in this report and its appendices. Each is accompanied by a definition that best reflects the meaning conveyed by the authors. A number of online resources and scientific references were consulted in preparation of the glossary. In many instances, the terms relate to fish population dynamics and quantitative concepts and, in these cases, the primary scientific references have been cited. The web sites used to develop definitions for more descriptive biological terminology include (1) A Glossary of Ecological Terms (<http://www.terrapsych.com/ecology.html>); (2) The Nature Education Knowledge Project (<http://www.nature.com/scitable/knowledge>); (3) Encyclopedia Britannica (<https://www.britannica.com/>); (4) FishBase (<http://www.fishbase.org/>); (5) Merriam-Webster Online (<http://www.merriam-webster.com/>); and (6) The Free Dictionary (<http://www.thefreedictionary.com/>). An extensive glossary of fishery science terms is presented in Mecklenburg and others (2002). Where appropriate, the definitions are presented with special attention to their application to meaning in the Chukchi and Beaufort Seas.

Science Terms

Abundance Generally, there are three types of abundance measures: total number of animals in a population (absolute abundance), number of animals per unit area (density), and abundance and density of one population to another (relative abundance). Because temporal variation in a population

is often described in density and biomass parameters, the distinction between biomass and other abundance measures is important. Biomass, expressed as mass per unit area, or mass per volume, reflects the quantity of resources incorporated by the population (that is, bioenergetics) and as such, is an indicator of its relative role in the ecosystem (Odum, 1985).

Age The length of time during which a being or thing has existed; the number of years of life completed (fishery statistics). Age estimation is a fundamental part of studies of the life history of fish and a key area in the monitoring, assessment, and management of fish stocks because age determined parameters underlie the population-dynamics models used for fish stock assessments. The age-determined parameters include age profiles and age at first maturity, and, when considered with length and weight measurements, provide valuable information about stock composition, age at maturity, life span, mortality, and stock production (Ricker, 1975).

Age at first maturity (t_m) Mean or median age at first maturity (that is, age at which 50 percent of a cohort spawn for the first time). Values are estimated from population parameters in the von Bertalanffy Growth Model (VBGM)¹ (Ricker, 1975).

Age and growth Basic information about the age and growth of a species and the environmental area inhabited by that species is foundational to effective fishery management. Habitat is the natural environment that influences and is used by a species population. The relations between length and weight and size and age form the basis for population dynamics (that is, population growth and production models) and quantitative analysis of environmental effects. Importantly, the relation between total length (L) and total weight (W) for nearly all species of fish is expressed by the equation (Ricker, 1975):

$$W = aL^b \text{ or } \ln W = \ln a + b \ln L \quad (1)$$

where

W	is weight, in kilograms;
L	is length, in centimeters;
a	is y-intercept; and
b	is slope.

¹The von Bertalanffy Growth Model is also expressed as the von Bertalanffy Growth Function (VBGF) and von Bertalanffy Growth Equation in the scientific literature.

A well-known growth model is the VBGM, which is based on a bioenergetics expression of fish growth converts length-frequency data into age composition (see, for example, Essington and others, 2001). The model expresses length (L) as a function of the age of the fish (t):

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \text{ or } L(t) \\ = L_\infty * \left[1 - \exp(-K * (t - t_0))\right] \quad (2)$$

where

- L_t is the length at time t ; t_0 the hypothetical age of the fish at zero length;
- K is the growth coefficient, the rate at which L_t approached expressed as the rate (per year) at which L_∞ is approached (also see “Carrying capacity”); and
- L_∞ is the asymptotic length, the mean length a given stock would reach if it were to grow indefinitely.

Estimation of growth parameters (K , L_∞ , t_0) of the VBGM are good indicators of stock condition and health. The right hand side of the equation contains the age, t , and some parameters. They are: “ L_∞ ” (read “ L -infinity”), “ K ” and “ t_0 ” (read “ t -zero”). Different growth curves will be created for each different set of parameters; therefore, it is possible to use the same basic model to describe the growth of different species simply by using a special set of parameters for each species.

Age structure The distribution of ages, or classes of ages, of individuals of a population. The presence of separate cohorts in fish populations may reflect adaptations in life strategies to cope against year to year variability in environmental conditions (Ricker, 1975).

Ammocoetes The larval stage of the primitive lamprey, known as an ammocoetes larva. Resembling a small eel, the larval lamprey can remain concealed in the sediments of rivers and estuaries from 7 to 17 years. Burrows are detectable as funnel shaped depressions, and in shallow, clear, flowing springs and streams, the ammocoetes larva will often expose their heads orienting their buccal cavities and gills into the current. Throughout the larval stage, there is a passive downstream migration of ammocoetes leading to maturity, and in some species, parasitism.

Amphidromy (of a migratory fish) that travels between freshwater and salt water, but does not travel to breed.

Anadromy (of a migratory fish) that lives in the sea and breeds in fresh water.

Arctic realm One of 12 marine realms as designated by the World Wildlife Federation and The Nature Conservancy. It includes the coastal regions and continental shelves of the Arctic Ocean and adjacent seas, including the Arctic Archipelago, Hudson Bay, and the Labrador Sea of northern Canada, the seas surrounding Greenland, the northern and eastern coasts of Iceland, and the eastern Bering Sea.

Axon An axon (from Greek, axis) also known as a nerve fiber, is a long, slender projection of a nerve cell, or neuron, that typically conducts electrical impulses away from the neuron’s cell body. The function of the axon is to transmit information to different neurons, muscles, and glands.

Axoplasm Axoplasm is the cytoplasm within the axon of a neuron (nerve cell). Neural processes (axons and dendrites) contain about 99.6 percent of the cell’s cytoplasm, and 99.7 percent of that is in the axons.

Baseline Initial collection of data, which serves as a basis for comparison with the subsequently acquired data.

Behavior Traditional fishing methods, scientific surveys, population modeling, and fishery management strategies are dependent upon a fundamental understanding of fish behavior. Behavioral research develops information about the relationships between fish behavior and environmental variables (physical and biological), and how this influences distribution, survival, and recruitment processes. Species have evolved particular behaviors to cope with environmental temperature and light, foods and predators, and reproduction.

Biodiversity Biological variety of the kind that preserves species and their DNA. Other definitions are (1) the number of species in an ecosystem, (2) the diversity between ecosystems, and (3) the diversity of entire regions. Depleted biodiversity leads to population crashes, declines in genetic variability, and extinctions.

Biogeography Biogeography is the study of the distribution of species and ecosystems in geographic space and through geological time. Organisms and biological communities vary in a highly regular fashion along geographic gradients of latitude, elevation, isolation, and habitat area.

Biogeographic province Provinces, as defined in biogeographic classification schemes, are nested within the realms.

Provinces are large areas defined by the presence of distinct biotas that have at least some cohesion over evolutionary time frames. Provinces will hold some level of endemism, principally at the level of species. Although historical isolation will play a role, many of these distinct biotas have arisen as a result of distinctive abiotic features that circumscribe their boundaries. These may include geomorphological features (isolated island and shelf systems, semienclosed seas); hydrographic features (currents, upwellings, ice dynamics); or geochemical influences (broadest-scale elements of nutrient supply and salinity) (Spalding and others, 2007, p. 575).

The BOEM Arctic Planning Areas are nested within the Arctic realm and the boundaries that include Chukchi and Beaufort Sea provinces. The Beaufort Sea province includes continental coast and shelf waters of the United States and Canada.

Brackish In the Arctic, brackish typically refers to salinity conditions of 10–25 practical salinity units (psu). Warm (5–10 °C) brackish waters have estuarine-like qualities (Craig, 1989a).

Carrying capacity (K) In nature, population growth must eventually slow, and population size ceases to increase. As resources are depleted, population growth rate slows and eventually stops, known as logistic growth. The population size at which growth stops is generally called the carrying capacity (K), which is the number of individuals of a particular population that the environment can support. At carrying capacity, because population size is approximately constant, birthrates must equal death rates, and population growth is zero. Growth rate $K(1 - L(t)/L_{\infty})$ decreases with time as the length of the fish reaches asymptotic length (Ricker, 1975).

Chukchi borderlands The gateway to the Arctic Ocean, located 600 miles north of the Bering Strait and 800 miles south of the North Pole. From Jakobsson and others (2008, p. 527):

The Chukchi Borderland is comprised of a group of generally less than 1000 m deep, north-trending ridges that surround the extensional Northwind Basin (Figure 2) (Hall, 1990). The easternmost of these ridges is the Northwind Ridge, which is deeper than its western neighbours and is characterized by an exceptionally steep slope towards the Canada Basin and a gently rounded to flat topped ridge crest. The Chukchi Spur–Chukchi Plateau composite ridge lies on the western side of the Northwind Basin and has a wide (>140 km at 78° N) flat topped crest mainly shallower than 600 m (Figure 2(a)). In addition to the large Northwind Ridge and Chukchi composite ridge, several much smaller ridges rise above the floor of the Northwind Basin.

Location of existing fish sampling and related catch characteristics is available in Mecklenburg and others (2014).

Colonization The spreading of a species into a new habitat. Successful colonization, as used in this report, implies the success of a reproductive event in the newly occupied habitat.

Compensation (density dependent processes) Population processes such as survival, growth, reproduction, and movement are considered density dependent if their rates change as a function of population abundance (Ricker, 1975). Processes that limit population growth at high abundances (for example, slower growth, increased emigration, and lower survival) or increase numerical growth at low population abundances (for example, faster growth, increased immigration, and higher survival) are examples of direct density dependence or compensation. Direct density dependent processes operate as a negative feedback and tend to stabilize population abundance.

Crepuscular feeder Crepuscular feeding occurs primarily at twilight (that is, during dawn and dusk). This is opposed to diurnal and nocturnal feeding behaviors, which occur respectively during hours of daylight and dark.

Dendrite Dendrites are the branched projections of a neuron that act to propagate the electrochemical stimulation received from other neural cells to the cell body, or soma, of the neuron from which the dendrites project. Electrical stimulation is transmitted onto dendrites by upstream neurons (usually their axons) through synapses located at various points throughout the dendritic tree. Dendrites play a critical role in integrating these synaptic inputs and in determining the extent to which action potentials are produced by the neuron.

Depensation (density independent processes) If population processes, such as survival and growth, decrease at low population abundances or increase at high abundances, they are referred to as inverse density dependence or depensation (Ricker, 1975). Inverse density dependent processes operate as a positive feedback and tend to destabilize populations.

Diadromy Migration of fish in either direction, from fresh to seawater or the reverse.

Ecosystem A biotic community and its surroundings, part inorganic (abiotic) and part organic (biotic), the latter including producers, consumers, and decomposers.

Ecological niche Describes the relational position of a species or population in an ecosystem. More formally, the niche includes how a population responds to the abundance of its resources and enemies (for example, by growing when resources are abundant and predators, parasites and pathogens are scarce) and how it affects those same factors (for example, by reducing the abundance of resources through consumption and contributing to the population growth of enemies by falling prey to them). The abiotic or physical environment also is part of the niche because it influences how populations affect, and are affected by, resources and enemies. The description of a niche may include descriptions of the organism's life history, habitat, and place in the food chain.

Endemism The ecological state of a species being unique to a defined geographic location, such as an island, nation, country or other defined zone, or habitat type; organisms that are indigenous to a place are not endemic to it if they are also found elsewhere.

Epipelagic Of, relating to, or constituting the part of the oceanic zone in which enough light penetrates for photosynthesis.

Extralimital (pertaining to a species) Not found within a given geographical area.

Eurythermic The animal is adaptable to a wide range of temperatures in the environment.

Food and feeding The numerical assignment of an organism to a trophic level has evolved to include ecological insight about a species position and interactions within a food web or ecosystem (Odum and Heald, 1975). In classic food web studies (Lindeman, 1942)², five (T1-5) trophic levels were recognized by ecologists. Lower trophic levels classified as producers (T1) and herbivores (T2), and higher trophic levels and primary and secondary carnivores (T3 and T4, respectively) and apex consumers (T5). Analysis of stomach contents often is used to associate a species with a specific level, intermediate standing between levels, or multiple levels. Recent models of trophic interactions (for example, Christensen and Pauly, 1992; Pauly and Watson, 2005) include a food-based fractional component in trophic level analysis to quantify the relative importance of prey in the consumers diet as well as the role of primary production. Model results present trophic level designations as continuous numbers ranging from 1 to 5. Age-related variations in foods habits are known in marine fish and thus, in reality, trophic level status will change over time. In most instances, deficiencies in life-history information have limited existing analyses to trophic level determinations based on combined data sets for juvenile and adult life stages. Although imperfect, the fractional analysis is meant to improve ecosystem understanding and energy flows because it more realistically addresses the complexities of consumer feeding behaviors (omnivory and feeding across multiple trophic levels) and predator-prey relationships. To illustrate, the mean trophic level for Blackline Prickleback (*Acantholumpenus mackayi*) is 3.1 (± 0.31). This mid food web value is indicative of a primary carnivore that feeds across trophic levels, in this case on lower level herbivores. The trophic level values reported herein are as reported in FishBase (Froese and Pauly, 2012).

Generation time The average age (t_g) of parents at the time their young are born. In most fishes, L_{opt} (derived as a growth parameter in the VBGM) is the size class with the maximum egg production. The corresponding age (t_{opt}) is a good approximation of generation time in fishes. It is calculated using the parameters of the VBGM as $t_g = t_{opt} = t_0 - \ln(1 - L_{opt} / L_{inf}) / K$. Note that in small fishes (<10 cm) maturity is often reached at a size larger than L_{opt} and closer to L_{inf} . In these cases, the length class where about 100 percent (instead of 50 percent) first reach maturity will contain the highest biomass of spawning fishes, usually resulting in the highest egg production. As an approximation for that length class, most fish most fish are assumed to have reached maturity at a length that is slightly longer than L_m , namely: $L_{m100} = L_m + (L_{inf} - L_m) / 4$, and generation time is calculated as the age at L_{m100} . This is applied whenever $L_m \gg L_{opt}$.

Gonochoristic The state (gonochorism) of having just one of at least two distinct sexes in any one individual organism.

Growth The study of growth means the determination of the body size as a function of age (Ricker, 1975). Therefore, all stock assessment methods work essentially with age composition data. This measures the growth of individuals in size and length. This is important in fisheries where the population is often measured in terms of biomass. The VBGM is widely to estimate of productivity parameters.

Specific growth rate (K) is given by:

$$K = (\ln w_t - \ln w_0) / t \quad (3)$$

where

w_t is the final weight and w_0 the initial weight,
 t is equal to the number of days considered, and
 K is assumed to be constant.

Hence, the individual growth is described by an exponential expression, relating the weight of the fish to time.

Growth model A primary interest of fisheries biologists is to estimate rates of fish population growth and understand the processes and factors that influence growth. Age and growth information is critical for research addressing questions about basic ecological relations and for managing fisheries. In the latter case, growth information is frequently used to populate assessment models with vital rates and age-specific length, weight, fecundity, and vulnerability to exploitation.

Additionally, information on growth may be used to estimate the age of fish based on size. Given the importance of understanding growth, much effort has been expended to understand factors that influence growth, to develop models to describe observed growth patterns, and to estimate the parameters of those models.

The decision about which growth model to use is important because most ecological models deal with transfer of energy or matter along the trophic chain. Growth can be constant or change during development periods. Although initial and final weights estimated with different models may be similar, growth curves as well as the total amount of energy or matter consumed over time may vary considerably during the growth period. It is suggested that the Gompertz or the parabolic growth models seem to be more appropriate for the description of young fish growth. For older fish, the VBGM equation or some modified form adjusted to seasonal change is preferable (Gamito, 1998).

Intrinsic rate of increase (r_m) The rate of increase in populations that reproduce within discrete time intervals and possess generations that do not overlap. The r_m is calculated as number of births minus number of deaths per generation time (reproduction rate less the death rate). Values greater than zero indicate that the population is increasing, the higher the value, the faster the growth rate. A population that has intrinsic rate of increase of zero is considered to have a stable age distribution (neither growing nor decreasing in numbers).

²Some scientific literature refers to trophic levels T1-5 as I-V.

A growing population has more individuals in the lower age classes than does a stable population, and a decreasing population has more individuals in the older age classes than a stable population (Musick, 1999).

Iteroporous A reproductive strategy (iteroparity) in which the species is characterized by multiple reproductive cycles over the course of a lifetime.

K-selection Species in stable environments tend to live longer and produce fewer, and sometimes larger, offspring. (K is the constant for carrying capacity in terms of population growth.)

Lateral line A system of sense organs in aquatic vertebrates, mainly fish, used to detect movement and vibration in the surrounding water. The sensory ability is achieved by modified epithelial cells, known as hair cells, which respond to displacement caused by motion and movement and transduce these signals into electrical impulses through excitatory synapses. Lateral lines serve an important role in schooling behavior, predation, and orientation.

Length (L) The length-frequency of a fish population is a key determinant in analyses of status and trends (Ricker, 1975). The length distributions of fish in samples give the simplest index of the composition of the stock from which the catch was taken. (Weight measurements are also required for determination of length-weight relationships and condition analysis.) Length measurements are reported as standard length, total length, and fork length by fishery investigators.

- **Standard length (SL)** refers to the length of a fish measured from the tip of the snout to the posterior end of the last vertebra or to the posterior end of the mid-lateral part of the hypural plate. This measurement excludes the length of the caudal fin.
- **Total length (TL)** refers to the length from the tip of the snout to the tip of the longer lobe of the caudal fin, usually measured with the lobes compressed along the midline. It is a straight-line measure, not measured over the curve of the body.
- **Fork length (FL)** refers to the length from the tip of the snout to the end of the middle caudal fin rays and is used in fishes in which it is difficult to tell where the vertebral column ends.

Life span (t_{max}) Life span is a central aspect of life history diversification. The parameter t_{max} is the approximate maximum age that fish of a given population would reach. It is calculated as the age at 95 percent of L_{∞} using the parameters of the VBGM. Life span is frequently estimated from maximum age and size data (Ricker, 1975).

Life span depends on the organism's survival schedule and is often associated with fecundity. The combination of survival and fecundity fitness components constitutes the basis for understanding the evolution of life histories. The theory of r - and K -selection expects that life histories can evolve toward

short or long life spans because of variation in ecological factors such as resource availability. Resource limitations impose trade-offs between different fitness components (for example, reproductive effort compared with individual growth rate) that are expected to translate into different demographic patterns. For example, as life span increases, the importance of fecundity for overall population dynamics is progressively replaced by that of survival.

Limiting factors All living things need food, water, shelter, and space to survive. As long as organisms have all of these things available to them their population will continue to grow. However, populations cannot grow forever. Some form of environmental resistance will stop the growth of a population (Ricker, 1975). The form of environmental resistance is called a limiting factor because it limits the population. However, limiting factors also may increase a population. In nature, population growth must eventually slow, and population size ceases to increase. As resources are depleted, population growth rate slows and eventually stops (known as logistic growth). The population size at which growth stops is generally called the carrying capacity (K), which is the number of individuals of a particular population that the environment can support. At carrying capacity, because population size is approximately constant, birthrates must equal death rates, and population growth is zero.

Limitations to population growth are either density-dependent or density-independent. Density-dependent factors include disease, competition, and predation. Density-dependent factors can have either a positive or a negative correlation to population size. With a positive relationship, these limiting factors increase with the size of the population and limit growth as population size increases. With a negative relationship, population growth is limited at low densities and becomes less limited as it grows.

- Density-dependent factors may influence the size of the population by changes in reproduction or survival (for example, food availability—effects on fecundity and [or] habitat condition)
- Density dependent factors also may affect population mortality and migration.

Factors that decrease population growth can be defined as environmental stress including limitations in food, predation, and other density-dependent factors. However, many sources of environmental stress affect population growth, irrespective of the density of the population. Density-independent factors, such as environmental stressors and catastrophe, are not influenced by population density change. Although the density-dependent factors are often biotic, density-independent factors are often abiotic. These density-independent factors include food or nutrient limitation, pollutants in the environment, and climate extremes, including seasonal cycles such as monsoons. Catastrophic factors such as fires and hurricanes also can affect population growth (Monterio, 2002).

Some important density-independent factors include:

- The quality of nutrients (for example, food quality, and amount of particular plant nutrients) in an environment affects the ability of an organism to survive, grow, and reproduce.
- Pollutants also contribute to environmental stress, limiting the growth rates of populations.
- Environmental catastrophes such as oil spills, fires, earthquakes, volcanoes, and floods can strongly affect population growth rates by direct mortality and habitat destruction.

Logistic population growth The geometric or exponential growth of all populations is eventually limited by food availability, competition for other resources, predation, disease, or some other ecological factor. If growth is limited by resources such as food, the exponential growth of the population begins to slow as competition for those resources increases. The growth of the population eventually slows nearly to zero as the population reaches the carrying capacity (*K*) for the environment. The result is an S-shaped curve of population growth known as the logistic curve (Ricker, 1975).

Myomeres The blocks of skeletal muscle tissue found commonly in chordates. They are commonly zig-zag, W- or V-shaped muscle fibers. The myomeres are separated from adjacent myomere by connective tissues and most easily seen in larval fishes. Myomere counts are sometimes used for identifying specimens because their number corresponds to the number of vertebrae in the adults.

Microphthalmia A developmental disorder of the eye that literally means small eye. One (unilateral microphthalmia) or both (bilateral microphthalmia) eyes may be involved.

Myosin structure Myosins are a family of Actin Motor Protein that are Adenosine triphosphate (ATP)-dependent motor proteins and are best known for their role in muscle contraction and their involvement in a wide range of other eukaryotic motility processes. They are responsible for actin-based motility. All myosins have head, neck, and tail domains with distinct functions.

Natural mortality (M) Natural mortality is a parameter in most fish stock assessment models (Ricker, 1975). Natural mortality can occur through predation or non-predation events such as senescence and disease. It is generally accepted that the natural mortality is high during larval stages and decreases as the age of fish increases, approaching a steady state. The rate then increases exponentially when the fish nears maximum age. Natural mortality also may vary with size, sex, parasite load, density, food availability, and predator numbers. However, in most cases, a single value—usually 0.2—for *M* is assumed for stock assessments.

Neritic Shallow marine waters extending from mean low water to 200-meter depths.

Neuromast The major unit of functionality of the lateral line is the neuromast. The neuromast is a mechanoreceptive organ that allows the sensing of mechanical changes in water. There are two main varieties of neuromasts in animals, superficial or freestanding neuromasts and canal neuromasts. Superficial neuromasts are located externally on the surface of the body, whereas canal neuromasts are located along the lateral lines in subdermal, fluid filled canals. Each neuromast consists of receptive hair cells whose tips are covered by a flexible and jellylike cupula. See “lateral line.”

Otophysic A connection between the swimbladder and the inner ear that enhances the hearing capability in various types of fish.

Oviparous Fishes producing eggs that hatch outside the body of the mother.

Poikilotherm An organism whose internal temperature varies with the temperature of its surroundings.

Paedomorphic Of, relating to, or resulting from the retention of juvenile characteristics by an adult.

Phylogenetic relationships In biology, phylogenetics is the study of evolutionary relationships among groups of organisms (for example, species and populations), which are discovered through molecular sequencing data and morphological data matrices. The result of phylogenetic studies is a hypothesis about the evolutionary history of taxonomic groups: their phylogeny.

Population distribution Variation of population density over a particular geographic area.

Population dynamics Major abiotic and biotic factors that tend to increase or decrease the population size, age, and sex composition of a species.

Populations or stocks The subdivision of species into local populations and the adaptive nature of genetic differences between these populations are interlinked by the ecological and genetic processes that subdivide and determine the discreteness of these stocks. Genetic discreteness implies some restriction of gene flow and spatial and temporal mechanisms of isolation. Differences in genetic stock structure reflect behavioral processes and adaptation within the species particular life history strategy.

Management at the stock-level is a cornerstone of conservation biology. In fisheries, the stock refers to the part of the fish population that is under actual or potential use. Population dynamics describes the ways in which a given population grows and shrinks over time as controlled by birth, death, and emigration or immigration. The population levels of exploited marine fish stocks are regulated through many underlying processes. Biological and environmental conditions as well as exploitation rate and pattern determine the balance between the increase in stock size due to recruitment and growth and losses caused by fishing and predation mortality. Critical parameters for population dynamics evaluations include stock size, age structure, recruitment, and growth (Ricker, 1975).

Relative abundance The contribution a species makes to the total abundance of the fishery community (Miller and Lea, 1976). It is a measure that provides an index of the number of individuals present, but not the actual numbers. Relative abundance terms, such as “abundant,” “common,” or “rare” often are used to express the general population status of a given species, but are most useful when they are defined by something that is measured or estimated in a manner that makes comparison meaningful. The definitions used in individual studies conducted in Chukchi Sea vary greatly and often reflect the differences in sampling gears, geographical localities and habitats sampled, time of sampling, and statistical approach. Thus, attempts to tie reported indices of abundance from catch summaries of individual studies (that is, species composition or catch-per-unit effort data) proved too challenging initially for this analysis, especially for the more poorly known fauna.

Recruitment The reaching of a certain size or reproductive state. For fisheries, recruitment usually means addition of new fish to the vulnerable population by growth from smaller size categories (Ricker, 1975).

Reproduction (Reproduction mode, chapter 3) The reproductive strategies of marine, amphidromous, and anadromous fishes demonstrate sharp contrasts related to their adaptation to cold Arctic conditions. Marine species generally have shorter lives, grow more quickly, and achieve earlier maturity than the anadromous counterparts. The low abundance of many species suggests tendencies for niche generalists, rather than specialists, animals that feed at lower trophic levels, and whose population may be more affected by density independent factors. For most Arctic species, marine and anadromous-like, population or stock information about the population characteristics (for example, sex ratios, age-at-maturity, and fecundity) that affect reproductive potential does not exist. Little is known about spawning times and locations or mating behaviors of marine species, and what is known has come from data collection outside the study area (chapter 3).

Resilience In ecology, resilience traditionally refers to the ability of a biotic community to sustain or return to its former state after a disturbance. The rate of recovery is a measure of resilience determined by the population processes involved in restoring abundance to healthy, sustainable, or pre-disturbance levels (Musick, 1999). Resilience also is thought of as a measure of the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures.

The competing definitions emphasize different aspects of stability. The practical application of resilience concepts requires substantial information about population status and trends (for example, intrinsic rate of population growth), biological interactions, genetic relationships, and effects of natural and anthropogenic stressors.

The American Fisheries Society proposed a method to classify a population's resilience (vulnerability to extinction) using VBGM parameters and other life history traits (Musick, 1999). In the two-tiered approach a population is initially assigned to one of four productivity categories. The second part of the vulnerability assessment examines recent trends in population size and further classifies the productivity categories according to observed rates of decline. This approach to studying population resilience is a first approximation of extinction risk. This means that a population that is determined to be vulnerable merits further study or status review.

In the first step, the five most important productivity parameters evaluated are (in order of importance): (1) intrinsic rate of growth (r_m , expressed as an instantaneous or annual percentage), (2) growth coefficient (K), (3) fecundity (number of eggs per year), (4) age at maturity (t_m), and (5) maximum age (t_{max}) (table 7.1). The intrinsic rate of increase is considered to be most important because its calculation incorporates all of the other parameters. Musick (1999) and others note that this parameter is the most difficult to estimate and is usually not available. As such, when information on r_m is available, it takes precedence in assignments to a productivity category. Age at maturity is the next most important parameter because it often is correlated with the growth coefficient (K) and maximum age. Musick (1999) noted that although fecundity also is a key indicator, it needs to be properly assessed in light of demographics features of the population, especially maximum age. Many fish populations exhibit a direct correlation between age or size and fecundity. Because of this, Musick (1999) recommended using fecundity-at-first-maturity to assess resilience.

As a rule, in the absence of an estimate of r_m , the fish population should be classified according to the lowest productivity category for which data are available (table 7.2).

Table 7.1. Productivity parameters proposed to the American Fisheries Society for classifying resilience of marine fish populations.

[Adapted from Musick (1999). **Life history parameter:** r_{max} , intrinsic rate of increase; K , growth coefficient; t_m , age at maturity; t_{max} , maximum age. <, less than; >, greater than]

Life history parameter	Productivity category			
	High	Medium	Low	Very low
r_{max} (1/year)	>0.5	0.16–0.50	0.05–0.15	<0.05
K (1/year)	>0.3	0.16–0.30	0.05–0.15	<0.05
Fecundity (1/year)	>10,000	100–1,000	10–100	<10
t_m (years)	<1	2–4	5–10	>10
t_{max} (years)	1–3	4–10	11–30	>30

Table 7.2. Decline thresholds as a function of resilience/productivity and population decline.

[Adapted from Musick (1999). **Observed population decline:** Threshold is percentage of rate of decline in numbers or biomass of mature individuals in a marine fish population over the longer of 10 years or 3 generations]

Decline thresholds	
Productivity category	Observed population decline
High	0.99
Medium	0.95
Low	0.85
Very Low	0.70

As an example, a fish with high fecundity ($>10^4$), but late maturity (5–10 years), and long life span (>30 years), would be classified under the Very Low Productivity category. Generally, populations having VBGM growth coefficients (K) less than 0.10 and (or) intrinsic rates of increase (r_{max}) less than 10 percent per year may be especially vulnerable.

Once a population’s productivity category is established, the second tier of the assessment considers rates of population decline (table 7.2). Population trends are analyzed over the longer of two periods: 1 decade or 3 generations. Information about decline (from Musick, 1999) is based on (1) population decline observed, estimated, inferred, or suspected in the past, or (2) population decline projected or suspected in the future based on (a) direct observation; (b) an index of abundance appropriate for the taxon; (c) a decrease in area of occupancy, extent of occurrence, and (or) quality of habitat; (d) actual or potential levels of exploitation; or (e) the effects of introduced taxa, hybridization, pathogens, pollutants, competitors, or parasites.

Richness Species richness is the number of different species represented in an ecological community, landscape, or region. Species richness is simply a count of species, and it does not take into account the abundances of the species or their relative abundance distributions. [3]

R-Selection Rapid growth and occupation through early reproduction, short life spans, low biomass, and many offspring.

Salinity The concentration of salts dissolved in water, measured in parts per thousand (‰) or practical salinity units (psu). Seawater averages 34 psu. Arctic salinities typically range from 27 to 32 psu. Ocean salinity is generally defined as the salt concentration (for example, sodium and chloride) in sea water. Salinity is most frequently measured in practical salinity units, a unit based on the properties of seawater conductivity, which is equivalent to parts per thousand or to grams per kilogram.

Semelparous Refers to a strategy whereas reproduction or breeding occurs only once in a lifetime.

Stock size (in weight) The weight of a fish stock or of some defined portion of a fish is known as biomass. Biomass is indicative of energy flows and the relative importance of a particular species to an assemblage or community level of organization. The established relations between fish length and weight are critical to the development of other key population parameters (Ricker, 1975).

Temperature Temperature is arguably the most important environmental variable to fish; Reynolds (1977, p. 734) describes this importance thusly:

Temperature serves as a proximate factor (cue, guidepost, sign stimulus, or directive factor) affecting locomotor responses of fishes. Although temperature can also serve as an ultimate ecological factor, as in behavioral thermoregulation, nonthermal factors may in some cases provide the ultimate adaptive or ecological value of a temperature response; some examples are habitat selection, intraspecific size segregation, interspecific niche differentiation, isolating mechanisms, predator avoidance, prey location, escape reactions, and migrations (thermoperiodic, diel, seasonal, spawning). Conversely, nonthermal variables such as light intensity or water depth may act as accessory proximate factors in thermoregulation. In spawning migrations, thermal requirements of eggs and larvae may take precedence over the (often different) preferenda or optima of adults. Although thermal responses of fishes are largely innate and species specific, ontogenetic and other changes can occur. Since temperature can serve as an unconditioned reinforcer in operant conditioning, thermal responses are not limited to simple kineses or taxes. Nonthermal factors such as photoperiod, circadian rhythms, currents, social and biotic interactions, stresses, infections, or chemicals can affect thermal responses, and may account for some lack of conformity between laboratory preferenda and field distributions and behaviors.

Trophic level The step in a nutritive series, or food chain, of an ecosystem. The organisms of a chain are classified into these levels on the basis of their feeding behavior. The first and lowest level contains the producers, green plants. The plants or their products are consumed by the second-level organisms—the herbivores, or plant eaters. At the third level, primary carnivores, or meat eaters, eat the herbivores; and at the fourth level, secondary carnivores, eat the primary carnivores. These categories are not strictly defined, as many organisms feed on several trophic levels; for example, some carnivores also consume plant materials or carrion and are called omnivores, and some herbivores occasionally consume animal matter. A separate trophic level, the decomposers, or transformers, consists of organisms such as bacteria and fungi that break down dead organisms and waste materials into nutrients usable by the producers.

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Appendixes

Appendix A. Ongoing and Recently Completed Fishery Studies Funded by Bureau of Ocean Energy Management in Arctic Outer Continental Shelf Lease Areas

Table A1 provides a comprehensive list with descriptions and access to reports of the following studies can be accessed at <http://www.boem.gov/Environmental-Stewardship/Environmental-Studies/Alaska/Index.aspx>.

Table A1. Ongoing studies in the Arctic Outer Continental Shelf lease areas.

[Blank cells indicate that the species occurrence has not been confirmed in that sea. Marine waters out to the U.S. Exclusive Economic Zone (200-mile limit) are included]

Bureau of Ocean Energy Management study	Research topic	Researcher organization
Genomics of Arctic Cod	Genetic structure and diversity	U.S. Geological Survey
U.S.-Canada Transboundary fish and lower trophic communities	Ecological baselines of marine fish and invertebrates in the Beaufort Sea	University of Alaska, Fairbanks, Department of Fisheries and Oceans Canada
Trophic links: Forage fish, their prey, and Ice Seals in the northeast Chukchi Sea	Food habits and trophic linkages of ice seals	University of Alaska, Fairbanks
Dispersal patterns and summer ocean distribution of adult Dolly Varden from the Wulik River, Alaska, using satellite tags	Coastal and ocean habitats of Dolly Varden	Alaska Department of Fish and Game
Population assessment of Snow Crab, <i>Chionoecetes opilio</i> , in the Chukchi and Beaufort Seas (including oil and gas lease areas)	Population dynamics of snow crabs	University of Alaska, Fairbanks
Distribution and habitat use of fish in the nearshore ecosystem of the Beaufort and Chukchi Seas (Alaska Coastal Ecosystem Survey)	Coastal habitat use by marine fish	National Oceanic and Atmospheric Administration Alaska Fisheries Science Center
Distribution of fish, crab, and lower trophic communities in the Chukchi Sea lease area (Arctic Integrated Ecosystem Survey)	Ecological baselines of fish and invertebrates in the northeastern Chukchi Sea	University of Alaska, Fairbanks, National Oceanic and Atmospheric Administration Alaska Fisheries Science Center

Table A2. Recently completed Bureau of Ocean Energy Management studies by year of completion.

Year	Bureau of Ocean Energy Management selected reference citations
2014	Bluhm, B., Huettmann, Falk, and Norcross, Brenda, 2014, Ecological analysis of 2008 western Beaufort Sea data: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEM 2014-014.
	Hopcroft, R.R., and Clarke, Cheryl, 2013, Retrieval of historical arctic fisheries survey data: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEM 2014-084, 45 p.
	Morris, M.C., 2014, Alaska shorezone coastal habitat mapping protocol: Seldovia, Alaska, Contract Report by Nuka Research and Planning Group LCC for the Bureau of Ocean Energy and Energy Management (BOEM), Anchorage, Alaska, 164 p. [Also available at http://alaskafisheries.noaa.gov/shorezone/chmprotocolO114.pdf].
	Talbot, S.L., Sage, G.K., Sonsthagen, S.A., and Fowler, M.C., 2014, Arctic Cod pilot genomics study—Preliminary results from analyses of mitochondrial DNA: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEM 2014-050, 29 p.
	Zimmerman, C.E., and von Biela, C.E., 2014, Investigation of population of origin and migration of Arctic Cisco found in the Colville River, Alaska using molecular and otolith tools: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEM 2014-019, 107 p.
2013	Carothers, C., Cotton, S., and Moerlein, K., 2013, Subsistence use and knowledge of salmon in Barrow and Nuiqsut, Alaska: Fairbanks, Alaska, University of Alaska Coastal Marine Institute and U.S. Department of the Interior, BOEM, Alaska OCS Region, OCS Study BOEM 2012-0115. [Also available at http://www.boem.gov/BOEM-Newsroom/Library/Publications/2013/BOEM-2013-0015pdf.aspx]
2012	Dunton, K.H., 2012, Chukchi Sea offshore monitoring in drilling area (COMIDA)—Chemical and Benthos (CAB): Anchorage, Alaska, prepared by University of Texas for U.S. Department of the Interior, BOEM Alaska OCS Region, Final Report, OCS Study BOEM 2012-012. [Also available at http://www.data.boem.gov/P1/PDFimages/ES_P1S/5/5182.pdf].
	Norcross, B.L., Holladay, B.A., and Mecklenburg, C.W., 2012, Recent and historical distribution and ecology of demersal fishes in the Chukchi Sea planning area: Fairbanks, Alaska, University of Alaska Coastal Marine Institute and U.S. Department of the Interior, BOEM, Alaska OCS Region, OCS Study BOEM 2012-073. [Also available at: http://www.boem.gov/BOEM-Newsroom/Library/Publications/2012/CMI-2012-073_pdf.aspx].
2011	Hardy, S.M., Iken, Katrin, Hundertmark, Kris, Albrecht, Greg, 2011, Defining genetic structure in Alaskan populations of the snow crab, <i>Chionoecetes opilio</i> : Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEMRE 2011-060, 31 p.
	Konar, Brenda, 2012, Recovery in a high Arctic kelp community: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEM 2012-0II, 24 p.
	Loggerwell, Elizabeth, Rand, Kimberly, Parker-Stetter, Sandra, Horne, John, Weingartner, Tom, and Bluhm, Bodil, 2010, Beaufort Sea marine fish monitoring 2008—Pilot survey and test of hypotheses: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEMRE 2010-048, 262 p.
	Pirtle, J.L., and Mueter, F.J., 2011, Beaufort Sea fish and their trophic linkages—Literature search and synthesis: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, BOEMRE 2011-021, 47 p.
2007	Murphy, S.M., Mueter, F.J., and Braund, S.R., 2007, Variation in the abundance of Arctic Cisco in the Colville River—Analysis of existing data and local knowledge, volumes I and II: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, MMS 2007-042, 240 p.
2004	MBC Applied Environmental Sciences, 2004, Proceedings of a workshop on the variability of Arctic Cisco (Qaaktaq) in the Colville River: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, MMS 2004-033, 90 p.
1998	Kline, T., Jr., and Goering, J., 1998, North Slope amphidromy assessment: Anchorage, Alaska, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, MMS 1998-006, 90 p.

Appendix B. Age-At-Size and Length-Weight Relationships for Arctic Marine Fishes

The Bureau of Ocean Energy Management (BOEM) Alaska Outer Continental Shelf (OCS) Region is in the process of publishing new age-at-size and length-weight relationships for marine fish species from new studies in the U.S. Chukchi and Beaufort Seas. As this report was nearing publication, a summary of the length-weight relationships from BOEM's U.S.–Canada Transboundary study in the Beaufort Sea was provided to the USGS (Brenda L. Norcross and others, University of Alaska, Fairbanks, written commun., 2016; and Kelly L. Walker, University of Alaska, Fairbanks, written commun., 2016). The transboundary study included field collections in offshore waters of the southeastern Beaufort and western Arctic Canada between 2012 and 2014.

There were 20 species for which sufficient numbers of fish were captured so that length-weight relationships could be established (table B1). The species are from nine families: Gadidae–*Boreogadus saida*, Cottidae–*Gymnocanthus tricuspidis*, *Icelus bicornis*, *I. spatula*, *Triglops nybelini*, and *Triglops pingelii*, Psychrolutidae–*Cottunculus microps*, Agonidae–*Aspidophoroides olrikii*, Cyclopteridae–*Eumicretremus derjugini*, Liparidae–*Careproctus* sp. and *Liparis fabricii*, Zoarcidae–*Lycodes adolfi*, *L. polaris*, *L. sagittarius* and *L. seminudus*, Stichaeidae–*Anisarchus medius*, *Lumpenus fabricii* and *Sticheaus punctatus*, and Pleuronectidae–*Reinhardtius hippoglossoides*. Fish sampling encompassed pelagic and benthic environments of the Beaufort Sea and the minimum and maximum lengths reported for each species varied greatly. The weight-at-length regressions fit the data closely, with r^2 values of 0.90–0.99 and all intercepts (a) were near zero (table B1). The range of slopes (b) was 2.49–3.59. A b value close to 3.0 indicates isometric growth, that is, growth of all body parts occurs at the same rate; values outside of that range indicate allometric growth, that is, the body changes shape with growth. The b value also indicates body shape; negative allometric growth ($b < 3$) and positive allometric growth ($b > 3$) indicate decreasing or increasing body thickness or plumpness with increasing fish length (Brenda L. Norcross and others, University of Alaska, Fairbanks, written commun., 2016; and Kelly L. Walker, University of Alaska, Fairbanks, written commun., 2016).

Table B1. Summary of length-weight relationships of marine fish collected in the U.S.–Canada transboundary study in the Beaufort Sea.

[Source: Brenda L. Norcross and others, University of Alaska, Fairbanks, written commun., 2016; and Kelly L. Walker, University of Alaska, Fairbanks, written commun., 2016. *a*: intercepts. *b*: range of slopes. *r*²: coefficient of determination. **Abbreviations:** g, gram; mm, millimeter]

Species	Number	Weight range (g)	Length range (mm)	<i>a</i> *10 ⁵	<i>b</i>	<i>r</i> ²
<i>Boreogadus saida</i>	2,877	0.03–106.13	15–240	0.587	3.01	0.98
<i>Artediellus scaber</i>	137	0.03–13.63	14–95	1.690	2.98	0.99
<i>Gymnocanthus tricuspid</i>	683	0.08–20.89	19–119	0.315	3.33	0.99
<i>Icelus bicornis</i>	97	0.23–4.45	27–68	0.270	3.37	0.96
<i>Icelus spatula</i>	412	0.09–7.86	24–89	0.488	3.20	0.90
<i>Triglops nybelini</i>	15	4.29–14.67	81–118	0.425	3.14	0.93
<i>Triglops pingelli</i>	234	0.15–14.30	26–130	0.834	2.97	0.98
<i>Cottonculus microps</i>	14	1.27–208.33	45–223	2.770	2.93	0.99
<i>Asidophoroides olrikii</i>	335	0.04–3.69	23–80	0.351	3.17	0.93
<i>Eumicretemus derjugini</i>	8	0.23–14.48	15–64	4.170	3.07	0.99
<i>Careproctus</i> sp.	41	0.72–112.53	47–145	0.071	3.59	0.98
<i>Liparis fabricii</i>	120	0.07–112.53	19–212	0.050	3.58	0.93
<i>Lycodes adolfi</i>	232	0.19–26.62	38–205	0.201	3.09	0.97
<i>Lycodes polaris</i>	64	0.24–26.79	40–164	0.161	3.26	0.99
<i>Lycodes saggittarius</i>	191	0.33–347.60	44–427	0.812	2.88	0.92
<i>Lycodes seminudus</i>	154	0.30–535.99	41–465	1.540	2.82	0.98
<i>Anisarchus medius</i>	65	0.23–5.15	49–134	2.790	2.49	0.93
<i>Lumpenus fabricii</i>	157	0.13–5.11	41–124	0.755	2.78	0.97
<i>Sticheaus punctatus</i>	7	0.17–0.71	29–48	0.122	3.42	0.94
<i>Reinhardtius hippoglossoides</i>	9	400.20–1,481.23	351–525	0.366	3.15	0.92

As part of this USGS study, the age and growth relationships for 19 marine fishes were reviewed and age-length and length-weight regressions are presented from collections in Arctic Alaska and adjacent seas. In certain instances, regressions are presented for data obtained from species collections in high-latitude areas far-removed from the Beaufort and Chukchi Seas, such as the Barents Sea. These examples highlight the limited availability of data for many species. In every case, the data are color-coded by investigator and area of fish collection. Because of the present-day ecological interest in *Boreogadus saida*, the most current length-weight relationship described for this species from the Beaufort Sea, as indicated in [table B1](#), is included for comparison with the historical data.

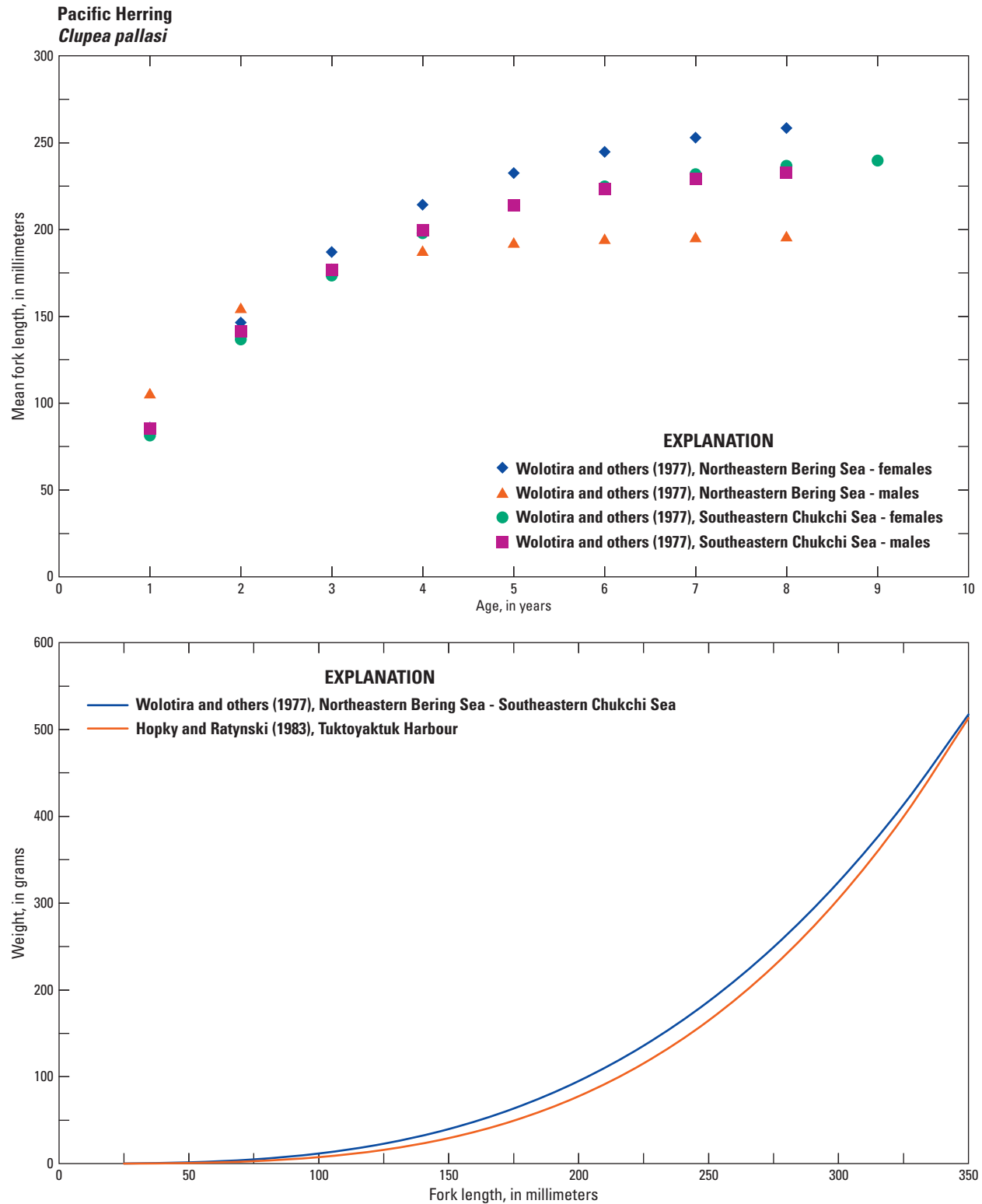


Figure B1. Age-at-length and length-weight relationships for Pacific Herring (*Clupea pallasii*). Data from Wolotira and others (1977).

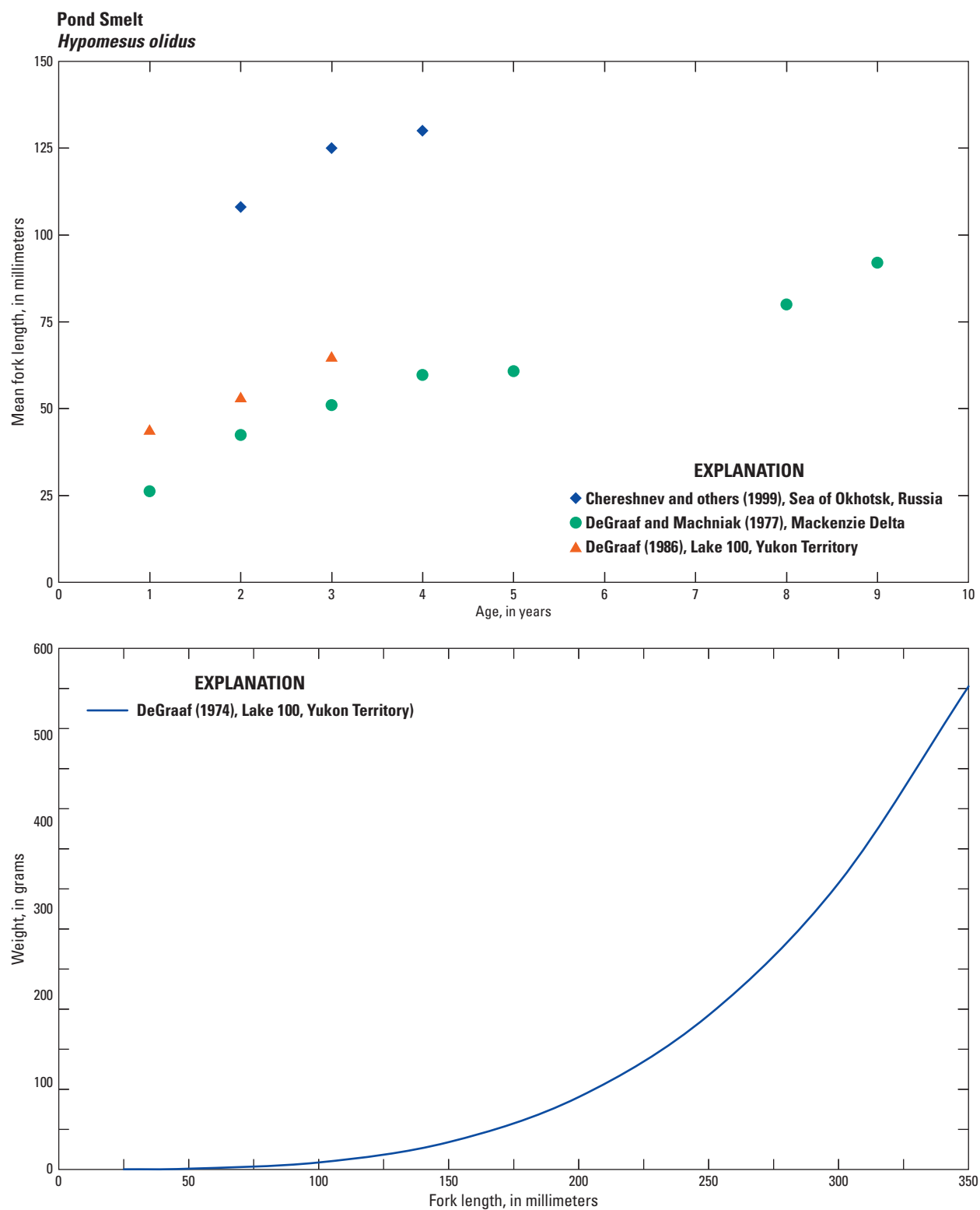


Figure B2. Age-at-length and length-weight relationships for Pond Smelt (*Hypomesus olidus*).

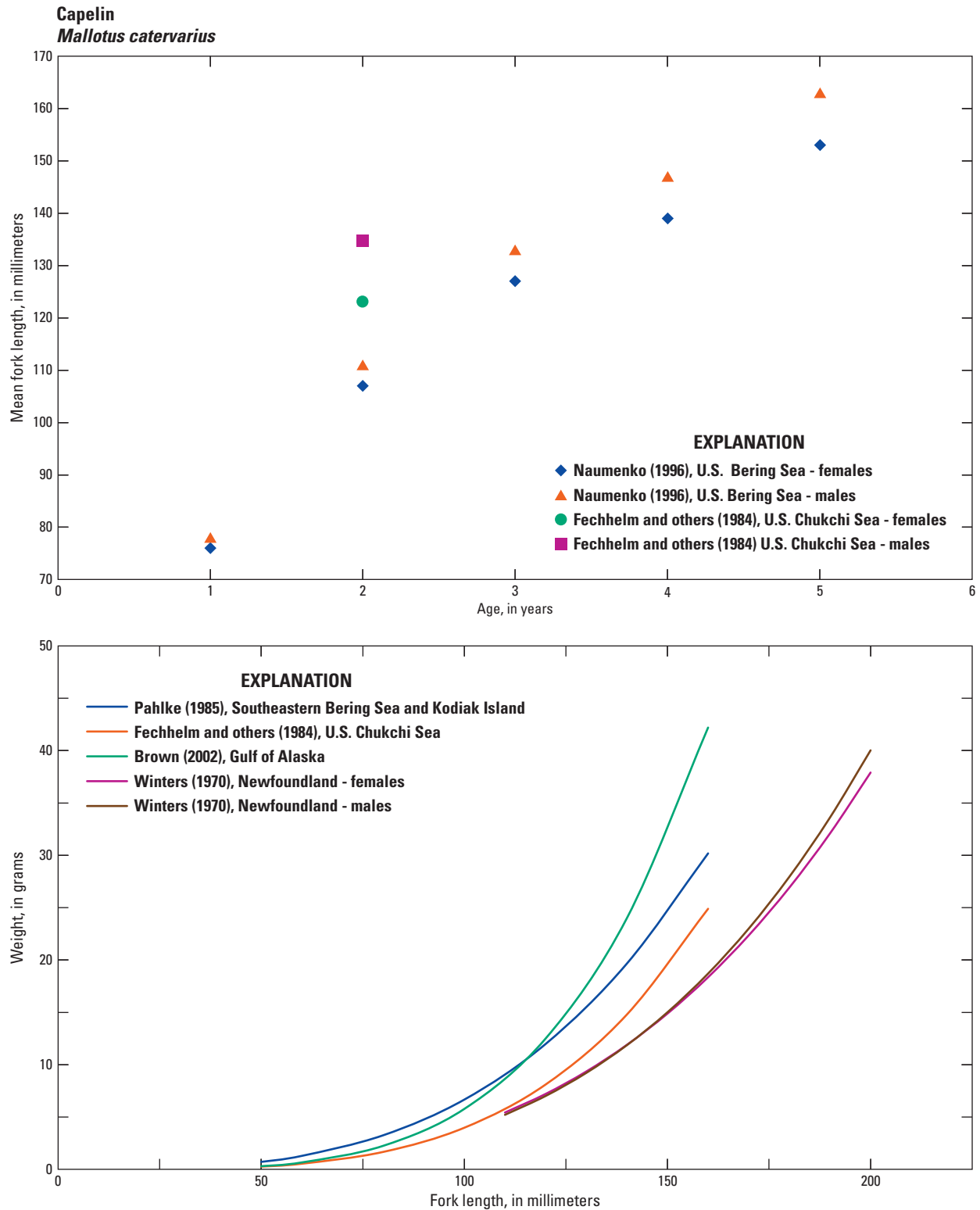


Figure B3. Age-at-length and length-weight relationships for Capelin (*Mallotus catervarius*).

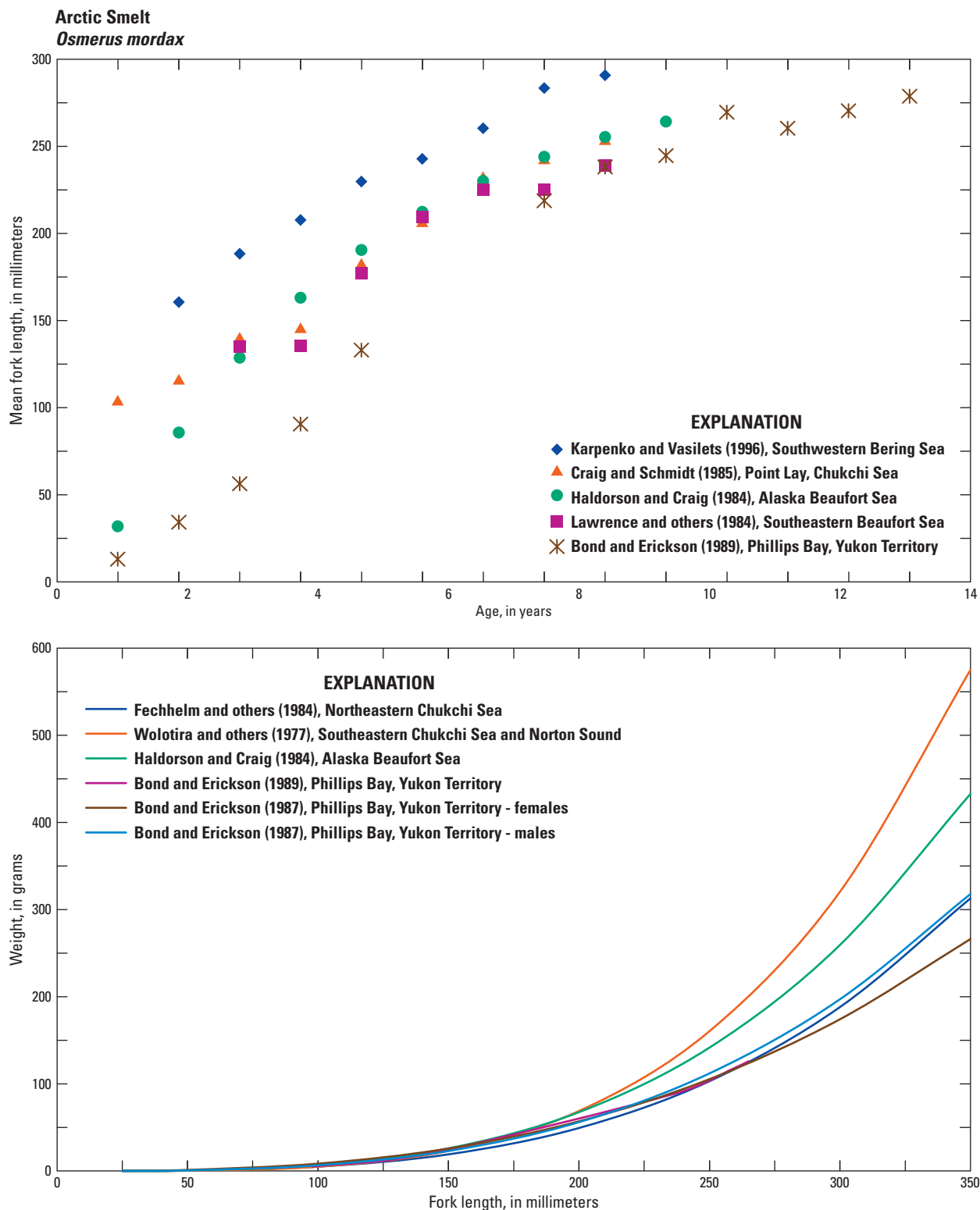


Figure B4. Age-at-length and length-weight relationships for Arctic Smelt (*Osmerus dentex*)

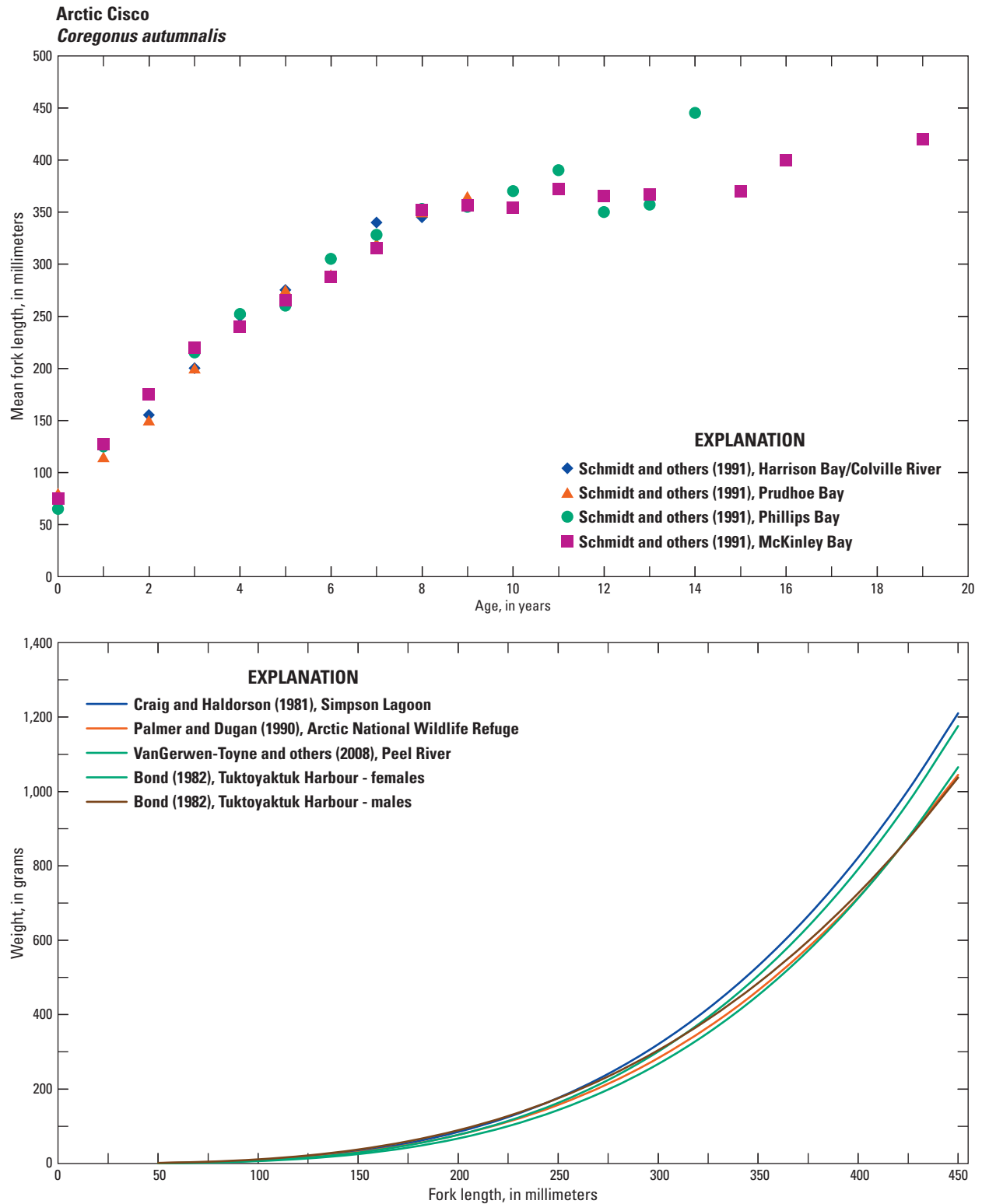


Figure B5. Age-at-length and length-weight relationships for Arctic Cisco (*Coregonus autumnalis*). Data from Schmidt and others (1991).

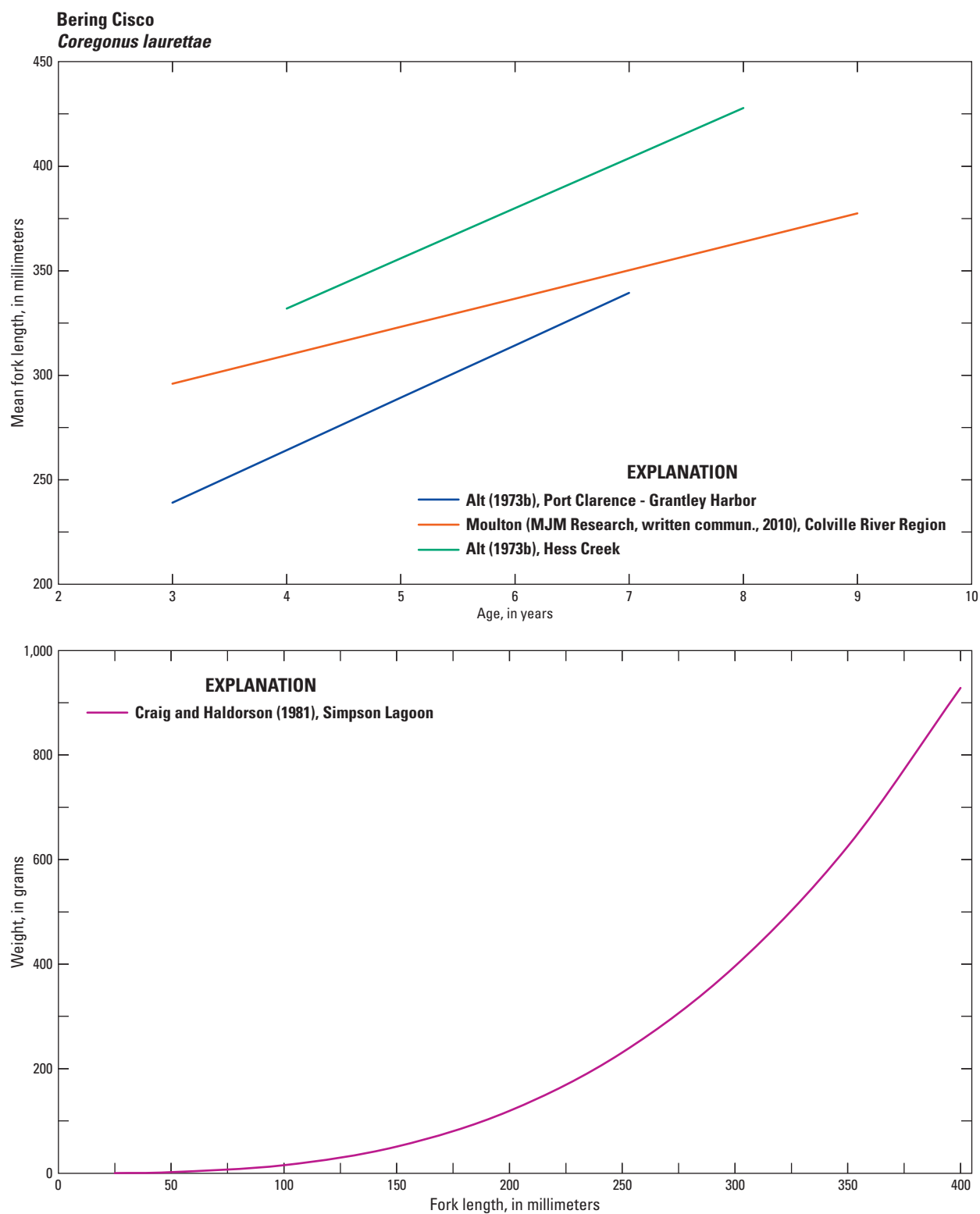


Figure B6. Age-at-length and length-weight relationships for Bering Cisco (*Coregonus laurettae*).

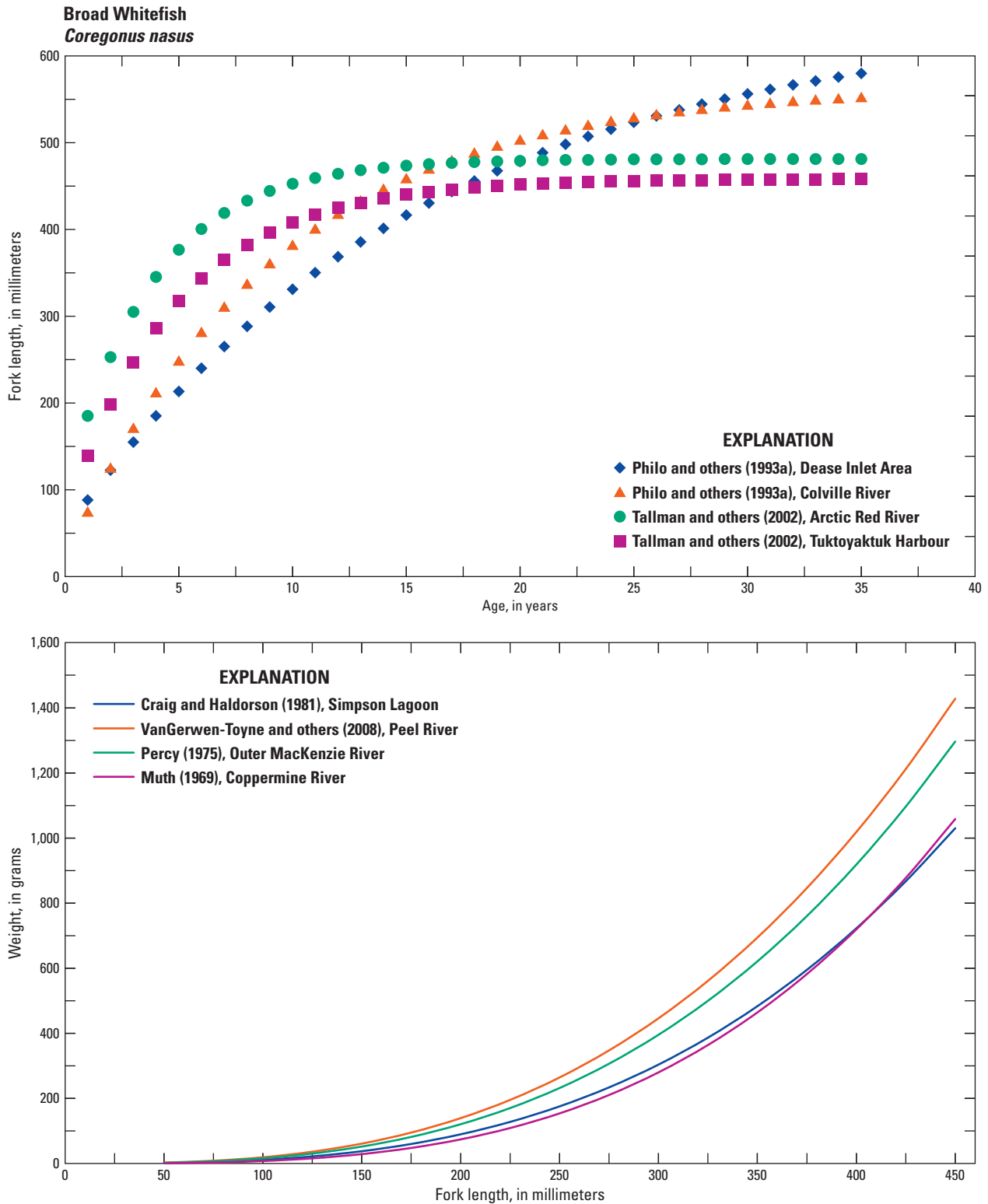


Figure B7. Age-at-length and length-weight relationships for Broad Whitefish (*Coregonus nasus*).

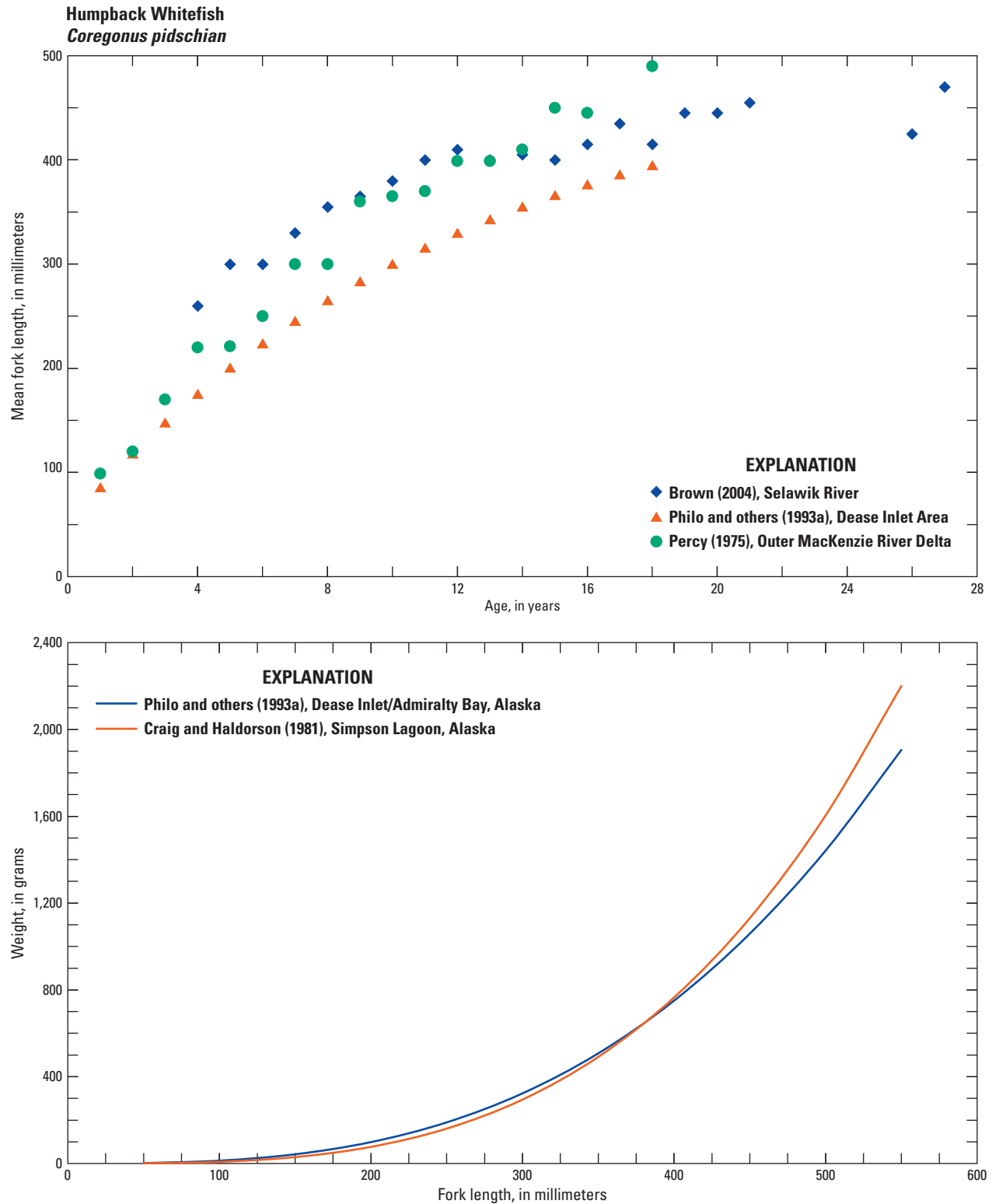


Figure B8. Age-at-length and length-weight relationships for Humpback Whitefish (*Coregonus pidschian*)

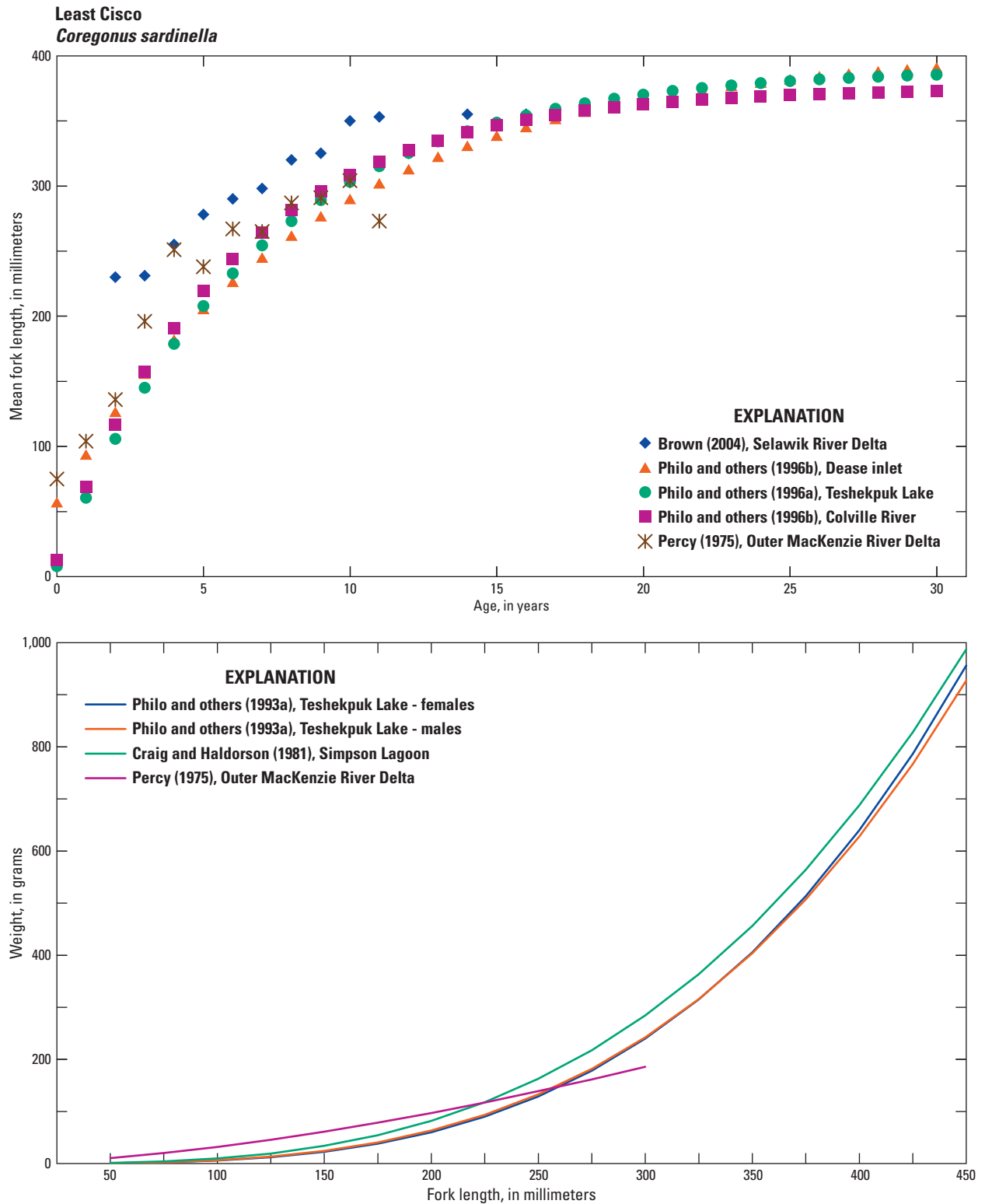


Figure B9. Age-at-length and length-weight relationships for Least Cisco (*Coregonus sardinella*).

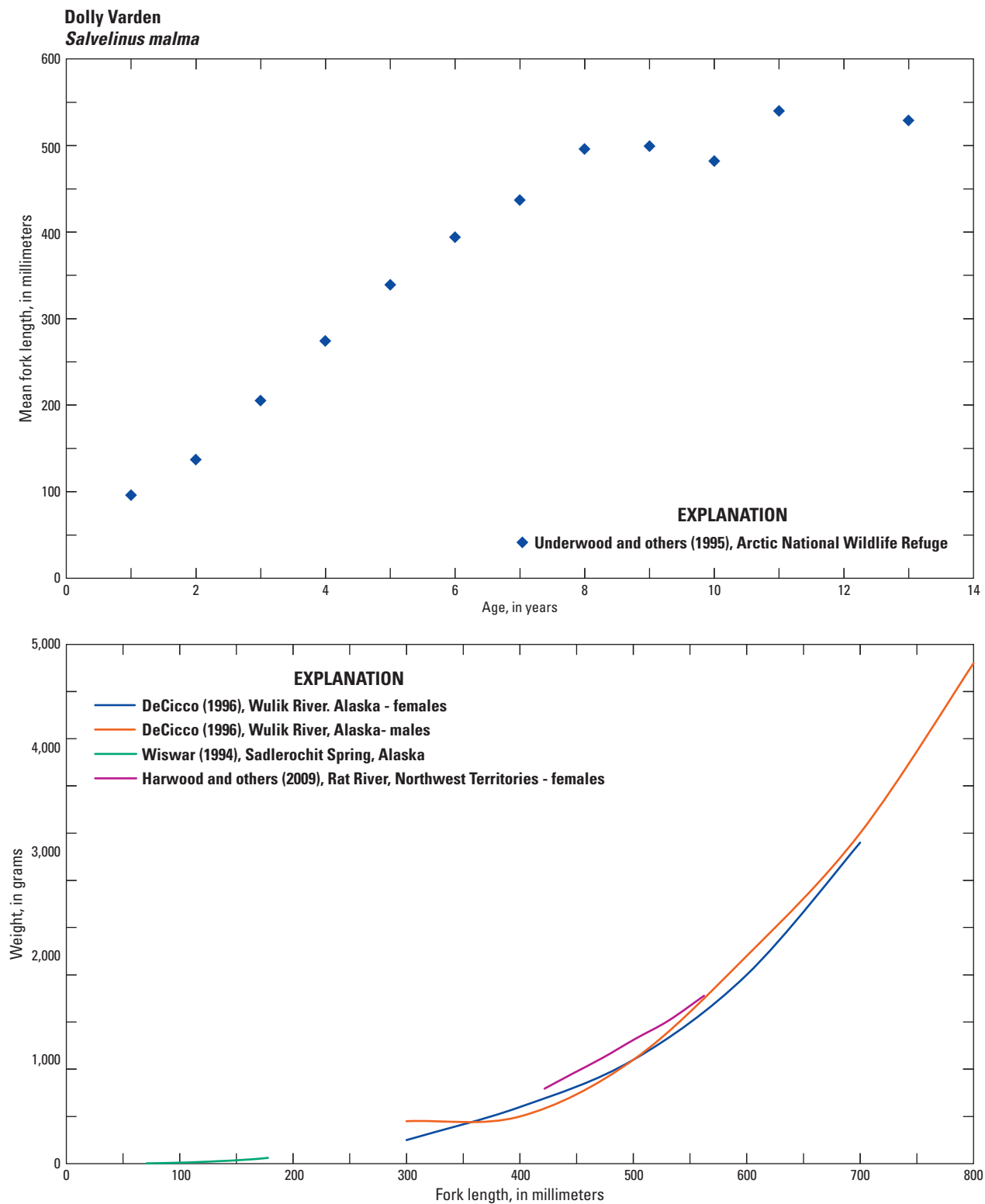


Figure B10. Age-at-length and length-weight relationships for Dolly Varden (*Salvelinus malma*). Age-length relationship not described from U.S. Beaufort and Chukchi Seas.

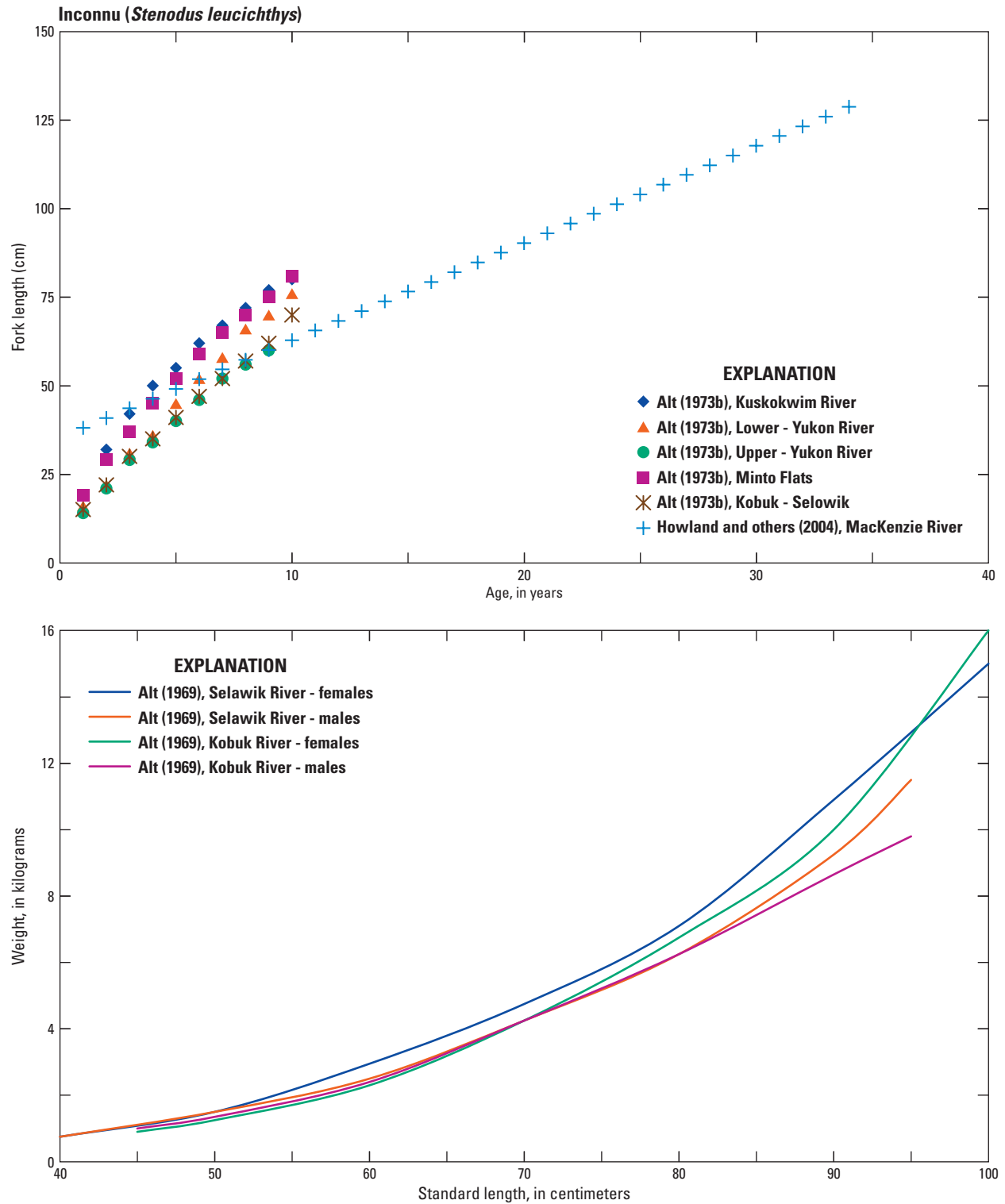


Figure B11. Age-at-length and length-weight relationships for Inconnu (*Stenodus leucichthys*).

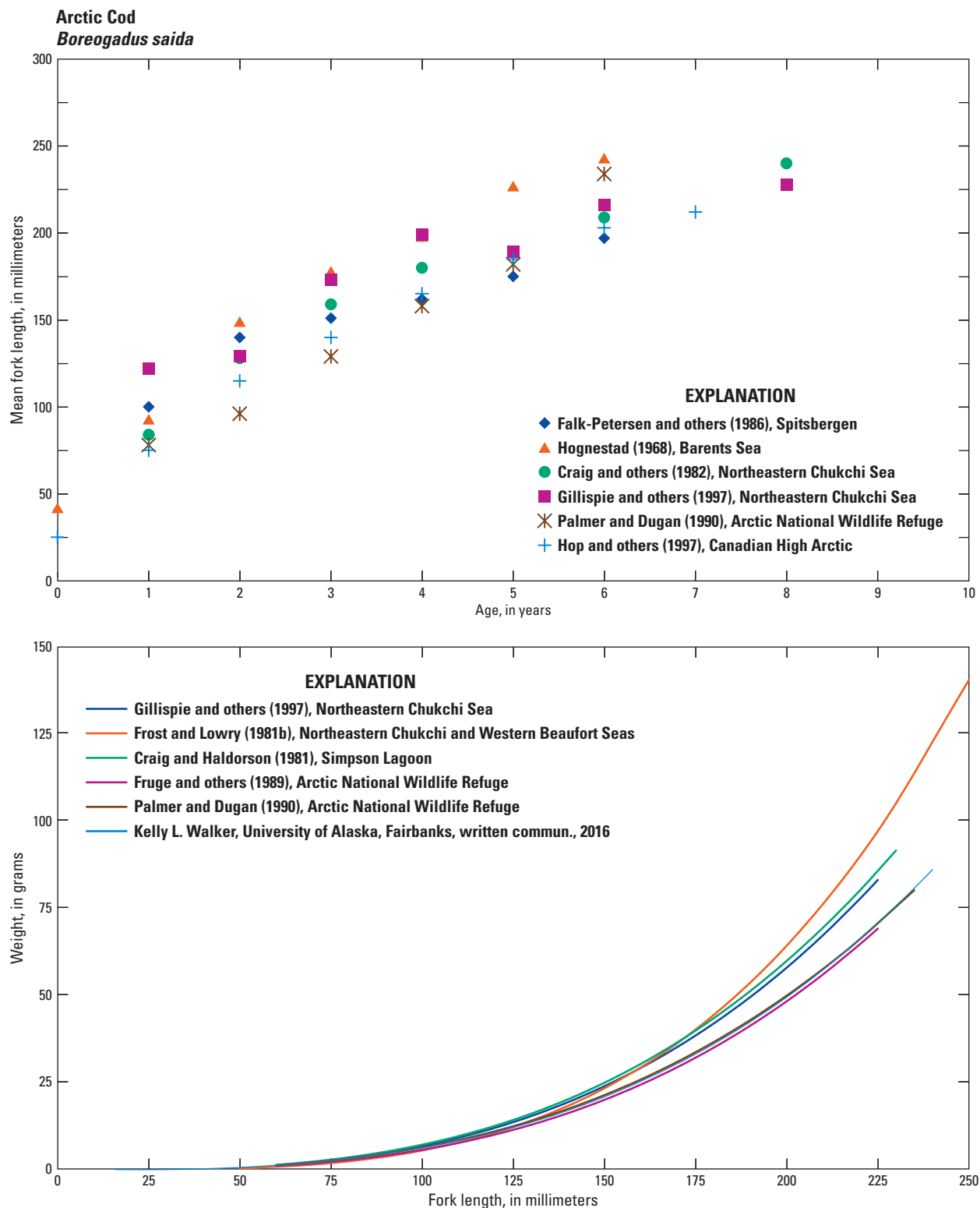


Figure B12. Age-at-length and length-weight relationships for Arctic Cod (*Boreogadus saida*).

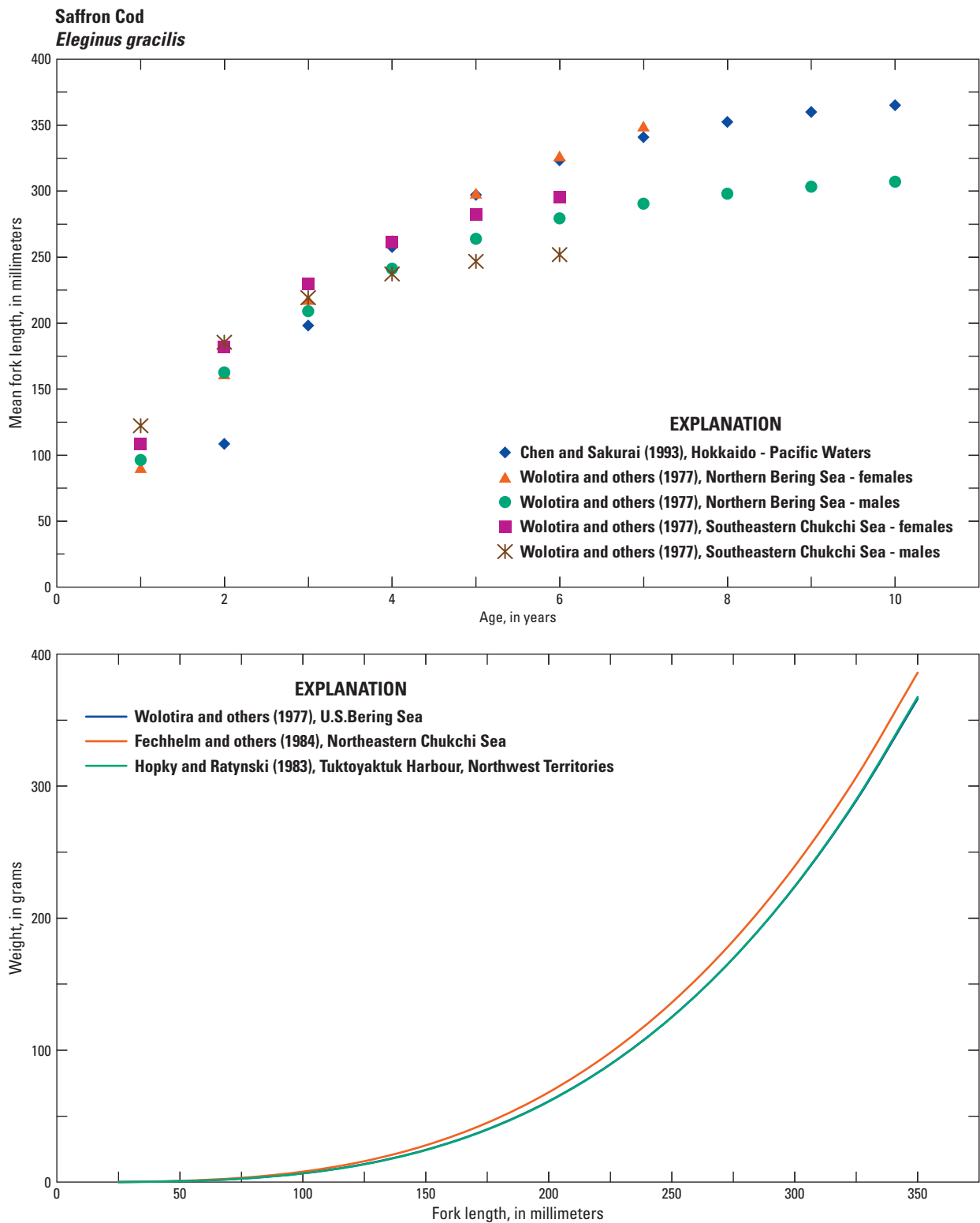


Figure B13. Age-at-length and length-weight relationships for Saffron Cod (*Eleginus gracilis*).

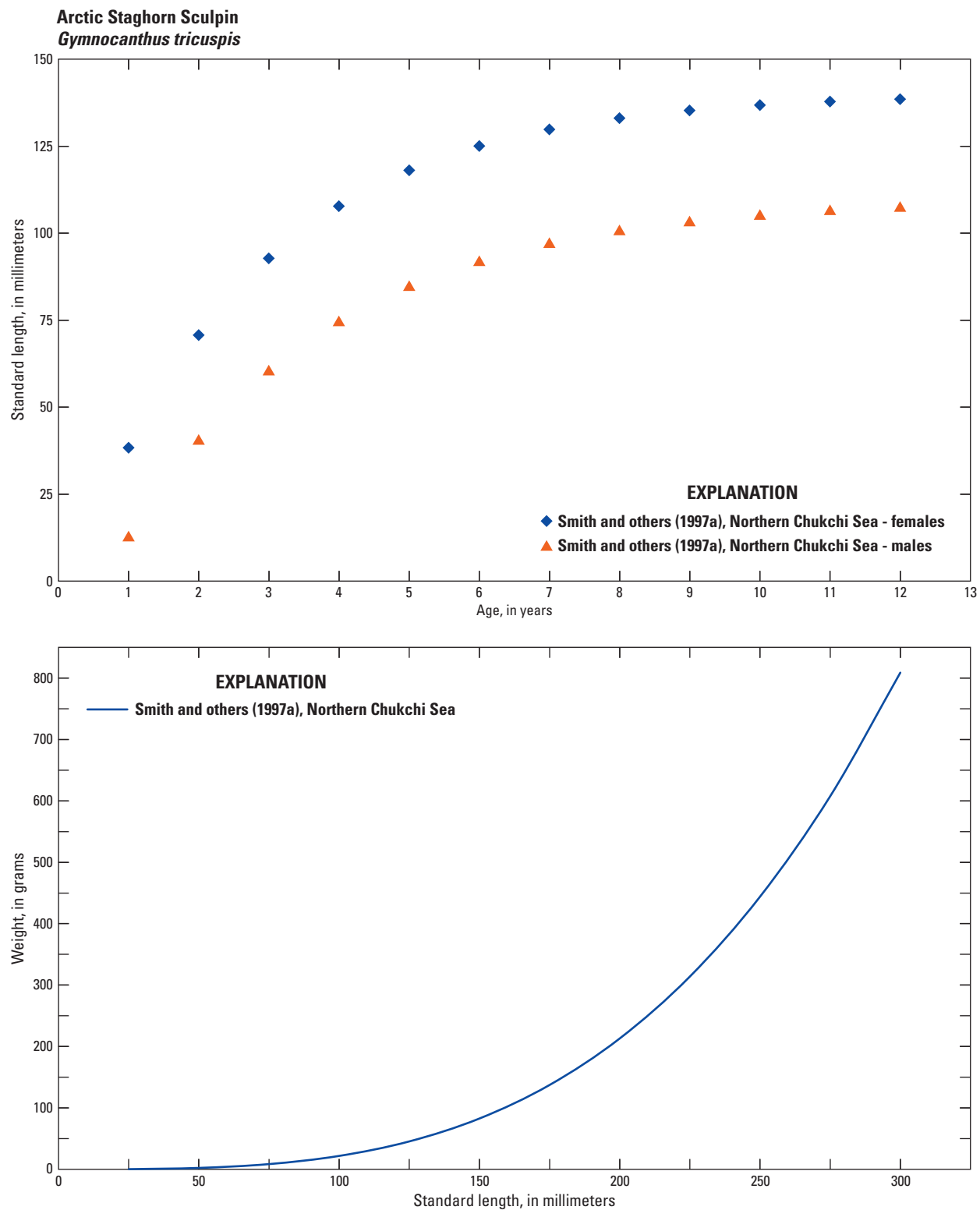


Figure B14. Age-at-length and length-weight relationships for Arctic Staghorn Sculpin (*Gymnochanthus tricusps*).

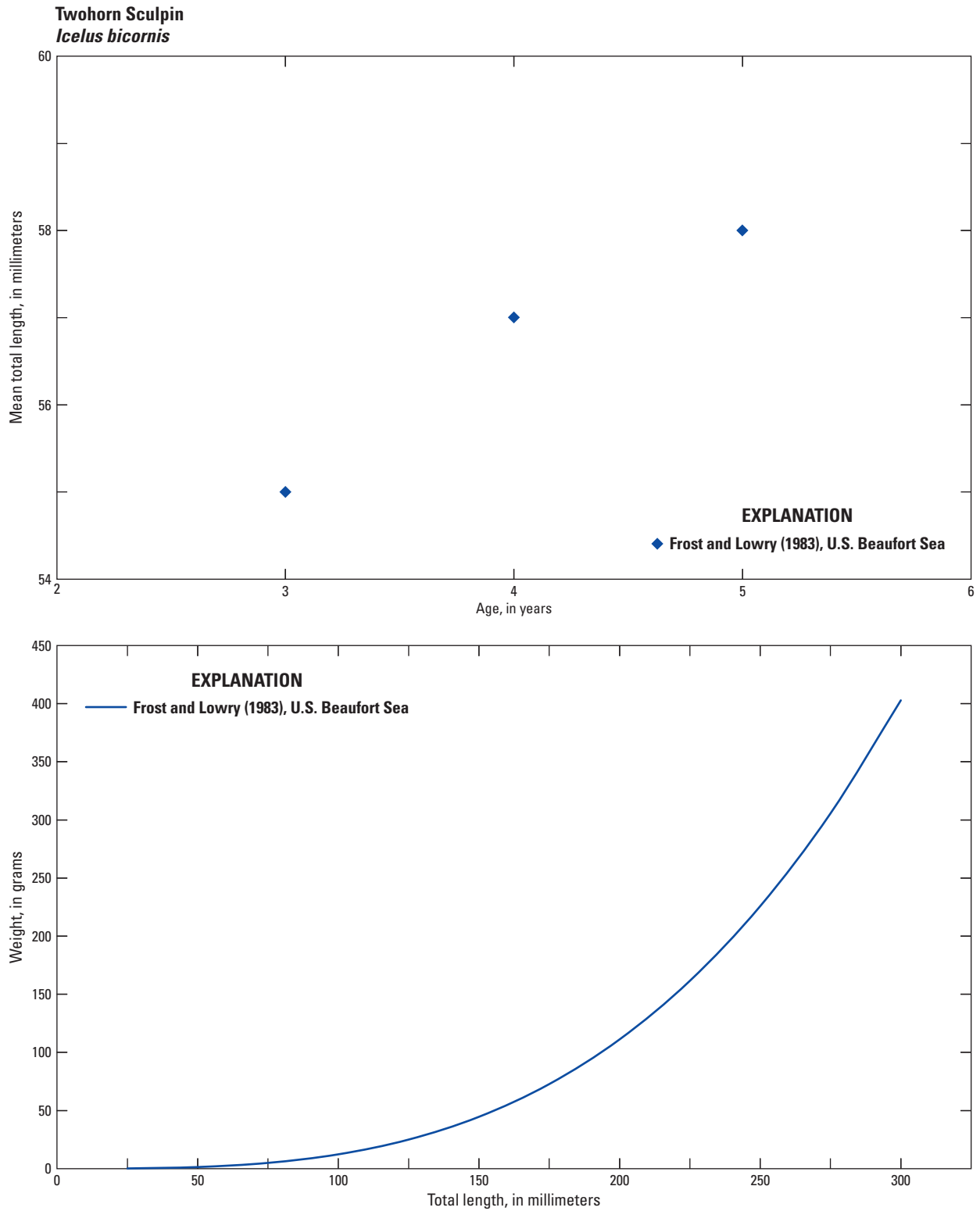


Figure B15. Age-at-length and length-weight relationships for Twohorn Sculpin (*Icelus bicornis*).

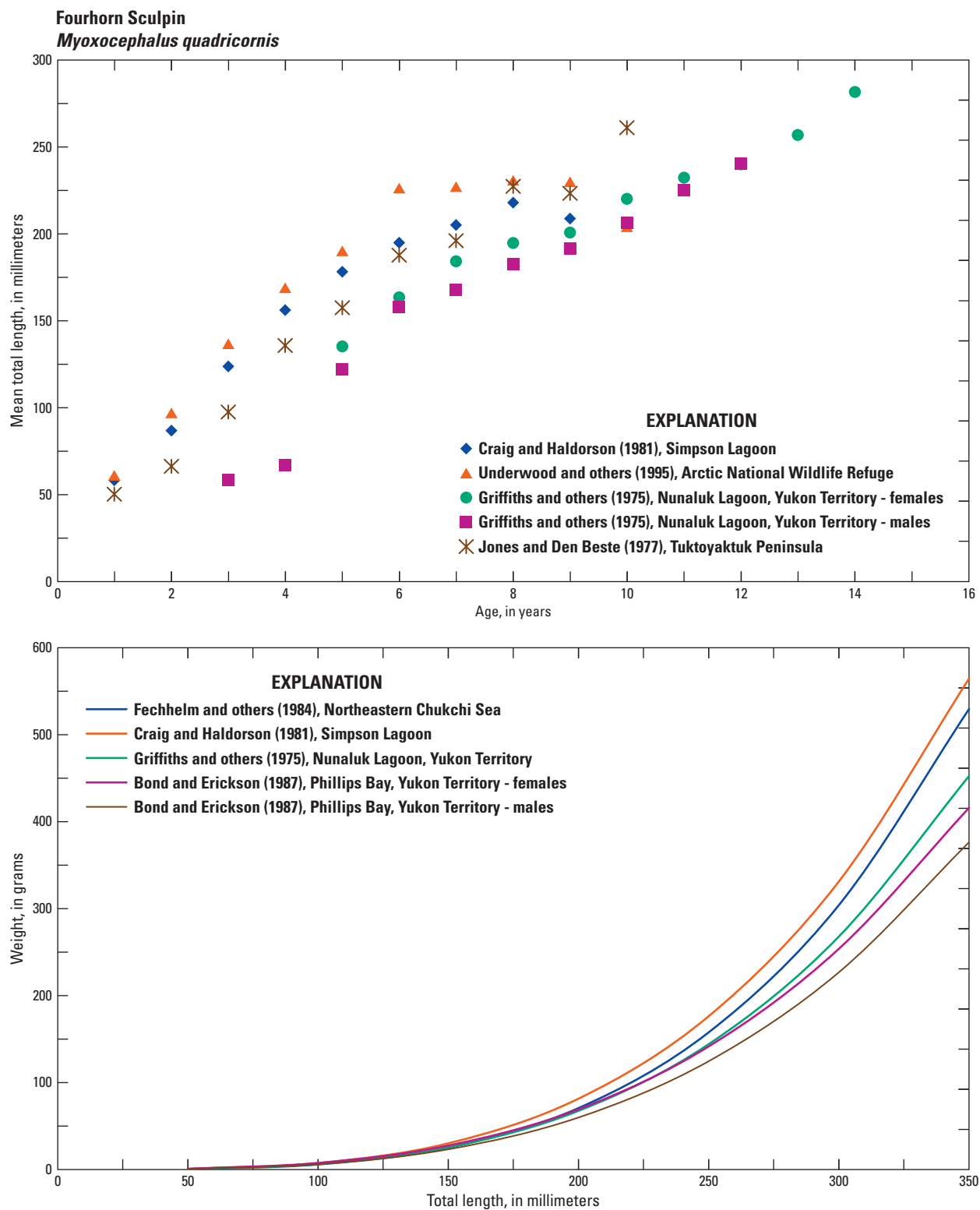


Figure B16. Age-at-length and length-weight relationships for Fourhorn Sculpin (*Myoxocephalus quadricornis*).

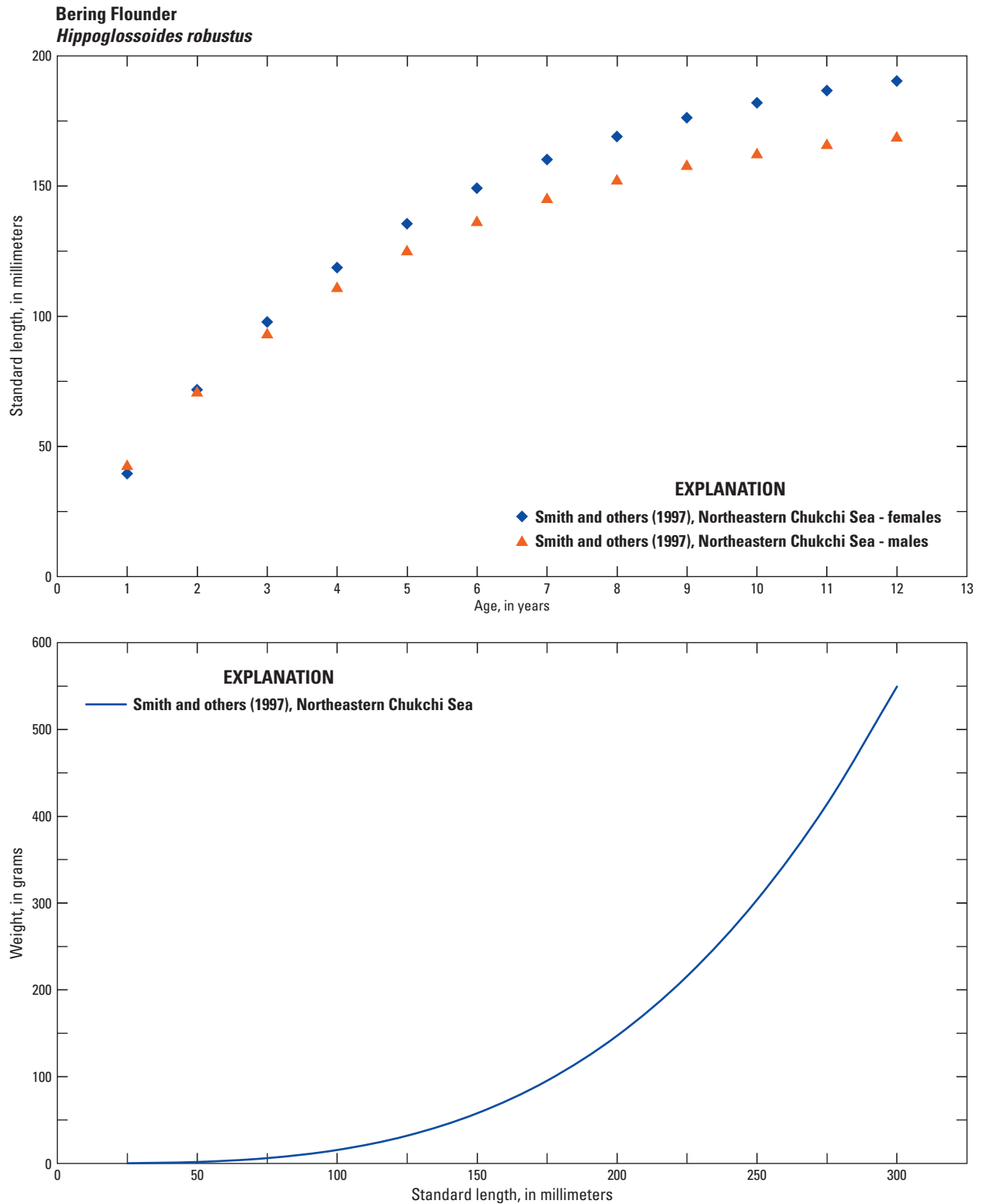


Figure B17. Age-at-length and length-weight relationships for Bering Flounder (*Hippoglossoides robustus*).

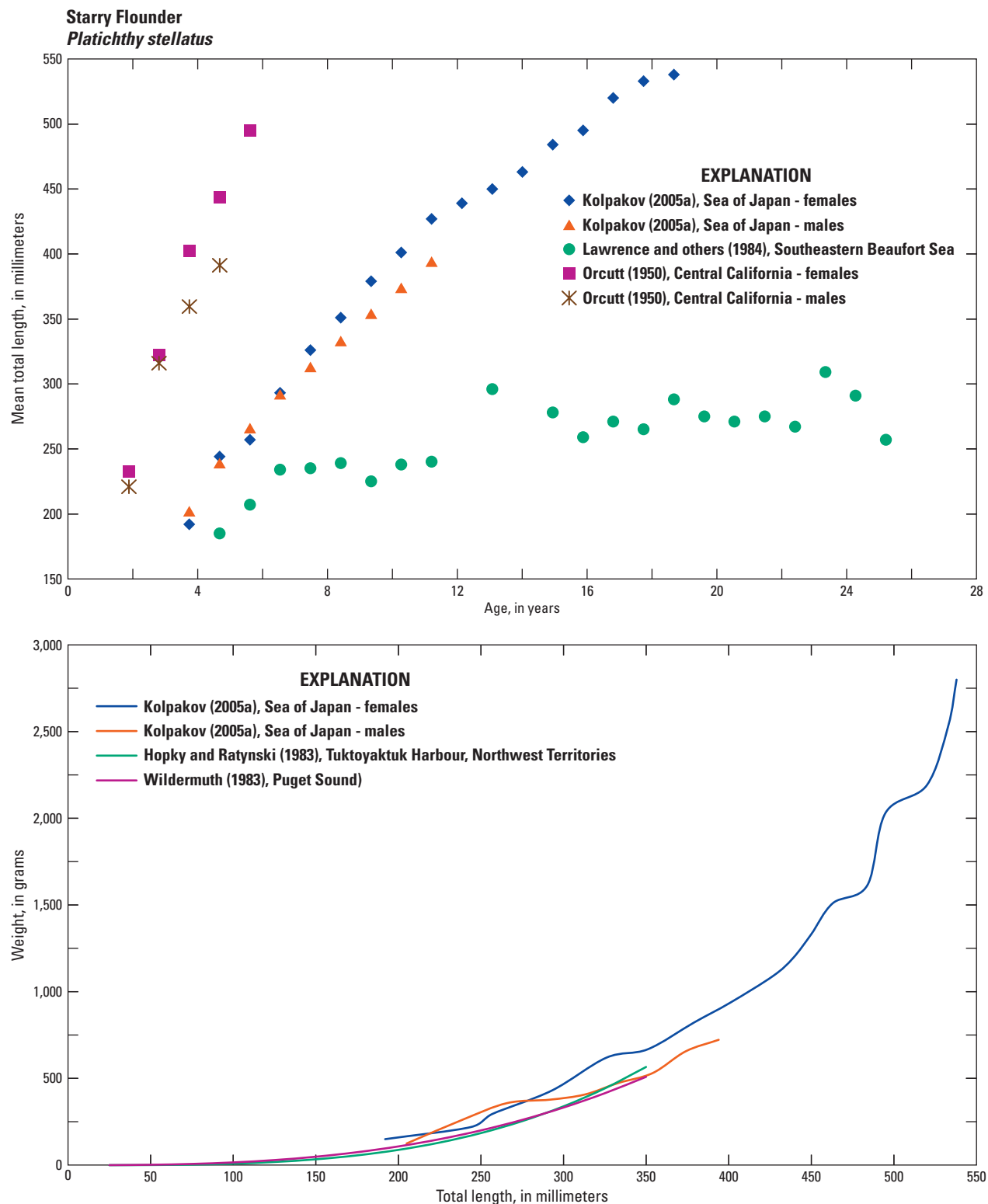


Figure B18. Age-at-length and length-weight relationships for Starry Flounder (*Platichthys stellatus*).

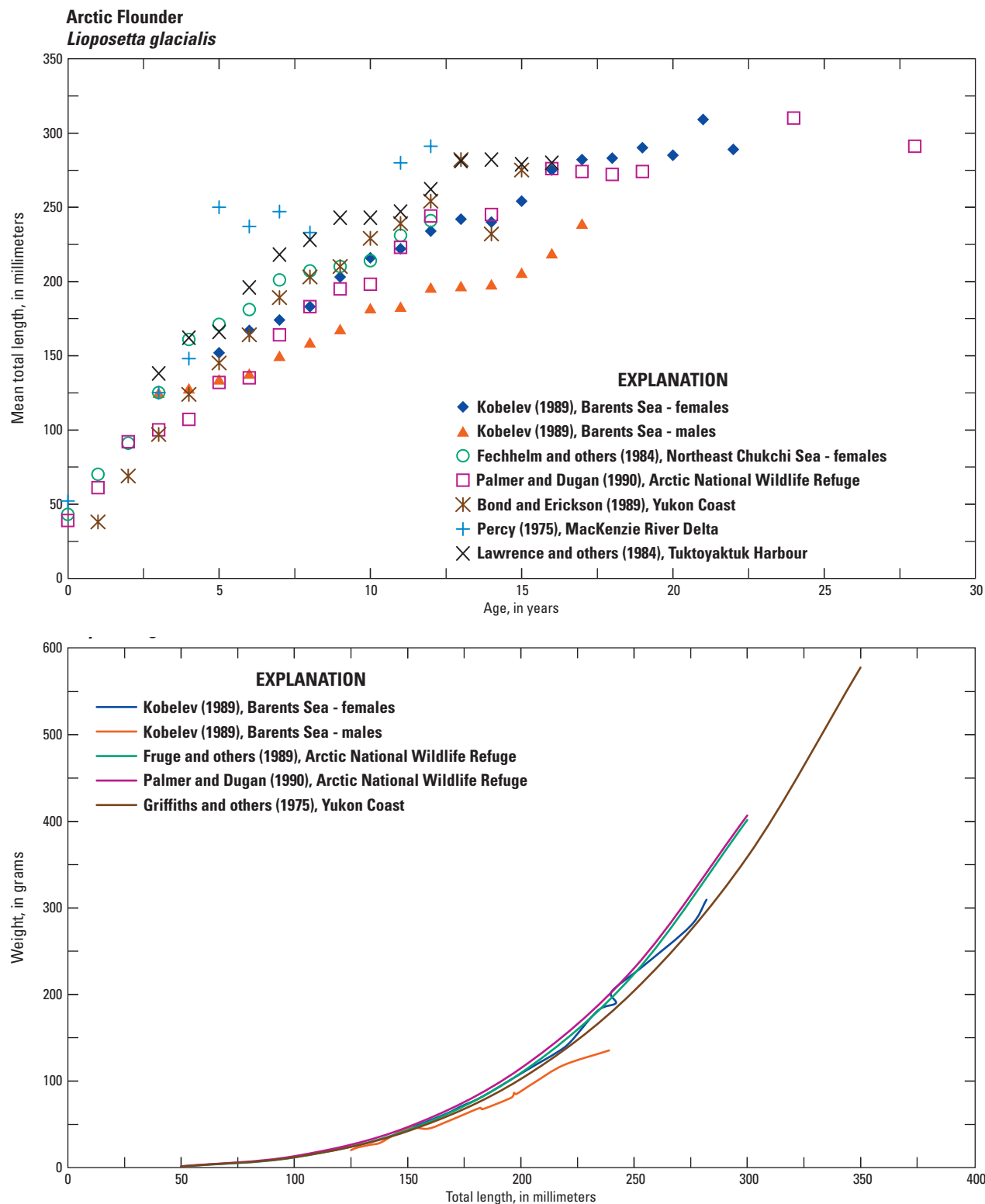


Figure B19. Age-at-length and length-weight relationships for Arctic Flounder (*Lioposetta glacialis*) from the Chukchi, Beaufort, and Barents Seas.

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Appendix C. Models Evaluated for Simulating Effects of Climate Change on the Distributions and Abundances of Arctic Cod and Saffron Cod in the Eastern Bering Sea

Table C1. Candidate models evaluated in search of a model to simulate the distribution (presence/absence) of Arctic Cod in the eastern Bering Sea using a smooth (s) GAM model.

[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Arctic Cod (<i>Boreogadus saida</i>) distribution models								
gam(<i>Boreogadus saida</i>) family=binomial,method="REML" smooth (s) models								
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n		FALSE	TRUE
s(GEAR_TEMPERATURE,BOTTOM_DEPTH,SURFACE_TEMPERATURE)	2,781.838	54.70	1,425.3	0.524	9,423	FALSE	8,349	339
						TRUE	173	562
s(GEAR_TEMPERATURE,BOTTOM_DEPTH)	2,941.793	51.30	1,504.3	0.484	9,423	FALSE	8,343	377
						TRUE	179	524
s(GEAR_TEMPERATURE,SURFACE_TEMPERATURE)	2,976.595	50.80	1,515.9	0.493	9,423	FALSE	8,356	388
						TRUE	166	513
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	2,797.761	53.50	1,419.1	0.511	9,423	FALSE	8,357	365
						TRUE	165	536
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH)	2,946.398	50.90	1,488.9	0.482	9,423	FALSE	8,355	388
						TRUE	167	513
s(GEAR_TEMPERATURE) + s(SURFACE_TEMPERATURE)	3,129.55	47.90	1,584.6	0.466	9,432	FALSE	8,366	419
						TRUE	156	482
s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	5,484.76	8.15	2,759.9	0.052	9,432	FALSE	8,521	899
						TRUE	1	2

Table C2. Candidate models evaluated in search of a model to predict the distribution of Arctic Cod in the eastern Bering Sea using a tensor smooth and (or) interaction smooth GAM models.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Arctic Cod (<i>Boreogadus saida</i>) distribution models								
Tensor product smooths (te) and Tensor product Interaction (ti) models gam(<i>Boreogadus saida</i>) family=binomial,method="REML"								
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n		FALSE	TRUE
te(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE) ¹	2,663.922	56.5	1,338	0.545	9,423	FALSE	8,367	314
						TRUE	155	587
te(GEAR_TEMPERATURE, BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	2,782.59	53.8	1,402.3	0.515	9,423	FALSE	8,349	351
						TRUE	173	550
te(GEAR_TEMPERATURE, BOTTOM_DEPTH)	2,915.461	51.4	1,463.2	0.487	9,423	FALSE	8,344	370
						TRUE	178	531
te(GEAR_TEMPERATURE, SURFACE_TEMPERATURE) + s(BOTTOM_DEPTH)	2,740.1	54.6	1,386.5	0.528	9,423	FALSE	8,342	326
						TRUE	180	575
te(GEAR_TEMPERATURE, SURFACE_TEMPERATURE) + te(GEAR_TEMPERATURE, BOTTOM_DEPTH)	2,708	55.3	1,377	0.534	9,423	FALSE	8,355	328
						TRUE	167	573
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE)	4,473.568	26.2	2,340.7	0.307	9,423	FALSE	8,428	625
						TRUE	94	276
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH) + te(SURFACE_TEMPERATURE)	3,452	42.50	1,766.4	0.447	9,423	FALSE	8,376	426
						TRUE	146	475

¹Selected as the best model based on model fit, low Akaike Information Criterion (AIC) score and the percent of deviance explained by the model.

Table C3. Candidate models evaluated in search of a model to predict abundance of Arctic Cod in the eastern Bering Sea using a smooth (s) GAM model.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Arctic Cod (<i>Boreogadus saida</i>) abundance models					
gam(ln(abundance +1)) method="REML" smooth (s) models					
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n
s(GEAR_TEMPERATURE,BOTTOM_DEPTH, SURFACE_TEMPERATURE)	20,072.9	51	10,190	0.505	9,423
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	19,500.69	53.25	9,794.7	0.531	9,423
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH)	19,618	52.50	9,846.2	0.524	9,423
s(GEAR_TEMPERATURE,BOTTOM_DEPTH)	23,235.07	30.50	11,671	0.303	9,423
s(GEAR_TEMPERATURE) + s(SURFACE_TEMPERATURE)	19,741.89	51.90	9,904.7	0.518	9,423
s(GEAR_TEMPERATURE,SURFACE_TEMPERATURE)	19,530.79	53.10	9,828.3	0.529	9,423
s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	26,186.95	4.64	13,120	0.0448	9,423

Table C4. Candidate models evaluated in search of a model to predict abundance of Arctic Cod in the eastern Bering Sea using a tensor smooth and (or) interaction smooth GAM model.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Arctic Cod (<i>Boreogadus saida</i>) abundance models					
Tensor product smooths (te) and Tensor product Interaction (ti) models gam(ln(abundance +1)) method="REML"					
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n
te(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE) ¹	18,772.98	57.10	9,501.1	0.568	9,423
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE)	24,648.37	19.50	12,413	0.191	9,423
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH)+ te(SURFACE_TEMPERATURE)	21,108.77	44.40	10,600	0.443	9,423
ti(GEAR_TEMPERATURE, SURFACE_TEMPERATURE)+ te(BOTTOM_DEPTH)	25,968.32	6.91	13,047	0.0672	9,432
te(GEAR_TEMPERATURE, SURFACE_TEMPERATURE)+ te(BOTTOM_DEPTH)	20,081.09	50.20	10,096	0.501	9,432
te(GEAR_TEMPERATURE)	20,833.78	45.80	10,428	0.458	9,432
te(SURFACE_TEMPERATURE)	26,546.83	0.68	13,281	0.00643	9,432
te(BOTTOM_DEPTH)	26,450.3	1.69	13,229	0.0165	9,423

¹Selected as the best model based on model fit, low Akaike Information Criterion (AIC) score and the percent of deviance explained by the model.

Table C5. Candidate models evaluated in search of a model to predict distribution of Saffron Cod in the eastern Bering Sea using a smooth (s) GAM model.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Saffron Cod (<i>Eleginus gracilis</i>) distribution models									
Models gam(<i>Eleginus gracilis</i>) family=binomial,method="REML" smooth(s) models									
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n		FALSE	TRUE	
s(GEAR_TEMPERATURE,BOTTOM_DEPTH, SURFACE_TEMPERATURE) ¹	2,026.113	51.60	1,022.6	0.422	9,423	FALSE	8,794	298	
						TRUE	98	233	
s(GEAR_TEMPERATURE,BOTTOM_DEPTH)	2,103.427	49.20	1,063.4	0.388	9,423	FALSE	8,798	316	
						TRUE	94	215	
s(GEAR_TEMPERATURE,SURFACE_TEMPERATURE)	2,628.688	36.70	1,329.5	0.325	9,423	FALSE	8,823	351	
						TRUE	69	180	
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE) ²	2,048.516	50.60	1,035.1	0.417	9,423	FALSE	8,796	286	
						TRUE	96	245	
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH)	2,134.97	48.10	1,072.6	0.38	9,423	FALSE	8,804	322	
						TRUE	88	209	
s(GEAR_TEMPERATURE) + s(SURFACE_TEMPERATURE)	2,662.401	35.50	1,346.5	0.312	9,423	FALSE	8,829	362	
						TRUE	63	169	
s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	2,061.879	50.00	1,039.2	0.408	9,423	FALSE	8,780	285	
						TRUE	112	246	
s(BOTTOM_DEPTH, SURFACE_TEMPERATURE)	2,069.542	50.00	1,044.4	0.398	9,423	FALSE	8,795	309	
						TRUE	97	222	

¹Identified as a potential best model.²Selected as the best model after reviewing the environmental response curves for the other models even though the Akaike Information Criterion (AIC) is higher and the deviance explained was lower.

Table C6. Candidate models evaluated in search of a model to predict distribution of Saffron Cod in the eastern Bering Sea using a tensor smooth and (or) interaction smooth GAM model.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Saffron Cod (<i>Eleginus gracilis</i>) distribution models									
gam(<i>Eleginus gracilis</i>) family=binomial,method="REML" tensor product smooths (te) and Tensor product Interaction (ti) models									
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n		FALSE	TRUE	
te(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE) ¹	1,953.825	53.80	967.42	0.45	9,423	FALSE	8,814	286	
						TRUE	78	245	
te(BOTTOM_DEPTH, SURFACE_TEMPERATURE)	2,041.313	50.60	1,022.7	0.414	9,423	FALSE	8,780	287	
						TRUE	112	244	
te(BOTTOM_DEPTH) + te(SURFACE_TEMPERATURE)	2,074.152	49.60	1,040.5	0.402	9,423	FALSE	8,784	305	
						TRUE	108	226	
te(GEAR_TEMPERATURE, BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	2,030.963	51.10	1,017.7	0.422	9,423	FALSE	8,805	295	
						TRUE	87	236	
te(GEAR_TEMPERATURE, BOTTOM_DEPTH)	2,109.372	48.90	1,051.7	0.387	9,423	FALSE	8,809	329	
						TRUE	83	202	
te(GEAR_TEMPERATURE, SURFACE_TEMPERATURE) + s(BOTTOM_DEPTH)	1,990.718	52.20	1,003.1	0.44	9,423	FALSE	8,806	281	
						TRUE	86	250	
te(GEAR_TEMPERATURE, SURFACE_TEMPERATURE) + te(GEAR_TEMPERATURE, BOTTOM_DEPTH)	1,964.257	53.10	998.51	0.446	9,423	FALSE	8,813	288	
						TRUE	79	243	
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE)	2,564.903	38.70	1,316.4	0.381	9,423	FALSE	8,827	320	
						TRUE	65	211	
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH) + te(SURFACE_TEMPERATURE)	2,365.397	42.90	1,203.3	0.375	9,423	FALSE	8,810	326	
						TRUE	82	205	
ti(BOTTOM_DEPTH, SURFACE_TEMPERATURE) + s(BOTTOM_DEPTH)	2,028.882	50.90	1,021.3	0.416	9,423	FALSE	8,772	281	
						TRUE	120	250	

¹Identified as a potential best model.

Table C7. Candidate models evaluated in search of a model to predict abundance of Saffron Cod in the eastern Bering Sea using a smooth (s) GAM model.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Saffron Cod (<i>Eleginus gracilis</i>) abundance models					
gam(ln(abundance +1)) method="REML" smooth (s) models					
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n
s(GEAR_TEMPERATURE,BOTTOM_DEPTH, SURFACE_TEMPERATURE)	18,888.36	56	9,597.5	0.55	9,423
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	19,871.85	49.90	9,997.6	0.497	9,423
s(GEAR_TEMPERATURE) + s(BOTTOM_DEPTH)	20,658.18	45.40	10,370	0.453	9,423
s(GEAR_TEMPERATURE,BOTTOM_DEPTH)	20,606.26	45.80	10,367	0.457	9,423
s(GEAR_TEMPERATURE) + s(SURFACE_TEMPERATURE)	21,309.22	41.50	10,699	0.414	9,423
s(GEAR_TEMPERATURE,SURFACE_TEMPERATURE)	20,304.42	47.50	10,219	0.474	9,423
s(BOTTOM_DEPTH) + s(SURFACE_TEMPERATURE)	20,783.68	44.70	10,434	0.446	9,423

Table C8. Candidate models evaluated in search of a model to predict abundance of Saffron Cod in the eastern Bering Sea using a tensor smooth and (or) interaction smooth GAM models.[Abbreviations: REML, restricted maximum likelihood; r^2 , coefficient of determination; n, number]

Saffron Cod (<i>Eleginus gracilis</i>) abundance models					
gam(ln(abundance + 1)) method="REML" tensor product smooths (te) and Tensor product Interaction (ti) models					
Model	Akaike Information Criterion	Deviance (percent)	REML score	r^2	n
te(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE) ¹	17,389.91	61.80	8,795.9	0.615	9,423
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH, SURFACE_TEMPERATURE)	18,566.81	56.50	9,408.1	0.563	9,423
ti(GEAR_TEMPERATURE, BOTTOM_DEPTH)+ te(SURFACE_TEMPERATURE)	20,012.76	49.00	10,046	0.489	9,423
ti(GEAR_TEMPERATURE, SURFACE_TEMPERATURE)+ te(BOTTOM_DEPTH)	20,115.11	48.50	10,135	0.484	9,423
te(GEAR_TEMPERATURE, SURFACE_TEMPERATURE)+ te(BOTTOM_DEPTH)	19,389.26	52.40	9,755	0.522	9,423
te(GEAR_TEMPERATURE)	22,310.26	34.70	11,165	0.347	9,423
te(SURFACE_TEMPERATURE)	25,199.78	11.30	12,612	0.113	9,423
te(BOTTOM_DEPTH)	22,614.04	32.60	11,319	0.326	9,423

¹Selected as the best model based on model fit, low Akaike Information Criterion (AIC) score and the percent of deviance explained by the model.

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For more information concerning the research in this report, contact the

Regional Director, Alaska
U.S. Geological Survey
4210 University Drive
Anchorage, Alaska 99508-4560

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