590

Distributions of Fishes in Fresh Water of Katmai National Monument, Alaska, and Their Zoogeographical Implications

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BUREAU OF COMMERCIAL FISHERIES

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By

WILLIAM R. HEARD,[1] RICHARD L. WALLACE,[2]
and WILBUR L. HARTMAN[1]

ABSTRACT

Katmai National Monument covers 10,916 km.^{2} on the base of the Alaska Peninsula and is divided by the Aleutian Mountain Range into two principal drainage areas. Streams north of the Aleutian Range flow into Bristol Bay of the Bering Sea, and those south of the mountains flow into Shelikof Strait of the North Pacific Ocean. The large multilake Naknek River system is the dominant drainage area on the Bristol Bay side of the monument, whereas small single lakes and short streams and rivers constitute many separate drainages on the Shelikof Strait side. Twenty-four species of fish occur in the Bristol Bay drainages of the monument, but only eight species were collected in streams and lakes draining into Shelikof Strait. Evidently the Aleutian Range has been a barrier to the southward movement of freshwater fishes in the monument. All eight species in Shelikof Strait drainages are capable of dispersal through salt water, whereas several forms in Bristol Bay drainages require fresh water for dispersal. Variable numbers of species occur in the interconnecting lakes of the Naknek River system. Naknek Lake, the downstream terminus of the lake system, contains 24 known species and each upstream lake contains fewer species than the one into which it drains. The present distribution of fishes in this system is discussed in terms of the sequential timing of species invasion and the postglacial development of barriers.

INTRODUCTION

Katmai National Monument is at the base of the Alaska Peninsula in southwestern Alaska (fig. 1). It was established by Presidential Proclamation in 1918, primarily to preserve the spectacular features of the Valley of Ten Thousand Smokes--a volcanic phenomenon that resulted in 1912 from the eruption of the volcano Mt. Novarupta. In subsequent years the boundaries were extended to include much of the area surrounding the Valley of Ten Thousand Smokes, and the monument now encompasses 10,916 km.^{2}. Interesting accounts of the discovery, description, and history of this remote scenic area were given by Griggs (1922) and Cahalane (1959).

The monument has many prominent features that influence the distribution of fishes. It is divided by the Aleutian Range along a northeast-southwest axis so that the general streamflow is to the sides of the Alaska Peninsula. The area has a long history of volcanism (Wahrhaftig, 1965), and glaciation was extensive during the Pleistocene (Muller, 1952; Karlstrom, 1957). Several streams on each slope of the Aleutian Range still originate from small, vestigial glaciers. One of the most important features influencing the distribution of fishes in the monument is the large complex of interconnecting streams and lakes in the Naknek River system. This system dominates the western half of the monument; it is here the Bureau of Commercial Fisheries has a cooperative arrangement with the National Park Service to do biological research on sockeye salmon, Oncorhynchus nerka (Walbaum). This research began at Brooks Lake in 1940 and was expanded in 1961 to include all of the Naknek system. Some of the studies have dealt with fishes associated with sockeye salmon.

We have been involved with various aspects of studies at Brooks Lake since 1957 and throughout the Naknek system since 1961. In 1962, we began to collect fishes from other drainage systems in the monument.

[1] Fishery Biologist, Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska 99821.

[2] Graduate student, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oreg. 97331.

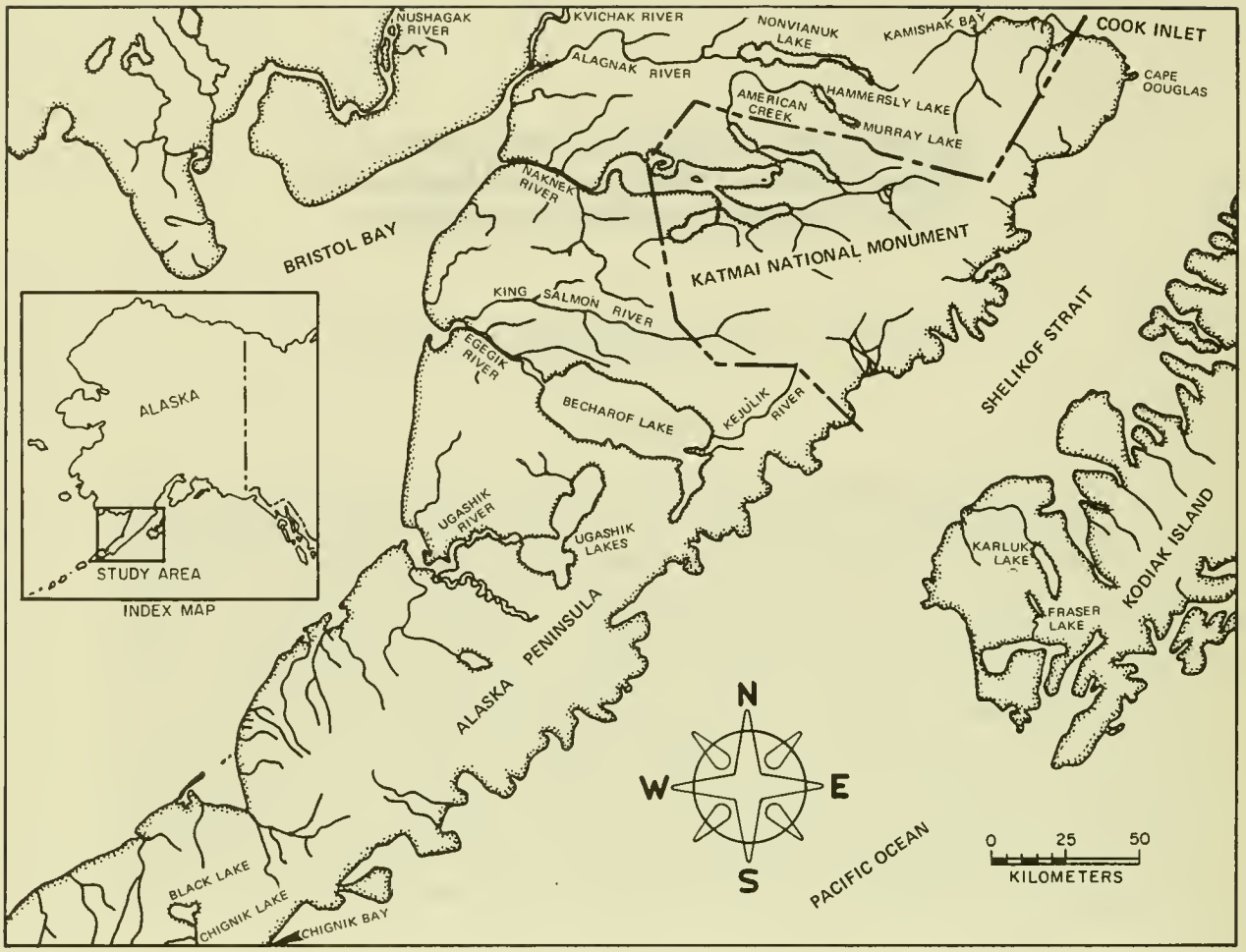

Figure 1.--Alaska Peninsula and adjacent areas, showing location of Katmai National Monument.

No general treatment of the occurrence and distribution of fishes in Katmai National Monument has been attempted, although Cahalane[3] in an interim report of the National Park Service Katmai Project mentioned a few species, and Greenbank[4] reported on a sport fishery survey of the Naknek system. Several publications concerned principally with aspects of sockeye salmon biology and a few published studies concerned with other species within the Naknek system provide an important background for the present study. Previous information concerning fishes in the monument other than in the Naknek system is confined mostly to data from reports[5] on commercial fishing in Shelikof Strait. These reports are concerned primarily with the species of salmon that spawn in particular streams.

Cahalane (1959) made a biological survey of the plant and vertebrate animal life in the monument but did not attempt to include fishes. The present study attempts to fill this gap in the general knowledge of fishes in the monument.

The purposes of this paper are (1) to report the known occurrence and distribution of fresh-water fishes in Katmai National Monument and (2) to consider the zoogeographical implications of these findings.

[3] Cahalane, Victor H. 1954. A biological survey of Katmai National Monument. In R. S. Luntey, Katmai Project interim report, Katmai National Monument, Alaska, pp. 75-109. U.S. Dept. Interior, Nat. Park Serv.

[4] Greenbank, John. 1954. Sport fish survey, Katmai National Monument. Manuscript on file, Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska, 30 pp.

[5] Information on the Shelikof Strait portion of the monument is included in the Management Reports, U.S. Bureau of Fisheries and Bureau of Commercial Fisheries, Kodiak Island District, for 1924-59. These reports are on file at the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay. Reports for this area since 1959 are available from the Alaska Department of Fish and Game, Juneau.

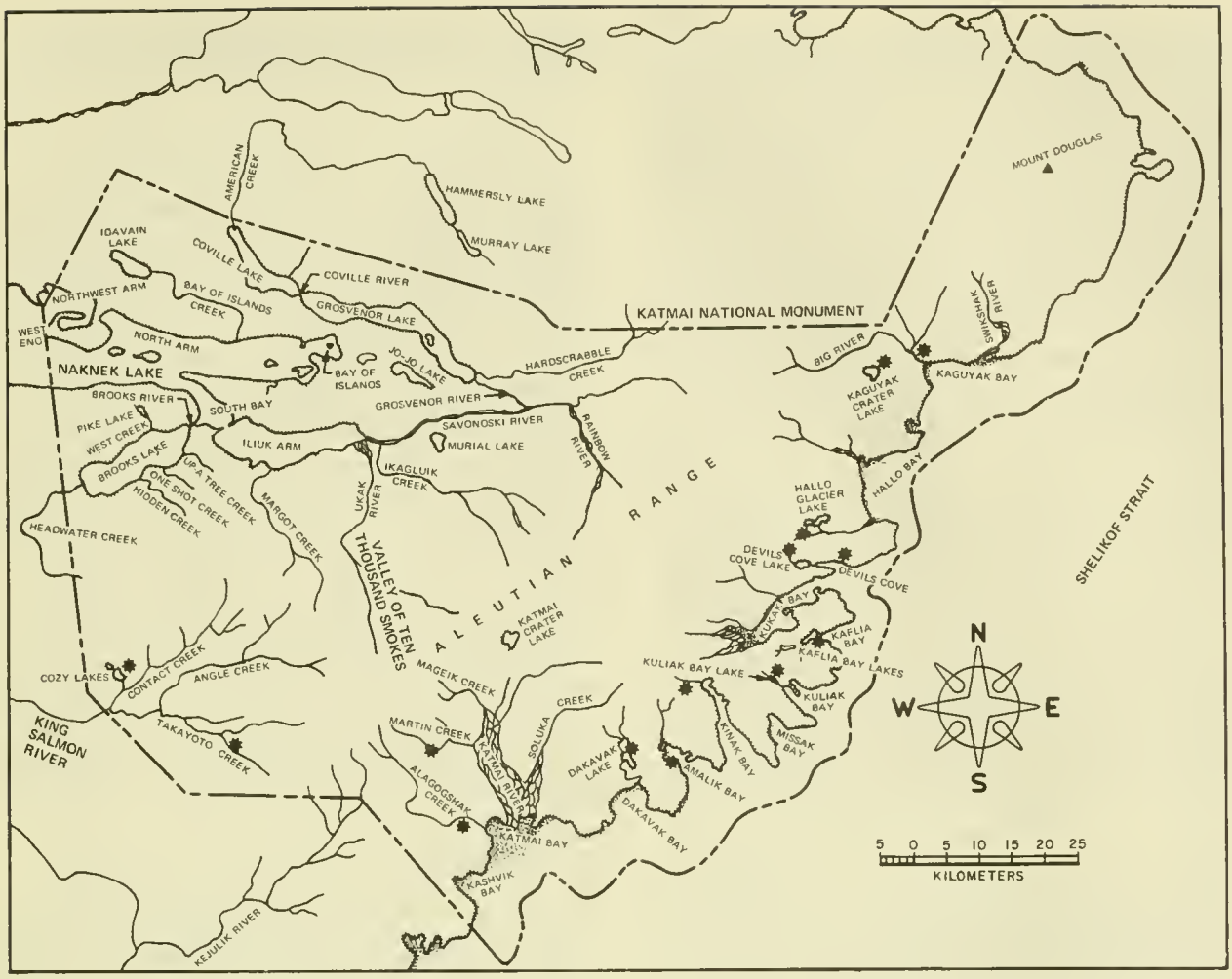

Figure 2.--Katmai National Monument, showing principal fresh-water areas. Asterisks indicate general locations where fish collections were made in the King Salmon River system and along Shelikof Strait, 1962-64. Hundreds of collections have been made throughout the Naknek River system beginning originally at Brooks Lake in 1940. Kuliak Bay Lake, Kafilia Bay Lake, Devils Cove Lake, Hallo Glacier Lake, Katmai Crater Lake, and Kaguyak Crater Lake are not official names. They are identified as such in this manuscript with nearby named geographic features for convenience only.

FRESH-WATER AREAS OF THE MONUMENT

The most important drainage feature of the monument is the arrangement of the Aleutian Range so that streams along the west side of the Alaska Peninsula flow into the Bering Sea through Bristol Bay and streams along the east side flow into the North Pacific Ocean through Shelikof Strait or Cook Inlet (fig. 1). A second important feature is the number, size, and relative complexity of drainage systems along the east and west sides of the monument (fig. 2). Although no major zoogeographical barriers lie between stream systems draining into Bristol Bay and interior Alaska, streams flowing into Shelikof Strait are essentially isolated from other fresh waters of the continent by the Aleutian Range.

BRISTOL BAY DRAINAGE

The principal fresh-water areas in the monument that drain into Bristol Bay are in the Naknek and King Salmon River systems. Of minor importance are the extreme headwaters of the Kejulik River in the Egegik River system, which lie just inside the southern boundary of the monument. These headwaters are small and of little significance to the distribution of fish in the monument (fig. 2).

Those portions of the King Salmon system that lie within the southwest corner of the monument are Contact, Angle, and Takayoto Creeks. Angle Creek is a tributary of Takayoto Creek which joins Contact Creek to form the King Salmon River. Two small interconnecting lakes, which Cahalane (1959) called Cozy Lakes, drain into Contact Creek.

The Naknek system has seven interconnecting lakes and is by far the largest and most complex drainage in the monument (fig. 2). Murray and Hammersly, the uppermost lakes, lie outside the north boundary of the monument; Coville, Grosvenor, Brooks, and Idavain Lakes all lie wholly in the monument; and the lower part of Naknek Lake is west of the monument. All of the lakes are of glacial origin (Muller, 1952). Six of them essentially occupy single basins, but Naknek Lake has six distinct basins (fig. 2): Iliuk Arm, North Arm, Northwest Arm, and South Bay are basins separated from each other by shallow, narrow connections; Bay of Islands is a distinct area at the east end of North Arm; and the West End is a shallow outwash plain of earlier glacial activity.

All of the lakes are dimictic oligotrophic lakes.[6] They are usually ice free from early May until early December. Murray and Hammersly Lakes lie about 488 m. elevation and are ice free 4 weeks less than the other lakes. Surface water temperatures during the summer reach 12° C. in all lakes except the shallowest lake, Coville, where they reach 15° C. Thermal stratification is seldom strongly developed or persistent during the summer. Oxygen is at or near saturation at all depths at all times of the year. Iliuk Arm is the only basin that receives drainage directly from glaciers and from the Valley of Ten Thousand Smokes; it is extremely turbid; visibility is usually less than 15 cm.

The largest streams in the Naknek system are American, Hardscrabble, Ikagluik, Margot, Bay of Islands, and Headwater Creeks, and Coville, Grosvenor, Savonoski, Rainbow, Ukak, and Brooks Rivers. In general, these streams have midsummer flows in excess of 3 $m.^3/sec.$ Naknek River itself, which drains Naknek Lake, lies outside the monument.

A number of tundra ponds, beaver ponds, and small tundra lakes occur along the western margin of the monument. These bodies of water are shallow, frequently contain submerged and emergent aquatic vegetation, and occasionally have no surface connections with major stream systems. Often a series of these ponds is connected by slow-flowing streams or marshes that go nearly dry during periods of low runoff. In the monument this aquatic habitat is confined to the Bristol Bay area; it becomes a prominent feature of the tundra west of the monument boundary.

[6] Hartman, Wilbur L., and Robert L. Burgner. 1968. Limnology of sockeye salmon-producing lakes in southwestern Alaska. Manuscript on file, Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska, 51 pp.

SHELIKOF STRAIT DRAINAGE

Fresh-water drainages in the Shelikof Strait area are characterized by numerous short and isolated systems, many of which consist only of stream habitats or of streams and small, insignificant lakes. Some drainage systems have lakes up to 4.8 km. long, but none have large interconnecting lakes. Variety in stream and lake habitat in Shelikof Strait drainages comes not from a single large complex system but from numerous small and relatively simple ones. The shoreline of the strait has gently curving bays and rugged fiords; about 20 distinct systems drain into the heads of the major bays. These bays, from south to north along the coast of the monument, are as follows: Kashvik, Katmai, Dakavak, Amalik, Kinak, Missak, Kuliak, Kaflia, Kukak, Hallo, and Kaguyak (fig. 2). The streams that flow into these bays are between 4.8 and 32.2 km. long, and generally have steep gradients. Most of them are unnamed; notable exceptions are Katmai River and Alagogshak and Soluka Creeks, which flow into Katmai Bay. Mageik and Martin Creeks flow into Katmai River. North of Hallo Bay the coastline becomes more regular and continues in a large sweeping arc that includes the easternmost promontory of the Alaska Peninsula, Cape Douglas (fig. 1). Big and Swikshak Rivers (fig. 2) drain much of this section of the coastline. In the northernmost part of the monument several small streams flow north from glaciers on Mt. Douglas into Kamishak Bay of Cook Inlet (fig. 1).

Coarse ash and pumice, principally from volcanic activity in 1912 (Griggs, 1922), is many meters deep over much of the terrain in the southeast portion of the monument. Several streams in this area, including Katmai River, Soluka Creek, and unnamed streams that flow into the head of Kukak Bay, carry heavy silt loads from the ash-laden watersheds. These streams have unstable beds and are extensively braided. Other large braided streams, which have less ash and pumice on their watersheds but carry silt loads from glaciers, are Swikshak River and two streams that flow into Hallo Bay. Not all streams along the strait, however, are braided or carry heavy silt loads. Those flowing from Dakavak Lake, from Kuliak Bay Lake, to and from Devils Cove Lake, Alagogshak Creek, and Big River all have fairly stable streambeds with moderate gradients.

Besides the principal terminal streams, short lateral streams drain the steep mountain slopes along the sides of the fiordlike bays along Shelikof Strait. Many of these

streams are precipitous and have irregular flows and unstable streambeds. In our limited sampling in these habitats, principally in the Amalik and Kinak Bay areas, we found that most of these streams had no established ichthyofauna.

The two largest streams along the Shelikof Strait side of the monument are Katmai and Big Rivers. Griggs (1922) has described the physical characteristics, some of them unique, of Katmai River. We collected fish on the east side of Katmai River about 3.2 km. above the mouth and from a clear-water tributary of the river, Martin Creek. Big River, which is about 32.2 km. long, arises to the west of Kaguyak Crater and flows in a large sweeping arc into the northwest corner of Kaguyak Bay (fig. 2). It has alternate stretches of pools and riffles, numerous small oxbows and cutoff meanders, and a low-gradient, slow-flowing lagoon section above the mouth. We collected fish from the main stream and from small flood plain cutoff ponds about 8.0 km. above the mouth.

Although they are generally small, the several lakes on the Shelikof Strait side of the monument provide a variety of lentic habitats for fishes in this area. Most of the lakes appear to be of glacial origin and are relatively deep for their size. Dakavak Lake, which drains into the head of Dakavak Bay through a 3.2-km.-long outlet stream, is the largest--about 4.8 km. long and 1.0 km. wide. Its watershed is heavily covered with pumice and ash, which give a chalky blue-gray color to the water. The maximum depth is unknown, although gill nets were fished as deep as 21 m. in 1962. Other smaller but generally clear lakes where fish were collected include Kuliak Bay Lake, Kaflia Bay Lake, and Devils Cove Lake. Small hanging lakes with high waterfalls occur at the heads of Amalik and Kinak Bays, but we did not collect from them; we did collect, however, in the outlet stream from a turbid glacier lake that forms along the face of Hallo Glacier.

Most lakes along Shelikof Strait had summer surface temperatures similar to those of lakes of the Naknek River system; Hallo Glacier Lake was only 1° C. in mid-August 1964.

Crater lakes occur in the calderas of Katmai and Kaguyak volcanoes. Although no attempt was made to collect fish in Katmai Crater Lake, one species was collected in Kaguyak Crater Lake.

Notably lacking in Shelikof Strait drainages is any extensive interconnecting stream-lake complex similar to that in the Naknek system. Except for common marine connections, Shelikof Strait streams and lakes in the monument are isolated from Bristol Bay drainages and from each other by mountains of the Aleutian Range.

METHODS AND EQUIPMENT

The intensity of fish collecting was much greater in the Naknek River drainage than in either the King Salmon River or the Shelikof Strait drainage. The occurrence and distribution of fishes in these two areas involve fewer species, however, and appear less complex than the Naknek system. The amount of fish collecting done in any one stream or lake varied greatly, depending on accessibility and the degree to which the location was involved in research on sockeye salmon. No attempt was made to document each collection from the Naknek system because hundreds of collections in most of this system have been made by the authors and many others engaged in salmon research. We collected from numerous smaller lakes, ponds, and streams in the Naknek system supplemental to salmon research to fill in gaps in the knowledge of fishes in the Naknek system. This report is the first attempt to bring together knowledge gained from this sampling concerning the occurrence of various species in specific lakes and streams.

Because of the large size, the remoteness of the area, and the general similarity of the drainages along Shelikof Strait, no attempt was made to collect in all of the streams there. We made about 25 collections at 13 locations in Shelikof Strait drainages and 3 collections at 2 locations in the King Salmon River system between 1962 and 1964. Locations of collections from Shelikof Strait and King Salmon River areas are shown in figure 2.

The problems of moving personnel and equipment to certain areas in the monument were challenging. Small boats and amphibious aircraft were available for travel throughout the larger Naknek system lakes. Overland treks were made on foot to small ponds and streams adjacent to larger waterways. We used small single-engine float planes to reach the most remote areas, particularly along Shelikof Strait. With aircraft, we used various sampling methods to collect in remote areas. The procedure usually followed involved a 2- or 3-day air trip with a series of stops at collecting sites to set gill nets, small traps, or fyke nets and to make seine and hook and line collections and general observations on fishes at each site. A return flight to the same area on the final day of the trip enabled us to haul the nets and traps left overnight and to process the collections. The collector in remote areas frequently wore a neoprene exposure suit and searched for fishes by snorkeling along the surface in shallow water. Exposure suits were also used during the setting

and lifting of gill nets and other gear when boats were not available.

We used several types of equipment to collect fishes. Beach seines and gill nets of various lengths and mesh sizes, tow nets 3.3 m. and 1 m. in diameter, small otter trawls, and small-meshed trap nets and fyke nets were used routinely through most of the Naknek system. Much of this equipment was also fished in other areas, although trawls and tow nets required powerboats, available only on the larger Naknek system lakes. Other sampling equipment included fish toxicants, sport fishing gear, hand nets, fish spears, small bobbinet "habitat" seines, and small-meshed collapsible nylon traps. Details on the use of much of this equipment have been discussed elsewhere (Hartman, Heard, and Strickland,[7] Ellis,[8] Heard, 1962; Merrell, 1964).

Fish weirs or counting fences operated by personnel of the Bureau of Commercial Fisheries at various times in the Naknek system on Naknek River, Brooks River, American Creek, Hardscrabble Creek, Hidden Creek, and West Creek, and along Shelikof Strait at the outlet of lower Kaflia Bay Lake have all contributed information on the occurrence and distribution of fishes considered in this report.

Fish collections were processed by identifying and counting the number of each species collected. In some collections, length and weights were recorded, and scales were collected for age analysis. Lengths of fish, except where otherwise noted, are reported as fork length. Field records from all Shelikof Strait and King Salmon River system collections, plus many of the Naknek system collections, are filed in the museum of the Bureau of Commercial Fisheries Biological Laboratory at Auke Bay, Alaska.

Identifications of fishes were made by the authors except where otherwise referenced. The principal taxonomic keys used were by Wilimovsky[9] and Clemens and Wilby (1961). Meristic counts follow Hubbs and Lagler (1958). Representative samples of all species collected in each of the principal drainages of the monument have been deposited either in the museum of the Laboratory at Auke Bay or in the Oregon State University fish collection. Nomenclature of fishes follows the American Fisheries Society (1960) except where otherwise noted.

ANNOTATED LIST OF SPECIES

The data on occurrence and distribution of fresh-water fishes in Katmai National Monument are presented in the following annotated list of 24 species from nine families known to occur in the monument. Within the family groups, six families--Petromyzontidae, Osmeridae, Umbridae, Esocidae, Catostomidae, and Gadidae--have only one species; whereas two families--Gasterosteidae and Cottidae--have two species each; and one large family--Salmonidae--has 14 species. In addition to information on fresh-water forms, we provide data on four euryhaline species, each from a separate family, that occur in or near fresh waters of the monument. Besides data on the occurrence and distribution of each species, the annotations include information on the life history and biology from various parts of the monument. Such information generally is not available from other sources. The quantity of this information varies greatly from species to species--a result of circumstance, not design.

FRESH-WATER FORMS

Many of the fishes occurring in fresh-water areas of Katmai National Monument either are or can be anadromous. A few forms that apparently are confined to fresh water throughout their life in southwest Alaska occur in estuarine environments in the Arctic (Walters, 1955). Only three families in the monument--Umbridae, Esocidae, and Catostomidae--are considered by Miller (1958) to be primary fresh-water fishes. All 24 forms listed below, however, at least spawn and spend their juvenile stages in fresh waters of the monument.

Petromyzontidae

Arctic lamprey, Lampetra japonica (Martens).--Arctic lamprey were collected only in the Naknek system, where fresh-water and anadromous forms coexist. We collected mature, spawning, or spent individuals of the smaller fresh-water form in May and June from Coville, Grosvenor, and Brooks Rivers; from most tributaries of Brooks Lake; from two small tributaries of Naknek Lake, one in North Arm and one on the south shore of the lake near the monument boundary; and from a tributary of Coville Lake about 1.6 km. north of the lake outlet. Only one specimen of

[7] Hartman, Wilbur L., William R. Heard, and Charles W. Strickland. 1962. Red salmon studies at Brooks Lake Biological Field Station, 1961. Manuscript on file, Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska, 53 pp.

[8] Ellis, Robert J. 1963. The abundance and distribution of juvenile red salmon and associated species in lakes of the Naknek River system and Karluk Lake. Manuscript on file, Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska, 80 pp.

[9] Wilimovsky, Norman J. 1958. Provisional keys to the fishes of Alaska. Manuscript on file, Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska, 113 pp.

the larger anadromous form was taken inside the monument--at the mouth of Brooks River, but several were collected in the Naknek River just outside the monument.

Immature adult Arctic lamprey were commonly collected during the summer in tow nets in limnetic areas of Coville, Grosvenor, and Brooks Lakes and of Iliuk Arm, South Bay, and North Arm of Naknek Lake. They were also caught in fyke nets (late summer and fall) from Coville, Grosvenor, and Brooks Rivers. Actively feeding parasitic-phase lampreys were observed attached to sockeye salmon, Oncorhynchus nerka (Walbaum); pygmy whitefish, Prosopium coulterii[10] (Eigenmann and Eigenmann); rainbow trout, Salmo gairdnerii Richardson; and threespine stickleback, Gasterosteus aculeatus Linnaeus. Parasitism by the lamprey, however, is not known to threaten any fish population in the Naknek system.

Morphologically, the parasitic Arctic lamprey is almost identical with the nonparasitic American brook lamprey, Lampetra lamotteii of eastern North America. Lampetra lamotteii has been reported in Alaska (Wilimovsky, 1954; Hubbs and Lagler, 1958), and it was initially believed to occur in the Naknek system. Available evidence suggests, however, that all lamprey in the Naknek system are parasitic (Heard, 1966). The report by Cahalane (see footnote 1) that Lampetra tridentata (Gairdner) occurred in Grosvenor Lake was apparently based on hearsay and cannot be accepted.

Salmonidae

Humpback whitefish, Coregonus pidschian (Gmelin).--Humpback whitefish were collected only in the Naknek system, where they occur in most of the principal lakes. They were collected in Iliuk Arm, South Bay, North Arm, and West End of Naknek Lake and in Coville and Grosvenor Lakes but not in Brooks Lake. Apparently, the greatest density of humpback whitefish in the monument is in Coville Lake, although numbers are substantial also in South Bay basin of Naknek Lake. Ripe humpback whitefish were caught in the autumn in South Bay near the mouth of Brooks River but were never observed spawning in the river. Observers in a low-flying aircraft saw thousands of fish on riffles in the lower portion of American Creek on October 27, 1963. The fish were believed to be humpback whitefish spawners from Coville Lake. The taxonomic and phyletic relation of this fish and the lake whitefish, Coregonus clupeaformis (Mitchill) in Alaska is not clear (Walters, 1955; Lindsey, 1962).

[10]Although the American Fisheries Society checklist uses the specific taxon spelling coulteri, the latest judgment of the International Code of Zoological Nomenclature holds that original spellings of "ii" on patronyms must be retained. This ruling also applies to Lampetra lamotteii (LeSueur) and Salmo gairdnerii Richardson.

Least cisco, Coregonus sardinella Valenciennes.--Least cisco were collected in the Naknek and King Salmon systems. They occurred in Coville, Grosvenor, and Naknek Lakes but not in Brooks Lake, although they were occasionally caught in lower Brooks River below the falls. Greenbank (see footnote 4) collected this species from a small lake east of the head of Bay of Islands which he called "Jo-Jo" Lake. At one time Jo-Jo Lake undoubtedly was continuous with the Bay of Islands, and high water levels may still connect the two through a series of marshes; this lake may also drain through a series of marshes into the Savonoski River. In the King Salmon River system least cisco were collected in lower Cozy Lake.

Most least cisco were caught in passive sampling gear such as trap nets and gill nets. The species seemed to escape readily from active sampling gear such as seines, tow nets, and trawls, especially in clearer waters.

Pink salmon, Oncorhynchus gorbuscha (Walbaum).--Pink salmon were collected in the Naknek and Shelikof Strait systems. They occurred in the monument portion of the Naknek system in small numbers: 100 passed through Brooks River weir into Brooks Lake in 1962, and about 200 spawned in Brooks River itself. Spawning pink salmon were observed in Up-a-Tree, One Shot, Hidden, and Headwater Creeks and in Coville River between 1960 and 1964.

Although accurate counts are few and some locality records are not specific, pink salmon are the most abundant and widely distributed species of salmon on the Shelikof Strait side of the monument. They have been reported from every bay along the coastline and probably spawn in streams at the head of most of these bays. Counts of adults through the Kaflia Bay weir in 1929 and 1934 were 291 and 375, respectively. In 1946, 100,000 pink salmon were caught in Swikshak Lagoon.

We collected and observed pink salmon in the Shelikof Strait area of the monument in 1962-64. We saw spawning runs of several thousand fish in Alagogshak Creek, Big River, and the stream that flows from Dakavak Lake into Dakavak Bay, and smaller runs in Katmai River and the principal terminal streams that flow into Amalik and Kuliak Bays and Devils Cove of Kukak Bay. Our observations were made during limited surveys and should only be considered as records of occurrence and not as indicators of total production. We were unable to observe streams in several of the areas, including Kashvik Bay, the main arm of Kukak Bay, and all of the area east and north of Big River.

Spawning by pink salmon in Katmai River was somewhat unexpected because the unstable stream bottom of this heavily braided river is composed primarily of water-soaked pumice. Nevertheless, adult pink salmon spawned in

small discontinuous pockets of gravel along the edge of a small bluff on the east bank of the river about 3.2 km. above the mouth. Surface velocity was 0.3-0.7 m./sec. in this area.

Chum salmon, Oncorhynchus keta (Walbaum).--Chum salmon were collected in the Naknek and Shelikof Strait systems. They are the least abundant salmon in the Naknek system, and the only information on their occurrence and distribution is that some adults (usually fewer than 10) pass through the Brooks River weir each year; a few have been reported in American Creek. We did not see chum salmon in the Shelikof Strait area of the monument, but they were reported in Big River and in Katmai, Kuliak, Kaflia, Kukak, Hallo, and Swikshak Bays, either in the early U.S. Bureau of Fisheries management reports or by biologists of Alaska Department of Fish and Game.

Coho salmon, Oncorhynchus kisutch (Walbaum).--Coho salmon, which are widely distributed in the monument, were collected in the Naknek, King Salmon, and Shelikof Strait systems. Most of the information on this species is based on samples of juveniles taken in the summer because the adult salmon do not appear until fall after much of the work on sockeye salmon has been discontinued. Within the Naknek system, annual counts of adult coho salmon through Brooks River weir in 1957-62 ranged from 194 to 1,844 (average 620). We collected juveniles or adult coho salmon in the Naknek system in Coville, Grosvenor, and Brooks Rivers; Coville, Grosvenor, and Brooks Lakes, and all basins of Naknek Lake; Hardscrabble, Margot, Headwater, Hidden, One Shot, and West Creeks; and unnamed creeks from Coville, Grosvenor, and lower Naknek Lakes. The only coho salmon collected from the King Salmon River system was a 62-mm. juvenile from lower Cozy Lake on June 29, 1962. The only area where we saw coho salmon along Shelikof Strait was in Big River; 71 juveniles (35-68 mm.) were seined there on August 15, 1964. Accounts of good runs of adult coho salmon in Kaflia Bay lakes and streams are given in some early management reports. Although coho salmon have been reported in Kashvik, Katmai, Kuliak, Kukak, Hallo, and Kaguyak Bays and in Swikshak Lagoon, they have not been reported from streams that enter those waters.

Sockeye salmon, Oncorhynchus nerka (Walbaum).--Sockeye salmon, the most evident and widely distributed species in the monument, were collected in the Naknek, King Salmon, and Shelikof Strait systems.

The Naknek system produces a large part of the valuable Bristol Bay catch of this species; annual escapements to the system have varied between 0.3 and 2.2 million fish. The major spawning areas of sockeye salmon in the Naknek system are the American, Hardscrabble, Margot, Headwater, and Bay of Islands Creeks and Grosvenor, Brooks, and Naknek Rivers. Many smaller streams and some lake beaches also support spawning populations. Juvenile sockeye salmon occurred in all areas of the larger Naknek system lakes except Idavain and Murray Lakes. Sport fishing for adults is popular in Brooks River.

No fresh-water (kokanee) populations of sockeye salmon are known to occur sympatrically with anadromous populations in the monument. We discovered kokanee salmon in two lakes that drain into Shelikof Strait, and Greenbank (see footnote 4) reported them in Jo-Jo Lake.

We saw several schools of young-of-the-year sockeye salmon (age 0) in lower Cozy Lake of the King Salmon River system and collected about 100 fish on June 29, 1962.

Apparently the largest run of anadromous sockeye salmon in the Shelikof Strait area of the monument is into two lakes at the head of Kaflia Bay. The lower lake has slightly brackish water either from seepage or possibly from flooding on extremely high tides. The upper lake is 15 to 23 m. higher than the lower, and the two are connected by a steep boulder-strewn stream about 305 m. long. The U.S. Bureau of Fisheries had a weir for counting adult salmon, presumably at the outlet of the lower lake at Kaflia Bay in 1929-32, and 1934; escapements of spawning sockeye salmon into the two lakes in these years averaged about 12,500 (see footnote 5). The estimated escapement of sockeye salmon to the two lakes in 1939 was 100,000 fish. On July 12, 1963, we saw about 2,000 adult sockeye salmon off the mouth of the interconnecting stream between the two lakes. We saw no adult salmon in the stream proper, but collected one juvenile (about 70 mm. long) from a pool just below the upper lake, so at least some adults ascend this precipitous stream.

Sockeye salmon runs of unknown size were reported in the early management reports and by local residents of the Kodiak Island area to occur in a small lake at the head of the west arm of Kuliak Bay (known locally as Halferty Bay). We saw no adults on two collecting trips to the Kuliak Bay Lake in August 1964, but collected several juveniles (age 0 and 1; from 52 to 92 mm.). The outlet stream had no barriers or obstructions that would prevent anadromous adults from entering the lake.

We collected juvenile sockeye salmon in 1962 from Dakavak Lake and a small lake above the Devils Cove portion of Kukak Bay. No records of adult sockeye salmon have been found in the commercial statistics for the bays into which these lakes drain. Moreover, the streams flowing from these lakes have barriers, and we believe that the populations in both lakes are landlocked kokanee salmon.

The outlet stream at Dakavak Lake is now subterranean; it flows or seeps through a 60- to 100-m. pumice and volcanic ash dike across the outlet end of the lake. The origin of the dike is unknown, although it likely developed, at least in part, from the extremely heavy ash deposits that followed the 1912 volcanic activity in the Dakavak Lake area. Possibly ash and rock slides in the narrow outlet arm of the lake, combined with large volumes of floating pumice on the lake surface, formed the dike. During its formation, and possibly later, surface water flowed over the top of the dike, as evidenced by high-water beach lines on the dike and margins of the lake. The top of the dike, about 25 feet above the current lake level, coincides with the top of a denuded high-water zone around the lake margin (Cahalane's [1959] frontispiece, photographed at Dakavak Lake on July 28, 1953, clearly shows this denuded zone.) Undoubtedly this dike has prevented anadromous fishes from going into the lake for several years. Nineteen sockeye salmon collected from the lake on June 30 and July 1, 1962, were 61 to 160 mm. long and averaged 125 mm. The larger of these (over 140 mm.) were in their fourth year of life and had maturing gonads. We believe these fish would have spawned in the fall. This population may have become landlocked during the eruption of 1912.

Anadromous sockeye salmon are probably excluded from the lake above Devils Cove in Kukak Bay by a 5- to 6-m. waterfall on the outlet stream. We caught 26 possible kokanee salmon, 28 to 139 mm. (average 105 mm.), by setting a gill net overnight and by beach seining in this lake on July 1, 1962. One fish, 136 mm. long, was in its fifth year of life; seven others, over 118 mm. long, were in their fourth year. These older fish had maturing gonads and probably would have spawned in the fall.

Perhaps the most unusual account of sockeye salmon in Katmai National Monument, one where this salmon apparently did not follow the usual pattern of using a lake for a juvenile rearing area, was given by Griggs (1922, p. 161). He quoted C. H. Gilbert who suggested that 5-year-old adult anadromous sockeye salmon collected in 1917 from a small unnamed tributary of the Katmai River had spent 2 years in fresh water, possibly in the tributary or in Katmai River itself in the years immediately after the 1912 eruption. We had hoped to recheck this stream to learn if sockeye salmon were still there but were unable to determine the stream's exact location.

Another group of anadromous sockeye salmon that does not have a lake nursery area occurs in the Swikshak River system. These fish spawn in a small stream that runs somewhat parallel with, and to the east of, Swikshak River and enters the river about 1.6 km. above its mouth. In its upper portion this stream is precipitous, but most of the lower portion is sluggish and forms a lagoon just before it joins the Swikshak River. Both portions are about 4 km. long. Sockeye salmon spawn in an area about 0.8 km. long between the two sections where the gradient first increases sufficiently to provide a silt-free gravel substrate.[11] Upstream, this gradient becomes too steep for a stable stream bottom. An estimated 2,700 sockeye salmon spawned in this stream on August 20, 1959.[12]

Chinook salmon, Oncorhynchus tshawytscha (Walbaum).--Chinook salmon were collected in the Naknek and King Salmon River systems. They occurred only in small numbers within the monument portion of the Naknek system. Adults were observed in Brooks River and in Headwater, Bay of Islands, and American Creeks between 1960 and 1964. Since 1940 an average of 15 adults per year have passed through Brooks River weir into Brooks Lake. The only juveniles observed within the monument portion of the Naknek system were seined from Hidden Creek Bay in Brooks Lake in 1961. Large numbers of chinook salmon occur outside the boundary of the monument in the lower portion of the Naknek system. Records from a weir on the Naknek River at the head of tidewater indicate that about 5,000 adult chinook salmon passed through the weir annually from 1953 to 1957; most of these spawned in Naknek River below the outlet of Naknek Lake. Substantial runs of chinook salmon spawn in Big Creek and King Salmon Creeks downstream from the Naknek River weir site.[13] We did not observe adult chinook salmon in the King Salmon River system within the monument, but we collected juveniles (34-51 mm.) from a small slough along Takayoto Creek in August 1964.

Pygmy whitefish, Prosopium coulterii (Eigenmann and Eigenmann).--Pygmy whitefish were collected only in the Naknek system. These small whitefish were collected from Iliuk Arm, South Bay, North Arm, and Bay of Islands in Naknek Lake; throughout Grosvenor and Brooks Lakes; from the eastern end of Coville Lake; and from near the outlet in Hammersly Lake. They were particularly abundant in Brooks Lake and South Bay of Naknek Lake. The fish were collected in shallow areas and in the deepest known freshwater area in the monument (171 m., Iliuk Arm). Large numbers of pygmy whitefish

[11] Personal communication, W. H. Noerenberg, Deputy Commissioner for Commercial Fisheries, Alaska Department of Fish and Game, January 24, 1966.

[12] Noerenberg, Wallace H. 1959. Stream surveys in the Kodiak area, 1959. Univ. Wash., Seattle, Fish. Res. Inst., Circ. 111, 40 pp.

[13] King Salmon Creek, a tributary of Naknek River west of King Salmon, should not be confused with the King Salmon River drainage.

from South Bay move into lower Brooks River in the summer and feed, primarily on immature insects. These fish spawn in Brooks River in November and December. The biology of pygmy whitefish in the Naknek system is reported by Heard and Hartman (1966).

Round whitefish, Prosopium cylindraceum (Pallas).--Round whitefish were collected in the Naknek and King Salmon systems. They occurred in Naknek, Coville, Grosvenor, and Brooks Lakes; American and Headwater Creeks; Hidden and West Creeks (tributaries of Brooks Lake); and Coville, Grosvenor, and Brooks Rivers. In the King Salmon River drainage, they occurred in lower Cozy Lake.

Round whitefish spawn in the autumn, apparently in streams similar to those inhabited by mountain whitefish, P. williamsoni (Girard), in Montana (Brown, 1952). About 200 adults in breeding condition were seined from South Bay of Naknek Lake off the mouth of Brooks River on November 7, 1962. Both sexes were tuberculate over much of the body and had brightly colored orange ventral fins and a bold longitudinal orange stripe along the body. Tony Malone, a trapper from Naknek, Alaska, reported that whitefish 12 to 16 inches (30 to 41 cm.) long were abundant in late autumn in Headwater Creek above the monument boundary. We believe these fish were round whitefish because only that species and pygmy whitefish occur in Brooks Lake or its tributaries, and pygmy whitefish never grow longer than about 20 cm.

Rainbow trout, Salmo gairdnerii Richardson.--Rainbow trout were collected only in the Naknek system. We found them in Coville, Grosvenor, and Brooks Lakes; South Bay and North Arm of Naknek Lake; Coville, Grosvenor, and Brooks Rivers; American, Headwater, West, and Margot Creeks; and one unnamed creek in South Bay at the base of Dumpling Mountain. We have seen adult rainbow trout spawning in Brooks River in May and have collected recently emerged fry in quiet water along the river in August. Greenbank (see footnote 4) presented age and growth data for rainbow trout caught by sports fishermen in Brooks River. A moderately heavy sport fishery for this fish also occurs in Naknek River. We do not know if steelhead occur in the Naknek system.

Arctic char, Salvelinus alpinus (Linnaeus).--We collected Arctic char from Iliuk Arm, South Bay, North Arm, and Northwest Arm of Naknek Lake; Coville, Grosvenor, Brooks and Idavain Lakes; and American and Margot Creeks. There are limited sport fisheries for Arctic char off the mouth of Margot Creek, in some unnamed creeks along the north shoreline of the North and Northwest Arms, and in Idavain Lake. Spawning Arctic char from Idavain Lake are brilliantly colored and are referred to by residents of the area as "golden trout."

Dolly Varden, Salvelinus malma (Walbaum).--Two types of Dolly Varden occur within the monument, one in the Naknek system and one in Shelikof Strait drainages. Dolly Varden in the Naknek system generally live in streams and are small, usually less than 25 cm. long. McPhail (1961), who recently evaluated the Dolly Varden-Arctic char complex in North America, recognized this small stream-dwelling Dolly Varden as a northern form, distinct from the more widely distributed southern form. The Aleutian Range on the Alaska Peninsula apparently represents the dividing line for these forms. McPhail's material from Karluk and Fraser Lakes on Kodiak Island was characteristic of the southern form, and material from Brooks Lake was characteristic of the northern form.

In the Naknek system we collected Dolly Varden from Grosvenor and Brooks Rivers, and from Brooks Lake, Up-a-Tree, One Shot, and Hidden Creeks. Greenbank (see footnote 4) reported that specimens he collected from Idavain Lake were Dolly Varden, but McPhail (1960), who made gill raker counts of Greenbank's specimens, suggested that the fish were Arctic char.

The southern form of Dolly Varden, which is widely distributed in streams and lakes along the Shelikof Strait area of the monument, is distinguished from the northern form principally by fewer gill rakers and fewer vertebrae; also, the southern form lives in lakes and streams and may be anadromous or landlocked (McPhail, 1961). We collected specimens of the southern form in lower Kaflia Bay Lake and in inlet and outlet streams of this lake; in Dakavak Lake, Kuliak Bay Lake, Devils Cove Lake, and the outlet stream of this lake below the high waterfalls; in a small pond on Martin Creek (tributary of Katmai River); in Big River; and in Kaguyak Crater Lake. An archaeological survey team from the University of Oregon collected this fish in 1963 from a small stream near the old village of Kukak. Counts of gill rakers on the lower limb of the first gill arch of Dolly Varden that we collected from various areas along Shelikof Strait agree with McPhail's (1961) counts for Dolly Varden from Karluk and Fraser Lakes on nearby Kodiak Island (table 1).

Arctic char from Idavain Lake were air-dropped into Kaguyak Crater Lake in 1956;[14] but none were observed in our collections. We collected nine specimens of char in Kaguyak Crater Lake in August 1964; gill raker counts of the specimens, however, indicate they were Dolly Varden, distinct from Idavain

[14] E. Siler, a guide and bush pilot at King Salmon, described this 1956 capture, transport, and air drop of about 20 "golden trout" to us at Brooks Lake in 1964.

Table 1.--Gill rakers in Arctic char and Dolly Varden from various parts of Katmai National Monument and in Dolly Varden from Karluk and Fraser Lakes on Kodiak Island

Species	Fish in sample	Gill rakers, lower half of first left gill arch	
		Range	Mean
	Number	Number	Number
Salvelinus alpinus			
Brooks Lake[1/]	1	14	--
Idavain Lake[1/]	4	14-16	14.7
Idavain Lake	20	13-16	14.2
Salvelinus malma			
Southern form			
Dakavak Lake	15	9-11	10.2
Devils Cove Lake	12	10-12	11.1
Fraser Lake[1/]	38	8-12	10
Kaguyak Crater Lake	9	10-11	10.8
Karluk Lake[1/]	33	8-12	11
Kuliak Bay Lake	18	9-12	10.4
Northern form			
Brooks Lake[1/] (tributaries)	20	11-14	12.6

[1/] Data from McPhail (1961).

Lake Arctic char (table 1). Kaguyak Crater Lake now has no outlet, although a low point in the northeast rim of the crater suggests that a stream may have flowed at an earlier date when water levels in the crater were higher (see Cahalane, 1959, plate 2, fig. 1). Sequential beach ridges attest to the former occurrence of higher water levels inside the crater. Dolly Varden live in the surrounding Big River drainage, and apparently dispersed into this unusual habitat.

Lake trout, Salvelinus namaycush (Walbaum).--Lake trout were collected only in the Naknek system. We collected them in almost all areas of Naknek, Coville, Grosvenor, and Brooks Lakes but not in any of the smaller lakes within the monument, although they occur in Hammersly and Murray Lakes. Although the species is found primarily in lakes, occasionally they are seen in the connecting rivers between lakes, such as Brooks and Coville Rivers. Grosvenor Lake has a limited sport fishery for lake trout just below the outlet of Coville River, where a concentration of fish remains at least from ice breakup in the spring until mid-September. This concentration of lake trout is undoubtedly related to the food that passes down the inlet stream. Lake trout have been observed at Colville River preying on migrating juvenile sockeye salmon. They also prey heavily on sticklebacks and pond smelt and occasionally on small rodents. Greenbank (see footnote 4) presented data on the average size of various age groups of lake trout from the Naknek system, and Lindsey

(1964) discussed the coexistence of lake trout and anadromous parasitic Arctic lamprey in the Naknek system.

Arctic grayling, Thymallus arcticus (Pallas).--Arctic grayling were collected only in the Naknek River system.[15] We collected them in Brooks River; Bay of Islands, Headwater, Hidden, and West Creeks; Brooks Lake; and South Bay and North Arm of Naknek Lake. Fish in the lakes were usually taken near one of the streams. Although their distribution was spotty, grayling were seasonally abundant in certain streams, particularly Brooks River. One grayling was seined from the morainal cut between Iliuk Arm and South Bay in 1962, about 4.8 km. from the mouth of Brooks River. Grayling spawn in Brooks River in May and early June; we collected fry (19-22 mm. long) from the river on July 11, 1963. Sport fishing for grayling is common in Brooks River (see footnote 4).

Osmeridae

Pond smelt, Hypomesus olidus (Pallas).--Pond smelt were collected in Coville and Grosvenor Lakes; North Arm, South Bay, and Iliuk Arm of Naknek Lake; and Coville River. Although we did not find them in Brooks Lake, we collected them in West Creek and Brooks River just below the outlet of Brooks Lake, so they probably live in the lake. Pond smelt are apparently more widely distributed and more abundant in Coville Lake than in other parts of the Naknek system.

Umbridae

Alaska blackfish, Dallia pectoralis Bean.--Blackfish were collected in Coville, Grosvenor, and Brooks Lakes; Bay of Islands and Northwest Arm of Naknek Lake; and West Creek and the ponds at the head of West Creek. Blackfish usually inhabit shallow tundra lakes and ponds (Walters, 1955) or sluggish marshes along streams (Blackett, 1962). Normally they are not considered to inhabit large lakes or deep water. In Brooks Lake, where they apparently are more abundant than anywhere else in the Naknek system, blackfish are commonly caught in water 15 to 20 m. deep; at this depth they are still within the range of submerged vegetation, particularly Chara and Nitella. A trap net set 8 m. deep on the bottom of Brooks Lake near the outlet from July 5 to September 9, 1963, took 583 blackfish. In general, the occurrence and distribution of blackfish in large lakes of the Naknek system seem to be associated with submerged aquatic vegetation.

Esocidae

Northern pike, Esox lucius Linnaeus.--Northern pike were prominent in many small lakes and ponds in the Naknek portion of the monument. They also live in the large lakes and streams but usually in areas of relatively shallow, quiet water with aquatic vegetation. Four such areas were Northwest Arm and Bay of Islands in Naknek Lake, the Grosvenor River Lagoon just below the outlet of Grosvenor Lake, and backwater lagoons along lower American Creek. Northern pike were also collected in Iliuk Arm, South Bay, and North Arm of Naknek Lake; Coville, Grosvenor, and Brooks Lakes; Coville, Grosvenor, and Brooks Rivers; and West and Hidden Creeks. Smaller lakes known to have pike populations include beaver ponds at the head of Hidden Creek, a series of lakes and beaver ponds at the head of West Creek (Greenbank [see footnote 4] referred to the larger of these as "Pike" Lake), Jo-Jo Lake, and a lake in the Savonoski Valley about 3 km. east of the Ukak River that Greenbank called "Murial" Lake. We did not sample Murial Lake, but Greenbank did.

Although northern pike now occur only rarely in the Brooks River area, they may have been abundant there in recent historical times. University of Oregon archaeologists have collected considerable quantities of fish remains in aboriginal occupation sites near Brooks River Falls. Considerable numbers of pike scales were found in the remains, most of which were from adult salmon. Radiocarbon dates and stratigraphic series of volcanic ash deposits indicate that most of these fish remains were deposited from A.D. 1500 to 1800.[16] Several swamp and marsh areas along the lower 400 m. of Brooks River now have water in them only for a brief period in late summer and early fall when the water level at Naknek Lake is highest. A few centuries ago when the mean water levels of Naknek Lake were high, the pike habitat in the present marshes and swamps was probably more stable. Under such conditions pike were probably abundant in the area.

Catostomidae

Longnose sucker, Catostomus catostomus (Forster).--Longnose suckers were collected in Coville and Grosvenor Lakes; Iliuk Arm, South Bay, and North Arm of Naknek Lake; American Creek; and Coville, Grosvenor,

[15] We received an unconfirmed report from sport fishermen in 1966 that they had caught grayling in Contact Creek in the headwaters of the King Salmon River system. Grayling are known to be common in the Ugashik River system farther out on the Alaska Peninsula (fig. 1), so it is likely they also live in the King Salmon River system.

[16] Cressman, L. S., and D. E. Dumond. 1962. Research on Northwest prehistory, prehistory in the Naknek drainage, southwestern Alaska. Univ. Oreg., Eugene, Dep. Anthropol., 54 pp.

Brooks, and Ukak Rivers. We did not collect them in Brooks Lake but found them in the lower portion of Brooks River below the falls. In the summer, many suckers occupy lagoon areas in lower Brooks River and in Coville and Grosvenor Rivers, apparently to feed. We presume that they spawn in early spring, because ripe females were collected just off the mouth of Brooks River in May and early June. Postlarval fry were taken in the Coville River Lagoon in July.

Gadidae

Burbot, Lota lota (Linnaeus).--Adult burbot were collected from Iliuk Arm, South Bay, North Arm, and Bay of Islands of Naknek Lake. One larval fish believed to be a burbot was taken in a plankton tow in Coville Lake, although no adults were taken in Coville or Grosvenor Lakes. No burbot was collected in Brooks Lake. Although no detailed data or specimens are available, there is a report[17] of dead burbot on the upstream face of Brooks weir in the late 1940's. By far the most extensive fish collecting in any area of Katmai National Monument during the past 10 years has been in Brooks Lake, and we doubt that burbot now live in this lake.

Gasterosteidae

Threespine stickleback, Gasterosteus aculeatus Linnaeus.--Threespine sticklebacks were collected in the Naknek and Shelikof Strait systems. Within the Naknek system they were collected from Coville, Grosvenor, and Brooks Lakes; all basins of Naknek Lake; Coville, Grosvenor, and Brooks Rivers; Headwater, Hidden, West, Margot, and unnamed creeks draining into North Arm; and Grosvenor and lower Naknek Lakes. Large numbers of threespine sticklebacks move from Grosvenor Lake and South Bay into lagoon areas in Coville and Brooks Rivers in early summer to spawn. We saw thousands of fry in these lagoons in late summer. The greatest concentrations of threespine sticklebacks in the Naknek system apparently are in the west end of Naknek Lake and in Northwest Arm (see footnote 8).

In Shelikof Strait drainages, we collected threespine sticklebacks in Katmai River, lower Kaflia Bay Lake, and Big River. Adults and fry were collected in July or August; apparently all of the populations were anadromous because the extent of lateral plate development on the adults suggested that they were from estuarine or marine environments (see Clemens and Wilby, 1961, p. 353). The fish were collected in fresh water, except for lower Kaflia Bay Lake, which is slightly brackish. The fresh-water areas were only a short and readily accessible distance from salt water.

Lateral plates on adult threespine sticklebacks from Shelikof Strait drainages were strongly developed, whereas those on Naknek system specimens were weakly developed or absent.

Ninespine stickleback, Pungitius pungitius (Linnaeus).--Ninespine sticklebacks were collected in the Naknek, King Salmon, and Shelikof Strait systems. They live throughout the Naknek system in the same lake and stream areas as threespine sticklebacks, except for Hardscrabble Creek and Savonoski River, where only ninespine sticklebacks were collected. In the large lakes, the ninespine stickleback seems to be more of a benthic fish than its relative, although both species occur in almost all lake habitats. One notable difference in the distribution of the two species of sticklebacks in the Naknek portion of the monument is that only ninespine sticklebacks live in many of the shallow bog lakes, tundra ponds, and beaver ponds. Examples of this distribution include the lakes and beaver ponds above West Creek, beaver ponds at the head of Hidden Creek, and Nystrom Lake--a small shallow lake near the mouth of Brooks River. Bond and Becker[18] also noted this peculiarity in the Iliamna Lake area. Robert and Alice Dewey, resident biologists at the BCF Brooks Lake Laboratory, found that ninespine sticklebacks were more tolerant to warmer aquarium water than threespine sticklebacks. Perhaps high summer temperatures in shallow ponds prevent establishment of stable populations of threespine sticklebacks. In the King Salmon River system, ninespine sticklebacks were collected in a slough of Takayoto Creek and in lower Cozy Lake, where they were very abundant. Only two specimens were collected from the Shelikof Strait area of the monument; these were both taken in Big River about 4.8 km. above salt water.

Cottidae

Coastrange sculpin, Cottus aleuticus Gilbert.--Coastrange sculpins were collected in the Naknek, King Salmon, and Shelikof Strait systems. In the Naknek system they were collected in Coville and Brooks Lakes; South Bay of Naknek Lake; Grosvenor, Brooks, and Ukak Rivers; Hidden, One Shot, and West Creeks; and unnamed creeks in Grosvenor and Naknek Lakes. In the King Salmon system they were

[17] George J. Eicher, Portland General Electric Company, in conversation with W. L. Hartman at Brooks Lake, June 1965.

[18] Bond, C. E., and C. D. Becker. 1963. Key to the fishes of the Kvichak River system. Univ. Wash., Seattle, Fish. Res. Inst., Circ. 189, 9 pp.

collected in lower Cozy Lake. In the Shelikof Strait systems they were collected in Big River, in a tributary of Dakavak Lake, and in outlet streams of lower Kaflia Bay and Devils Cove Lakes.

Slimy sculpin, Cottus cognatus Richardson.--Slimy sculpins were collected in the Naknek and King Salmon systems. In the Naknek system, they were taken in Coville, Grosvenor, Brooks, and Idavain Lakes; all basins of Naknek Lake; Coville, Grosvenor, Brooks, Savonoski, and Ukak Rivers; and American, Margot, Headwater, Hidden, One Shot, and West Creeks. This sculpin also occurs in Hammersly Lake. In the King Salmon system, slimy sculpins were collected in Takayoto Creek.

Both species of cottids in the monument spawn in the spring, although their spawning sites and behavior have not been observed. Although the two species occur sympatrically in streams and lakes of the Naknek system, collections from Brooks Lake and its tributaries suggest the coastrange sculpin is usually the dominant stream form and the slimy sculpin is usually prevalent in lakes. Slimy sculpin was the only cottid collected from depths greater than 30 m. in any lake.

EURYHALINE FORMS

At least four marine fishes occur in freshwater portions of streams that lie within the monument or flow from the monument. We collected specims of three of the species between 1962 and 1964, and Greenbank (see footnote 4) reported the fourth. These fishes were collected upstream from the upper zones of tidal influence, and although no corroborative salinity data are available for any of the collections, the species are all listed as euryhaline forms by Gunter (1956).

Osmeridae

Arctic smelt, Osmerus dentex Steindachner.--Arctic smelt move into Naknek River from Bristol Bay in late winter and early spring on their spawning migrations. They were collected as far upstream as the Naknek Rapids, a fast-water section of Naknek River about midway between the outlet of Naknek Lake and the town of King Salmon. Some of these smelt may move into Naknek Lake near the outlet of the river.

Gadidae

Pacific cod, Gadus macrocephalus Tilesius.--Greenbank (see footnote 4) reported that a Pacific cod was taken by an angler in Naknek River just below the outlet of Naknek Lake. He speculated that cod might occasionally stray into the lake. According to Gunter (1956) Greenbank's account was the first euryhaline record of this species.

Cottidae

Pacific staghorn sculpin, Leptocottus armatus Girard.--We collected 10 staghorn sculpins (14-65 mm. total length) from Katmai River 3.2 km. above the stream mouth on August 21, 1964.

Pleuronectidae

Starry flounder, Platichthys stellatus (Pallas).--Several starry flounders have been taken in Naknek River as far upstream as Naknek Rapids, and C. J. DiCostanzo[19] reported that he has observed this fish in Naknek River at the outlet of Naknek Lake. We collected eight small starry flounders (34-44 mm. total length) from a shallow riffle area of Katmai River about 3.2 km. above the stream mouth on August 21, 1964.

ZOOGEOGRAPHICAL IMPLICATIONS

Additional collecting will undoubtedly reveal new locality records, but sufficient data are now available to define the basic distribution of fish in the principal drainages of Katmai National Monument. Striking differences occur in these drainages, and the mountains of the Aleutian Range (fig. 2) appear to have been an effective barrier to the southward dispersal of many fishes now in the Bristol Bay drainages.

All fishes along the Shelikof Strait side of the monument--salmon, char, sticklebacks, and sculpins--are from groups known to have high tolerance to salinity and to be capable of marine dispersal. None of the principally fresh-water fishes north of the Aleutian Range--whitefishes, lake trout, grayling, blackfish, pike, suckers, and burbot--occur in the Shelikof Strait drainages (table 2).

The term "primary freshwater fishes" was used by Miller (1958) for families that have been restricted to fresh water throughout their known history. His classification applied to fishes in the monument would include only blackfish, pike, and suckers, although Walters (1955, p. 334) reported that the longnose sucker "readily enters coastal waters" in the Arctic. Other cold-water fishes such as whitefishes, lake trout, grayling, and burbot that are normally confined to fresh-water streams and lakes in the southern parts of their ranges do invade coastal waters in the Arctic (Walters, 1955). We have no evidence that any of

[19]Chief, Salmon Investigations, Bureau of Commercial Fisheries Biological Laboratory, Box 155, Auke Bay, Alaska 99821. Personal communication, 1964.

Table 2.--Fishes collected in principal drainages of Katmai National Monument

Common name	Scientific name	Bristol Bay drainages		
		Naknek River system	King Salmon River system	Shelikof Strait drainages
Arctic lamprey	Lampetra japonica	x		
Humpback whitefish	Coregonus pidschian	x		
Least cisco	C. sardinella	x	x	
Pink salmon	Oncorhynchus gorbuscha	x		x
Chum salmon	O. keta	x		[1]/ x
Coho salmon	O. kisutch	x	x	x
Sockeye salmon	O. nerka	x	x	x
Chinook salmon	O. tshawytscha	x	x	
Pygmy whitefish	Prosopium coulteri	x		
Round whitefish	P. cylindraceum	x	x	
Rainbow trout	Salmo gairdnerii	x		
Arctic char	Salvelinus alpinus	x		
Dolly Varden	S. malma	x		x
Lake trout	S. namaycush	x		
Arctic grayling	Thymallus arcticus	x		
Pond smelt	Hypomesus olidus	x		
Alaska blackfish	Dallia pectoralis	x		
Northern pike	Esox lucius	x		
Longnose sucker	Catostomus catostomus	x		
Burbot	Lota lota	x		
Threespine stickleback	Gasterosteus aculeatus	x		x
Ninespine stickleback	Pungitius pungitius	x	x	x
Coastrange sculpin	Cottus aleuticus	x	x	x
Slimy sculpin	C. cognatus	x	x	

[1] Not personally verified by us (see footnote 5).

these fishes now live in brackish waters in the vicinity of Katmai National Monument, and assume their dispersal in southwest Alaska was essentially by fresh-water pathways or via bridges of low salinity during early postglacial stages.

The presence of pygmy whitefish (Kendall, 1917), pond smelt (Narver, 1966), and blackfish (Roos, 1959) in the Chignik River system supports the concept of the Aleutian Range barrier. This system is about 274 km. southwest of the monument at a point on the Alaska Peninsula where the mountains become discontinuous. It drains into the Pacific Ocean southwest of Shelikof Strait, but the headwaters are flat, low in elevation, and only slightly separated from other streams that flow northwest into Bristol Bay. Headwater stream transfer, which in the Chignik system would amount to a lowlands transfer, or flooding as discussed by Walters (1955, pp. 329-330), could easily account for the occurrence of these fresh-water fishes in the system, illustrating that where the Aleutian Range breaks down the fishes from Bristol Bay drainages are dispersed southward.

That pygmy whitefish, pond smelt, and blackfish occur in the Chignik system and apparently in no other drainages flowing into the Pacific Ocean side of the Alaska Peninsula illustrates that most Shelikof Strait drainages are isolated not only from fresh-water areas north of the Aleutian Range but also from each other. Adjacent drainages along Shelikof Strait, particularly in much of the monument, flow parallel to each other but are separated and isolated by buttress ranges and deep fiords. It seems unlikely that species incapable of tolerating high salinity would be dispersed along the Shelikof Strait coastline.

Similarities in the ichthyofauna of Shelikof Strait drainages and nearby Kodiak Island emphasize the isolation of these areas from continental sources of fresh-water fishes. The only fishes reported from Karluk or Bare Lakes on Kodiak Island (Greenbank and Nelson, 1959) that were not found in fresh waters along Shelikof Strait of the monument were chinook salmon, Arctic char, and rainbow trout. Each of these species could occur in Shelikof Strait drainages because they commonly live in the sea during part of their life cycle.

The scarcity of species in the King Salmon River system portion of the monument may be related to the limited diversity of habitat in the headwaters. Although we collected only eight species in this system, zoogeographically it has the same potential for fresh-water fishes as the Naknek system because it lies north of the Aleutian Range barrier and adjacent to the Naknek system. The collections in the King Salmon River system were admittedly small, but this system probably does not have all of the fishes that occur in the Naknek system because it is a stream environment without the ecological diversity of a multilake-stream complex.

The Naknek River system has by far the most diverse ecological habitats of the drainages in Katmai National Monument. This interconnecting stream-lake complex has also been open to invasion by fresh-water fishes from the Bering Refugeum (see McPhail, 1963, and Flint, 1945) without significant barriers since early postglacial times. It has the largest number of fishes (24 species) of the major drainages in the monument, and includes all species found in the other drainages (table 2).

We believe that open avenues of fresh-water dispersal account for the principal differences in fishes in the Naknek system and Shelikof Strait drainages. Although no single Shelikof Strait drainage approaches the ecological diversity of habitats in the Naknek system, they afford a variety of stream and lake environments. These environments along the Shelikof Strait side of Katmai National Monument suggest that many (though probably not all) fishes in the Naknek system could survive in various parts of the Shelikof Strait systems if given access to them. Differences between fishes in the Naknek and King Salmon River systems, on the other hand, appear mostly related to the lack of a diverse habitat in the King Salmon River system. This lack is particularly noteworthy in that portion of the King Salmon River system that lies within the monument. Additional collections in the King Salmon River downstream from the monument should help clarify this point.

The number of species in various lakes of the Naknek system differed considerably. All 24 known species in the Naknek system occur in Naknek Lake (table 3). Naknek Lake as the downstream terminus of the multilake system is the first area to be invaded by fish through existing drainage patterns. All upstream lakes that drain directly or indirectly into Naknek Lake have fewer species than Naknek Lake, and in each upstream lake a barrier or potentially adverse environment now exists between it and Naknek Lake.

The heterogeneity of species in different lakes of the Naknek system appears to be related to the development of barriers and the sequential timing of the invasion of species into the system. Physical barriers such as falls or rapids or ecological barriers such as unfavorable environments may have prevented dispersal of certain species within the system. Development of barriers before the invasion of species would prevent dispersal beyond the barriers, whereas earlier invasion before barriers formed could allow more extensive dispersal.

The Naknek system has been extensively glaciated. Muller (1952) discussed at least four major glacial episodes in the system,

Table 3.--Occurrence of fishes in the major lakes and basin complexes in the Naknek River system of southwest Alaska

[Surface elevations in meters above sea level for each basin are in parentheses]

Fishes present	Naknek Lake (10 m.)	Brooks Lake (19 m.)	Coville-Grosvenor Lake (32 m.)	Idavain Lake (232 m.)	Hammersly-Murray Lake (488 m.)
Arctic lamprey	x	x	x		
Humpback whitefish	x		x		
Least cisco	x		x		
Pink salmon	x	x	x		
Chum salmon	x	x	x		
Coho salmon	x	x	x		
Sockeye salmon	x	x	x		x
Chinook salmon	x	x	x		
Pygmy whitefish	x	x	x		x
Round whitefish	x	x	x		
Rainbow trout	x	x	x		x
Arctic char	x	x	x	x	x
Dolly Varden	x	x	x		
Lake trout	x	x	x		x
Arctic grayling	x	x			
Pond smelt	x	x	x		
Alaska blackfish	x	x	x		
Northern pike	x	x	x		
Longnose sucker	x		x		
Burbot	x		x(?)		
Threespine stickleback	x	x	x		
Ninespine stickleback	x	x	x		
Coastrange sculpin	x	x	x		
Slimy sculpin	x	x	x	x	x
Total known species	24	20	23	2	6

the earliest of which was probably pre-Wisconsin. The present lakes and basins in the Naknek system were formed by glacial activity during Wisconsin times, which Muller (1952) called the Brooks Lake glaciation. This glacial episode consisted of one main glacier--Naknek Glacier--which occupied all the present basins of Naknek Lake and had prominent tongues projecting through the present Coville-Grosvenor and Brooks Lake basins. The last major glaciation in the Naknek system probably ended about 8,000 B.C.; a minor readvance into Iliuk Arm of Naknek Lake ended about 4,000 B.C. (Karlstrom, 1957).

Invasion of fish in the Naknek system probably began with the initial glacial recession and the first development of postglacial drainage systems. At various times the entire system, including Naknek River, was covered with ice, so the fresh-water fishes invading the system would have come directly or indirectly from the Bering Refugeum. Anadromous and salinity-tolerant forms could have come from the Bering Sea or Pacific Ocean.

Although Brooks Lake drains directly into Naknek Lake, four species in Naknek Lake--humpback whitefish, least cisco, longnose sucker, and burbot--apparently do not occur in Brooks Lake. These fishes probably were barred from Brooks Lake by a 1.5- to 2-m. falls that developed on Brooks River. These species may have been late invaders of the Naknek system. During certain phases of the postglacial development of the system, Brooks and Naknek Lakes were one lake, but continued downcutting of end moraines on Naknek Lake subsequently lowered the lake level, separated Brooks and Naknek Lakes, and developed Brooks River. The time of sufficient separation of the two lakes to allow the formation of Brooks Falls has been suggested at 2,000 B.C.[20] Many species now in Brooks Lake, such as pygmy whitefish, pond smelt, blackfish, sticklebacks, and sculpins, probably could not surmount Brooks Falls as it now exists;

[20] D. E. Dumond, Department of Anthropology, University of Oregon, Eugene, Oregon. Personal communication, 1965.

these species probably were present when Brooks and Naknek Lakes were continuous.

Only one species in Naknek Lake, Arctic grayling, does not occur in the Coville-Grosvenor Lakes complex (table 3). Three anadromous fishes, pink, chum, and chinook salmon, occur only rarely in this area. The absence of grayling in these lakes is puzzling because no major physical barriers exist between Grosvenor and Naknek Lakes, and the Grosvenor River and lower American Creek appear to be excellent grayling habitat. If grayling are a relatively late arrival and still in the process of dispersal in the system, cautious speculation suggests that their dispersal may be limited by the extreme turbidity of Iliuk Arm and Savonoski River. The general distribution and abundance of grayling in the system are limited, and no large numbers of this species are available to probe routinely through adverse environments. Other more complex environmental factors may be limiting grayling distribution in the system.

We know of only two fishes, Arctic char and slimy sculpin, that inhabit Idavain Lake, which drains into Naknek Lake through the 26-km.-long Bay of Islands Creek. Two series of falls, about 4.8 and 16.1 km. below the lake, have probably prevented access to the lake by other fishes since an early stage of glacial recession. Arctic char and slimy sculpin are the only species common to all of the major basin complexes (table 3) and were probably among the earliest fishes to invade the Naknek system.

Hammersly and Murray Lakes, the highest lakes in the Naknek River system (about 488 m.) have only six species (table 3). These lakes drain into Coville Lake through 87-km.-long American Creek. This creek has no complete barriers, and anadromous sockeye salmon annually spawn at the outlet of Hammersly Lake. A series of precipitous rapids in American Creek, however, probably forms an effective barrier to many species in Coville Lake and lower American Creek that do not occur in Hammersly and Murray Lakes.

Hammersly and Murray Lakes and upper American Creek at one time may have drained north into the present Alagnak River system (fig. 1). The Coville-Grosvenor tongue of the main Naknek Glacier pushed north almost to the Alagnak River (Keller and Reiser, 1959, plate 29) and coalesced with ice from the basin of Nonvianuk Lake (Muller, 1952, p. 62). Drainage diversions associated with the retreat of glaciers in this area may have caused the headwaters of what is now American Creek to flow north into the Alagnak River. Certain physiographic features of the area suggest this possibility (see footnote 19). If this diversion did occur some of the fishes now in Hammersly and Murray Lakes could have invaded the lake via the Alagnak River system rather than the Naknek River system.

SUMMARY

1. Katmai National Monument is divided by the Aleutian Mountain Range into two principal drainage areas: (1) streams flowing into Bristol Bay of the Bering Sea (dominated by the multilake Naknek River system) and (2) streams flowing into Shelikof Strait of the North Pacific Ocean (characterized by many short streams and rivers and a few small lakes).

2. Twenty-four species of fresh-water fishes, many of which are or can be anadromous, occur in the monument. All 24 species occur in the Naknek system, at least eight of them occur in the King Salmon River system, and at least eight of them occur collectively in the 18 to 20 systems draining into Shelikof Strait.

3. Four marine fishes, all known euryhaline forms, occur in fresh water in or near the monument.

4. The Aleutian Range has been a barrier to the southeastward movement of fresh-water fishes within the monument area. All species in Shelikof Strait drainages are capable of dispersal through salt water, whereas many forms in Bristol Bay drainages require fresh water for dispersal.

5. Dolly Varden occur, apparently through natural dispersion, in the crater lake in the caldera of Kaguyak Volcano.

6. The last major glaciation of the Naknek system ended about 10,000 years ago. Sequential timing of species invasion and the postglacial development of barriers have strongly influenced the present distribution of fishes in this system. All upstream lakes in the Naknek system have fewer species than the lakes below them, and barriers exist between each upstream and downstream lake.

7. Arctic char and slimy sculpin, the only species common to all basin complexes of the Naknek system, were apparently early invaders. Lake trout, pygmy whitefish, rainbow trout, and sockeye salmon are present in all basins except Idavain Lake.

8. Least cisco, humpback whitefish, and longnose suckers could have been late invaders of the Naknek system because these fish apparently are restricted from Brooks Lake by a falls on Brooks River. Sufficient separation of Brooks and Naknek Lakes to allow the development of Brooks Falls is estimated to have occurred around 4,000 years ago.

9. Hammersly and Murray Lakes, although not in the monument, are important in the distribution of fishes in the Naknek system. These lakes and the upper portion of American Creek may have drained north into the Alagnak River system during early postglacial drainage development.

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