AN ASSESSMENT OF POTENTIAL MINING IMPACTS ON SALMON ECOSYSTEMS OF BRISTOL BAY, ALASKA

VOLUME 2—APPENDICES A-D

Appendix B: Non-Salmon Freshwater Fishes of the Nushagak and Kvichak River Drainages

Author: Michael Wiedmer, Malma Consulting (mwiedmer_malma@gci.net)

NON-SALMON FRESHWATER FISHES OF THE NUSHAGAK AND KVICHAK RIVER DRAINAGES

INTRODUCTION

The fresh waters of the Nushagak and Kvichak river drainages in southwest Alaska (Figure 2-3, 2-4 in main assessment report) support diverse fish assemblages that combined total at least 9 families, 17 genera, and 29 species (Table Appendix B-1). An additional six species: Pacific herring *Clupea pallasii*, Pacific cod *Gadus macrocephalus*, saffron cod *Eleginus gracilis,* Pacific staghorn sculpin *Leptocottus armatus*, Arctic flounder *Pleuronectes glacialis,* and starry flounder *Platichthys stellatus* are primarily marine species that venture into the lower reaches of the drainages (Mecklenburg et al. 2002; Morrow 1980b) and are not discussed here. The five species of North American Pacific salmon, keystones of the region's ecological and economic systems, are reviewed in Appendix A of this assessment. Appendix B provides biological, ecological, and human use information for the other 24 species supported by the waters of the Nushagak and Kvichak river drainages.

This appendix is divided in two sections. The *Harvested fish* section describes seven species that are, or have been, targeted by subsistence, sport, and/or commercial fisheries within the fresh waters of the Nushagak and Kvichak river drainages, and that are well distributed across the two drainages. The *Other species* section covers, in less detail, the remaining species that are not major targets of local fisheries or species that are not broadly distributed across the watersheds, but that nonetheless play important ecological roles in the Nushagak and Kvichak river drainages. The relative lack of directed studies limits the information available on the abundance, life history, and ecology of many non-harvested fish species.

HARVESTED FISH

Each of the species described in this section: northern pike, humpback whitefish, rainbow trout, Arctic char, Dolly Varden, lake trout, and Arctic grayling, are distributed across much of both the Nushagak and Kvichak river drainages. Unlike the *obligate anadromous*[1] Pacific salmon populations of the Nushagak and Kvichak river drainages, in which essentially all individuals migrate from natal lakes and streams to the sea to feed and grow, individual fish in these seven species do not need to journey to marine waters to successfully complete their life cycle, although some individuals of certain species (e.g., Dolly Varden and humpback whitefish) may. Also unlike the North American Pacific salmon, individuals in each of these seven species can

[1] Among migratory fishes, Myers (1949) defined, in part, the following distinct movement patterns:

Diadromous. Fishes which migrate between the sea and fresh water.

Anadromous. Diadromous fishes which spend most of their lives in the sea and migrate to fresh water to breed. [A pattern expressed by many Alaska fishes].

Catadromous. Diadromous fishes which spend most of their lives in fresh water and migrate to the sea to breed. [Not a pattern expressed by Alaska fishes].

Amphidromous. Diadromous fishes whose migration from fresh water to the sea, or vice-versa, is not for the purpose of breeding, but occurs regularly at some other definite stage of the life-cycle. [A pattern expressed by a few primarily marine Alaska fishes (e.g., starry flounder)].

Potamodromous. Fishes whose migrations occur wholly within fresh water. [A pattern expressed by many Alaska fishes].

Table Appendix B-1.Fish species[2,3] reported in the Nushagak and Kvichak river drainages (ADF&G 2012b; Bond and Becker 1963; Burgner et al. 1965; Fall et al. 2006; Krieg et al. 2009; Mecklenburg et al. 2002; Morrow 1980b; Russell 1980).

Scientific/Common Family Name	Common Name	Scientific Name	Principal Migratory Patterns[4]	Relative Abundance	Abundance relative to other Bristol Bay basins
Petromyzontidae/ lampreys	Arctic lamprey	*Lethenteron camtschaticum*[5]	Anadromous	Juveniles common/widespread in sluggish flows where fine sediments accumulate[6]	Unknown, presumably similar
	Alaskan brook lamprey	*L. alaskense*[5]	Nonanadromous		
	Pacific lamprey	*Entosphenus tridentatus*[5]	Anadromous	Rare	Unknown, presumably similar. Not known west of Nushagak drainage
Catostomidae/ suckers	longnose sucker	*Catostomus catostomus*	Nonanadromous	Common in slower flows in larger streams	Unknown, presumably similar
Esocidae/pikes	northern pike	*Esox lucius*	Nonanadromous	Common/widespread in still or sluggish waters	Unknown, presumably similar
Umbridae/ mudminnows	Alaska blackfish	*Dallia pectoralis*	Nonanadromous	Locally common/abundant in still or sluggish waters in flat terrain	Unknown, presumably similar
Osmeridae/smelts	rainbow smelt	*Osmerus mordax*	Anadromous	Seasonally abundant in streams near the coast	Unknown, presumably similar
	pond smelt	*Hypomesus olidus*	Nonanadromous	Locally common in coastal lakes and rivers, Iliamna Lake, inlet spawning streams, and the upper Kvichak River; abundance varies widely interannually	Unknown, presumably similar
	eulachon	*Thaleichthys pacificus*	Anadromous	No or few specific reports; if present, distribution appears limited and abundance low	Unknown, presumably similar
Salmonidae/salmonids	Bering cisco	*Coregonus laurettae*	Nonanadromous and Anadromous[7]	Rare? Very few specific reports	Unknown; perhaps more abundant than elsewhere
	humpback whitefish	*C. pidschian*	Nonanadromous and Anadromous[7]	Common in large upland lakes; locally and seasonally common in large rivers	Unknown; perhaps more abundant than elsewhere
	least cisco	*C. sardinella*	Nonanadromous and Anadromous[7]	Locally common in some lakes (e.g., Lake Clark, morainal lakes near Iliamna Lake); less common in Iliamna Lake and large slow moving rivers such as the Chulitna, Kvichak, and lower Alagnak	Unknown; perhaps more abundant than elsewhere
	pygmy whitefish	*Prosopium coulterii*	Nonanadromous	Locally common in a few upland lakes	Unknown, presumably similar
	round whitefish	*P. cylindraceum*	Nonanadromous	Abundant/widespread throughout larger streams in upland drainages; but not in headwaters or coastal plain	Unknown, presumably similar

-continued-

[2] Does not include primarily marine species that periodically venture into the lower reaches of coastal Bristol Bay streams.

[3] No species listed here has either Federal or State of Alaska special status (e.g., endangered, threatened) except that the State of Alaska has identified Kvichak sockeye salmon as a stock of yield concern (ADF&G 2012c).

[4] **Anadromous**: fishes that spawn in fresh waters and migrate to marine waters to feed; **Nonanadromous**: fishes that spend their entire life in fresh waters, with possible migrations between habitats within a drainage (potamodromous and nonmigratory freshwater fishes); **Nonanadromous and Anadromous**: fish populations in which some individuals have nonanadromous migratory patterns and some have anadromous migratory patterns.

[5] Nomenclature follows Brown et al. (2009).

[6] Juveniles, the most commonly encountered life stage, of Arctic and Alaska brook lamprey are morphologically indistinguishable, so these two species are combined here.

[7] Anadromy known elsewhere in Alaska, but not verified within either the Nushagak or Kvichak river drainages.

Table Appendix B-1.-Page 2 of 2.

Scientific/Common Family Name	Common Name	Scientific Name	Principal Migratory Patterns	Relative Abundance	Abundance relative to other Bristol Bay basins
Salmonidae/salmonids (continued)	coho salmon	*Oncorhynchus kisutch*	Anadromous	Juveniles abundant/widespread in Nushagak drainage upland flowing waters and in some Kvichak R. tributaries downstream of Iliamna Lake; present in some Iliamna Lake tributaries; not recorded in the Lake Clark drainage	More abundant in Nushagak drainage than elsewhere in Bristol Bay, except for the North Alaska Peninsula Basin
	Chinook salmon	*O. tshawytscha*	Anadromous	Juveniles abundant and widespread in upland flowing waters of the Nushagak River watershed and in the Alagnak River; infrequent upstream of Iliamna Lake	More abundant in Nushagak drainage than elsewhere in Bristol Bay
	sockeye salmon	*O. nerka*	Anadromous	Abundant	More abundant than elsewhere, comparable to Egegik basin.
	chum salmon	*O. keta*	Anadromous	Abundant in Nushagak drainage upland flowing waters and in some Kvichak R. tributaries downstream of Iliamna Lake. Infrequent upstream of Iliamna Lake.	More abundant than elsewhere
	pink salmon	*O. gorbuscha*	Anadromous	Abundant, in even years, in Nushagak drainage, with restricted distribution, and in some Kvichak R. tributaries downstream of Iliamna Lake. Rare upstream of Iliamna Lake.	More abundant than elsewhere in even years
	rainbow trout	*O. mykiss*	Nonanadromous[8]	Frequent/common; closely associated during summer with spawning salmon	More abundant/larger body size than much of Bristol Bay
	Arctic char	*Salvelinus alpinus*	Nonanadromous	Locally common in upland lakes	Unknown, presumably similar
	Dolly Varden	*S. malma*	Nonanadromous and Anadromous	Abundant in upland headwaters and selected lakes	Unknown, presumably similar
	lake trout	*S. namaycush*	Nonanadromous	Common in larger upland lakes and seasonally present in lake outlets; absent from the Wood River lakes	Unknown, presumably similar
	Arctic grayling	*Thymallus arcticus*	Nonanadromous	Abundant/widespread	Unknown, presumably similar
Gadidae/cods	burbot	*Lota lota*	Nonanadromous	Infrequent to common in deep, sluggish or still waters	Unknown, presumably similar
Gasterosteidae/ sticklebacks	threespine stickleback	*Gasterosteus aculeatus*	Nonanadromous and Anadromous	Locally abundant in still or sluggish waters; abundant in Iliamna Lake	Unknown, presumably similar
	ninespine stickleback	*Pungitius pungitius*	Nonanadromous	Abundant/widespread in still or sluggish waters	Unknown, presumably similar
Cottidae/sculpins	coastrange sculpin	*Cottus aleuticus*	Nonanadromous	Abundant/widespread[9]	Unknown, presumably similar
	slimy sculpin	*C. cognatus*	Nonanadromous		

[8] In Bristol Bay, anadromous individuals (steelhead) are known to spawn and rear only in the North Alaska Peninsula basin (Figure 2-3).

[9] These two sculpin species are not reliably or frequently distinguished in field collections; slimy sculpin is thought to be the more abundant and widely distributed species (Bond and Becker 1963).

survive to spawn more than once (they are *iteroparous*, Stearns 1992, p. 180) and, compared to salmon, have longer potential life spans (see the following species descriptions).

Northern pike *Esox lucius*

Freshwater distribution and habitats

The Northern pike has a circumpolar distribution across the northern hemisphere and is the only species in the family Esocidae that has colonized arctic waters (Crossman 1978). In North America northern pike inhabit lakes and low gradient rivers from the Arctic Ocean south to the Missouri and Mississippi river drainages, and from the North Atlantic Ocean west to the Rocky Mountains (Scott and Crossman 1998, p. 357). In Alaska, northern pike are native primarily north of the Alaska Range, including waters of the Nushagak and Kvichak river drainages (Mecklenburg et al. 2002, p. 144; Morrow 1980b, p. 168), but were illegally introduced and are now established in several regions south of the Alaska Range, particularly in the Susitna River drainage (Rutz 1999, p. 1). In Bristol Bay, northern pike occur in coastal plain lakes (Hildreth 2008, p. 9), inland lakes (Burgner et al. 1965, p. 4; Dye et al. 2002, p. 1; Russell 1980, p. 87), and river systems (ADF&G 2012) providing suitable habitat. The Nushagak and Nuyakuk river mainstems, Lake Aleknagik, and the Lake Clark drainage (Figure 2-4 in main assessment report) support the largest sport fisheries within the Nushagak and Kvichak river drainages (Jennings et al. 2011, p. 126, 128).

Northern pike primarily spawn in sections of lakes, wetlands, or very low gradient streams providing shallow (less than 1 m), slow or still waters with soft substrates and aquatic vegetation (Cheney 1971d, p. 13; Chihuly 1979, p. 48, 57; Dye et al. 2002, p. 5, 6-7; Russell 1974. p. 42; Rutz 1999, p. 15). Summer habitat is in slightly deeper, but still warm water with dense aquatic vegetation (Chihuly 1979, p. 46, 58; Dye et al. 2002, p. 5; Joy and Burr 2004, p. 22; Roach 1998, p. 3; Rutz 1999, p. 9). In southcentral Alaska's Susitna River drainage, river-dwelling northern pike are often found in side sloughs where water temperatures are several degrees warmer than the adjacent main channel (Rutz 1999, p. 19). Among the large, deep, cold, glacially-formed lakes of the Nushagak and Kvichak river drainages, shallow, vegetated habitats are scarce, making those found in Lake Clark's Chulitna Bay and the shallow bays of Lake Aleknagik particularly important northern pike concentration areas (Chihuly 1979, p. 48; Dye et al. 2002, p. 6-7; Russell 1980, p. 91).

Northern pike overwinter in lakes, spring-fed rivers, or larger deep rivers where there is likely to be sufficient water and oxygen to survive until spring (Dye et al. 2002, p. 5; Roach 1998, p. 18-21; Scanlon 2009, p. 17; Taube and Lubinski 1996, p. 5-8). Water depth beneath winter ice may be 0.8 m or less (Taube and Lubinski 1996, p. 8). In winter, local residents ice fish for northern pike along the large rivers of the Nushagak and Kvichak river drainages (Krieg et al. 2009, p. 135, 220, 215, 344).

Life cycle

At spring ice-out in Lake Aleknagik, in the Nushagak River drainage, large fish are in water 1 to 1.5 m deep and within 10 m of shore. In late May to mid-June, as water temperatures rise to about 6 °C, mature fish move inshore to spawn in brush and aquatic vegetation (Dye et al. 2002. p. 5). Female northern pike can produce over 100,000 adhesive 3-mm diameter ova, which they scatter in small batches among aquatic vegetation or rocks, while an attending male fertilizes them. Neither females nor males construct redds (Morrow 1980b, p. 166-167; Scott and Crossman 1998, p. 359). After spawning, as Lake Aleknagik water temperatures rise above 8 °C, fish move slightly offshore, to 1 to 3 m of water, but remain in the bays where they spawned, moving little for the remainder of the summer (Dye et al. 2002, p. 5). As water levels and temperatures drop in mid-September through October, fish move out of shallow bays to depths of 3 to 5 m in the main lake and then move little until the following spring (Dye et al. 2002, p. 5).

Mature northern pike living in Alaska river systems and river-lake complexes ascend tributaries in spring, beneath the ice. Spawning occurs from mid-May to early July as ice melts in side-channel slack waters or lake margins. After spawning, mature pike move to deeper water to feed, where they remain until moving in September and October to lakes, spring-fed streams, and larger, deeper rivers where they overwinter (Cheney 1971d, p. 13-14; Cheney 1972, p. 5; Chythlook and Burr 2002, p. 13; Kepler 1973, p. 75; Russell 1980, p. 91; Taube and Lubinski 1996, p. 6-8).

Northern pike eggs hatch in less than a month. At hatching, fry are 6 to 9 mm long, and have a yolk sac, but no mouth. Before they start actively feeding, fry cling to the substrate, debris, or vegetation for around 10 days, absorbing their yolk sacs while their mouths develop (Morrow 1980b, p. 167; Scott and Crossman 1998, p. 359). In Nushagak and Kvichak river drainage lakes, young-of-the-year northern pike are actively swimming by at least late June to early July and grow rapidly through the summer (Chihuly 1979, p. 32, 34; Russell 1980, p. 91, 93). In river systems, fry remain near or downstream of spawning areas (Cheney 1971d, p. 13). In interior Alaska, age-0 fish reach a mean length of 140 mm by September (Cheney 1972, p. 15). In Lake Aleknagik, northern pike grow rapidly to about age 4 and a total length of around 419 mm, then growth slows to about an average of 25 mm per year (Chihuly 1979, p. 27-28, 33). Some male northern pike in Lake Aleknagik mature at age 3, and by around age 5 and lengths of approximately 438 to 469 mm, all fish are mature (Chihuly 1979, p. 34).

Many mature northern pike do not travel far (Chihuly 1979, p. 64; Dye et al. 2002, p. 5; Joy and Burr 2004, p. 25; Rutz 1999, p. 8), but some river-system individuals make extensive seasonal migrations between spawning, feeding, and overwintering areas (Scanlon 2009, p. 11), sometimes moving at least 290 km per year (180 mi per year, Cheney 1971a, p. 7). Mature northern pike may disperse through the summer and then aggregate prior to moving to overwintering locations and while overwintering (Roach 1998, p. 14). Mature northern pike show high fidelity to spawning (Joy and Burr 2004, p. 29; Roach 1998, p. 13) and winter areas (Scanlon 2009, p. 20; Taube and Lubinski 1996, p. 8) and moderate fidelity to summer feeding areas (Taube and Lubinski 1996, p. 8). Because fish must exceed a minimum size before they can be successfully tracked with standard telemetry methods, most movement studies are limited to bigger individuals and seasonal movements of immature Alaska northern pike are largely unknown.

Mature females often tend to be larger than males of the same age (Clark et al. 1988, p. 22, 25; Pearse 1991, p. 36; Rutz 1999, p. 9), but males appear to have a greater mortality rate (Cheney 1971c, p. 17; Chihuly 1979, p. 26; Pearse 1991, p. 36). In the Nushagak and Kvichak river drainages, northern pike can reach total lengths of at least 1.04 m, weights in excess of 7 kg, and ages of 18 years (Chihuly 1979, p. 33, 37; Dye et al. 2002, p. 6; Russell 1980, p. 92, 93). In the

Yukon River drainage, fish can reach 1.2 m in length (Scanlon 2009, p. 20), and 26 years in age (Cheney 1971c, p. 15).

Predator–prey relationships

Northern pike are highly adaptable predators able to consume a wide range of invertebrates and vertebrates, but they are particularly efficient consumers of fish (Craig 2008). Where they are available, a wide variety of fish dominate the diet of larger Nushagak and Kvichak river drainages northern pike, including Alaska blackfish, round whitefish, least cisco, smaller northern pike, ninespine and threespine stickleback, juvenile sockeye salmon, Arctic char, pygmy whitefish, sculpins, longnose suckers, and lake trout (Chihuly 1979, p. 79-86; Russell 1980, p. 95-97). The diet of larger northern pike illegally introduced into southcentral Alaska's Susitna River drainage was dominated by coho and sockeye salmon, whitefish species, stickleback species, and rainbow trout (Rutz 1999, p. 17). Immediately after hatching, young-of-the-year fry eat zooplankton and immature aquatic insects, but quickly transition to small sticklebacks and other small fish (Chihuly 1979, p. 85-88; Morrow 1980b, p. 167). Northern pike smaller than 200 mm feed substantially on invertebrates; fish over 400 mm eat invertebrates (e.g., crustaceans, leeches, beetle larvae, and mollusks, Russell 1980, p. 95-97) only incidentally (Cheney 1972, p. 29; Chihuly 1979, p. 79-88). Northern pike diets are adaptable and can include a wide variety of foods in the absence of fish prey, although growth rates are then lower (Cheney 1971b, p. 23). Northern pike are keystone predators and often the greatest predator of northern pike are larger northern pike (Cheney 1972, p. 27; Chihuly 1979, p. 82; Craig 2008).

Abundance and harvest

Total abundance of northern pike in the Nushagak and Kvichak river drainages is unknown. Dye et al. (2002, p. 6) estimated that in 1998 and 1999, the abundance of northern pike longer than 299 mm in Lake Aleknagik was more than 11,580. Chulitna Bay on Lake Clark has supported a large subsistence fishery; in June 1978 an estimated 350 to 500 large northern pike were harvested from Turner Bay at the head of Chulitna Bay (Russell 1980, p. 91). In the mid-2000s, residents in ten of the Nushagak and Kvichak river drainage villages annually harvested an estimated 4,385 northern pike (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202), and they were the most important non-salmon fish in four of those villages (Fall et al. 2006, p. 152; Krieg et al. 2009, p. 46, 124, 171). From the mid-1970s to the mid-2000s, northern pike were estimated to represent between 9.9 and 14.1% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214). In 2009, sport anglers caught an estimated 8,217 northern pike in the Nushagak and Kvichak river drainages and the adjacent Togiak River (Figure 2-3 in main assessment report) drainage (10% of the statewide total) and harvested (kept) an estimated 1,177 (6% of the statewide total; Jennings et al. 2011, p. 75). Annual sport harvests have declined, due at least in part to both lower bag limits and the increasing popularity of catch-and-release fishing (Dye and Schwanke 2009, p. 6). In 1966 and 1967, an experimental freshwater commercial fishery on Tikchik Lake harvested 316 northern pike, the third-most commonly harvested fish (6% of total number of fish harvested; Yanagawa 1967, p. 10).

Stressors

Because northern pike are long-lived, have a piscivorous diet, and prefer relatively warm water, they bioaccumulate and biomagnify atmospherically deposited mercury, and tissue mercury concentrations correlate strongly with length and age (Headlee 1996; Mueller et al. 1996, p. 36). Lindesjöö and Thulin (1992) reported that wild northern pike exposed to pulp mill effluents developed severe jaw deformities. They did not determine if the deformities were directly caused by constituents of the effluents, if the deformities resulted from a secondary reduction of dissolved oxygen (DO) levels, or through some other mechanism. Northern pike are highly tolerant of low DO levels. In laboratory experiments, juvenile northern pike survived DO levels down to at least 0.25 $mg \cdot l^{-1}$ (Petrosky and Magnuson 1973).

Casselman (1978) found that, for a Canadian stock of northern pike, maximum summer growth occurred at 19 °C, growth stopped at 28 °C, and 29.4 °C was the upper incipient lethal temperature. For an Ohio stock, Bevelhimer et al. (1985) reported maximum summer growth occurred at 25 °C and that northern pike continued to grow at 30 °C. Combined, these results suggest a possible latitudinal cline in temperature tolerances and optimal and lethal temperatures for Nushagak and Kvichak river drainages northern pike may be lower than those reported by Casselman (1978).

Humpback whitefish *Coregonus pidschian*

The taxonomic status of humpback whitefish remains unsettled. Some sources (e.g., Mecklenburg et al. 2002, p. 180; Morrow 1980b, p. 24) distinguish three separate Alaska whitefish species (lake *C. clupeaformis,* Alaska *C. nelsonii, and* humpback *C. pidschian*) based on gill raker counts; other authors (e.g., Alt 1979; Brown 2006, p. 2; McDermid et al. 2007) consider them a single variable species (the *C. clupeaformis* complex). This appendix treats the three forms synonymously. In addition, Bernatchez and Dodson (1994) suggest that this species should be considered synonymous with the European whitefish *C. lavaretus*.

Freshwater distribution and habitats

In combination with the European whitefish, the humpback whitefish has a circumpolar distribution across the northern hemisphere (Bernatchez and Dodson 1994). In North America, the humpback whitefish freshwater range extends from the Arctic Ocean coastal plain south to near Canada's southern border, and from the Atlantic seaboard to the Bering Strait (Scott and Crossman 1998, p. 271). Humpback whitefish are found in lakes, streams, and brackish water across much of Alaska, primarily north of the Alaska Range (Alt 1979; Mecklenburg et al. 2002, p. 186-188). In the Nushagak and Kvichak river drainages, humpback whitefish are reported in deeper lakes, mainstem rivers, and slow-flowing tributaries (ADF&G 2012; Burgner et al. 1965, p. 4, 5; Fall et al. 2006, p. 321, 337, 354, 381; Krieg et al. 2009, p. 301, 318, 339, 365, 370; Metsker 1967, p. 6; Russell 1980, p. 72-76; Woody and Young 2007, p. 8; Yanagawa 1967, p. 12).

In northwest Ontario, lake spawning sites were found in nearshore areas at average depths of 2.7 to 3.5 m; primarily over boulders, cobbles, and detritus (Anras et al. 1999). In western and interior Alaska, stream spawning sites are in spatially discrete reaches, often glacially-fed, with moderate to high gradients, moderate to swift currents, and gravel substrates (Alt 1979; Brown 2006, p. 25-26; Harper et al. 2009, p. 17; Kepler 1973, p. 71). In interior Alaska's Chatanika River, fish spawn in water 1.3 to 2.6 m deep, flowing at approximately 0.5 $m \cdot s^{-1}$ (Kepler 1973, p. 71).

After spawning, adults migrate downstream to more slowly flowing waters with fine substrates (Brown 2006, p. 26). In Canada's Mackenzie River system, overwintering locations are in deep mainstem channels or delta areas (Reist and Bond 1988). Lakes and sloughs supporting summer feeding aggregations in southcentral and interior Alaska are well connected to mainstem channels, ensuring that feeding fish can reliably enter in spring and exit in late summer during migrations from and to spawning and overwintering areas (ADF&G 1983b, p. G-15; ADF&G 2006, p. 31).

In early August, apparently mature fish were collected in the lower Swan River), about 2 km upstream of the confluence with the Koktuli River (ADF&G 2012, sites FSN0604A02, FSN0604A04), and mature fish were collected at the mouth of Koggiling Creek, at its confluence with the lower Nushagak River (ADF&G 2012, sites FSN0607C08, FSN0607C10). The stomachs of most of the Koggiling Creek fish were empty (Wiedmer *unpublished*). These fish may have recently left summer feeding lakes in the Swan River and Koggiling Creek drainages and were staging before beginning their upstream spawning migration (see Life cycle and Predator-prey discussions below).

In late August, apparently mature and perhaps larger immature fish were collected in small upland lakes draining to the upper North Fork Koktuli River (ADF&G 2012, sites PEB91NK011, PEB91NK019). Whether humpback whitefish overwinter in these lakes is not known. In fall, residents of the Nushagak and Kvichak river drainages harvest humpback whitefish in mainstem rivers, as the whitefish move upstream to spawn. In winter, residents also harvest humpback whitefish in Sixmile and Iliamna lakes, Lake Clark (Figure 2-4 in main assessment report), and mainstem rivers (Fall et al. 2006, p. 39, 200, 289, 321, 337, 354, 381; Krieg et al. 2009, p. 55, 135, 159, 178, 220, 301, 339, 365).

In Alaska, the habitat preferences of juvenile humpback whitefish have been particularly difficult to define (Brown 2004, p. 19; Brown 2006, p. 25, 30; Brown et al. 2002, p. 18). In the lower Mackenzie River, nursery habitats and foraging areas for young-of-the-year are in delta lakes and main delta channels (Chang-Kue and Jessop 1992, p. 27). No young-of-the-year were found in main-channel rivers and streams in the Nushagak River drainage in August 2006 (ADF&G 2012), suggesting either a year-class failure (Bogdanov et al. 1992) or that they were occupying off-channel habitats. In Lake Clark and adjacent lakes, juveniles were captured mostly in shallow (less than 3 m) nearshore areas, while larger fish were more broadly distributed (Woody and Young 2007, p. 8).

Life cycle

North of the Nushagak and Kvichak river drainages, some humpback whitefish populations include anadromous individuals, but the proportion of anadromous individuals within populations appears to decrease with increasing distance from marine waters (Brown 2004, p. 17; Brown 2006, p. 14; Harper et al. 2007, p. 11; Sundet and Pechek 1985, p. 34). Within the Nushagak and Kvichak river drainages, limited otolith isotope analyses have yet to reveal evidence for anadromy in fish collected in Lake Clark or the lower Nushagak River (Randy Brown, U. S. Fish and Wildlife Service, Fairbanks, personal communication; Woody and Young 2007, p. 12).

In interior Alaska, large fish feed in lakes until late summer. They then move into mainstem rivers and stay near lake outlets for up to 3 weeks before beginning to migrate upstream to spawning areas in late August to early September. Most adults arrive in the spawning areas by mid-September, and spawning extends from late September to mid-October (Brown 2006, p. 26). Russell (1980, p. 72) reported spawning in late September in Nushagak and Kvichak river drainage lakes. Lake spawning in northwest Ontario occurs at temperatures between 2 and 6 °C, shortly before lake surfaces begin to freeze (Anras et al. 1999). Kepler (1973, p. 71) reported spawning in an interior Alaska stream from mid-September to early October, at temperatures ranging from 0 to 3 °C.

In interior Alaska, males mature at ages 4 to 6; females at ages 5 to 7 (Alt 1979; Brown 2006, p. 28). Fish are reported to mature at lengths of about 310 to 380 mm (FL; Alt 1979; Brown 2004, p. 19; Brown 2006, p. 23; Chang-Kue and Jessop 1992, p. 17; Kepler 1973, p. 71), and age and length at maturity may vary among locations (Alt 1979; Brown 2004, p. 19; Chang-Kue and Jessop 1992, p. 17). Three females from the lower Nushagak River (ADF&G 2012, sites FSN0607C08, FSN0607C10) with fork lengths ranging from 435 to 460 mm were mature, while one 370-mm female was not (Wiedmer *unpublished*). In interior Alaska, females apparently spawn every year (Brown 2006, p. 29). Farther north, at least some females do not spawn every year, although males may (Brown 2004, p. 16, 17).

Humpback whitefish broadcast spawn instead of digging redds; after fertilization their 2- to 3-mm diameter eggs sink and lodge in the interstitial spaces of the substrate (Anras et al. 1999; Morrow 1980b, p. 36, 38; Scott and Crossman 1998, p. 271). Fecundity of interior Alaska humpback whitefish ranges from 8,400 to 65,400 ova for females ranging in length from 320 to 520 mm (Clark and Bernard 1992). The estimated fecundity of three mature females collected in August in the mouth of Koggiling Creek in the Nushagak River drainage (ADF&G 2012, Site FSN0607C10) fell within this range (Wiedmer *unpublished*).

In Siberian rivers, the time from spawning to hatching is about 185 to 190 days and survival from egg to fry appears to vary greatly from year to year (Bogdanov et al. 1992). Larval fish, weighing 4.9 to 6.3 mg, with lengths of 9 to 13 mm, drift downstream immediately after hatching (Bogdanov et al. 1992; Shestakov 1991). Studies in both Norway and Siberia found that these fry still have yolk sacs and do not begin feeding for the first several days of their downstream drift (Næsje et al. 1986; Shestakov 1991). In Siberia's Anadyr River, larvae drift downstream for two to three weeks, from late May to early June (Shestakov 1991; Shestakov 1992). The scale and speed of downstream migrations correlate with increases in river discharge (Bogdanov et al. 1992; Næsje et al. 1986; Shestakov 1991). Russell (1980, p. 72) observed fry in the shallows of Kvichak River drainage lakes by mid-June.

In interior Alaska and northern Canada, immature fish, from age 0 to about age 4, appear to rear far downstream of spawning areas in off-channel sites such as deltas, lakes, and sloughs, or in mainstem eddies (Brown 2006, p. 31; Reist and Bond 1988). Age-0 juveniles in the Anadyr River primarily inhabit lakes that connect to the mainstem during spring high flows (Shestakov 1992). By mid-July, age-0 fish reach 43 mm, with growth faster in floodplain lakes than in streams (Shestakov 1992).

In the Nushagak and Kvichak river drainages, humpback whitefish reach at least age 27 and lengths to 584 mm (Woody and Young 2007, p. 8). Elsewhere, maximum age can be up to 57 years (Power 1978). In interior Alaska, maturing and mature fish show fidelity to both summer feeding (Brown 2006, p. 21; Brown et al. 2002, p. 16; Harper et al. 2007, p. 14; Harper et al. 2009, p. 11, 17), and fall spawning areas, which can be more than 600 km apart (Harper et al. 2007, p. 15; Harper et al. 2009, p, 30).

Predator–prey relationships

Large humpback whitefish from Nushagak and Kvichak river drainage lakes feed predominantly on benthic invertebrates, particularly mollusks, chironomids (non-biting midges), planktonic crustaceans, and caddis fly larvae (Metsker 1967, p. 29; Russell 1980, p. 76), but will apparently feed on salmon eggs and small fry when available (Van Whye and Peck 1968, p. 37; Woody and Young 2007, p. 13). Adults preparing to spawn stop eating earlier than mature non-spawners, and large humpback whitefish feed little during the spawning migration and while overwintering (Brown 2004, p. 21; Brown et al. 2002, p. 16). In lakes, young-of-the-year fry initially feed primarily on planktonic crustaceans (Claramunt et al. 2010; Hoyle et al. 2011). After they reach lengths greater than 40 mm, their diet transitions to benthic macroinvertebrates, particularly chironomids (Claramunt et al. 2010).

Round whitefish and Arctic grayling feed on humpback whitefish eggs (Brown 2006, p. 23; Kepler 1973, p. 71), and other species likely do as well. Humpback whitefish are vulnerable to predation by piscivorous fish, such as lake trout (Van Whye and Peck 1968, p. 37) and in the Nushagak and Kvichak river drainages, northern pike may be important predators (Russell 1980, p. 95).

Abundance and harvest

The total abundance of humpback whitefish in the Nushagak and Kvichak river drainages is not known. The estimated mid-2000s annual subsistence harvests in nine of the villages within the Nushagak and Kvichak river drainages totaled over 4,000 fish (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202). From the mid-1970s to the mid-2000s, whitefish, the majority of which were humpback whitefish, were estimated to represent between 8.3 to 26.8% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214).

The 2009 estimated sport catch of all whitefish species in the Nushagak and Kvichak river drainages plus the Togiak River drainage was 1,118 fish (11% of the total statewide catch of all whitefish species excluding sheefish *Stenodus leucichthys*), and the estimated harvest was 520 (18% of the total statewide harvest of all whitefish species, excluding sheefish; Jennings et al. 2011, p. 76). In the mid-1960s, Iliamna Lake and Lake Clark supported a commercial humpback whitefish fishery (Metsker 1967, p. 8, 10). In 1966 and 1967, humpback whitefish comprised 62% of the total number of fish harvested in a freshwater commercial fishery on Tikchik Lake (Yanagawa 1967, p. 12).

Stressors

Mature humpback whitefish aggregate in discrete spawning habitats, leaving them at risk to both acute events during fall spawning and chronic changes to spawning habitat (Brown 2006, p. 32).

Extreme high water events shortly before fall spawning may cause adult whitefish to leave spawning areas and delay spawning to another year (Underwood et al. 1998, p. 13). The spawning success of lake-dwelling whitefish is vulnerable to lake level manipulation during the winter incubating period (Anras et al. 1999) and to elevated substrate sedimentation (Fudge and Bodaly 1984). Age-0 fish are vulnerable to low flows in spring, which can prevent access to preferred floodplain lake habitats (Shestakov 1992).

Mature humpback whitefish appear not to feed during spawning migrations or during the winter (Brown 2004, p. 21; Brown et al. 2002, p. 16). Almost all annual feeding occurs in summer, often in off-channel lakes and sloughs. Mature whitefish must have access to and from these off-channel habitats, both in spring to immigrate and in late summer to emigrate (Brown 2006, p. 26; Harper et al. 2007, p. 16).

Fertilized eggs need cold water (optimally around 0.5 °C; Morrow 1980b) during development; eggs incubating in 10 °C waters suffer 99% mortality rates (Scott and Crossman 1998, p. 272). In an experiment mimicking Great Lakes summer conditions, Edsall (1999) found juvenile survival peaked at water temperatures of 10 to 15 °C and declined at lower and warmer temperatures and that juvenile growth peaked at 18.5 °C. For Great Lakes young-of-the-year acclimated to warmer waters, the upper lethal temperature was 26.6 °C (Edsall and Rottiers 1976). Metabolically, whitefish do not swim as efficiently as other salmonids (Bernatchez and Dodson 1985). Swimming performance peaks at around 12 °C and declines at lower temperatures. Bernatchez and Dodson (1985) speculate that the timing of seasonal migrations may be a function of the combined influence of seasonal stream velocities and temperatures. Optimal and lethal temperatures may be lower for Alaska populations.

Rainbow trout *Oncorhynchus mykiss*

Rainbow trout and steelhead are two forms of one species and belong to the same genus (*Oncorhynchus*) as the Pacific salmon. Rainbow trout is the common name for individuals with nonanadromous life histories and steelhead is the common name for individuals with anadromous life histories. Unlike the region's Pacific salmon, southwest Alaska rainbow trout/steelhead are mostly nonanadromous. In Bristol Bay, the Alaska Department of Fish and Game (ADF&G) documents steelhead only in a few spawning streams near Port Moller, in the southwestern portion of the basin, outside the Nushagak and Kvichak river drainages (Johnson and Blanche 2012, Chignik and Port Moller 1:250,000 quadrangles). As no steelhead are known to occur in the fresh waters of the Nushagak and Kvichak river drainages (e.g., Russell 1977, p. 44), they are not discussed further here.

Freshwater distribution and habitats

The native freshwater range of rainbow trout is largely restricted to Pacific Ocean drainages: in North America from Alaska's Kuskokwim River system south to mountain drainages of central Mexico (MacCrimmon 1971, p. 664), and in Asia in the Kamchatka region (Froese and Pauly 2012). Native rainbow trout in Alaska fresh waters are restricted to southwest, southcentral, and southeast Alaska, from the Holitna River region south to Dixon Entrance (Morrow 1980b, p. 78). Rainbow trout have been extensively and successfully transplanted outside their native range, including sites in interior Alaska (MacCrimmon 1971; Morrow 1980b, p. 51). While rainbow trout of the Nushagak and Kvichak river drainages are near the northern limit of their global native range, they are broadly distributed across the Nushagak and Kvichak river drainages, except in Lake Clark and its tributaries (Minard and Dunaway 1991, p. 2; Minard et al. 1998, p. 32), and the Tikchik Lakes system, except for Tikchik Lake itself (Burgner et al. 1965, p. 11; Yanagawa 1967, p. 16-17). They are found in small streams to mainstem rivers and in lakes (ADF&G 2012; Meka et al. 2003).

Rainbow trout typically spawn in flowing water, but can spawn along lake shores, near groundwater upwellings (Northcote and Bull 2007). Rainbow trout in the Naknek River (Figure 2-3 in main assessment report), downstream of several large lakes, spawn in fast water of the mainstem, with much of the spawning occurring in the transition between the upstream confined reach and the downstream unconfined reach (Gwartney 1982, p. 9; Gwartney 1985, p. 47). Females deposit eggs, which are immediately fertilized by males, into excavated redds (Morrow 1980b, p. 51). In Lower Talarik Creek, Russell (1977, p. 9) reported that redds were dug in the gravel of side channels, near the upstream ends of islands, and in pool tails above riffles. Typical water depths at Lower Talarik Creek redd locations were less than 0.6 m and current velocities were 0.3 to 0.6 $m \cdot s^{-1}$. The most suitable sites for rainbow trout spawning in southcentral Alaska's Copper River system had water temperatures ranging from 2 to 9 °C, average depths ranging from 0.3 to 0.4 m, average current velocities of 0.5 to 0.7 $m \cdot s^{-1}$, and substrate diameters ranging from 20 to 60 mm (Brink 1995, p.71-75). In northern Idaho, rainbow trout spawned after the peak of spring snowmelt, and redds had a mean area of 1.19 m^2 (standard deviation (SD) = 0.62; range = 0.27 to 2.40 m^2), a mean water depth at the pit head of 0.18 m (SD = 0.08; range = 0.05 to 0.38 m), and a mean water velocity at the pit head of 0.39 $m \cdot s^{-1}$ (SD = 0.15; range = 0.08 to 0.67 $m \cdot s^{-1}$) (Holecek and Walters 2007). Steelhead in Alaska's Copper River, the size of large Nushagak and Kvichak river drainages rainbow trout, dug redds averaging 3.4 m^2 in area (Brink 1995, p. 125).

As the only spring-spawning member of its genus in the Nushagak and Kvichak river drainages, with eggs hatching later in the summer than other Bristol Bay freshwater fish, young-of-the-year rainbow trout have a very short time to complete incubation and initial growth before the onset of winter. Therefore, spawning and early rearing habitats may be limited to locations with warmer summer temperatures and abundant food, as fry size in late fall is positively related to winter survival (Smith and Griffith 1994). Spawning areas in southcentral Alaska's Susitna and Copper river tributaries are often near lake outlets, presumably because of warmer water there (Brink 1995, p. 16-18, 99; Sundet and Pechek 1985, p. 37). Spawning begins in spring when Lower Talarik Creek water temperatures reach 2 to 3 °C, peaks at 4 to 7 °C, and stops at temperatures greater than 16 °C (Russell 1977, p. 12).

In streams, rainbow trout summer rearing density increases with pool depth and overhead cover (Bryant and Woodsmith 2009; Nakano and Kaeiryama 1995). Winter rearing density increases with increasing availability of multiple cover types (Bjornn and Reiser 1991, p. 135). In summer in southeast Alaska, rearing juveniles leave small tributaries and are relatively more abundant in larger streams ($\geq 3^{rd}$ order; *sensu* Strahler 1952, p. 1120). In spring and fall, juveniles are equally distributed in both headwater tributaries and larger streams (Bramblett et al. 2002). However, beginning in September, juvenile rainbow in Idaho move downstream from summer rearing to winter overwintering areas (Chapman and Bjornn 1968, p. 165). Given the very low winter flows and water temperatures in southwest Alaska low-order streams (e.g., USGS 2012), Nushagak and Kvichak river drainages juvenile rainbow trout may follow the movement pattern of Idaho fish.

In southeast Alaska, juvenile rainbow trout rear in streams with gradients up to at least 16% (Bryant et al. 2004), but there are no reports of trout in such steep streams within the Nushagak and Kvichak river drainages (ADF&G 2012). In streams of southwestern Alaska, in spring and early summer before the arrival of adult salmon, large rainbow trout are lower in drainages, in slower velocity currents, often in sloughs (Alt 1986). Later in the summer the distribution of age-1 and older Alaska rainbow trout is closely tied to the distribution of spawning salmon (Alt 1986; Brink 1995, p. 102, 104; Meka et al. 2003; Sundet and Pechek 1985, p. 39-40). In fall, after salmon spawning (except for coho) is complete, large southwestern Alaska rainbow trout occupy stream reaches with moderate currents and gravel substrates, often near grassy banks (Alt 1986). Stream fish may congregate in discrete overwintering habitats with moderate currents, often in areas of groundwater upwelling (Sundet and Pechek 1985, p. 40), and in late winter rainbow trout appear to select areas with ice cover (Sundet 1986, p. 39). In general, groundwater influence may be an important habitat characteristic because in regions where they are non-native, rainbow trout invasions can be limited to only groundwater-fed streams with stable flows (Inoue et al. 2009).

Radio telemetry, tagging, and genetic studies indicate the presence of multiple rainbow trout populations, including resident and adfluvial forms, within Bristol Bay watersheds (Burger and Gwartney 1986, p. 22, 26; Gwartney 1985, p. 70-71; Krueger et al. 1999; Meka et al. 2003; Minard et al. 1992, p. 34; PLP 2011, p. 15.1-85).

Life cycle

Rainbow trout spawning in the Bristol Bay region is associated with spring ice-out and occurs from late March through mid-June (Burger and Gwartney 1986, p. 22; Dye 2008, p. 21; Gwartney 1985, p. 45-46, 51; Minard et al. 1992, p. 2; PLP 2011, p. 15.1-85; Russell 1977, p. 41). Pre-spawner movements to spawning tributaries begins prior to ice-out, in early March (Dye 2008, p. 13). Within a given drainage, the timing of spawning can vary by several weeks depending on spatial and interannual stream temperature patterns (Burger and Gwartney 1986, p. 22; Hartman et al. 1962, p. 195; Russell 1977, p. 12). While post-spawners are often in poor physical condition (Russell 1977, p. 15), rainbow trout in the Nushagak and Kvichak river drainages can spawn in consecutive years and some spawn at least three years in a row (Minard et al. 1992, p. 17, 22; Russell 1977, p. 15).

In small lakes in southcentral Alaska, males matured at a smaller size than females and approximately one-third of males smaller than 178 mm (SL, standard length; 7 in) were mature. In this population most females did not mature until about 300 mm (SL; 12 in), while all males matured at about 250 mm (SL; 10 in) (Allin 1954, p. 36). In Moose Creek, in the Wood River lake system (Figure 2-4 in main assessment report), half of the fish over 376 mm (FL) were sexually mature (Dye 2008, p. 22). In Lower Talarik Creek, most spawners were ages 7 to 9 (Russell 1977, p. 17); in the upper Kvichak River, from 1989 to 1991, spawners were primarily ages 5 to 7 (Minard et al. 1992, p. 15). Fecundity of Lower Talarik Creek females (lengths ranging from 533 to 692 mm FL) averaged 3,431 (n = 16, SD = 1,053) and ova diameter averaged 5.5 mm (n = 25, SD = 0.6, Russell 1977, p. 18). In the Nushagak and Kvichak river drainages rainbow trout can reach at least age 14 (Minard and Dunaway 1991, p. 111, 189; determined by scale pattern analysis, a conservative measure; e.g., Sharp and Bernard 1988), with lengths to at least 814 mm (FL; Russell 1977, p. 30).

Post-spawning adults exhibit multiple movement patterns (Gwartney 1985, p. 68, 70; Meka et al. 2003). In Bristol Bay watersheds, many adults migrate shortly after spawning in the inlet or outlet streams of large lakes to feeding areas in large lakes (Burger and Gwartney 1986, p. 20; Meka et al. 2003; Minard et al. 1992, p. 2; Russell 1977, p. 44). After a summer of feeding in lakes, from September through November these mature rainbow trout move back to, or near, lake inlets and outlets to overwinter (Burger and Gwartney 1986, p. 20; Meka et al. 2003; Minard et al. 1992, p. 2; Russell 1977, p. 32). In late summer, some large adults move from Iliamna Lake into tributaries to forage amongst the spawning sockeye salmon, and then return to Iliamna Lake (PLP 2011, p. 15.1-85). In the Wood River lakes system, mature rainbow trout from many spawning streams aggregate to feed in the inter-lake rivers and remain there, or nearby in the adjacent lakes, through the following winter (Dye 2008, p. 13). After spawning in tributaries to southcentral Alaska's Susitna River, some mature rainbow trout remained near spawning areas, some moved downstream, some moved into other tributaries, and some moved upstream (Sundet and Pechek 1985, p. 39). Even in watersheds with large lakes, some fish may remain in outlet rivers year-round (Meka et al. 2003). Fish grow little in winter (Russell 1977, p. 32).

While some mature fish may not undergo large seasonal migrations, others move considerable distances (Dye 2008, p. 15; Meka et al. 2003; Minard et al. 1992, p. 33; Russell 1977, p. 23), to at least 200 km (122 mi) or more (Burger and Gwartney 1986, p. 16). Meka et al. (2003) speculated that seasonal migrations may be longer in watersheds with large lakes than in watersheds without large lakes. In southwest Alaska's Goodnews River, most adult fish moved less than 10 km throughout the year, and the movement that does occur is primarily upstream to spring spawning locations, and downstream to overwintering locations (Faustini 1996. p. 19-20).

Incubating rainbow trout eggs develop much more rapidly than do those of salmon, and juveniles emerge from spawning gravels between mid-July and mid-August at about 28 mm long (ADF&G 2012, e.g., site FSN0616E01; Johnson et al. 1994; Russell 1977, p. 30). Juveniles grow quickly during late summer and early fall, nearly doubling their length by late September (Russell 1977, p. 30). Immature fish may remain in their natal stream for several years before moving to other habitats (Russell 1977, p.18, 22).

In the Alagnak River (Figure 2-4 in main assessment report), within the Kvichak River drainage, Meka et al. (2003) distinguished three unique adult migratory patterns: lake-resident, lake-river, and river-resident. Each of these populations migrates seasonally, and Meka et al. (2003) suggested that Alagnak rainbow trout evolved these movements to take advantage of seasonal food sources (salmon eggs and carcasses) and warmer winter water temperatures. A similar pattern was observed in Upper Talarik Creek (PLP 2011, p. 15.1-85). Russell (1977, p. 37) noted that Lower Talarik Creek trout were in better condition following large Kvichak drainage sockeye salmon escapements than after small escapements.

Predator–prey relationships

The diet of rearing rainbow trout includes a broad range of aquatic and terrestrial invertebrates (Nakano and Kaeiryama 1995). When available, sockeye salmon eggs dominate rainbow trout diet in Lower Talarik Creek. While their diet is highly varied, other important Lower Talarik Creek rainbow trout food items includes aquatic dipterans (chironomids) and caddis fly larvae (Russell 1977, p. 36). Many larger Lower Talarik Creek rainbow trout appear to feed primarily in Iliamna Lake and not in the stream (Russell 1977, p. 35). In streams of the Nushagak and

Kvichak river drainages, Russell (1980, p. 103) reported that aquatic insects, salmon eggs, shrews and voles, unidentified fish and Chinook salmon fry, and salmon carcasses made up the bulk of the summer and fall diet of rainbow trout.

In studies within the Nushagak and Kvichak river drainages, Scheuerell et al. (2007) reported that before the seasonal arrival of adult salmon, rainbow trout primarily feed on dipterans (39%), stoneflies (18%), mayflies (12%), and caddis flies (11%). When spawning sockeye salmon arrive, rainbow trout diet shifts to salmon eggs (64%), larval blowflies (which feed on salmon carcasses; (11%)), and salmon carcasses (9%). This diet shift in conjunction with seasonal salmon spawning activity increases rainbow trout energy intake more than five-fold (Scheuerell et al. 2007).

In the laboratory, slimy sculpin, a ubiquitous species throughout the lakes and streams of the Nushagak and Kvichak river drainages, consume rainbow trout eggs (Fitzsimons et al. 2006). While Nushagak and Kvichak river drainages rainbow trout are certainly consumed by predators, they are not specifically identified in the diet of regional predatory fish (Metsker 1967, p. 26, 29; Russell 1980, p. 55-56, 62-63, 67, 73, 76, 81-83, 95-97, 103, 108), perhaps due in part to their comparatively low abundance relative to other available prey species.

Abundance and harvest

In the Nushagak and Kvichak river drainages total rainbow trout abundance is unknown, but there have been population estimates of larger (those targeted by anglers) fish in selected streams. From 2,000 to 4,500 fish available to hook and line angling gather in the upper Kvichak River in spring (Minard et al. 1992, p. 30); an average of 950 fish spawn in Lower Talarik Creek (Russell 1977, p. 9); and 950 fish larger than 199 mm occur in the Tazimina River, north of Iliamna Lake (Schwanke and Evans 2005, p. 9). In the Wood River lakes system, counts have been as high as 13,700 rainbow trout larger than 250 mm in the Agulowak River and 2,400 larger than 340 mm in the Agulukpak River (Dunaway 1993, p. 10, 24).

In the Nushagak and Kvichak river drainages and the adjacent Togiak River drainage, sport anglers caught more rainbow trout in 2009 (an estimated 159,685, or 22% of the statewide total) than all other non-salmon fish species combined (Jennings et al. 2011, p. 69). In 2009 sport anglers harvested 225 rainbow trout within the Nushagak and Kvichak river drainages and adjacent Togiak River drainage (Jennings et al. 2011, p. 69). Annual sport harvests have declined, due at least in part to the increasing popularity of catch-and-release fishing (Dye and Schwanke 2009, p. 6). The State of Alaska's Southwest Alaska Rainbow Trout Management Plan includes policies to manage Nushagak and Kvichak river drainages rainbow trout populations to maintain historic size and age composition without relying on hatcheries, to provide a range of harvest opportunities, and to economically develop the sport fishing industry while acknowledging the intrinsic value of the resource to Alaskans (Dye and Schwanke 2009, p. 32).

From the mid-1970s to the mid-2000s, rainbow trout were estimated to represent between 19 and 30.9% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214). In the mid-2000s, villagers from nine of the Nushagak and Kvichak river drainage communities annually harvested, as part of their subsistence activities, an estimated 3,740 rainbow trout (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202).

Stressors

Low pH (less than or equal to pH 5.5) impairs adult egg and sperm development and reduces early embryonic survival (Weiner et al. 1986). Pre-emergent embryo survival depends strongly on elevated DO concentrations and movement of groundwater through redds. Embryo survival is minimal where mean DO is less than 5.2 $mg{\cdot}l^{-1}$; at higher DO levels, embryo survival increases in relation to the velocity of intergravel flows greater than 5 $cm{\cdot}h^{-1}$ (Sowden and Power 1985). Bjornn and Reiser (1991, p. 84, 85) concluded that upstream migrating large trout need stream depths no less than 0.18 m, velocities no more than 2.44 $m{\cdot}s^{-1}$, and DO levels at least 80% of saturation and never less than 5.0 $mg{\cdot}l^{-1}$. For spawning rainbow trout in the central part of their North American range, Bell (1986, p. 96) recommended water temperatures between 2.2 and 20 °C (36 to 68 °F), and optimally 10 °C (49.5 °F). Russell (1977, p. 12) observed that Lower Talarik Creek rainbows stopped spawning at stream temperatures above 16 °C. In the laboratory, at temperatures below 2.8 °C, age-0 fry become inactive and seek refuge within the stream substrate. At temperatures below 5.5 °C, fry stop feeding (Chapman and Bjornn 1968, p. 168).

The survival of incubating embryos rapidly declines as the proportion of fines (sediments less than 6.35 mm in diameter) increases in spawning gravels, probably because the fines reduce intragravel flow (Bjornn and Reiser 1991, p. 99, 100). The success rate of fry emergence from spawning gravels and juvenile rearing density also declines with increasing proportion of fines in the substrate (Bjornn and Reiser 1991, p. 103, 132). Rainbow trout populations are particularly vulnerable when adult fish aggregate in spring spawning grounds and overwintering locations.

Ten steelhead population segments in California, Oregon, and Washington are currently listed as threatened or endangered primarily due to the lack of access to their historic range that has resulted from constructed barriers to migration and to stream dewatering. Nonanadromous rainbow trout populations are not listed (NMFS 2006).

Char

The Nushagak and Kvichak river drainages are home to three species of char: Arctic char, Dolly Varden, and lake trout. These char all spawn in fall. Bristol Bay Dolly Varden are often anadromous; Arctic char and lake trout are typically nonanadromous. The habitats of Dolly Varden and Arctic char occasionally overlap within the Nushagak and Kvichak river drainages, and when they do these species may hybridize (Taylor et al. 2008).

Taxonomic distinctions between Arctic char and Dolly Varden historically have been inconsistent. Some earlier authors (e.g., Craig 1978; Craig and Poulin 1975; Yoshihara 1973) called riverine and anadromous Alaska char “Arctic char” *Salvelinus alpinus*. More recent assessments suggest these fish are Dolly Varden (Behnke 1980, p. 454; Cavender 1980, p. 319-320; Taylor et al. 2008). In general, researchers currently believe that the North American char west of Canada’s Mackenzie River living primarily in flowing water are Dolly Varden, and Arctic char (and lake trout) are largely limited to lakes and adjacent reaches of their inlet and outlet streams (Reist et al. 1996).

The State of Alaska's 2012 edition of the *Catalog of Waters Important for the Spawning, Rearing or Migration of Anadromous Fishes*, or "Anadromous Waters Catalog" (AWC; e.g., Johnson and Blanche 2012) identifies Dolly Varden as the anadromous char across most of the state. However, in Bristol Bay the AWC identifies some streams as anadromous Dolly Varden habitat and some as anadromous Arctic char habitat. The AWC lists both anadromous Dolly Varden and anadromous Arctic char in the Kvichak River drainage, but only anadromous Arctic char in the Nushagak River drainage. These distinctions result from the history of regional variations in species naming and do not accurately reflect the ranges of different species and life histories. Current terminology labels the river-dwelling char of the Nushagak and Kvichak river drainages Dolly Varden. That is, the rivers and streams in the AWC currently designated as Arctic char habitat should, in almost all cases, be interpreted as Dolly Varden habitat. As a result of recent field work, ADF&G concluded that the Nushagak River, and the Koktuli River in particular, likely supported anadromous Dolly Varden (Schwanke 2007, p. 14).

Arctic char *Salvelinus alpinus*

Freshwater distribution and habitats

The Arctic char is a circumpolar species, distributed at high latitudes across the northern hemisphere (Brunner et al. 2001). In fresh water, Arctic char range closer to the North Pole than any other fish species (Johnson 1980, p. 16). In the fresh waters of North America, Arctic char are not typically far from the ocean. They range from Maine and New Hampshire north to the Canadian mainland Arctic Coast and through the Canadian Arctic archipelago (Scott and Crossman 1998, p. 203). The Alaska Arctic char distribution is disjunct. They occur in the Brooks Range, on the North Slope and the Seward Peninsula, in Bristol Bay, and a few other isolated locations in southcentral and interior Alaska (Mecklenburg et al. 2002, p. 199). Multiple distinct Arctic char races, differing in growth rate and migratory strategies, can occupy a single lake (Baroudy and Elliott 1994; Sandlund et al. 1992).

Alaska Arctic char appear primarily restricted to lakes and adjacent reaches of their inlet and outlet streams in well-drained areas (Morrow 1980b, p. 58; Scanlon 2000, p. 56, 58; Taylor et al. 2008, Wiedmer *unpublished*) and do not appear to undertake extensive seasonal migrations outside their home lakes (McBride 1980, p. 17). However, some Alaska Arctic char are known to move 15 to 20 km upstream and downstream between connected lakes (Troyer and Johnson 1994, p. 49) and Scanlon (2000, p. 43-48) suggested some move seasonally to estuarine or marine areas. Within the Nushagak and Kvichak river drainages, they are reported in the Tikchik and Wood River lakes, Iliamna Lake, and other upland lakes (Bond and Becker 1963; Burgner et al. 1965; Russell 1980, p. 49; Taylor et al. 2008), but they are apparently absent from Bristol Bay's coastal tundra lakes (Hildreth 2008, p. 9). Metsker (1967, p. 23) believed that Intricate Bay in Iliamna Lake is a particularly important spawning area. Adults and juveniles are common in the east end of Iliamna Lake, but not in tributaries (Bond and Becker 1963).

The depth of Arctic char lake spawning habitat can vary from 1 to 100 m (reviewed in Johnson 1980, p. 44), but is often in gravel shoals less than 5 m deep (Klemetsen et al. 2003, p. 31). McBride (1980, p. 6) found Wood River lakes spawners concentrated in the mouths of small tributary streams. DeLacy and Morton (1943) concluded that Kodiak Island's Karluk Lake Arctic char spawn in the lake and not in the tributary streams.

During the spring and early summer, McBride (1980, p. 20) estimated that approximately 40% (approximately 65,000) of the Wood River lakes Arctic char population greater than 300 mm long congregated in the inlets and outlets of the inter-lake rivers to feed on the sockeye salmon smolt outmigration. In Bristol Bay's Ugashik lakes (Figure 2-3 in main assessment report), Plumb (2006, p. 14-15) found Arctic char at depths greater than 75 m; but 90% of her catch was in waters less than 10 m deep. Fish sizes were not segregated by depth (Plumb 2006, p. 19-20). Similar to Dolly Varden (discussed below), Arctic char often occupy different habitats depending on the presence or absence of competitors (reviewed in Klemetsen et al. 2003, p. 29-30).

Life cycle

Arctic char in Bristol Bay are thought to be primarily nonanadromous (e.g., Reynolds 2000, p. 16), but Scanlon (2000, p. 43-48) suggested that some Becharof Lake Arctic char were anadromous. In Nushagak and Kvichak river drainage lakes, maturity is reached at around ages 3 to 6, at a length of approximately 330 mm (FL; 13 in.) (Metsker 1967, p. 23; Russell 1980, p. 48, 54). Metsker (1967, p. 23, 26) concluded that individual Iliamna Lake Arctic char spawned in alternating years, but McBride (1980, p. 16) provided evidence that at least some Lake Aleknagik Arctic char return annually to spawning locations. Wood River lakes Arctic char demonstrated high level of interannual fidelity to both spawning and feeding sites (McBride 1980, p. 6, 8, 19). Lake Aleknagik Arctic char periodically provide eggs for Alaska's sport fish hatcheries (Dunaway and Sonnichsen 2001, p. 138).

In the Nushagak and Kvichak river drainages Russell (1980, p. 48) found individuals ready to spawn in mid-September and McBride (1980, p. 6) collected Wood River lakes spawning fish between mid-September and mid-October. Ripening females in Brooks Range lakes have ova diameters ranging from 1.6 to 4.7 mm and fecundity ranges from 3,200 to 4,000 ova (Troyer and Johnson 1994, p. 41). If the substrate is not too coarse (approximately 10 cm or more, Sigurjónsdóttir and Gunnarsson 1989) females excavate redds into which they deposit their ova, which males immediately fertilize (Johnson 1980, p. 45). The incubating eggs and alevins remain in spawning gravels until the following spring (summarized in Johnson 1980, p. 47-48). Bristol Bay Arctic char live at least 15 years (Plumb 2006, p. 19), are particularly slow growing (Russell 1980, p. 48), reach fork lengths to at least 684 mm, and weights to at least 3.8 kg (Scanlon 2000, Appendix Table A). As with Dolly Varden, multiple migratory patterns and morphologies (Klemetsen et al. 2003, p. 36) occur with the basin (Russell 1980, p. 48; Scanlon 2000, p. 63-64). Tagging studies indicated that the Wood River lakes supported at least 20 discrete stocks (McBride 1980, p. 20).

Predator–prey relationships

The diet of young-of-the-year is poorly understood, but is thought in general to be dominated by small benthic and planktonic invertebrates (reviewed in Klemetsen et al. 2003, p. 32). In larger Brooks Range fish, planktonic crustaceans, insects, and snails were the most frequently occurring food items and fish were not an important part of the diet (Troyer and Johnson 1994, p. 44). In Iliamna Lake, summer diet was dominated by snails (Bond and Becker 1963) and winter diet was dominated by threespine stickleback (Metsker 1967, p. 26, 28). In other Nushagak and Kvichak river drainage lakes, mollusks and caddis fly larvae were the dominant benthic organisms consumed (Russell 1980, p. 55-56). In summer, freshwater crustaceans dominated the diet of Ugashik Lakes Arctic char (Plumb 2006, p. 27) and crustaceans, sticklebacks, insects, pygmy whitefish, sculpins, and juvenile sockeye salmon dominated the diet of Becharof Lake Arctic char (Scanlon 2000, p. 51, 53-54).

In the Nushagak and Kvichak river drainages, larger Arctic char eat outmigrating sockeye salmon smolt, often in spring and early summer at lake outlets (McBride 1980, p. 1; Metsker 1967, p. 29). Karluk Lake Arctic char eat mostly insects until the arrival of spawning sockeye, when their diet shifts to drifting salmon eggs, benthic invertebrates dislodged by salmon redd excavation, and adult salmon carcasses (DeLacy and Morton 1943).

Arctic char are eaten by other predatory fish, including lake trout (Troyer and Johnson 1994, p. 42) and larger Arctic char (Klemetsen et al. 2003, p. 33). Mink *Mustela vison* eat mature Wood River lakes Arctic char when they have the opportunity (Dunaway and Sonnichsen 2001, p. 138).

Abundance and harvest

In the Nushagak and Kvichak river drainages total Arctic char abundance is unknown. Meacham (reported in McBride 1980, p. 20) estimated that in the 1970s the Wood River lakes supported between 135,000 and 210,000 (presumably larger) Arctic char. Russell (1980, p. 48, 49) considered them common in some lakes in the Lake Clark area, but absent or rare in lakes of the upper Mulchatna River watershed and Lake Clark itself. In the mid-1960s, Iliamna Lake supported a commercial fishery and char made up 84% (2,979 kg, 6,553 lb) of the total dressed weight harvest (Metsker 1967, p. 9). These fish are thought to be mostly Arctic char (Bond and Becker 1963; Taylor et al. 2008).

Between 1971 and 1980, the annual estimated abundance of Arctic char larger than 249 mm ranged from 8,000 to 12,000 fish at the mouth of the Agulowak River and 4,300 to 7,800 fish at the mouth of the Agulukpak River (Minard et al. 1998, p. 131). By 1993 the estimated abundance of the Agulowak River population declined to only 5,400 fish, prompting a substantial reduction in bag limits and harvest means (Minard and Hasbrouck 1994, p. 13, 22). While excessive sport harvests were thought to be responsible for the decline (Minard et al. 1998, p. 16), anecdotal reports suggested that the more conservative sport harvest regulations were leading to the recovery of the stock (Dunaway and Sonnichsen 2001, p. 131). Minard et al. (1998, p. 16) also reported a similar apparently significant decline in Iliamna River stocks, both in overall abundance and in larger, older age classes. These observations prompted adoption of a catch-and-release fishing regulation.

The State of Alaska's sport and subsistence fisheries statistics do not distinguish between Arctic char and Dolly Varden. Sport anglers caught an estimated 48,438 Arctic char/Dolly Varden in the Nushagak and Kvichak river drainages and the adjacent Togiak River system in 2009 (8% of the statewide total) and harvested (kept) an estimated 2,159 (5% of the statewide total; Jennings et al. 2011, p. 73). Arctic char/Dolly Varden consistently support the greatest sport harvest of any non-salmon freshwater fish in Bristol Bay (Dye and Schwanke 2009, p. 8). Sport harvests have declined, due at least in part to both lower bag limits and the increasing popularity of catch-and-release fishing (Dye and Schwanke 2009, p. 6).

In the mid-2000s, villagers from ten of the Nushagak and Kvichak river drainage communities annually harvested, as part of their subsistence activities, an estimated 3,450 Arctic char and

Dolly Varden combined (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202). Arctic char and Dolly Varden combined were the most important non-salmon fish harvested in the villages of Iliamna, Newhalen, and Pedro Bay (Fall et al. 2006, p. 49, 84, 117). From the mid-1970s to the mid-2000s, Arctic char/Dolly Varden were estimated to represent between 16.2 and 26.9% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214).

Stressors

Arctic char are not tolerant of warm water. In tests of European Arctic char, egg mortality was 100% at temperatures at or above 12 to 13 °C (Jungwirth and Winkler 1984). Even when acclimated to water temperatures between 15 and 20 °C, pre-emergent fry could not survive exposures to temperatures above 26.6 °C for more than 10 minutes and could not survive temperatures over 21° C for more than a week (Elliott and Klemetsen 2002). Apparent over-harvests have been implicated for historic population declines within the Nushagak and Kvichak river drainages (Minard et al. 1998, p. 16).

Dolly Varden *Salvelinus malma*

Dolly Varden is a highly plastic species: multiple genetically, morphologically, and ecologically distinct morphs (e.g., benthic specialist, riverine specialist, lacustrine generalist, specialized piscivore) can exist in the same water body (Ostberg et al. 2009). Researchers currently recognize two geographically distinct forms of Dolly Varden: northern and southern, based on differences in life history (Armstrong and Morrow 1980, p. 107-130), phenotype (Behnke 1980, 465-466; Cavender 1980, p. 299-318), and genotype (Taylor et al. 2008). Dolly Varden in the Nushagak and Kvichak river drainages are of the northern form (Behnke 1980, p. 465).

Freshwater distribution and habitats

The global native freshwater range of Dolly Varden is restricted to waters draining to the Beaufort, Chukchi, and Bering seas and the North Pacific. The North American range extends from the Arctic coast of Alaska and Canada west of the Mackenzie River south to northern Washington. The Asian range stretches from the Chukotka Peninsula south to Japan and Korea (Mecklenburg et al. 2002, p. 200). In Alaska, Dolly Varden are found in waters draining to all coasts (Mecklenburg et al. 2002, p. 200) and the Alaska Peninsula (Figure 2-3 in main assessment report) divides the northern and southern forms (Behnke 1980, p. 453). Dolly Varden are known to occur widely in Bristol Bay, but their true distribution across the waters of the Nushagak and Kvichak river drainages is underreported. Within the Nushagak and Kvichak river drainages, popular sport fishing areas include the Alagnak, Newhalen, Nushagak, Mulchatna, and the Wood River–Tikchik Lakes systems (Minard et al. 1998, p. 188).

As in southeast Alaska (Bryant et al. 2004), Nushagak and Kvichak river drainage Dolly Varden occur farther upstream in high-gradient headwater streams than other fish species (ADF&G 2012, e.g., Site FSN0604E01). In both southeast Alaska (Bramblett et al. 2002; Wissmar et al. 2010) and the Nushagak and Kvichak river drainages (ADF&G 2012, e.g., Site FSN0616E01; e.g., Tazimina Lakes, Russell 1980, p. 31-32, 73), nonanadromous Dolly Varden occur above migratory barriers that currently prevent access to anadromous salmon populations.

Spawning occurs well upstream from areas used for overwintering (DeCicco 1992). Northern-form anadromous Dolly Varden overwinter primarily in lakes and in lower mainstem rivers where sufficient groundwater provides suitable volumes of free-flowing water (DeCicco 1997; Lisac 2009, p. 13, 15-16). In stream systems, spawning occurs in fast-flowing channels, primarily in upper reaches (Bramblett et al. 2002; Fausch et al. 1994; Hagen and Taylor 2001; Kishi and Maekawa 2009; Koizumi et al. 2006) and small, spring-fed tributaries (Hagen and Taylor 2001). Stream-resident Dolly Varden are reported to spawn in channels that are 1 to 3 m wide and 10 to 35 cm deep (Hino et al. 1990; Maekawa et al. 1993), with a mean depth of 9 cm, mean velocity of 21 $cm \cdot s^{-1}$, and median substrate diameter of 1.6 cm (Hagen and Taylor 2001). Stream-resident females select spawning sites where gravel is prevalent (Kitano and Shimazaki 1995). Spawning site substrate and current velocity do not correlate significantly with female size, but redd depth does (Kitano and Shimazaki 1995). Anadromous individuals spawn in deeper water than nonanadromous fish, ranging from 20 to 60 cm (Blackett 1968). They construct redds approximately 30 cm long, 15 to 25 cm wide, and 15 cm deep (Blackett 1968); composite redds, potentially containing several individual nests can be up to 3.5 m long and 1.2 m wide (Yoshihara 1973, p. 47).

In Kamchatka, Eberle and Stanford (2010) found rearing Dolly Varden in floodplain springbrooks and 7^{th}-order mainstem channels. Within the Nushagak and Kvichak river drainages, juveniles appear to be limited primarily to low-order headwaters (ADF&G 2012), and infrequently to side channels and the main channel of larger rivers downstream to the confluence of 5^{th}-order streams (ADF&G 2012, e.g., Site FSN0609A02). In southeast Alaska Dolly Varden rear in channels with gradients steeper than 20% (Wissmar et al. 2010), but in the Nushagak and Kvichak river drainages, Dolly Varden have been reported only in gradients of 12% or less (ADF&G 2012, e.g., Site FSM0503A07). Rearing Dolly Varden normally stay close to the stream bottom over gravels and cobbles (Dolloff and Reeves 1990; Hagen and Taylor 2001; Nakano and Kaeiryama 1995). Fry density is inversely related to stream depth (Bryant et al. 2004) and use of shallows increases if cover is available (Bugert et al. 1991). Different juvenile age classes can segregate in different micro- (Bugert et al. 1991; Dolloff and Reeves 1990) and macro- (ADF&G 2012; Denton et al. 2009) habitats. Affinity for cover, including cobbles and boulders, increases with age and tolerance for other Dolly Varden declines (Dolloff and Reeves 1990). Gregory (1988, p. 49-53) found stream-resident juvenile Dolly Varden in beaver ponds, where they grow faster than fish in adjacent streams, because of relatively warmer water temperatures and increased productivity.

Dolly Varden occur in upland Bristol Bay lakes, often in large numbers, feeding both at the surface and on the lake bottom, but they are uncommon or absent in lakes supporting Arctic char populations (Russell 1980, p. 49, 69-72; Scanlon 2000, p. 56). Dolly Varden will use all lake habitats in the absence of competitors (other salmonids), but concentrate in offshore and near-bottom habitats where competitors occupy nearshore and near-surface habitats (Andrew et al. 1992; Jonsson et al. 2008; Schutz and Northcote 1972). In the absence of competitors, lake-dwelling Dolly Varden move from deeper offshore waters, where they spend the day, perhaps in loose aggregations, to spend the night in onshore waters, near the surface (Andrusak and Northcote 1971). Dolly Varden vision is more sensitive to low light than competing salmonids (Henderson and Northcote 1985; Henderson and Northcote 1988; Schutz and Northcote 1972), allowing them to feed in deeper water and at night.

Life cycle

Northern-form Dolly Varden express several migratory patterns, including anadromous, nonanadromous stream-resident, nonanadromous spring-resident, nonanadromous lake-resident, nonanadromous lake-river-resident, and nonanadromous residuals (nonanadromous male offspring of anadromous parents; (Armstrong and Morrow 1980, p. 107-130; Behnke 1980, p. 466). Bristol Bay supports Dolly Varden with both anadromous (Reynolds 2000, p. 16-17; Scanlon 2000, p. 48-51) and nonanadromous (Denton et al. 2009; Scanlon 2000, p. 48-51) life histories.

Anadromous Dolly Varden exhibit very complex migratory patterns (Armstrong and Morrow 1980, p. 108-109), frequently leaving one drainage, traveling through marine waters, and reentering distant drainages, including those on separate continents (DeCicco 1992; DeCicco 1997; Lisac 2009, p. 14; Morrow 1980a). Even apparently nonanadromous fish can seasonally move more than 200 km within complex Bristol Bay watersheds (Scanlon 2000, p. 60).

Anadromous Dolly Varden of the Togiak River system, just west of the Nushagak and Kvichak river drainages, spawn from approximately mid-September to mid-October, overwinter downstream from spawning locations, and migrate annually to sea, where they spend approximately six weeks feeding (Lisac and Nelle 2000, p. 31-34). The timing of adult seaward migration generally corresponds with spring ice-out and high water, with adults migrating to sea in May and June. Their return to fresh water appears to relate to decreased stream discharge (Lisac and Nelle 2000, p. 33-34, 35). Anadromous Dolly Varden migrate upstream from the ocean to spawning areas in July and August (Lisac 2011). Russell (1980, p. 72) observed Dolly Varden spawning in the upper Mulchatna River system in mid-September.

Anadromous Dolly Varden home to spawn (Crane et al. 2003; Lisac and Nelle 2000, p. 31), but stocks can mix at sea and in overwintering areas (DeCicco 1992). In northwest Alaska anadromous Dolly Varden usually undertake three to five ocean migrations before reaching sexual maturity (DeCicco 1992). In the Togiak River, some anadromous fish mature at age 2 and most mature at age 4 (Lisac and Nelle 2000, p. 31; Reynolds 2000). Bristol Bay Dolly Varden can live at least 14 years (Plumb 2006, p. 19; Scanlon 2000, Appendix Table B) and reach lengths of 740 mm or more (Faustini 1996, p. 16). The minimum length of anadromous spawners in southwest Alaska’s Goodnews River is about 330 to 360 mm (Lisac 2010, p. 4).

Stream-residents mature from age 2 to 5 (Blackett 1973; Craig and Poulin 1975; Maekawa and Hino 1986; Russell 1980, p. 72) and live at least to age 7 (Blackett 1973). They are smaller than their anadromous counterparts, ranging at maturity from 113 mm (Hagen and Taylor 2001) to 520 mm (Gregory 1988, p. 29) in length, with most less than 200 mm (Gregory 1988, p. 21-25). Like anadromous individuals, after spawning stream-resident adults move quickly to downstream overwinter areas (Maekawa and Hino 1986).

Although anadromous Dolly Varden in northern Alaska tend to spawn only every second year (DeCicco 1997), Lisac and Nelle (2000, p. 31) speculated that most anadromous Dolly Varden in the Togiak River near the Nushagak and Kvichak river drainages can spawn in consecutive years. Female fecundity is a function of size (Jonsson et al. 1984), and anadromous females can produce up to 7,000 ova (Armstrong and Morrow 1980, p. 102), a productivity more than 50 times that of nonanadromous females (Blackett 1973). Ripe ova of anadromous females are 3.5

to 6 mm in diameter; ripe ova of nonanadromous females can be as small as 2.8 mm (Armstrong and Morrow 1980, p. 101, 102).

In most cases, a spawning group consists of one female and several males, one of which is a dominant male that actively courts the female (Hino et al. 1990; Maekawa et al. 1993). Females excavate redds in stream gravels, and then deposit their eggs while a male fertilizes them. Chars show little evidence of nest-guarding behavior (Kitano and Shimazaki 1995). Males appear to suffer a much higher post-spawning mortality than do females (Armstrong 1974).

In streams on both sides of the Bering Strait, egg hatching peaks from the end of April to mid-May (Radtke et al. 1996). Embryos are 15 to 20 mm long at hatching and remain in the spawning substrate while they absorb their yolk sac. Alevins emerge from the nest around the time of ice break-up (April to June), at a length of about 25 mm (Armstrong and Morrow 1980, p. 108). Radtke et al. (1996) found that fry begin actively feeding in June to early July, 42 to 52 days after hatching. Newly emerged alevins tend to stay on the bottom of pools and are relatively inactive except when feeding (Armstrong and Morrow 1980, p. 108). Growth greatly increases through the summer as water becomes warmer; by September, age-0 fish average about 60 mm long (Armstrong and Morrow 1980, p. 108). Young anadromous Togiak River Dolly Varden make their first seaward migration between their first summer and age 3 (Reynolds 2000, p. 15). Size, rather than age, appears to govern the timing of initial smolt out-migration (Armstrong 1970).

Predator–prey relationships

Dolly Varden primarily target benthic invertebrates in streams (Eberle and Stanford 2010; Russell 1980, p. 73; Stevens and Deschermeier 1986) and lakes (Scanlon 2000, p. 53-55; Schutz and Northcote 1972). During the day, foraging from stream drift (food drifting in the current) is more important than benthic foraging, but the relative importance of benthic foraging increases at night; surface feeding is not important (Hagen and Taylor 2001). Dolly Varden also switch to benthic feeding when drift availability is limited (Fausch et al. 1997; Nakano et al. 1999; Nakano and Kaeiryama 1995).

Dolly Varden eat juvenile salmon (Armstrong 1970; Bond and Becker 1963), but they have been largely exonerated (Armstrong and Morrow 1980, p. 133; DeLacy and Morton 1943; Morton 1982) from earlier accusations that they were salmon run destroyers. From 1921 to 1939, Alaska Dolly Varden were the target of a bounty program designed to increase salmon abundance. Now it is believed that Dolly Varden were not responsible for the declines in salmon abundance (Harding and Coyle 2011, p. 19). When spawning salmon are present, salmon eggs–probably those flushed by high flows and superposed redd construction–can be important food (Armstrong 1970, p. 53-54; Scanlon 2000). Denton et al. (2009) reported that nonanadromous age-1 and older Dolly Varden in certain ponds near Iliamna Lake feed on sockeye salmon fry for a brief time in late June to mid-July, then migrate to sockeye spawning areas and feed almost exclusively on eggs from late July to mid-September. From late August through September they also eat blowfly larvae that had fed on adult sockeye salmon carcasses. Salmon eggs are too big for age-0 fry to consume, but blowfly maggots, when available, dominate their diet. Some nonanadromous Dolly Varden actively follow adult sockeye salmon to spawning areas and grow significantly faster after the arrival of spawning salmon (Denton et al. 2009; Wipfli et al. 2003). In May in Iliamna Lake tributaries such as the Copper River, Dolly Varden feed heavily on the spawning run of mature pond smelt (Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication).

The summer diet of stream-resident Dolly Varden in northcentral British Columbia is primarily adult dipterans (true flies; 33.6%) and hymenopterans (wasps, bees, and ants; 7.5%), with other aquatic insects comprising the remainder (Hagen and Taylor 2001). In southeast Alaska Dolly Varden also feed on terrestrial insects, but do so less than other salmonids occupying the same habitat (Wipfli 1997). Juvenile stream-rearing Dolly Varden consume a wide variety of predominantly aquatic invertebrates (Eberle and Stanford 2010), preferentially selecting immature blackflies, non-biting midges (chironomids), and mayflies (Milner 1994; Nakano and Kaeiryama 1995), but also feed on terrestrial invertebrates (Baxter et al. 2007; Nakano et al. 1999), particularly in the absence of competing salmonids (Baxter et al. 2004; Baxter et al. 2007). Some juvenile Dolly Varden eat age-0 Arctic grayling (Stevens and Deschermeier 1986).

In the absence of competitors, lake-dwelling Dolly Varden feed heavily in summer on terrestrial insects and during fall on zooplankton. In the presence of competition, they feed heavily on chironomids (both pupae and larvae) and trichopterans (caddis flies; Andrusak and Northcote 1971; Hindar et al. 1988).

River otters *Lutra canadensis* can extensively prey on rearing Dolly Varden (Dolloff 1993). Armstrong and Morrow (1980, p. 110) noted that bears and wolves take some mature fish from spawning areas (also observed by Wiedmer; ADF&G 2012, Site FSS0424A07) and speculated that fish-eating birds also take a few. Fish-eating birds such as harlequin ducks *Histrionicus histrionicus*, common *Mergus merganser* and red-breasted *M. serrator* mergansers, and bald eagles *Haliaeetus leucocephalus* are common in southwest Alaska throughout the year and ospreys (*Pandion haliaetus*, a fish-eating raptor) are more abundant along the waters of Bristol Bay than elsewhere in Alaska (Armstrong 1980, p. 69, 80, 81, 89, 92). Russell (1980, p. 81) reported that Lake Clark National Park and Preserve (Figure 2-3 in main assessment report) lake trout feed on Dolly Varden. Perhaps the greatest predators on smaller Dolly Varden are larger Dolly Varden (Armstrong and Morrow 1980, p. 110; Russell 1980, p. 73). Wiedmer (ADF&G 2012, Site FSS0406A01) collected a 195-mm (FL) northern-form Dolly Varden that had partially swallowed a 98-mm Dolly Varden.

Abundance and harvest

In the Nushagak and Kvichak river drainages total Dolly Varden abundance is unknown. Between 2002 and 2010 (excluding 2006), annual runs of anadromous Dolly Varden to southwest Alaska's Kanektok River averaged 13,115 (range: 8,140 to 43,292, Lisac 2011). The State of Alaska's sport and subsistence fisheries statistics do not distinguish between Arctic char and Dolly Varden. Sport anglers caught an estimated 48,438 Arctic char/Dolly Varden in the Nushagak and Kvichak river drainages and the adjacent Togiak River system in 2009 (8% of the statewide total) and harvested (kept) an estimated 2,159 (5% of the statewide total; Jennings et al. 2011, p. 73). In combination, Arctic char and Dolly Varden consistently support the greatest harvest of any non-salmon freshwater fish in Bristol Bay (Dye and Schwanke 2009, p. 8). Sport harvests have declined, due at least in part to both lower bag limits and the increasing popularity of catch-and-release fishing (Dye and Schwanke 2009, p. 6).

In the mid-2000s, villagers from ten of the Nushagak and Kvichak river drainage communities annually harvested, as part of their subsistence activities, an estimated 3,450 Dolly Varden and Arctic char combined (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202). Dolly Varden and Arctic char combined were the most important non-salmon fish harvested in the villages of Iliamna, Newhalen, and Pedro Bay (Fall et al. 2006, p. 49, 84, 117). From the mid-1970s to the mid-2000s, Dolly Varden/Arctic char were estimated to represent between 16.2 and 26.9% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214).

Stressors

Dolly Varden are not tolerant of warm water (Fausch et al. 1994; Kishi et al. 2004; Nakano et al. 1996). Feeding activity declines to low levels at water temperatures above 16 °C and their upper lethal limit is 24 °C (Takami et al. 1997). As a result, activities that increase water temperatures beyond tolerance levels will reduce available habitat (Kishi et al. 2004; Nakano et al. 1996), including the refuge from potential competitors that cold stream temperatures provide (Fausch et al. 2010).

Total dissolved solids (TDS) do not have a significant impact on Dolly Varden fertilization, up to the highest concentrations evaluated (1,817 $mg \cdot l^{-1}$); however, elevated TDS did significantly affect embryo water absorption at concentrations as low as 964 $mg \cdot l^{-1}$ (Brix et al. 2010). Brix et al. (2010) concluded that the water-hardening phase immediately following fertilization was the most sensitive life stage to elevated TDS.

McDonald et al. (2010) reported that Dolly Varden are relatively insensitive to selenium exposure (perhaps due to low rearing temperatures) and estimated that concentrations of 44 and 49 $mg \cdot kg^{-1}$, dry weight affected 10 and 20% of the study population, respectively. Dolly Varden in fresh water metabolize naphthalene much more rapidly than seawater, which may explain the greater toxicity of naphthalene to fish when in seawater (Thomas and Rice 1980). Whether in fresh water or sea water, toluene is more readily metabolized by Dolly Varden than is naphthalene (Thomas and Rice 1986b), and toluene is more rapidly metabolized in warmer water (Thomas and Rice 1986a).

In southeast Alaska Dolly Varden are typically the first salmonid colonizers of new streams formed by glacial retreat, suggesting they have lower requirements for microhabitat features (e.g., pools) that are a function of stream age (Milner 1994). Because they often use small isolated stream habitats and spawning populations can be small, both anadromous and nonanadromous Dolly Varden are particularly vulnerable to barriers to migration (Dunham et al. 2008; Fausch et al. 2010; Kishi and Maekawa 2009; Koizumi 2011; Koizumi and Maekawa 2004) and to alterations of the small headwater streams in which they spawn and rear (Armstrong and Morrow 1980, p. 133). The closely related bull trout *S. confluentus* is listed as threatened in the contiguous United States (USFWS 1999), due in large part to habitat fragmentation and warming stream temperatures.

Lake trout *Salvelinus namaycush*

Freshwater distribution and habitats

The global native distribution of lake trout is limited almost entirely to Canada and Alaska, from the just south of Canada's southern border north to the Canadian Arctic archipelago and from Canada's eastern maritime provinces west to near the Bering Sea coast (Martin and Olver 1980, p. 209-210). This native range is almost entirely restricted to the limits of North American late-Pleistocene glaciations (Lindsey 1964). In Alaska lake trout occur in suitable habitats across most of the state except for southern southeast Alaska, much of western Alaska, and maritime islands (Mecklenburg et al. 2002, p. 198), but within that broad range, there are great discontinuities between occupied habitats (Lindsey 1964). Bristol Bay marks the westernmost limit of the lake trout's native range (Mecklenburg et al. 2002, p. 198). Bristol Bay lake trout appear to be restricted to upland lakes and their inlet and outlet streams (ADF&G 2012, Site FSN0616C03; Burgner et al. 1965; Metsker 1967, p. 9, 11; Russell 1980, p. 47, 78, 79; Yanagawa 1967, p. 10). They are common in the Tikchik Lake system but absent from the main Wood River lakes (Burgner et al. 1965). Russell (1980, p. 77) considered them widely distributed in the Lake Clark area and their diet indicated they fed at lake surfaces and bottoms, and throughout water columns. Anglers target lake trout in many Nushagak and Kvichak river drainage upland lakes, particularly Lake Clark, Iliamna Lake, and the Tikchik Lakes (Minard et al. 1998, p. 152-155).

Almost all spawning occurs along lake shorelines or shoals, above coarse, often angular substrate (Martin and Olver 1980, p. 218; Scott and Crossman 1998, p. 222; Viavant 1997, p. 6-7). Lake trout typically spawn along exposed shorelines off points or islands or in mid-lake shoals (Martin and Olver 1980, p. 218). Russell (1980, p. 77) reported apparent spawning habitats on shoals around islands in Lake Clark. Spawning can occur in very spatially discrete locations (Viavant 1997, p. 6-7). Spawning areas appear to be kept clean of fine sediments by wind-driven or deep-water currents and not by springs or seeps. The maximum depth of spawning may be positively related to lake size, particularly fetch length, but is often less than 6 m (Martin and Olver 1980, p. 218; Royce 1951). In lakes that thermally stratify, lake trout may migrate seasonally from warming surface waters to cool deep waters (Martin and Olver 1980, p. 228-230).

Life cycle

Compared to many other salmonids, lake trout exhibit little tendency toward anadromy (Rounsefell 1958), but some individuals in far northern areas do migrate seasonally to marine waters (Swanson et al. 2010). Like other char, lake trout is a highly variable species and multiple forms, differing in diet, growth, and life span can occupy a single lake (Martin 1966). Adults can live to at least 51 years (Keyse et al. 2007); in the Nushagak and Kvichak river drainages, lake trout are known to live at least 29 years, begin to reach maturity at about 6 years (Russell 1980, p. 77), reach lengths of at least 910 mm (FL; Wiedmer *unpublished*), and weights of at least 14.5 kg (Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication). In some southcentral Alaska lakes, lake trout mature at ages 7 to 10 at lengths of 450 to 550 mm (FL; Van Whye and Peck 1968, p. 35). In the Nushagak and Kvichak river drainages and lakes in southcentral and interior Alaska, lake trout spawn in mid- to late September and perhaps later (Russell 1980, p. 77; Van Whye and Peck 1968, p. 35; Viavant 1997, p. 6). Mature lake trout, particularly those in more northern habitats, may not spawn annually, but will skip one or two years between spawning events (Martin and Olver 1980, p. 215). Most lake trout appear to home each year to specific spawning sites, but not all do (Martin and Olver 1980, p. 218).

The number of ova produced by mature females is a function of size and perhaps stock; reported average fecundities range from 996 to 15,842, and the diameter of ripe ova range from 3.7 to 6.8 mm (Martin and Olver 1980, p. 211, 213, 214). Lake trout may clean fine debris from the general area of spawning locations, but they do not construct redds, nor cover or guard their fertilized eggs (Royce 1951). Eggs and alevins incubate in spawning substrates until the following spring (Martin and Olver 1980, p. 224). The movements of young-of-the-year fry are poorly understood, but they are suspected to move to deeper water, often using the cover of coarse substrates (Martin 1966, p. 224, 226; Royce 1951). Larger fish can be nomadic within their home lake (Martin and Olver 1980, p. 226-227), and may move short distances between lakes (Scanlon 2010, p. 22). A probably mature, and apparently healthy 565 mm (FL) lake trout was captured in mid-August in the Tikchik River approximately 14 km from the nearest large lake (ADF&G 2012, site FSN0616C03), and sub-adult and adult lake trout are regularly encountered by summer anglers in the Alagnak River, downstream of Kukaklek and Nonvianuk lakes (Charles Summerville, Alaska Trophy Adventures, King Salmon, AK, personal communication). As a result of spawning stress, some adults move from lakes downstream into outlet rivers, and many likely do not survive to return to their natal waters (Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication).

Predator–prey relationships

In Lake Clark, growth remains fairly constant up to lengths of about 560 mm (FL), after which the relationship between weight and length significantly increases. Metsker (1967) attributed this to a transition, occurring at a length of about 480 mm (FL), from a diet of invertebrates to a diet of fish, primarily least cisco. A similar diet transition from insects and mollusks to fish, coupled with a potential influence on growth rate, was observed in lake trout from lakes in southcentral Alaska (Van Whye and Peck 1968, p. 30, 37).

Aquatic and terrestrial insects and small crustaceans are important foods for young-of-the-year fry (Martin and Olver 1980, p. 234). In Alaska, Arctic grayling, sculpins, humpback, round, and pygmy whitefish, least cisco, sockeye salmon fry, salmon eggs, ninespine stickleback, longnose suckers, Dolly Varden, Arctic char, rodents, shrews, and smaller lake trout are all prey items for large lake trout (Plumb 2006, p. 29; Russell 1980, p. 81-83; Troyer and Johnson 1994, p. 42; Van Whye and Peck 1968, p. 37). Lake trout observed in August in the Tikchik and Alagnak rivers likely were attracted to high densities of spawning salmon. In the absence of fish prey, large lake trout in arctic Alaska lakes are generalist feeders and feed primarily on benthic invertebrates (Keyse et al. 2007). In the presence of large lake trout, small lake trout limit their use of available habitats to avoid predation (Hanson et al. 1992; Keyse et al. 2007; McDonald and Hershey 1992).

In the laboratory, slimy sculpin consume lake trout eggs (Fitzsimons et al. 2006). In the wild, small lake trout (Royce 1951) are known to feed on lake trout eggs, as are round whitefish (Loftus 1958), which are found throughout the Nushagak and Kvichak river drainages (ADF&G 2012). Royce (1951) suspected that humpback whitefish, which are found in many of the same Nushagak and Kvichak river drainage lakes as lake trout, also feed on lake trout eggs. Burbot and large lake trout in the Nushagak and Kvichak river drainages feed on small lake trout (Russell 1980, p. 67, 82-83). Power and Gregoire (1978) concluded that, of the all the members of the fish community in Lower Seal Lake, Quebec, lake trout were the species most affected by freshwater seal *Phoca vitulina* predation. In 1998, Small (2001) reported that Iliamna Lake in the Kvichak River drainage supported a minimum harbor seal population of 321.

Abundance and harvest

In Bristol Bay total lake trout abundance is unknown, but in 2009 the Nushagak and Kvichak river drainages and the adjacent Togiak River system supported an estimated sport catch of 3,651 (12% of the statewide total) and harvest of 588 (11% of the statewide total; Jennings et al. 2011, p. 72). Dye and Schwanke (2009, p. 6) speculated that the trend of decreasing sport harvests are due in part to increasing catch-and-release practices.

In the mid-1960s, Iliamna Lake and Lake Clark supported a commercial winter lake trout fishery (Metsker 1967, p. 8, 10). In 1966 and 1967 Tikchik Lake also supported an experimental commercial freshwater fishery (Yanagawa 1967). Lake trout were the second-most commonly harvested species in that fishery, representing 30% of the overall harvest. The Tikchik Lake fishery harvested 1,502 lake trout, which averaged 2.2 kg in weight, and ranged in length from 500 to 575 mm and in age to more than 15 years (Yanagawa 1967).

In the mid-2000s, villagers from ten of the Nushagak and Kvichak river drainage communities annually harvested, as part of their subsistence activities, about an estimated 1,030 lake trout (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202). From the mid-1970s to the mid-2000s, lake trout were estimated to represent between 4.6 and 11.8% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214).

Stressors

As with lake-spawning humpback whitefish, excessive variation in lake level is suspected to reduce egg and alevin survival (Martin and Olver 1980, p. 223). Sedimentation of lake spawning areas has resulted in declines or elimination of successful reproduction (reviewed in Martin and Olver 1980, p. 223-224). In nature, lake trout are reported in water temperatures ranging from -0.8 to 18 °C, appear to prefer summer temperatures around 6 to 13 °C (Martin and Olver 1980. p. 230-231), and to have an upper lethal temperature of approximately 23.5 °C (Gibson and Fry 1954). Martin and Olver (1980, p. 231) concluded that a DO level of approximately 4 $mg \cdot l^{-1}$ is the minimum tolerated by lake trout. Late maturity, long life, and slow growth make lake trout particularly vulnerable to over-harvest (Martin and Olver 1980, p. 259). Like the similarly long-lived piscivore, northern pike, lake trout bioaccumulate and biomagnify atmospherically deposited mercury (Swanson et al. 2011). Lake acidification has extirpated lake trout from some Canadian lakes (Matuszek et al. 1992).

Arctic grayling *Thymallus arcticus*

Freshwater distribution and habitats

Arctic grayling are found in fresh waters at higher latitudes in the Northern Hemisphere, from Hudson Bay west across the Bering Strait to the Ob and Kara river drainages east of Asia's Ural Mountains. In North America, the current native distribution of Arctic grayling is almost entirely restricted to northwestern Canada and Alaska (Scott and Crossman 1998, p. 301, 302). Arctic grayling native to northern Michigan were extirpated by around 1936 (Scott and Crossman 1998, p. 301), and by the 1990s their former broad distribution in streams of the Upper Missouri River were limited to the Big Hole River in southwestern Montana (Lohr et al. 1996). In Alaska, the Arctic grayling native range stretches across the entire mainland, but they are absent from most islands, except those formerly part of the Bering land bridge (Morrow 1980b, p. 145-146). Throughout their range, Arctic grayling are primarily restricted to fresh waters. Along the Arctic Ocean coast, they will descend downstream to feed in nearshore marine waters, but they appear to remain in the low salinity plume at the mouths of rivers or in lagoons (Furniss 1975; Tack 1980, p. 26).

Arctic grayling are widely distributed in Bristol Bay lakes (Burgner et al. 1965; Russell 1980, p. 49, 57; Yanagawa 1967, p. 12) and streams (Coggins 1992). They can occur in slow-flowing lowland streams where salmon, rainbow trout, and Dolly Varden are absent (ADF&G 2012), but they do not occur in many of the small shallow ponds on the coastal plain (Hildreth 2008, p. 9). In the absence of headwater lakes, their range often does not extend quite as far up the higher gradient headwater streams of the Nushagak and Kvichak river drainages as do Dolly Varden and rearing coho salmon, but they are found, at some time of the year, in most tributaries and downstream to the lower Nushagak and Kvichak rivers (ADF&G 2012; Krieg et al. 2009, p.365, 383). Sport anglers catch Arctic grayling across most of the Nushagak and Kvichak river drainages, with a particular focus on the Kvichak, Alagnak, Newhalen, Tazimina, Nushagak, Mulchatna, and Koktuli rivers, Lake Clark, and the Wood River and Tikchik lake systems (Minard et al. 1998, p. 189).

Nushagak and Kvichak river drainages stream spawning locations may represent sites that provide both warm spring and summer temperatures and suitable hydrology (Tack 1980, p. 3-4, 14-16, 27; Warner 1957). Some spawning may occur in lakes, at stream outlets (Warner 1957). Arctic grayling and rainbow trout are the only spring-spawning salmonids in the Nushagak and Kvichak river drainages, and both likely seek spawning sites that enhance incubation rates and early fry growth. Tack (1980, p. 14) reported that most interior Alaska spawning occurred in riffles with sand and gravel substrates and minimal silt, in currents ranging from 0.25 to 1 $m \cdot s^{-1}$. Reed (1964, p. 14) concluded that Alaska Arctic grayling did not target specific spawning substrates.

Best egg survival in the closely-related European grayling *T. thymallus* was 6 to 13.5 °C (Jungwirth and Winkler 1984). For much of the summer, age-0 fish tend to remain near the sites where they emerged from the spawning substrate (Craig and Poulin 1975; MacPhee and Watt 1973, p. 14, 15; Tack 1980, p. 27; Tripp and McCart 1974, p. 56). Given the August distribution of age-0 fry in the Nushagak–Mulchatna drainage (ADF&G 2012), it appears that most Arctic grayling spawning in this system occurs in tributaries.

When food is not limiting, optimal growth for age-0 juveniles in interior Alaska is at about 17 °C (Dion and Hughes 2004; Mallet et al. 1999). Older age classes may segregate to different habitats (Craig and Poulin 1975; Tack 1980, p. 29; Vincent-Lang and Alexandersdottir 1990, p. 50), but the details of that segregation may depend on the drainage-specific patterns of water temperature and food availability (Hughes 1998).

After spawning, adults may migrate further upstream (Hughes and Reynolds 1994; Vascotto 1970, p. 77; Wojcik 1954), or descend back to the mainstem (Craig and Poulin 1975; MacPhee and Watt 1973, p. 14; Tripp and McCart 1974, p. 49-51; Warner 1957), often using the same summer feeding areas annually (Ridder 1998, p. 17; Tack 1980, p. 21). Juveniles age 1 and older often follow adults, perhaps to imprint the complex migratory routes (Tack 1980, p. 20). In interior and southcentral Alaska, adult Arctic grayling overwinter in deep lakes and large rivers (Reed 1964, p. 13; Ridder 1998, p. 10-15; Sundet and Pechek 1985, p. 44; Tack 1980, p. 8, 28). Available evidence suggests the same pattern applies in the Nushagak River drainage. In August, Arctic grayling are absent or uncommon in the lower mainstem of the Nushagak River (ADF&G 2012). However, in this same area, local residents harvest large numbers of Arctic grayling through the ice during winter (Krieg et al. 2009, p. 220, 383).

Life cycle

Arctic grayling are nonanadromous, but often do undertake extensive seasonal migrations. Prior to spring breakup, large fish concentrate in mainstem rivers, at the mouths of tributaries. During and immediately after breakup, fish begin entering tributaries, even below ice cover and through channels on the ice surface (Reed 1964, p. 12-13; Warner 1957). In at least parts of Alaska, the upstream migration correlates with the peak of the spring freshet (Tack 1980, p. 13) and adults appear to show some fidelity to spawning areas (Craig and Poulin 1975; Tack 1980, p. 27). Nushagak and Kvichak river drainages Arctic grayling spawn in May through early June, shortly after breakup (Dye 2008, p. 26; Russell 1980, p. 57).

Mature female fecundity probably averages between about 4,000 and 7,000 ova, with some large fish producing much more (Scott and Crossman 1998, p. 303). Water-hardened eggs have an average diameter of around 3 mm and are non-adhesive (Reed 1964, p 14). Spawning adults do not actively construct redds (Craig and Poulin 1975), but their actions may create slight depressions in the stream substrate (Reed 1964, p. 13-14). Fertilized eggs fall into interstitial spaces, hatch in 2 to 3 weeks at lengths of about 8 mm (Scott and Crossman 1998, p. 303), and fry start feeding a few days later (Morrow 1980b, p. 146). Some age-0 fish in the Nushagak and Kvichak river drainages are free-swimming in early June, and perhaps even earlier in certain locations (Russell 1980, p. 57). Early growth rates appear related to temperature and benthic invertebrate densities (Tripp and McCart 1974, p. 21); on Alaska's North Slope, growth rates of age-0 Arctic grayling correlate positively to stream temperature (Luecke and MacKinnon 2008).

In the Nushagak and Kvichak river drainages, age-0 fish reach a mean fork length of about 69 mm (n = 700, SD = 13.6 mm) by August (calculated from data provided by ADF&G 2012). After age 0, Arctic grayling in the Nushagak and Kvichak river drainages grow about 47 $mm \cdot y^{-1}$ until age 5 when growth begins to slow (Russell 1980, p. 60). Fish begin maturing at lengths of about 300 mm (FL), and once mature, grayling appear to spawn every year (Craig and Poulin 1975; Engel 1973, p. 8; Tripp and McCart 1974, p. 34). Bristol Bay Arctic grayling mature around age 5 (Russell 1980, p. 57), can live at least 13 years (Plumb 2006, p. 56), reach lengths of at least 650 mm (FL; MacDonald 1995, Table 7) and weights at least 0.9 kg (Russell 1980, p. 57). Alaska Arctic grayling may travel over 320 km between spawning, summer feeding, and overwintering locations (Reed 1964, p. 13; Ridder 1998, p. 10; Tripp and McCart 1974, p. 53).

Predator–prey relationships

Arctic grayling appear to feed on whatever is available to them, primarily aquatic and terrestrial insects, sequentially taking advantage of temporary peaks of abundance of different invertebrate populations (Plumb 2006, p. 62; Reed 1964, p. 20; Scheuerell et al. 2007; Tripp and McCart 1974, p. 60-61). Arctic grayling typically feed at the surface and mid-depth in the water column (Vascotto 1970), but food items include benthic slimy sculpin and slimy sculpin eggs (Bond and Becker 1963) and humpback whitefish eggs (Kepler 1973, p. 71). Scheuerell et al. (2007) discovered that in the Nushagak River drainage, after the arrival of spawning sockeye salmon, the energy intake of Arctic grayling increases more than five-fold, due primarily to the increased availability of benthic invertebrates. As spawning salmon construct redds and bury fertilized eggs, they disturb the substrate, displacing benthic macroinvertebrates, thus making them more available to Arctic grayling predation. In addition, Arctic grayling feed on salmon eggs and the larval blowflies that colonize salmon carcasses. These salmon-derived resources contribute a large majority of the energy necessary for the annual growth of nonanadromous Arctic grayling (Scheuerell et al. 2007). In lakes, Arctic grayling can be the most important prey species of lake trout (Troyer and Johnson 1994, p. 42). In Alaska Arctic streams, Stevens and Deschermeier (1986) found that some juvenile Dolly Varden eat age-0 Arctic grayling fry .

Abundance and harvest

In Bristol Bay total Arctic grayling abundance is unknown, but in 2009 the Nushagak and Kvichak river drainages and the adjacent Togiak River drainage supported an estimated sport fish catch of 44,762 fish (11% of the statewide total) and a harvest of 1,094 (4% of the statewide total; Jennings et al. 2011, p. 74). Dye and Schwanke (2009, p. 6) speculated that the ongoing trend of decreasing sport harvests are due in part to increasing catch-and-release practices.

In the mid-2000s, villagers from nine of the Nushagak and Kvichak river drainage communities annually harvested, as part of their subsistence activities, about an estimated 7,790 Arctic grayling (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202). From the mid-1970s to the mid-2000s, Arctic grayling were estimated to represent between 6.9 and 9.7% of the total weight of the Kvichak River drainage non-salmon freshwater fish subsistence harvest (Krieg et al. 2005, p. 214).

Stressors

Total dissolved solids up to 2,782 $mg \cdot l^{-1}$ do not have a significant impact on Arctic grayling egg fertilization; however, concentrations as low as 1,402 $mg \cdot l^{-1}$ do significantly affect water absorption during the water-hardening phase immediately following fertilization, when embryos gain resistance to mechanical damage (Brix et al. 2010). As a result, Brix et al. (2010) identified that period as the most sensitive early developmental stage.

Egg mortality in the closely-related European grayling *T. thymallus* was 100% at temperatures over 16 °C or under 4 °C (Jungwirth and Winkler 1984). In interior Alaska, the minimum and maximum temperatures at which growth occurs are 4.5 °C and 21 °C (Dion and Hughes 2004; Mallet et al. 1999). In interior Alaska, age-0 fish are more tolerant of high water temperatures than alevins and older juveniles, with a median tolerance limit in excess of 24.5 °C, compared to 20 to 24.5 °C for the other life stages (LaPerrier and Carlson 1973, p. 29).

In North Slope streams, the growth of age-0 fry is positively correlated with temperature, while adult growth has no temperature correlation (Deegan et al. 1999; Luecke and MacKinnon 2008). Adult and age-0 juveniles may also respond differently to stream discharge. Adult growth in North Slope streams is positively correlated with discharge, while age-0 growth is negatively correlated with it (Deegan et al. 1999; Luecke and MacKinnon 2008). Wojick (1954, p. 67) speculated that elevated stream discharges during the incubation and early fry rearing stage would harm Arctic grayling stocks.

Although reasons for the dramatic contraction in the native range of stream-resident Upper Missouri River Arctic grayling is not well understood, constructed barriers to fish migration and stream dewatering appear to be major contributing factors (Barndt and Kaya 2000).

OTHER SPECIES

Lampreys (Family Petromyzontidae)

Lamprey taxonomy is unsettled (e.g., Renaud et al. 2009), with particular confusion regarding the relationship between, and the taxonomic status of, nonparasitic nonanadromous forms and parasitic anadromous forms. Currently, the Nushagak and Kvichak river drainages are thought by some (ADF&G 2012; Docker 2009; Lang et al. 2009; Mecklenburg et al. 2002; Renaud et al. 2009) to be home to three lamprey species: Arctic lamprey *Lethenteron camtschaticum*, Alaskan brook lamprey *L. alaskense*, and Pacific lamprey *Entosphenus tridentatus* (nomenclature follows Brown et al. 2009). Arctic and Alaskan brook lamprey are closely allied, but are thought, at least by some, to be distinct, valid species (Vladykov and Kott 1978). The Arctic lamprey is believed to be the ancestral form, from which the species Alaskan brook lamprey is derived (a *satellite species*) (Renaud et al. 2009; Vladykov and Kott 1979). Summer field surveys typically capture juvenile lampreys (called *ammocoetes*) and there is no simple morphological method to distinguish juvenile Arctic lamprey from juvenile Alaskan brook lamprey, so some sources (e.g., ADF&G 2012) record the observations of juveniles that may represent either of the species collectively as "*Arctic-Alaskan brook lamprey paired species*". The spawning run of Arctic lamprey is targeted by subsistence fishers in the Yukon River (Brown et al. 2005; Osgood 1958, p. 48), but lamprey in the Nushagak and Kvichak river drainage are not targeted by subsistence (Fall et al. 2006; Krieg et al. 2009) or sport (Jennings et al. 2011) fisheries.

Freshwater distribution and habitats

The distribution of Arctic lamprey is almost circumpolar; in Alaska it is found in fresh waters in coastal drainages from the Kenai Peninsula west along the Alaska Peninsula and Aleutian Islands, and north to the Arctic coastal plain, as well as in the Yukon River system upstream to Canada (Mecklenburg et al. 2002, p. 62). The reported distribution of Alaskan brook lamprey is much more limited and disjunct, with isolated observations in Bristol Bay, the Kuskokwim, the lower and central Yukon River drainage (but see Sutton et al. 2011), and the Mackenzie River system (ADF&G 2012; Vladykov and Kott 1978). This reported limited and disjunct distribution is likely due in large part to limited appropriate field sampling efforts and ongoing taxonomic uncertainty. The same, or a very closely related species is reported in fresh waters of eastern Russia (Shmidt 1965, p. 16). Juveniles of the species combination "Arctic-Alaskan brook lamprey paired species", as well as individuals recorded as metamorphosed Alaskan brook lamprey have been observed widely across the Nushagak River drainage (there has been less basin-scale survey work conducted in the Kvichak River drainage) from mainstem habitats to smaller streams, but they appear absent from high gradient headwaters, as was reported for central Yukon River tributaries (Sutton et al. 2011). Most observations of adult Arctic lamprey in Bristol Bay are from near the coast (Heard 1966). Heard (1966) found that Alaskan brook lamprey were more common than Arctic lamprey in the Naknek River system.

Pacific lamprey are known to range in North American fresh waters from the Nushagak River drainage south to northern Baja California and in Asia from Bering Sea drainages south to Hokkaido, northern Japan (Froese and Pauly 2012). Pacific lamprey are rarely reported in Bristol Bay drainages (Heard 1966; Russell 2010).

Adults of all three Bristol Bay-area lamprey species spawn in gravel-bedded streams (Heard 1966; Russell 2010). Alaskan brook lamprey excavate small redds and spawn in streams ranging in width from 1.5 to more than 30 m wide, out of the main current in water depths ranging from 0.08 to 0.20 m deep, with velocities of 0.14 to 0.3 $m \cdot s^{-1}$ (Heard 1966). Juvenile lamprey select low velocity sites with fine sediments, into which they burrow (Sutton et al. 2011). While these sites have slow local currents, they are well oxygenated (Potter 1980). In Bristol Bay, juvenile Arctic-Alaskan brook lamprey are found in lakes as well as streams (ADF&G 2012; Heard 1966). Both Arctic and Alaskan brook lamprey were reported spawning in tributaries (Lower Talarik Creek and Copper River) to Iliamna Lake (Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication).

Life cycle

In the Naknek River system, adult Arctic lamprey range in length from 219 to 311 mm (Heard 1966), while adult Alaskan brook lamprey reach lengths of only 150 and 168 mm and females produce 2,200 to 3,500 ova, each averaging 0.9 mm in diameter (Vladykov and Kott 1978). Mature Pacific lamprey have a mean total length of around 537 mm (Docker 2009). Russell (2010) estimated the lengths of three Pacific lamprey spawning in a Naknek River tributary at between 406 and 574 mm.

In Alaska, including the Nushagak and Kvichak river drainages, anadromous adult Arctic lamprey migrate upstream from marine waters during fall and winter and overwinter in fresh water before spawning in tributary streams in May to early July (Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication; Bradford et al. 2008; Brown et al. 2005). Heard (1966) reported that Alaskan brook lamprey in Bristol Bay's Naknek River system also spawned from late May through early July and Russell (1974, p. 42) observed spawning in mid-May in Lower Talarik Creek. Pacific lamprey in the Naknek River system were observed spawning in late June (Russell 2010). All three Bristol Bay-area species excavate redds, often communally, in gravel and cobble substrates, into which they deposit their eggs (Heard 1966; Russell 2010). Lamprey are semelparous; all spawners die soon after breeding once.

Lamprey eggs hatch after incubating ~2 weeks and following an additional 1 to 3 weeks of development, larval fish emerge from redds and move downstream to slow-velocity sites where they burrow into fine sediments (Potter 1980). Larval Arctic lamprey leave the spawning redd at lengths of ~8 mm (Kucheryavyi et al. 2007). Juvenile movements tend to be downstream, but they may move short distances upstream or remain in one location for multiple years (Potter 1980). Lampreys have an extended larval stage lasting several years followed by a relatively brief adult stage. The larval form is referred to as an ammocoete, and its appearance and behavior contrasts markedly from the adult form. During a transformative period (metamorphosis) of a few months, ammocoetes develop eyes, fins, and a tooth-bearing oral disk and then usually live less than a year for nonanadromous forms to one or two years for anadromous forms before spawning once, then dying (Docker 2009; Hardisty 2006, p. 181; Lang et al. 2009).

Arctic and Alaskan brook lamprey transform at lengths of around 125 to 210 mm (ADF&G 2012; Docker 2009; Vladykov and Kott 1978). In the Naknek River system this transformation begins in early summer and is completed by August (Heard 1966).

Age at metamorphosis depends on growth rates, which are positively related to stream size and water temperature, and may take as long as 18 years (Potter 1980). Alaska Arctic lamprey can remain in their larval form for at least 8 years (Sutton et al. 2011). After metamorphosis, anadromous species migrate to marine waters to feed on the body fluids of fish and marine mammals (Scott and Crossman 1998, p. 44-45). Nonanadromous Alaskan brook lamprey feed little or not at all after transformation, and their lengths often shrink prior to spawning (ADF&G 2012; Vladykov and Kott 1978). Larval lamprey appear to produce pheromones which migrating adults use as cues to find spawning streams and other larval lamprey may use to find suitable rearing habitats (Fine and Sorensen 2010; Fine et al. 2004; Wagner et al. 2009).

Predator–prey relationships

Juvenile lamprey typically filter feed on organic detritus (Sutton et al. 2011), but will seasonally consume decaying carcasses of adult Pacific salmon (Kucheryavyi et al. 2007). Kucheryavyi et al. (2007) speculate that those larval lamprey with access to salmon carcasses grow more rapidly and accumulate enough energy stores so that they forego the parasitic, anadromous life stage, and transform to adults directly.

Whether Alaskan brook lamprey parasitize freshwater fish remains unsettled; but if they do, they do not seem detrimental to Bristol Bay fish populations (Greenbank 1954; Heard 1966; Vladykov and Kott 1978). Heard (1966) reported that adult Alaskan brook lamprey have been seen attached to, or are suspected of attaching to, Bristol Bay adult and juvenile sockeye salmon, rainbow trout, pygmy whitefish, and threespine sticklebacks.

Rainbow trout, among other fish, are known to eat lamprey eggs and larvae (Manion 1968). In Bristol Bay, a wide variety of birds and mammals feed on lamprey ammoecoetes, including Arctic terns *Sterna paradisaea*, mew, Bonaparte's, and herring gulls *Larus canus*, *L. philadelphia, and L. argentatus*, common goldeneye *Bucephala clangula*, greater yellowlegs *Tringa melanoleuca*, black-bellied plovers *Pluvialis squatarola*, American golden-plovers *P. dominica*, Hudonian godwits *Limosa haemastica*, common and red-breasted mergansers *Mergus merganser* and *M. serrator*, common loons *Gavia immer*, black-billed magpies *Pica hudsonia*, and river otters *Lutra canadensis* (Russell 2010; Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication).

Suckers (Family Catostomidae)

Alaska is home to one member of the sucker family, the longnose sucker *Catostomus catostomus*. In recent years, an estimated 2,800 longnose suckers were harvested annually in

Nushagak and Kvichak river drainage subsistence fisheries (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 126, 162, 202, 231), both for human consumption and for sled-dog food. Often longnose suckers were harvested incidentally in subsistence fisheries targeting other species (Krieg et al. 2009, p. 206). They are not a target of sport fisheries (Jennings et al. 2011).

Freshwater distribution and habitats

Longnose suckers range across Canada and northern United States from the Atlantic to the Pacific and north to Arctic Ocean drainages and west to far northeastern Asia (Scott and Crossman 1998). In Alaska, longnose suckers are widely distributed throughout the mainland (Morrow 1980b). Sundet and Pechek (1985) considered longnose suckers to be the most abundant large nonanadromous species in the lower mainstem of southcentral Alaska's Susitna River and they are common in the mainstem of the Yukon River and its major tributaries (Andersen 1983; Bradford et al. 2008). Longnose suckers are widely distributed and often abundant in the lakes, rivers, and larger streams of Bristol Bay, but they are largely absent from headwater areas (ADF&G 2012; Greenbank 1954; Russell 1980).

During summer in the Susitna River system, longnose suckers are found in a variety of habitats, including tributaries, side and upland sloughs, and the mainstem and do not appear to be very particular about water velocities or hydraulic conditions. They are found most frequently in the mainstem during spring and fall (and likely winter), and seem to move into off-channel and tributary habitats in mid-summer (ADF&G 1983b). Spawning has been observed in water depths of 15–30 cm deep, velocities of 0.3–0.45 $m \cdot s^{-1}$, over gravels and small cobbles (Geen et al. 1966).

Longnose suckers often are relatively sedentary or move randomly in summer, but may seasonally migrate hundreds of kilometers per year, and can move at least 60 km per day (Geen et al. 1966; Pierce 1977; Sundet and Pechek 1985; Tripp and McCart 1974).

Life cycle

Mature longnose suckers likely home to spawn in natal streams. In northern Canada, southcentral Alaska, and the Nushagak and Kvichak river drainages, they migrate upstream shortly after ice-out in the second half of May to spawn in mainstems and tributaries in late May to early June (Pierce 1977; Russell 1974, p. 42; Sundet and Pechek 1985; Tripp and McCart 1974). Spawning appears to occur in specific areas (Tripp and McCart 1974).

In Canada's Mackenzie River system, mean female fecundity (mean length 471 mm, range 425 to 525 mm) was 49,278 ova (range 23,935 to 107,988; Tripp and McCart 1974). In a small southcentral Alaska stream, mean fecundity was 26,248, with a range of 8,325 to 55,500 ova (Pierce 1977). Mature ova are 1.5–2 mm in diameter (Pierce 1977; Tripp and McCart 1974). Longnose suckers do not excavate redds and fertilized eggs fall into the interstitial spaces of the stream substrate (Geen et al. 1966).

In central British Columbia, eggs incubate for about 2 weeks at a temperature of 10° C before hatching. Larval fish emerge from the spawning gravel another 1 to 2 weeks later (Tripp and McCart 1974). Around one month after spawning, fry emerge from spawning gravels at a length of approximately 22 mm and begin migrating downstream to rearing areas, primarily at night, when stream levels are high and turbid, or on dark nights (Geen et al. 1966; Tripp and McCart 1974). Russell (1980) reported age-0 fry in Lake Clark's Chulitna Bay as early as June 20. Age-0 fish emigrate from southcentral Alaska spawning streams gradually from mid-July through mid-October (Pierce 1977).

Growth can be slow and fish can live at least 22 years; in some northern populations males may not begin to mature until age 9 and females until age 12 (Tripp and McCart 1974). In southcentral Alaska, males begin to mature at age 5 at lengths of around 208 mm, and most are mature at age 6; females mature begin to mature at age 7 at lengths of around 250 mm and most are mature at age 8 (Pierce 1977). Once longnose suckers mature, they probably spawn every year and can reach lengths of 575 mm (Tripp and McCart 1974).

Predator–prey relationships

Longnose suckers consume a wide range of benthic invertebrates and plants (Beamish et al. 1998; Scott and Crossman 1998). Longnose suckers are a favorite food of river otters (Crait and Ben-David 2006; Wengeler et al. 2010) and are known to be eaten by lake trout, northern pike, and burbot (Beamish et al. 1998; Russell 1980, p. 81, 96).

Mudminnows (Family Umbridae)

The taxonomy of the genus *Dallia* remains unsettled (Crossman and Ráb 1996), but currently most authors report a single species of mudminnow in Alaska—the Alaska blackfish *Dallia pectoralis*. Alaska blackfish were once harvested in large quantities in western Alaska subsistence fisheries (Brown et al. 2005; Osgood 1958, p. 241-242). In recent years, however, only an estimated 100 Alaska blackfish are harvested annually in Nushagak and Kvichak river drainage subsistence fisheries. (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 39, 77, 117, 161, 201). They are not a target of Nushagak and Kvichak river drainage sport fisheries (Jennings et al. 2011).

Freshwater distribution and habitats

Alaska blackfish are native only to the western half of Alaska and the tip of Chukotka Peninsula at the extreme northeastern limit of Asia. This species is found only in and near the limits of Pleistocene Beringian refugia, and with the exception of Chukotkan populations, is endemic to Alaska (Scott and Crossman 1998, p. 339). In Alaska they range from the central North Slope west and south along the Bering Sea coast to Bristol Bay and up the Yukon drainage to the Fairbanks area. They also have been accidentally introduced to the Anchorage area (Morrow 1980b, p. 162). In Bristol Bay, Alaska blackfish are locally common or abundant in ponds, large lakes, and slow-moving or stagnant, small- to large-sized streams draining large flat expanses, particularly on the coastal plain. While they are present in the Wood River lakes near the coast, they seem absent or rare in the Tikchik lakes and Lake Clark and adjacent lakes further from the coast, and in higher gradient headwater streams (ADF&G 2012; Burgner et al. 1965; Hildreth 2008, p. 9; Payne and Moore 2006; Rogers et al. 1963; Russell 1980).

On Alaska's North Slope, Alaska blackfish were found among aquatic vegetation in slow-flowing channels and adjacent shallow lakes (Ostdiek 1956). Alaska blackfish typically occur on substrates composed of silt, mud, or decaying vegetation (Blackett 1962).

Life cycle

In the Nushagak River drainage's Lake Aleknagik, spawning occurs in the second half of July (Aspinwall 1965). Water-hardened eggs are about 2 mm in diameter, are very adhesive, and sink to the bottom or adhere to vegetation. About 10 days after spawning, fry hatch at a length of about 6 mm and reach 20 mm six weeks later (Aspinwall 1965).

In Bristol Bay, most females reach maturity at age 3 at lengths ≥49 mm and individuals reach at least age 8 and lengths of 220 mm (Aspinwall 1965; Hildreth 2008, p. 9). Most females appear to spawn annually, but some may spawn in alternate years (Aspinwall 1965). Individual lake-dwelling Alaska blackfish are not thought to make broad-scale movements, but remain relatively sedentary (Payne and Moore 2006); however Blackett (1962), in an interior Alaska stream, identified an apparent upstream migration after the mid-May ice break-up.

The esophagus is modified as an accessory respiratory organ, and Alaska blackfish can tolerated summer dissolved oxygen levels down to 2.30 ppm (Crawford 1974; Ostdiek 1956).

Predator–prey relationships

Alaska blackfish diet is dominated by benthic invertebrates including cladocerans, copepods, ostracods, larval dipterans, larval caddisflies, snails, and algae (Ostdiek 1956; Ostdiek and Nardone 1959; Payne and Moore 2006). In the Nushagak River drainage, northern pike are known to feed on Alaska blackfish (Chihuly 1979, p. 79-86), but because they are often the only fish species present in their preferred habitats (Scott and Crossman 1998, p. 340), perhaps the most important predators on small Alaska blackfish are larger Alaska blackfish.

Smelts (Family Osmeridae)

The smelt family has a circumpolar distribution across the northern hemisphere and is comprised of approximately 10 marine, anadromous, and freshwater species. As with many fish families, smelt taxonomy is unsettled (Scott and Crossman 1998, p. 311-312). Three smelt species have been reported in Bristol Bay fresh waters: rainbow smelt *Osmerus mordax*, pond smelt *Hypomesus olidus*, and eulachon *Thaleichthys pacificus* (Mecklenburg et al. 2002; Morrow 1980b; Nelle 2003).

In recent years, an estimated 3,200 pounds of smelt (likely a mix of rainbow and pond smelt; Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication) were harvested annually in Nushagak and Kvichak river drainage subsistence fisheries (Fall et al. 2006, p. 44, 79, 112, 149, 193; Krieg et al. 2009, p. 38, 76, 116, 160, 200). In 2009 an estimated 10,000 smelt (likely rainbow smelt) were harvested in the Kvichak, Nushagak, and Togiak drainage sport fisheries (Jennings et al. 2011, p. 79).

Freshwater distribution and habitats

rainbow smelt

In North America, the native freshwater range of rainbow smelt extends along the east coast from New Jersey to Labrador; and along the west coast from Vancouver Island through the Gulf of Alaska, and along the Bering Sea and Arctic Ocean coasts to the Mackenzie River delta area. In Asia, rainbow smelt range from Hokkaido to Arctic Ocean drainages west to the North

Atlantic. They have been introduced to the Great Lakes, where they are now abundant (Scott and Crossman 1998, p. 312-313).

Russell (2010) reported that rainbow smelt were abundant in winter, often under ice, in the lower and intertidal reaches of Bristol Bay mainstems and tributaries. They apparently begin moving from marine waters into the lower reaches of mainstem rivers in mid- to late September, where they remain until spawning in coarse substrates of mainstems and tributaries the following spring (Nelle 2003; Richard Russell, Alaska Department of Fish and Game (retired), King Salmon, AK, personal communication). They do not appear to range far inland from the Bristol Bay coast (Burgner et al. 1965; Greenbank 1954; Nelle 2003; Russell 1980).

pond smelt

Pond smelt have a very disjunct global distribution. In Asia they range from Korea to the Alazeya River, and after a gap of over 2700 km, occur again near the Kara Sea in the west-central Russian arctic. In North America they are restricted to Alaska and northwestern Canada, where they range from southcentral Alaska's Copper River delta westward to the Bering Sea coast and northward to the Kobuk River drainage, and after a gap of over 1000 km, in the lower Mackenzie River system (Scott and Crossman 1998, p. 308-309).

In Bristol Bay, pond smelt are reported only in low-elevation ponds and lakes near the coast, their tributaries and outlets, and mainstem estuaries (Burgner 1962; Froese and Pauly 2012; Hartman and Burgner 1972; Heard and Hartman 1966; Hildreth 2008, p. 9). They are known in Iliamna Lake, some of its tributaries, and the Kvichak River (Hartman and Burgner 1972; Siedelman et al. 1973, p. 22; Wiedmer *unpublished*), but they have not been reported in the lakes or streams of the upper Nushagak or Kvichak river drainages (ADF&G 2012; Burgner et al. 1965; Russell 1980). Age-1 and older pond smelt in lakes and ponds primarily feed in off-shore, open water habitats, except when mature adults move inshore to spawn in shallow, nearshore areas (Narver 1966).

eulachon

The global freshwater range of eulachon is limited to North America's Pacific coast from northern California to southwestern Alaska, and Bristol Bay is at the northwest limit of this distribution (Willson et al. 2006, p. 3). Eulachon appear to occur in Bristol Bay fresh waters in very low numbers (Nelle 2003) and because of the lack of specific observations within the Nushagak and Kvichak river drainages, eulachon are not examined further here.

Life cycle

rainbow smelt

Most or all Bristol Bay rainbow smelt populations appear to be anadromous (Mecklenburg et al. 2002, p. 174), and mature individuals have fork lengths from around 163 mm to 298 mm (Dion and Bromaghin 2008; Nelle 2003; Russell 2010). Across various river systems in Bristol Bay, rainbow smelt migrate upstream to spawning areas and spawn from mid-April to the second half of June (Dion and Bromaghin 2008; Nelle 2003; Russell 2010; Wiedmer *unpublished*). Estimated fecundity of Bristol Bay's Togiak River females range from 17,000 to 90,000 and average 52,000 (Dion and Bromaghin 2008). By late June, some rainbow smelt fry are free swimming, schooling, and migrating downstream to marine waters (Russell 2010).

In the Togiak River, both males and females begin to mature at age 2, and males live to at least age 8; females to at least age 6 (Dion and Bromaghin 2008). More northerly Alaska populations mature later and live to at least age 15 (Haldorson and Craig 1984).

pond smelt

Alaska pond smelt appear to be nonanadromous (Harvey et al. 1997). Pond smelt are capable of repeat spawning (Degraaf 1986), but in southwest Alaska, most pond smelt spawn only once, then die (Narver 1966). Adult pond smelt in southwest Alaska, including the Nushagak and Kvichak river drainages, migrate upstream in May and spawn from late May to late June in both shallow open nearshore lake habitats with organic sediments and in lake tributaries (Harvey et al. 1997; Narver 1966; Russell 1974, p. 42). Eggs are adhesive and 6-mm-long fry hatch in about 18 days (Scott and Crossman 1998, p. 309) and are free swimming by the end of July (Narver 1966). In late August and September, young-of-the-year fry, 20–30 mm long, migrate downstream to overwintering areas (Harvey et al. 1997).

By August of the following year, pond smelt reach ~58 mm, and the year after they are ~82 mm long (Narver 1966). In southwest Alaska, most pond smelt live until age 2, or at most age 3 (Narver 1966), but in more slowly growing arctic populations age of maturity is 3 and fish may live to at least age 9 (Degraaf 1986). In southwest Alaska lakes where population estimates were made across multiple years, pond smelt abundance varies widely from year to year (Narver 1966).

Predator–prey relationships

rainbow smelt

Rainbow smelt are known to prey on both invertebrates and fish, including young-of-the-year slimy sculpin (Brandt and Madon 1986; Dion and Bromaghin 2008; Haldorson and Craig 1984), but the feeding of anadromous individuals may be largely limited to marine and estuarine areas (Dion and Bromaghin 2008; Haldorson and Craig 1984). In Bristol Bay, during their spawning migrations, high densities of rainbow smelt attract an abundant and diverse assemblage of predators, including mergansers, osprey, bald eagles, mew and glaucous-winged gulls, rainbow trout, and river otters (Russell 2010; Wiedmer *unpublished*).

pond smelt

Pond smelt feed primarily on zooplankton (Degraaf 1986; Hartman and Burgner 1972). While pond smelt may compete with young sockeye salmon for food, no population-level impacts have been demonstrated in Bristol Bay. Pond smelt may provide sockeye salmon fry a buffer from the predations of Arctic char and lake trout (Burgner et al. 1969; Hartman and Burgner 1972).

Salmonids (Family Salmonidae)

In abundance, diversity, ecosystem function, and human use and interest, the 15 extant salmonid species dominate most Nushagak and Kvichak river drainage freshwater fish communities. The Nushagak and Kvichak river drainages annually produce many hundreds of millions of juvenile salmonids, yielding tens of millions of adults (Eggers and Yuen 1984; West et al. 2012). The salmonid family is comprised of three subfamilies, each with representatives in Bristol Bay: salmon, trout, and char (Subfamily Salmoninae); grayling (Subfamily Thymallinae); and whitefish (Subfamily Coregoninae) (Mecklenburg et al. 2002, p. 178-209). The Nushagak and

Kvichak river drainages are home to five species of Pacific salmon, one trout, and three char. The five salmon species: coho salmon *Oncorhynchus kisutch*, Chinook salmon *O. tshawytscha*, sockeye salmon *O. nerka*, chum salmon *O. keta*, and pink salmon *O. gorbuscha* are grouped taxonomically in the same genus with rainbow trout/steelhead *O. mykiss*. Appendix A of this report details the life history traits of the five native Pacific salmon species and rainbow trout are covered in the *Harvested Fish* section of Appendix B. The three char species are members of the genus *Salvelinus*: Dolly Varden *S. malma*, Arctic char *S. alpinus*, and lake trout *S. namaycush* and each are discussed earlier in this appendix, as is Arctic grayling *Thymallus arcticus*. Five species in two whitefish genera are also reported in the Nushagak and Kvichak river drainages: Bering cisco *Coregonus laurettae*, least cisco *C. sardinella*, humpback whitefish *C. pidschian*, pygmy whitefish *Prosopium coulterii*, and round whitefish *P. cylindraceum.* The taxonomic status of members of the genus *Coregonus* is particularly unsettled (e.g., Scott and Crossman 1998, p. 230). Humpback whitefish are described earlier in this appendix. Specific observations of Bering cisco in the Nushagak and Kvichak river drainages are absent or rare, and this species may be largely limited to the area's estuaries (Froese and Pauly 2012), so they will not be discussed further in this report. The remaining three species are outlined below.

In recent years, an estimated 600 round whitefish and less than 50 least cisco were harvested annually in Nushagak and Kvichak river drainage subsistence fisheries (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 40, 78, 118, 162, 202), and neither species is targeted by sport fisheries (Jennings et al. 2011). Pygmy whitefish are not targeted by subsistence or sport fisheries in the Nushagak and Kvichak river drainages (Fall et al. 2006; Jennings et al. 2011; Krieg et al. 2009).

Freshwater distribution and habitats

least cisco

The least cisco is nearly circumpolar in its range, which extends in Arctic Ocean drainages from the central Canadian arctic to northern Europe, and in Bering Sea drainages in both Asia and North America (Scott and Crossman 1998, p. 263-264). In Alaska it is widely distributed in lakes and rivers across the mainland north of the Alaska Range (Mecklenburg et al. 2002, p. 182). In the Nushagak and Kvichak river drainages, the reported distribution of least cisco is centered in and around Lake Clark, including Hoknede and Lower Pickeral lakes and the Chulitna River (Russell 1980, p. 77). While abundant in Lake Clark's offshore, open-water zone (Schlenger 1996, p. 78, 88), it is appears to be less so in Iliamna Lake (Kerns 1968) and low velocity sites in the Kvichak and Alagnak rivers (Wiedmer *unpublished*). Least cisco occur in the Nushagak River's Tikchik lakes, but not in the Wood River lakes (Burgner et al. 1965, p. 4), nor in Bristol Bay tundra ponds near the coast (Hildreth 2008, p. 9). Haas (2004; identification corroborated by Dan Young NPS, Port Alsworth, AK, personal communication) tentatively identified least cisco in morainal lakes west of Iliamna Lake. In Lake Clark, least ciscos are much more abundant in the northern, glacially turbid waters, perhaps in response to predation risk (Schlenger 1996, p. 78, 88).

The Chulitna River system may provide spawning and/or juvenile rearing habitat for Lake Clark least cisco, as local residents reported that in late June juvenile least ciscos migrate out of the Chulitna River to Lake Clark (Russell 1980, p. 77).

pygmy whitefish

The pygmy whitefish is a nonanadromous species with a strikingly disjunct global distribution in north-central and northwestern North America and far northeastern Asia (Eschmeyer and Bailey 1955; Wiedmer et al. 2010). Pygmy whitefish typically inhabit cold, deep lakes and glacially fed rivers, most within the footprint of the Laurentide and Cordilleran ice sheets (Weisel et al. 1973). Even where they occur regionally, researchers have noted the apparent absence of pygmy whitefish from seemingly suitable habitats, perhaps because they are particularly vulnerable to predation or competition (Bird and Roberson 1979; Chereshnev and Skopets 1992). Their extirpation from an estimated 40% of their historic habitats in Washington State, at the southern limit of their range, was attributed to piscicides, introduction of exotic fish species, and/or declining water quality (Hallock and Mongillo 1998, p. 9).

In the Nushagak and Kvichak river drainages, pygmy whitefish have been reported in Iliamna, Kontrashibuna, Tikchik, Nuyakuk, and Little Togiak lakes; Twin Lakes; lakes Clark, Beverley, Nerka, and Aleknagik; southern tributaries to the Chulitna River near Nikabuna Lakes (mapped by Wiedmer et al. 2010); Caribou Lakes (local name for lakes in the headwaters of the Koksetna River, Woods and Young 2010), and Summit Lakes (Dan Young, NPS, Port Alsworth, AK, personal communication). They are not known to occur in Bristol Bay tundra ponds (Haas 2004; Hildreth 2008, p. 9), and their distribution in rivers and streams appears to be very limited (ADF&G 2012).

Where they do occur, pygmy whitefish occupy a wide variety of ecological habitats in Bristol Bay lake systems; from shallow nearshore areas less than 1 m deep to offshore zones at depths of at least 168 m, and from near the bottom to the surface over deep water and in some adjacent streams. (ADF&G 2012, sites PEB91CH001 and PEB91CH007; Heard and Hartman 1966; Russell 1980, p. 98). In the absence of competitors or predators, pygmy whitefish will feed during the day in shallow, nearshore areas (Zemlak and McPhail 2006). However, in low turbidity lakes with competitors and/or predators, pygmy whitefish are often found only at depth, particularly during the day (Eschmeyer and Bailey 1955; McCart 1965; Plumb 2006; Rankin 2004, p. 95). Pygmy whitefish may segregate by age, with younger fish in shallower nearshore areas, and older fish in offshore benthic habitats (Eschmeyer and Bailey 1955, p. 179; Heard and Hartman 1966). Pygmy whitefish often spawn in lake inlet or outlet streams (Heard and Hartman 1966; Weisel et al. 1973), but will spawn in lakes (Hallock and Mongillo 1998, p. 4).

Pygmy whitefish are typically found in water temperatures below 10° C (Hallock and Mongillo 1998, p. 6), but they can tolerate dissolved oxygen levels less than 1.0 $mg \cdot l^{-1}$ (Zemlak and McPhail 2006). Because they tend to aggregate in large, mobile schools (Zemlak and McPhail 2006), the abundance of pygmy whitefish in particular locations may appear to vary dramatically.

round whitefish

In North America, round whitefish range from Connecticut north along the North Atlantic coast, including the St. Lawrence River/Great Lakes system, and west across Canada’s and Alaska’s Arctic Ocean and Bering Sea drainages, and south to the Gulf of Alaska. In Asia it is distributed from the Kamachatka Peninsula north and west to the Yenisei River in the central Russian arctic (Scott and Crossman 1998, p. 287-289). Round whitefish are distributed across all of mainland Alaska except for southern Southeast (Mecklenburg et al. 2002, p. 189; Morrow 1980b, p. 41).

Round whitefish are broadly distributed and abundant in many of the streams and lakes of the Nushagak and Kvichak river drainages, but they are absent or uncommon in headwater streams or coastal tundra streams or lakes (ADF&G 2012; Burgner et al. 1965; Hildreth 2008, p. 9; Russell 1980, p. 104).

In southcentral Alaska's Susitna River, round whitefish are more likely to be found feeding in tributaries and off-channel habitats in summer, and migrating in the mainstem in spring and fall from and to mainstem overwintering habitats (ADF&G 1983b, p. G-20 - G-21; Sundet and Pechek 1985, p. 44-45). During summer, they do not demonstrate a preference for water velocity (ADF&G 1983b, p. F-28). While they prefer Susitna River tributaries, they are commonly encountered during the summer in the mainstem Yukon (Andersen 1983, p. 15, 18, 21; Bradford et al. 2008) and Nushagak and Kvichak rivers (ADF&G 2012).

Spawning areas include mainstem rivers, tributary mouths, and inshore areas of lakes (Morrow 1980b, p. 33; Sundet and Pechek 1985, p. 45). Juvenile round whitefish in the Susitna River system were found more often in the turbid mainstem and in off-channel sites than in tributaries, presumably using higher turbidity water as cover from predation (Sundet and Pechek 1985, p. 44-45).

Life cycle

least cisco

The life history patterns of least cisco are broadly similar to those of the humpback whitefish discussed earlier in this appendix. Both species have populations that migrate seasonally between lakes and rivers and populations that are nonmigratory lake residents (Morrow 1980b, p. 29). The least cisco of the Nushagak and Kvichak river drainages may not undertake large migrations, and some may spend their entire lives in single lakes. At least some of the putative least cisco found by Haas (2004) live in lakes with no apparent inlets or outlets, suggesting that these fish remain in their natal lake for life.

Unlike least ciscos in the lower Kuskokwim River drainage (Harper et al. 2007, p. 13) to the north, populations in the Nushagak and Kvichak river drainages appear to be nonanadromous (Mecklenburg et al. 2002, p. 182). While anadromous lower Kuskokwim River drainage individuals do not mature until they reach lengths of 300 mm and age 3, and can grow to at least 450 mm and live to at least age 14 (Harper et al. 2007, p. 13); Lake Clark area least cisco also mature at age 3, but at lengths of only ~145–180 mm, and reach a maximum length of ~276 mm and a reported maximum age of 9 (Russell 1980, p. 77, 85; Schlenger 1996, p. 42).

Mature least cisco in the Kuskokwim River drainage may not spawn every year (Harper et al. 2007, p. 13, 21), but the frequency of spawning in Bristol Bay waters is unknown. The fecundity of sampled large (280 to 420 mm FL) migratory female least cisco in interior Alaska ranges from 11,500 to 111,600 ≤1-mm diameter ova, but the fecundity of the much smaller Nushagak and Kvichak river drainage fish is not reported, and presumably averages less than 11,000 (Clark and Bernard 1992; Morrow 1980b, p. 28).

pygmy whitefish

Pygmy whitefish grow slowly, have low fecundity, and most live short lives (Eschmeyer and Bailey 1955; Heard and Hartman 1966), although some individuals can live to at least age 16 (Rankin 2004, p. 90-92). Maximum total length for individuals in many populations is around 120–140 mm (Chereshnev and Skopets 1992; Eschmeyer and Bailey 1955; Plumb 2006, p. 14; Russell 1980, p. 91). In Bristol Bay, the longest reported length was 163 mm for an age-5 female (Heard and Hartman 1966), and the greatest age was 7 years (Plumb 2006, p. 19). In some Bristol Bay lakes, the maximum age of sampled fish was only 3, and the maximum length was only 83 mm (Heard and Hartman 1966). Across their global range, males and females mature at ages 1 to 4 and lengths as small as 53 to 56 mm (Bird and Roberson 1979; Chereshnev and Skopets 1992; Eschmeyer and Bailey 1955; Heard and Hartman 1966; McCart 1965; Weisel et al. 1973). Heard and Hartman (1966) reported that mature female pygmy whitefish in the lakes of Bristol Bay's Naknek River system produced from 103 to 1,153 ova per year, each measuring an average of 2.4 mm in diameter. Once mature, pygmy whitefish appear to spawn annually (Chereshnev and Skopets 1992; Weisel et al. 1973). Heard and Hartman (1966) concluded that pygmy whitefish in the Naknek River system spawn at night from mid-November to mid-December.

round whitefish

Round whitefish are nonanadromous freshwater residents (Mecklenburg et al. 2002, p. 189) and many do not appear to undertake lengthy migrations (Morrow 1980b, p. 33). In interior Alaska lakes and in the Nushagak and Kvichak river drainages, round whitefish mature at lengths between 220 mm and 290 mm (TL), at ages between 4 and 8 years, and once mature, most spawn annually (Russell 1980, p. 104; Van Whye and Peck 1968, p. 36). In southwest Alaska round whitefish live to at least age 14 and reach lengths of around 420 mm (Russell 1980, p. 104). Furniss (1974, p. 11) reported that the fecundity of northern Alaska round whitefish (mean length = 409 mm) was around 5,300 ova.

Sundet and Pechek (1985, p. 45) concluded that the peak of spawning in the Susitna River system was from mid- to late October. Round whitefish deposit their eggs on the substrate, but do not excavate redds (Morrow 1980b, p. 33). Eggs incubate through the winter and after the young hatch, they remain in the redd absorbing their yolk sac for several more weeks before emerging in late winter to early spring (Scott and Crossman 1998, p. 288).

Predator–prey relationships

least cisco

The diet of Lake Clark-area least cisco includes a wide range of invertebrates including plecoptera nymphs, chironomid nymphs and adults, trichoptera adults, and copepods (Russell 1980, p. 87, 88; Schlenger 1996, p. 57). Because of their diet overlap, Kerns (1968) considered least cisco the most important competitor of juvenile Lake Clark sockeye salmon. Lake Clark lake trout and northern pike are known to feed on least cisco (Metsker 1967, p. 29; Russell 1980, p. 83, 96), and burbot and predatory birds are reported to feed on them in other parts of Alaska (Morrow 1980b, p. 29).

pygmy whitefish

Multiple morphological and ecological pygmy whitefish morphs can occur in individual Bristol Bay lakes (McCart 1970), but invertebrates dominate the diet of all morphs. Pelagic morphs feed primarily on plankton while benthic morphs feed primarily on larval insects (particularly chironomids) and mollusks (Chereshnev and Skopets 1992; Heard and Hartman 1966; McCart 1970). Pygmy whitefish are flexible in their diet (Heard and Hartman 1966; Plumb 2006, p. 46, 51-52; Weisel et al. 1973), and will eat the eggs of whitefish when they are available (Eschmeyer and Bailey 1955). Terns, Dolly Varden, lake trout, and Arctic char are all known to feed on pygmy whitefish (Hallock and Mongillo 1998; Russell 1980, p. 98; Scanlon 2000, p. 51, 53-54; Snyder 1917).

round whitefish

In the Nushagak and Kvichak river drainages, adjacent areas, and elsewhere in Alaska, round whitefish eat primarily benthic invertebrates, including trichopteran and chironomid larvae and snails (Furniss 1974, p. 11, 22, 36; Russell 1980, p. 108; Van Whye and Peck 1968, p. 37). Round whitefish will feed on salmon and other whitefish eggs when they are available (Brown 2006, p. 23; Van Whye and Peck 1968, p. 37). In the Nushagak and Kvichak river drainages and adjacent areas, burbot, lake trout, and northern pike are known to prey on round whitefish (Russell 1980, p. 67, 81-82, 95-96).

Cods (Family Gadidae)

Almost all of the approximately 30 to 60 cod species worldwide are found in cool marine waters, mostly in the northern hemisphere. Like many orders of fish, taxonomy, in this case at the family level, remains unsettled (Froese and Pauly 2012; Mecklenburg et al. 2002, p. 269; Scott and Crossman 1998, p. 640), explaining in part the broad range of species reported in the cod family. Two of the primarily marine cods, Pacific cod *Gadus macrocephalus*, and saffron cod *Eleginus gracilis*, may periodically enter the lower reaches of the Nushagak and Kvichak rivers, but their freshwater distribution appears very limited (Mecklenburg et al. 2002, p. 293, 296; Morrow 1980b, p. 185-188), and they are not discussed further here. Only one of the cods, the burbot *Lota lota*, is exclusively a freshwater resident everywhere it occurs and it is discussed below.

Less than an estimated ~400 burbot are harvested annually in Nushagak and Kvichak river drainage subsistence fisheries (Fall et al. 2006, p. 45, 80, 113, 150, 194; Krieg et al. 2009, p. 39, 76, 117, 161, 201) and they are not a target of the regional sport fishery (Jennings et al. 2011, p. 77).

Freshwater distribution and habitats

Burbot range broadly across the mainland fresh waters of both North America and Eurasia, north of about 40° N (Scott and Crossman 1998, p. 642). Burbot are found throughout mainland Alaska, except for southern Southeast (Mecklenburg et al. 2002, p. 289; Morrow 1980b, p. 187). Burbot are reported in many lakes and streams across the Nushagak and Kvichak river drainages, but they are uncommon or absent in small headwater streams or the lakes and streams of the coastal tundra plain (ADF&G 2012; Burgner et al. 1965, p. 4; Hildreth 2008, p. 9; Russell 1980, p. 64-65; Yanagawa 1967, p. 10).

Burbot live in Alaska lakes (e.g., Schwanke and McCormick 2010), and in large river systems like the Yukon River drainage (Andersen 1983, p. 18, 21; Evenson 1998). In southcentral Alaska's Susitna River, burbot reside mostly in highly turbid waters, both in the mainstem and in off-channel habitats (ADF&G 1983a, p. F-26; ADF&G 1983b, p. F-21, G-20; Sundet 1986, p. 33; Sundet and Pechek 1985, p. 32). In the Susitna River system they spawn both in the mainstem and in low-gradient tributaries at sites with water velocities of 0–0.6 $m \cdot s^{-1}$ (0.0-2.1 $ft \cdot s^{-1}$), depths of 0.6–2.7 m (0.2–9.0 ft), over sand to cobble substrates, possibly in conjunction with upwelling and in areas where anchor ice does not form (Sundet 1986, p. 36-37) (Sundet 1986; Sundet and Pechek 1985, p. 33, 42). In Lake Michigan, their preferred summer water temperature range is 8–13° C (Edsall et al. 1993). Large Alaska river systems may support multiple discrete burbot stocks (Evenson 1988).

Life cycle

Burbot are nonanadromous, freshwater residents, although they may venture into brackish or marine waters (Chen 1969, p. 1). Size at maturity appears to vary across Alaska, and burbot may mature at lengths from 310 to 500 mm, at ages of around 4 to 7 (Chen 1969, p. 36; Evenson 1990; Sundet and Pechek 1985, p. 33). After they mature, most, but not all, individuals spawn each year (Chen 1969, p. 35; Clark et al. 1991, p. 5; Evenson 1990; Sundet and Pechek 1985, p. 33).

In the Susitna River system, mature burbot begin migrating from mainstem summer feeding areas to spawning areas in mid-September to mid-October. While most individuals may move little, some fish will seasonally migrate several hundred kilometers (Evenson 1988, p. 14, 30; Sundet 1986, p. 37; Sundet and Pechek 1985, p. 33). In southcentral and interior Alaska, burbot spawn from mid-January to early February (Chen 1969, p. 20; Sundet 1986. p. 37; Sundet and Pechek 1985. p. 33).

Interior Alaska female burbot (lengths ranging from 504 to 1,040 mm) have estimated fecundities ranging from 184,000 to 2,910,000 ova (Clark et al. 1991, p. 6-8). Eggs are demersal, nonadhesive, and 0.4 to 0.7 mm in diameter (Clark et al. 1991, p. 5). Because it occurs under the ice, details are limited, but Alaska burbot are thought to communally spawn and scatter their eggs near the substrate, where they fall into interstitial spaces. In the Tanana River drainage, eggs are thought to hatch in late April, young-of-the-year fry reach 20 mm long in June, and grow rapidly to lengths of at least 108 mm by early October (Chen 1969, p. 20, 29).

In Alaska, burbot can reach an age of at least 24 years, but most do not appear to live longer than 15 years (Chen 1969, p. 27, 28). In interior Alaska, burbot can reach lengths of at least 1,135 mm (TL; Hallberg 1986), but the largest reported by Russell (1980, p. 64) in the lakes and rivers of the Nushagak and Kvichak river drainages was only 597 mm TL and the oldest was only 11. Burbot of the Nushagak and Kvichak river drainages may mature at a smaller size and younger age and be less fecund than those of the Yukon and Tanana river drainages.

Predator–prey relationships

The diet of young-of-the-year burbot is primarily aquatic insects (Plecoptera, Ephemeroptera, Diptera, and Trichoptera), but as they grow, fish become an increasingly important part of their diet (Chen 1969, p. 42, 43). In the Nushagak and Kvichak river drainages, burbot feed primarily on least cisco, lake trout, round whitefish, sculpin, and larval and adult insects (Russell 1980, p.

67). In other areas, burbot are also known to eat large quantities of whitefish eggs (Bailey 1972), which are available late in the year in the Nushagak and Kvichak river drainages, and lamprey, longnose suckers, and northern pike. Large burbot also prey on small burbot (Chen 1969, p. 42).

Sticklebacks (Family Gasterosteidae)

Members of the stickleback family occur in fresh and nearshore marine waters throughout much of the northern hemisphere north of about 30° N (Scott and Crossman 1998, p. 656). Two, the threespine stickleback *Gasterosteus aculeatus*, and the ninespine stickleback *Pungitius pungitius* are found in the waters of the Nushagak and Kvichak river drainages (Scott and Crossman 1998, p. 656). Across their global ranges, both threespine and ninespine sticklebacks exhibit extensive morphological variations, and some authors (e.g., Nelson 1971) refer to them as species complexes. Here we refer collectively to all members of each species complex by their common names. While sticklebacks may once have been the target of directed harvests by Nushagak and Kvichak river drainage residents (e.g., Krieg et al. 2009, p. 190), they are currently caught only in small numbers in a few locations, principally through the ice in subsistence fisheries (Fall et al. 2006, p. 69, 80, 335), and are not harvested in sport fisheries (Jennings et al. 2011).

Freshwater distribution and habitats

threespine stickleback

This species is nearly circumpolar in distribution, although that distribution has considerable discontinuities (Scott and Crossman 1998, p. 666). In Alaska, where up to four distinct phenotypes have been reported (Narver 1969; Willacker et al. 2010), threespine sticklebacks are reported near the coast from southern Southeast to the Bering Strait, but records west and north of Bristol Bay are uncommon (ADF&G 2012; Mecklenburg et al. 2002, p. 333; Morrow 1980b, p. 333). In and near the Nushagak and Kvichak river drainages, threespine stickleback are reported both in lowland and upland lakes and in river systems from estuaries to medium-sized streams, where they are primarily associated with sites with low current velocity (ADF&G 2012; Burgner et al. 1965; Haas 2004; Hildreth 2008, p. 9; Kerns 1968; Russell 1980, p. 111). They are common in the Kvichak River and in the lower reaches of some Iliamna Lake tributaries. Many of the large individuals encountered during the late summer in the Kvichak River appear to be moribund post-spawners (Wiedmer *unpublished*), a pattern observed elsewhere in southwest Alaska (Harvey et al. 1997). They can occur in swifter streams (Bond and Becker 1963), but appear largely absent from headwaters (ADF&G 2012).

In streams, they have a significant preference for low velocity, deeper (>0.2 m) habitats with extensive aquatic vegetation and high oxygen concentrations. They prefer to be away from stream banks and riparian cover, perhaps to avoid the fish predators that dwell there (Copp and Kováč 2003). In some Nushagak and Kvichak river drainage lakes, such as Iliamna Lake, they are abundant in offshore open waters (Hartman and Burgner 1972; Kerns 1968). Stickleback have an affinity for their native habitat type (lake or stream), and that affinity parallels morphological and genetic divergence (Bolnick et al. 2009), leading to genetically distinct populations, even in a given drainage (Reusch et al. 2001). In lakes of southwest Alaska, spawning and early development is in shallow, nearshore areas; as fish mature they may remain nearshore or move to open, offshore waters (Hartman and Burgner 1972; Narver 1966).

ninespine stickleback

The ninespine stickleback has a circumpolar distribution across the northern hemisphere (Scott and Crossman 1998, p. 672, 673). In Alaska it is found from the Kenai Peninsula west and north to waters draining to the Arctic Ocean. While Mecklenburg et al. (2002, p. 334) map its range across most of mainland Alaska, it appears to be absent or infrequent away from coastal areas (ADF&G 2012; Morrow 1980b, p. 194). In the Nushagak and Kvichak river drainages, ninespine stickleback are more widespread than threespine stickleback. Ninespine sticklebacks can tolerate low dissolved oxygen concentrations and are reported both in lowland and upland ponds and lakes (Burgner et al. 1965; Hartman and Burgner 1972; Hildreth 2008, p. 9; Morrow 1980b, p. 192; Russell 1980, p. 87). They occur from the lower mainstem rivers to headwaters (ADF&G 2012), but are primarily associated with shallow, low velocity sites with emergent vegetation (Russell 1980, p. 87). In southwest Alaska lakes, spawning occurs in shallow, nearshore areas with organic substrates and rooted aquatic plants (Narver 1966). In Iliamna Lake and Lake Clark, they are largely absent from offshore areas (Kerns 1968).

Life cycle

threespine stickleback

Threespine sticklebacks can have either anadromous or nonanadromous life histories, and anadromous individuals migrate in May (Harvey et al. 1997; Sundet and Pechek 1985) from the sea to spawning areas at least 60 km up major North American Pacific coast river systems (Virgl and McPhail 1994). The distribution of anadromous individuals in the Nushagak and Kvichak river drainages is unknown. In southwest Alaska, including the Nushagak and Kvichak river drainages, most spawners are age 2 or 3, most spawning occurs in June and early July, and often occurs in beds of aquatic plants (Bond and Becker 1963; Narver 1966; Russell 1974, p. 42). Males establish and defend territories, and construct, with vegetation and sand, barrel-shaped nests into which females deposit eggs (Morrow 1980b, p. 190). Total fecundity varies considerably depending on food availability during the mating season (Wootton and Evans 1976) and can range from 80 to 1,300 ova (Morrow 1980b, p. 190). Young-of-the-year fry emerge from their nests at lengths of around 7 mm in late July to early August, and by the end of August reach lengths of around 27 mm (Dunn 1962; Harvey et al. 1997; Morrow 1980b, p. 190; Narver 1966). In southwest Alaska, most individuals do not live beyond two or three years, reach lengths to around 80 mm, and probably only spawn once (Dunn 1962; Narver 1966; Russell 1980, p. 111).

ninespine stickleback

Alaska ninespine sticklebacks are primarily nonanadromous (Morrow 1980b, p. 192-193). In some southwest Alaska lakes, ninespine sticklebacks mature at ages 1 to 2 and migrate upstream in May to spawn (Harvey et al. 1997; Narver 1966). Spawning occurs from late June through at least mid-July and, like threespine sticklebacks, males construct nests in which multiple females lay batches of eggs, perhaps 50 to 80 at a time. Total female fecundity reportedly ranges up to 1,000 ova (Froese and Pauly 2012). Eggs hatch in about a week to ten days and the male parent guards and fans the nest while the eggs incubate and the larval fish develop (Morrow 1980b, p. 193; Narver 1966). By late July young-of-the-year fry are free-swimming and some may migrate to downstream feeding and overwintering habitats (Harvey et al. 1997). Egg development and early growth is very rapid; by the end of August fry reach lengths of around 36 mm (Narver

1966). In southwest Alaska, ninespine stickleback reach lengths of around 60 mm and most spawn only once (ADF&G 2012, e.g., Site FSB0318A06; Harvey et al. 1997; Narver 1966).

Predator–prey relationships

threespine stickleback

Copp and Kováč (2003) reported that the diet of threespine sticklebacks was dominated by cladocerans, copepods, amphipods, chrinomids, and ostracods. Considerable competition between age-0 sockeye and similarly sized age-1 threespine stickleback may occur in lakes of the Nushagak and Kvichak river drainages, and dense populations of sockeye fry may displace threespine sticklebacks from open water habitats (Hartman and Burgner 1972; Kerns 1968).

A wide variety of birds and fish in the Nushagak and Kvichak river drainages feed on threespine sticklebacks, including adult Arctic char, northern pike, and rainbow trout (Bond and Becker 1963; Hartman and Burgner 1972; Metsker 1967). Threespine sticklebacks are also preyed on by large aquatic macroinvertebrates such as immature dragonflies (Lescak et al. 2012) and are particularly vulnerable to a host of parasites (Scott and Crossman 1998, p. 667-668; Wiedmer unpublished).

ninespine stickleback

The diet of ninespine sticklebacks is dominated by small aquatic invertebrates, similar to the diet of threespine sticklebacks (Morrow 1980b, p. 194). In the Nushagak and Kvichak river drainages, ninespine sticklebacks are preyed on by a wide variety of birds and fish, including lake trout, northern pike, and rainbow trout (Bond and Becker 1963; Russell 1980, p. 67, 96).

Sculpins (Family Cottidae)

Most of the approximately 70 genera and 300 species of sculpins making up the Family Cottidae live near the bottom of northern marine waters. While only a few species are primarily freshwater residents (Mecklenburg et al. 2002, p. 398), they can be important parts of salmonid stream ecosystems (Petrosky and Waters 1975). Two nonanadromous freshwater sculpin species occur in the Nushagak and Kvichak river drainages: coastrange sculpin *Cottus aleuticus*, and slimy sculpin *C. cognatus*. Because of their very similar appearance, many field surveys do not distinguish between these two species, so the relative distribution of each species within the Nushagak and Kvichak river drainages is uncertain. Sculpins are not a target of Nushagak and Kvichak river drainage subsistence (Fall et al. 2006; Krieg et al. 2009) or sport fisheries (Jennings et al. 2011).

Freshwater distribution and habitats

coastrange sculpin

Coastrange sculpin occupy a narrow (≤200 km wide) fringe along North America's Pacific Ocean coast from southern California to the Aleutian Islands (Scott and Crossman 1998, p. 820-821). Morrow (1980b) reported an isolated population in the Kobuk River draining to Kotzebue Sound. Because this species is readily confused with slimy sculpin, its distribution in the Nushagak and Kvichak river drainages is uncertain, but appears more restricted than slimy sculpin (Bond and Becker 1963). In Bristol Bay they are found in both lakes and in streams; in streams they seem to prefer swift open riffles with coarse substrates (Heard 1965).

Coastrange sculpin often spawn in steep gradients with coarse substrates (McLarney 1968). In July and August, during the first weeks after hatching, coastrange sculpin fry are planktonic near the water surface as they drift downstream to lakes or quiet stream backwaters (Heard 1965; McLarney 1968). In stream-dwelling populations, after the post-hatching fry drift downstream, they migrate back upstream later in the summer after adopting a benthic life-style (McLarney 1968). At least in some lakes, larger coastrange sculpin have a pronounced daily vertical migration: from the bottom during the day to near the surface at night (Ikusemiju 1975).

slimy sculpin

Slimy sculpin range across northern North America from Virginia on the Atlantic Ocean coast, north into Canada's arctic mainland, and west to Alaska and across the Bering Sea to Asia's Chukotka Peninsula. In North America, slimy sculpin is the most widespread member of its genus (Scott and Crossman 1998, p. 832). In Alaska, they range across all of the mainland and the island remnants of the currently submerged Beringia, from headwaters to lower mainstems (Craig and Wells 1976; Morrow 1980b, p. 210).

In southcentral Alaska's Susitna River, slimy sculpin are found in diverse habitats and do not exhibit strong preferences for particular hydraulic conditions, water sources, or velocities (ADF&G 1983b, p. F-28). Because of their tolerance for a wide range of stream conditions, both Bond (1963) and Russell (1980, p. 104) considered them the most widespread of the nonanadromous fishes in the lakes and streams of the Nushagak and Kvichak river drainages. They occur throughout these two drainages, in upland lakes (Burgner et al. 1965) and from small headwater streams to the intertidal zone, but they are uncommon in very low gradient streams with fine sediments (ADF&G 2012) or in shallow coastal tundra ponds (Hildreth 2008, p. 9).

Across their global range, slimy sculpin are found in cool streams and lakes (Craig and Wells 1976; DiLauro and Bennett 2001; Halliwell et al. 2001). They are thought to exhibit site fidelity and do not appear to undertake long-distance seasonal spawning migrations (Cunjak et al. 2005; Galloway et al. 2003; Gray et al. 2004; Morgan and Ringler 1992), but will migrate in lakes in response to seasonal food availability (e.g., sockeye salmon eggs, Foote and Brown 1998).

In streams, slimy sculpins, particularly age-0 juveniles, tend to use shallower habitats with faster velocities, often under the cover of coarse substrates (van Snik Gray and Stauffer 1999). In Bristol Bay they occur at all depths in lakes (Heard 1965). In Lake Ontario, slimy sculpins were found to more than 150 m deep, with younger, smaller individuals typically in shallower waters (Brandt 1986). However, they may not occur in isolated shallow lakes subject to extensive winter freezing (Hershey et al. 2006). Slimy sculpin spawn in streams in areas with shallow water (~0.16 m) and coarse substrates (Keeler and Cunjak 2007) and in lakes (Bond and Becker 1963).

In streams, they prefer cool, stable riffles and are strongly affected by flood, drought, and elevated turbidity (Danehy et al. 1998; Edwards and Cunjak 2007; Keeler et al. 2007; Langdon 2001; Petrosky and Waters 1975). Their preferred temperature is reported to be 11.5-13.5° C (Symons et al. 1976). Young-of-the-year juveniles appear to have the greatest intolerance for warmer water and completely avoid water ≥25° C (Gray et al. 2005).

Life cycle

coastrange sculpin

Coastrange sculpins appear to be nonanadromous freshwater residents (Scott and Crossman 1998, p. 821-822). Individuals mature at lengths of around 40 to 50 mm (Ikusemiju 1975), at ages of 2 or 3, and female fecundity ranges from 100-1764 ova (Patten 1971). In coastal streams in southcentral and southeast Alaska, in May to early June females deposit adhesive eggs (<1.5 mm diameter; Scott and Crossman 1998) on the underside of large, stable rocks. Males fertilize, then guard the eggs, which hatch from late May to early July (McLarney 1968). Newly hatched larvae are ~7 mm (Ikusemiju 1975) and by late July to mid-August fry reach lengths of 20 to 30 mm (Brown et al. 1995; Ikusemiju 1975; McLarney 1968). In the central part of their range, coastrange sculpin reach lengths of at least 101 mm and may not live much beyond age 4 (Patten 1971).

slimy sculpin

Slimy sculpin are nonanadromous freshwater residents (Mecklenburg et al. 2002, p. 468). In arctic Alaska, fish mature between the ages of 3 and 5, at lengths of around 70 mm, and spawn in late May, a week or so after breakup (Craig and Wells 1976). About a week before the onset of spawning, males select and defend nest sites (the undersides of stable rocks or submerged debris) in areas with shallow water (~0.16 m deep) and coarse substrates (Keeler and Cunjak 2007). Males can court multiple females and will guard nests with multiple egg clutches (Majeski and Cochran 2009). Females deposit adhesive eggs 2.5 to 3 mm in diameter (Morrow 1980b) and interior Alaska females have a mean fecundity of around 200 ova (Craig and Wells 1976). Young-of-the-year fry are 11 to 13 mm long at the beginning of August and reach 19 to 24 mm by late September (Craig and Wells 1976). Once mature, they spawn annually (Craig and Wells 1976), can reach age 8 in arctic waters (Hanson et al. 1992; McDonald et al. 1982), and lengths of at least 117 mm in waters of the Nushagak and Kvichak river drainages (Russell 1980, p. 104).

Predator–prey relationships

coastrange sculpin

In California, the diet for coastrange sculpin stream populations is dominated by immature aquatic insects and other aquatic arthropods (Brown et al. 1995). In the Nushagak and Kvichak river drainages, coastrange sculpin prey on sockeye salmon eggs, alevins, and emerging fry (Bond and Becker 1963), particularly on the eggs of Iliamna Lake island beach sockeye salmon spawners (Foote and Brown 1998). In turn, during the summer, age-0 planktonic coastrange sculpin are preyed on by age-1 sockeye salmon fry (Heard 1965) and Nushagak and Kvichak river drainage area sculpin of all sizes (both species combined) are eaten by burbot, humpback whitefish, lake trout, northern pike, rainbow trout, and round whitefish (Russell 1980, p. 67, 76, 81, 82, 83, 96, 97, 103, 108).

slimy sculpin

The diet of slimy sculpins typically is dominated by aquatic invertebrates such as benthic arthropods and small mollusks (Craig and Wells 1976; Hershey and McDonald 1985; Hudson et al. 1995; Petrosky and Waters 1975), but where and when available, they will feed on sockeye salmon eggs, alevins, and emerging fry (Bond and Becker 1963; Foote and Brown 1998), and lake trout eggs and alevins (Fitzsimons et al. 2006; Fitzsimons et al. 2007; Fitzsimons et al. 2002; Savino and Henry 1991). They are more successful feeding on salmonid eggs deposited in coarser substrates, such as those selected by lake trout and island beach-spawning sockeye salmon (Biga et al. 1998). Slimy sculpin predation of successfully buried salmonid eggs and alevins in typical stream substrates may be limited (Moyle 1977).

A wide variety of larger fish eat slimy sculpin; including Arctic grayling, burbot, rainbow smelt, humpback whitefish, lake trout, Arctic char, northern pike, rainbow trout, and round whitefish (Bond and Becker 1963; Brandt and Madon 1986; Elrod and Ogorman 1991; Hudson et al. 1995; Owens and Bergstedt 1994; Russell 1980, p. 67, 76, 81, 82, 83, 96, 97, 103, 108; Scanlon 2000, p. 51, 53-54).

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