

By

Alaska Dept. of Fish & Game, Habitat Inv.

for

U.S. FISH AND WILDLIFE SERVICE

- | | |
|--------------------|----------------------|
| 1. Chum salmon | 5. Arctic grayling |
| 2. Pink salmon | 6. Dolly Varden char |
| 3. Broad whitefish | 7. Threespine |
| 4. Round whitefish | stickleback |

1981



United States Department of the Interior

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FISH AND WILDLIFE SERVICE

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IN REPLY REFER TO:

To: Government agencies, private organizations and individuals interested in Alaskan fish/habitat relationships

Descriptions of freshwater fish habitat relationships for the following Alaskan species are enclosed:

1. Chum salmon (Oncorhynchus keta)
2. Pink salmon (Oncorhynchus gorbuscha)
3. Broad whitefish (Coregonus nasus)
4. Round whitefish (Prosopium cylindraceum)
5. Arctic grayling (Thymallus arcticus)
6. Dolly Varden char (Salvelinus malma (Walbaum))
7. Threespine stickleback (Gasterosteus aculeatus)

These descriptions were prepared by the Habitat Division of the Alaska Department of Fish and Game under contract to the U.S. Fish and Wildlife Service (FWS). Habitat descriptions for coho salmon and rainbow trout are currently being developed by the FWS.

We hope these descriptions will be a useful reference in your Alaskan natural resource work. If you know others who could use this information, please contact:

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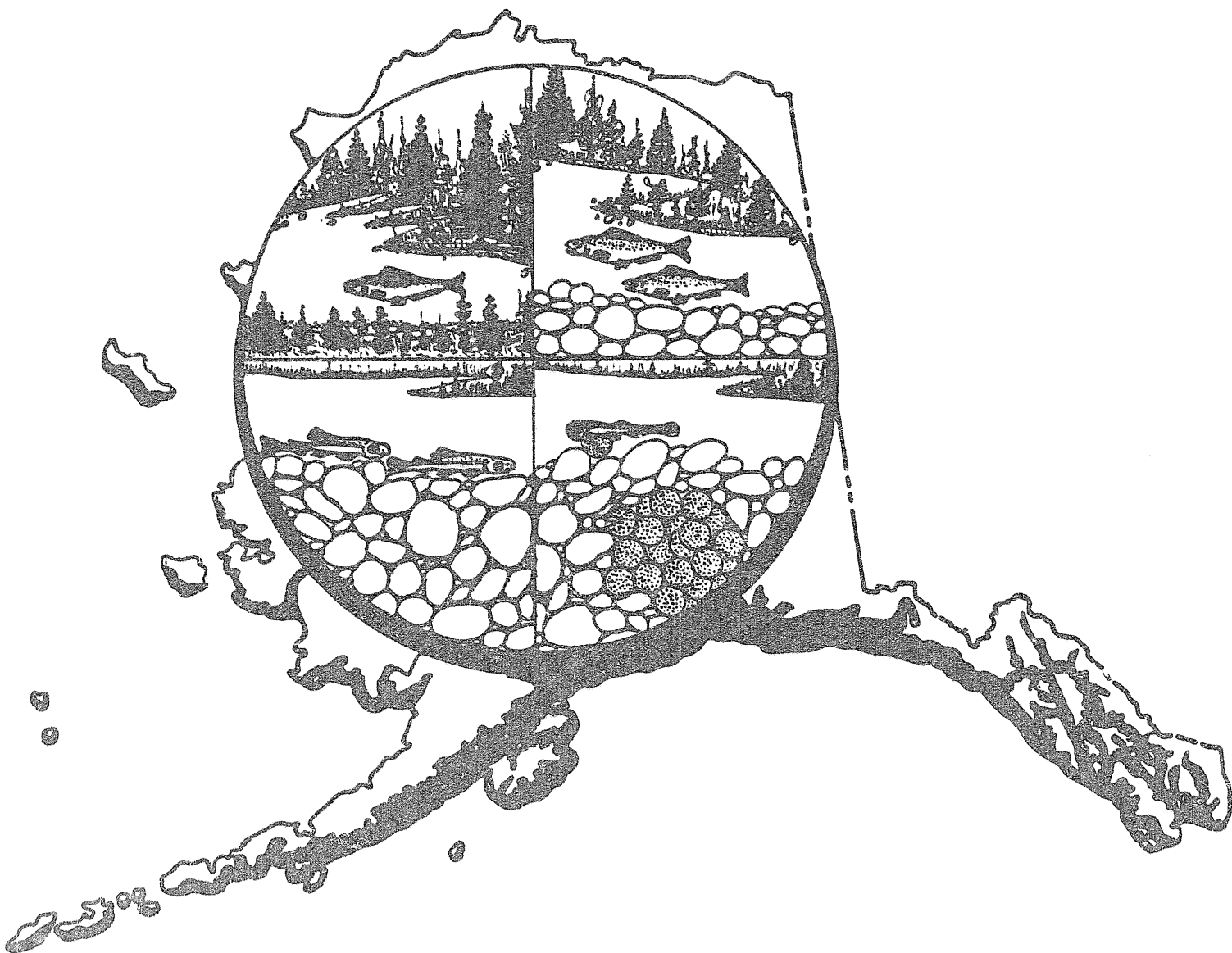
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FRESHWATER HABITAT RELATIONSHIPS

CHUM SALMON - ONCORHYNCHUS KETA



ALASKA DEPARTMENT OF FISH & GAME
HABITAT PROTECTION SECTION
RESOURCE ASSESSMENT BRANCH

APRIL, 1981

FRESHWATER HABITAT RELATIONSHIPS
CHUM SALMON (ONCORHYNCHUS KETA)

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I. INTRODUCTION

A. Purpose

The purpose of this report is to present available information about the freshwater habitat tolerances, preferences, and requirements of the chum salmon, Oncorhynchus keta (Walbaum), and to evaluate habitat which parameters are most important to the species or are most often critical to survival or limiting to production. This information is intended to provide a data base for habitat evaluation activities. In particular, Section III, which attempts to relate various levels of certain environmental parameters to habitat suitability, is intended to be used with the Habitat Evaluation Procedures and instream flow methods of the U.S. Fish and Wildlife Service. These procedures and methods are tools for assessing the effect of land use development projects on aquatic habitat.

Bakkala (1970) has presented a comprehensive summary of biological data on the chum salmon. The present report is restricted to habitat data and to the freshwater stage of the life history and expands upon the relationship between the chum salmon and habitat parameters. It also considers recent information and emphasizes data from Alaska, particularly unpublished data and personal communications from fishery biologists who have worked with chums in the State. Habitat parameters emphasized are those of a physical or chemical nature. Certain biological factors affecting the well being of the population such as feeding, predation, competition, parasites, and disease are not comprehensively treated.

Although information has been examined from throughout the range of the species, emphasis is placed upon Alaska because it is expected that this is where habitat evaluations using this report will be made. Populations from different geographic areas

undoubtedly have habitat needs which differ to some extent; however, data to document such differences are available only in rare instances. Caution must be used when extending information from one stock to other stocks. Research in Siberia has shown differences in habitat preferences between summer chum and fall chum.

Habitat requirements described in this report are for chum salmon; however, it occasionally was considered useful to include data for other species of Pacific salmon where such information was lacking for chums. In these cases, the other species are always mentioned by name or referred to by the phrase "Pacific salmon" if the information is of a general nature. Any reference to salmon without naming a particular species or using the phrase "Pacific salmon" always refers specifically to chum salmon. Reviews of factors constituting the freshwater habitat of Pacific salmon have been done by Macy (1954), Nicola et al. (1966), and Reiser and Bjornn (1979).

Chum salmon, also commonly called dog salmon in Alaska, are anadromous as are other North American species of Pacific salmon, but the time spent in freshwater is primarily for reproduction. Chums migrate to the ocean in their first spring or summer of life and spend little time, if any, rearing in freshwater as do king, sockeye, and coho salmon. Most of the chum salmon's life is spent at sea.

Four periods in the freshwater life history can be distinguished: upstream migration of adults, spawning, intragravel period of eggs and alevins, and downstream migration of fry. The period from egg deposition to emergence from the gravel is usually the stage of highest mortality and is probably the stage where habitat requirements are most critical.

This report presents a general summary of the life history and then, in Section II, gives a detailed discussion of habitat needs for each life stage in the freshwater environment. Section III attempts to synthesize the relationship between various environmental parameters and habitat quality.

Aquatic habitat and chum salmon relationships presented in this paper are very general. They are not appropriate for applications to specific watersheds.

B. Distribution

Chum salmon have the widest distribution of any of the Pacific salmon, occurring in the northern North Pacific Ocean, the Bering Sea, the Chukchi Sea, and along the Arctic Ocean coasts of Siberia, Alaska and northwest Canada. Spawning has been documented in streams and rivers in North America from the Sacramento River in California to the Mackenzie and Anderson Rivers on the Arctic coast of Canada (Hart, 1973) and, in Asia, from the Nakdong River in Korea and the Tone River in Japan to the Lena River in Siberia (Bakkala, 1970). More chum salmon are apparently produced on the Asian side of the Pacific than on the North American side (Merrell, 1970). Spawning has been recorded in at least 1,270 streams in the United States (Atkinson et al., 1967). Chums occur only in small numbers on the North American coast south of central Oregon or north of Kotzebue Sound in Alaska (Helle, 1979).

Chum salmon generally occur throughout Alaska except for certain streams in the Copper River drainage and in the eastern Brooks Range (Alaska Department of Fish and Game, 1978; Atkinson et al., 1967; Merrell, 1970; Morrow, 1980). Chums are abundant in Southeast Alaska, especially in the northern part of the area. There are both summer runs, primarily in northern Southeast, and fall runs mainly in southern Southeast. Chums are abundant in

Prince William Sound, where there are early runs which enter the Sound in late April to early July and spawn in non-lake-fed streams of the mainland, middle runs which enter the Sound in mid to late July and spawn in lake-fed streams of the mainland and in streams of the outer islands, and late runs which enter the Sound in late July, enter freshwater in August and early September and spawn almost exclusively in spring-fed creeks of the mainland. Cook Inlet chums enter freshwater between early July and mid-September. Chums in the southern part of Cook Inlet spawn in coastal streams, while those of the northern part utilize the large river systems. They are uncommon on the east side. Chums are abundant in streams of Kodiak Island. They are present in bays and estuaries of the island from mid June to early September and in freshwater from mid August to early October. Chums are also abundant in the south Alaska Peninsula area where they enter streams from mid July to mid September. Little is known about the distribution of spawning chums in the Aleutian Islands. The Nushagak and Togiak areas are the main chum salmon producers in the Bristol Bay drainage. Chums enter streams of Bristol Bay from mid June to mid August and spawn mostly in the lower portion of the larger clearwater tributaries of the main river systems. Chum salmon are the most abundant salmon species in the Kuskokwim Bay and River area. There are sixteen or more major spawning streams in the Kuskokwim River system. Chums are also the most abundant salmon in the Yukon River drainage. The Yukon River drainage is the greatest single river system producer of chums in the state. There are distinct runs of summer chums and fall chums in the Yukon River. The summer chums enter the mouth of the river from late May through mid July and spawn in tributaries of the lower and middle portion of the river. The Anvik River is one of the major producers of summer chums. Fall chums enter the river from mid July through early September and spawn primarily in the tributaries of the upper river. In the Norton Sound and Kotzebue Sound areas, chums are again the most abundant salmon. Norton Sound chums arrive in bays and estuaries from June to late

July. Kotzebue Sound has two major run components in July and August. Most of the Kobuk River chums arrive in the Sound and migrate up river before the Noatak River chums. The Noatak River is the major chum producer in the area. Although chum salmon occur in streams along the entire Alaskan coast to the Canadian border and beyond, there are relatively few north of the Kotzebue Sound drainage and numbers along the Arctic coast are very limited. This area is the most northern part of the chum salmon's distribution in North America (Alaska Department of Fish and Game, 1978). Figure 1 shows the distribution of chum salmon in Alaska and indicates some of the major study sites where data mentioned in this report was collected.

C. Life History Summary

Most of this section has been summarized from Bakkala (1970).

In the summer and fall, adult chum salmon leave marine waters and begin the upstream migration to spawning areas. Spawning migrations vary in length from short distances in some coastal streams, where spawning may take place in the intertidal zone, up to as much as 3200 km in long rivers such as the Amur River in Siberia or the Yukon River (Bakkala, 1970; Morrow, 1980).

Many streams have more than one run of chums, including distinct runs of summer and fall chums.

Fall chums in the Yukon River average about 0.5 kg more than the summer chums, spawn farther upriver, and are more likely to spawn in springs or areas of ground water seepage. Similar differences exist between summer and fall chums in the Amur River of Siberia; the fall chums also have a greater fecundity (Sano, 1966). The spawning grounds of fall chums are different from those of summer chums in the Amur River in that the former tend to be shallower, have a narrower range of temperature variation, have a weaker

flow, have a lower dissolved oxygen content and a higher carbon dioxide content, and have a lower pH (Smirnov, 1947).

Adults do not feed on the upstream migration. The rate of migration in the Amur in Siberia has been found to be 56 to 115 km per day, and in shorter streams, 1.9 to 4.2 km per day (Bakkala, 1970). Lebida (1964) found that chums in the Yukon migrated from about 1 to 53 km per day with a mean rate around 20 to 30 km/day.

On the spawning grounds, the female excavates the redd in gravel by turning to one side and rapidly flexing the body, creating water currents with the caudal fin. After a depression is completed, the female and the dominant of several males in attendance enter and simultaneously extrude the eggs and milt. The female excavates another depression slightly upstream which serves to cover the fertilized eggs just deposited. The female may dig several nests and spawn with more than one male. After spawning, she may stay near the redd and protect the site from other spawners. Males often spawn with more than one female. Both sexes die within one to six days after spawning.

The eggs are deposited at depths of 8 to 43 cm below the surface of the gravel (Bakkala, 1970; Burner, 1951). Fecundity of chum salmon ranges from about 1,000 to 8,000 eggs with 2,000 to 3,000 being most common. In Asia, summer chum salmon are at the low end of this range and autumn chums are at the high end (Bakkala, 1970). The average fecundity of 36 females taken in the Noatak River was 3,365 (Bird, 1980). Noatak River chum salmon are considered to be an autumn race.

Chum salmon spawn from June to January, but the peak for northern populations occurs from July to early September and the peak for southern populations occurs in October or November.

MAIN STUDY SITES

- 1 NOATAK RIVER
- 2 CHENA RIVER
- 3 DELTA RIVER
- 4 TERROR/KIZHUYAK RIVERS
- 5 OLSEN CREEK
- 6 SASHIN CREEK
- 7 KASAAN BAY AREA

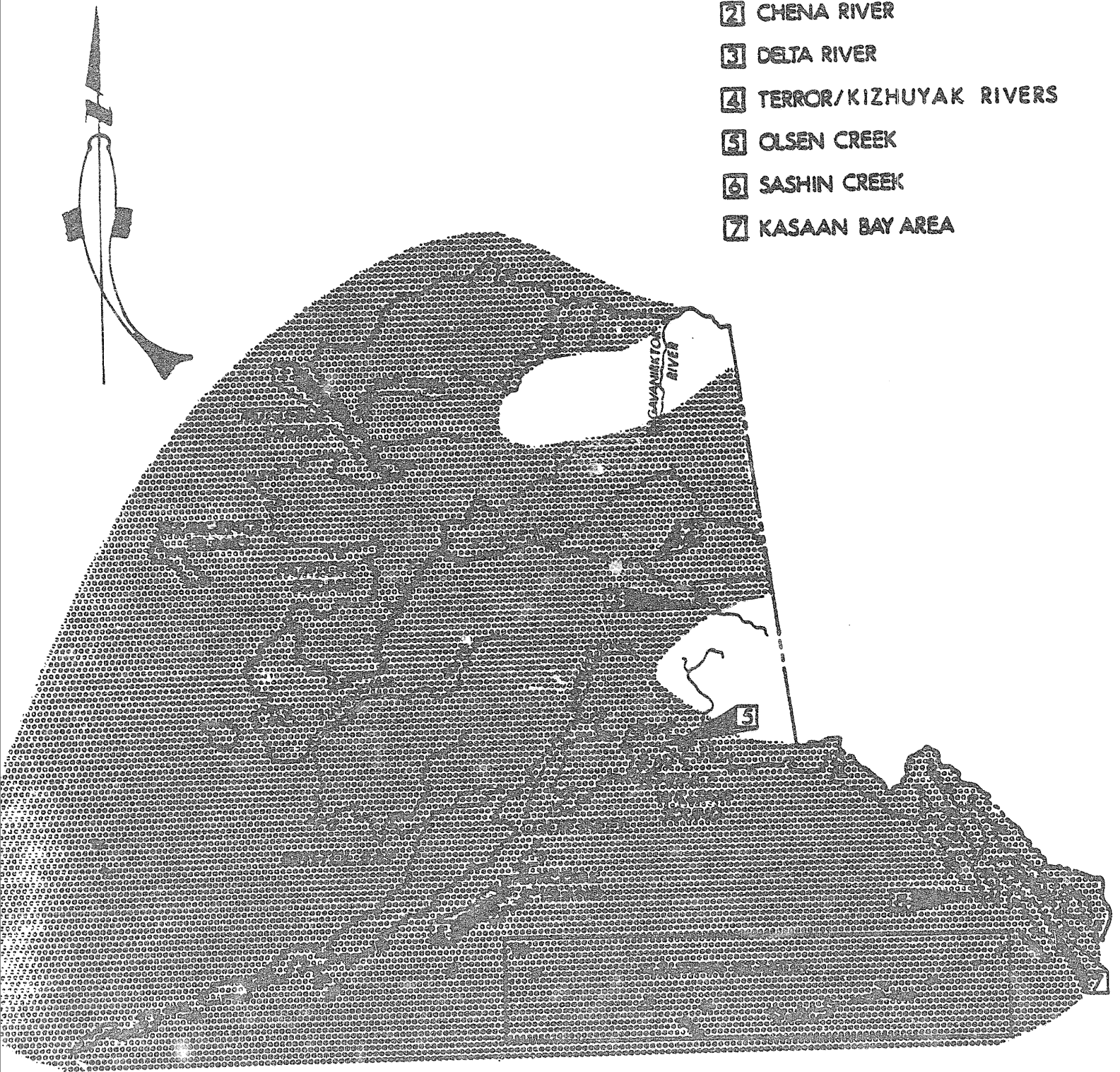


FIGURE 1. DISTRIBUTION OF CHUM SALMON IN ALASKA (FROM ALASKA DEPARTMENT OF FISH AND GAME, 1978) AND MAIN STUDY SITES.

The time spent in freshwater (time from entering the stream to time of expiration) for adult salmon in a stream in southeastern Alaska was 11 to 18 days (Mattson et al., 1964). The time spent in freshwater for other stocks such as those spawning hundreds of kilometers up the Yukon River could last up to two months. The actual redd life, or time spent at the spawning sites, in Traitors River was 5 to 9 days (Mattson and Rowland, 1963).

Chum salmon eggs incubate in the gravel 50 to 130 days. After hatching, the larvae with yolk sacs still attached are known as alevins. The alevins remain in the gravel until their yolk sacs are nearly or completely absorbed which takes about 30 to 50 days (Bakkala, 1970). The alevins are largely dependent on the yolk sac for nourishment although Disler (1953) has reported that preemergent alevins consume small amounts of benthic organisms such as diatoms and chironomid larvae. The alevins are about 22 mm long and weigh approximately 0.16 g at hatching; after absorption of the yolk sac, they are 27 to 32 mm long and weigh 0.20 to 0.23 g (Bakkala, 1970).

The period spent in the gravel by the eggs and alevins is a time of heavy mortality. The survival rate from eggs to fry in natural streams typically averages less than 10%.

The alevins emerge from the gravel in the spring (March, April, and May). Those that still have remnants of the yolk sac absorb it shortly after emergence. The young chums are now commonly called fry. Most chum salmon fry begin their downstream migration to the ocean soon after emergence. Some may remain in freshwater for several weeks, especially those that are hundreds of kilometers from the ocean. The outmigration occurs mainly at night in April and May and is a combination of displacement and active swimming.

Most of the fry travel near the surface and in the center of the stream where the water currents are strongest (Hunter, 1959). Sano and Kobayashi (1953, cited by Bakkala, 1970) found that chum fry in a Japanese stream migrated from three to five kilometers per day. In large rivers, the fry travel by day as well as night, particularly if the river is turbid.

The bulk of the diet of fry in freshwater consists of benthic organisms, chiefly aquatic insects such as chironomid larvae, mayfly nymphs, stonefly nymphs, caddisfly larvae, and blackfly larvae (Bakkala, 1970). Occasionally, planktonic organisms are taken.

Predation is a major source of mortality to chum fry during the downstream migration period. Common predators in North American streams are cutthroat and rainbow trout, Dolly Varden, coho salmon smolts, squawfish, sculpins, and predaceous birds such as kingfishers, and mergansers.

Chum fry show an increasing preference for seawater with increasing age. Those that have completely absorbed their yolk sacs can tolerate direct entrance into full strength seawater.

When chum fry emerge from the gravel, they are about 30 to 32 mm long. At the time of entry into marine waters they range from about 30 to 60 mm in length and their weight ranges from 0.20 to 3.82 g. Chum fry entering an estuary in southeastern Alaska averaged 35 mm in length (Bakkala, 1970).

The fry form schools when entering the estuary if they have not done so before. Entry into salt water is usually complete by June. The young chum remain near shore until mid or late summer, feeding in estuarine areas and even moving back into freshwater areas with the tides to feed (Mason, 1974). The fry switch from benthic organisms, which were their main food source in

freshwater, to zooplankton including cladocerans, copepods, and barnacle nauplii and cyprids. By the middle of August, almost all juveniles have left the estuaries. By mid summer, the young chums are 100 to 150 mm long and by September, about 150 to 225 mm long.

After leaving coastal waters, the immature chums become widely distributed in the North Pacific Ocean and Bering Sea. By their second summer at sea, they are distributed from the Asian to American coasts with a southern limit of about 40° to 44° N and a northern limit in the Arctic Ocean (Bakkala, 1970). Chum salmon experience a high mortality, much of it due to predation, during their early ocean life. The main types of food taken by chums consist of polychaetes, pteropods, squid, crustacean larvae, copepods, amphipods, euphausiids, and fish (Bakkala, 1970). The average mean size of immature chums in marine waters in early summer ranges from a fork length of 34 cm and weight of 0.5 kg for age one fish to 55 cm and 1.9 kg for age five fish (Bakkala, 1970). Younger chums have a greater growth rate than older fish. The immature stage lasts from half a year up to five and a half years.

Bakkala (1970) considered the adult phase of chum salmon to begin on January 1 of the year in which the fish matures sexually and spawns. Therefore, this phase lasts from about six months for those adults spawning in June to about twelve months for those spawning in December.

Mature chum salmon range from age one to age seven. Most chums mature at age two or three in southern parts of the species range and at age three or four in northern parts (an age three fish is one that has spent three winters in the ocean, has three annuli, and is in its fourth year of life). Age six and seven fish are rare. Age three fish are usually the most common in southeast

Alaska. Age four fish predominate from Prince William Sound northward, with age three and age five being next in abundance. Adults range from 45 to 96 cm in fork length and from 0.8 to 13.4 kg in weight; the average size for mature fish is about 60 to 75 cm and 4.0 to 7.0 kg (Bakkala, 1970; Merrell, 1970; Morrow, 1980). The record fish cited by Bakkala was 108.8 cm and 20.8 kg. Age three fish are slightly smaller in northern parts of Alaska (55 to 62 cm) than in southern parts (67 to 71 cm) (Bakkala, 1970).

Maturing adults begin the migration back to the natal streams in the last few months of their lives. The majority of them have spent two to four years at sea. They leave the high seas feeding grounds during the period from May to November and enter coastal waters. Little time is spent in coastal waters before the upstream migration to the spawning grounds begins.

D. Economic Importance

The annual commercial harvest of chum salmon in Alaska in the years 1971 to 1976 ranged from 4.3 to 7.7 million fish, weighed from 32.1 to 64.8 million pounds, and had a monetary value to the fishermen ranging from 7.5 to 18.6 million dollars. In 1976, the first wholesale value of the statewide production of chum salmon was 35.1 million dollars (Alaska Department of Fish and Game, 1979a).

In 1980, 9.9 million chums were harvested commercially in Alaska. Most of these were taken in southeast Alaska, Kodiak Island, the Alaska Peninsula, Bristol Bay, the Kuskokwim River, and the Yukon River. The total statewide production was 65.3 million pounds (Alaska Department of Fish and Game, 1980b).

A further harvest of chum salmon produced in Alaskan streams occurs in the high seas fishery of the Bering Sea. The Japanese mothership fishery harvests two to four million fish annually. Significant numbers of these are believed to originate in western Alaska (Alaska Department of Fish and Game, 1979b).

The commercial salmon catch in Alaska north of Bristol Bay, which is predominantly chum salmon, may produce a large percentage of the total cash income for many villagers in western and northwestern Alaska.

In addition to the commercial catch, large numbers of chum salmon are taken for subsistence use. Chums are used for subsistence throughout the state, but the bulk are taken in western and northwestern areas including the Yukon River drainage in the interior. The annual statewide subsistence harvest of chums ranks in the hundreds of thousands. In former years, large numbers of chums were taken for sled-dog food, but this use declined with, among other things, the increasing use of snowmachines starting in the mid 1960s. Renewed interest in sled dogs in the last few years has apparently resulted in an increased chum salmon harvest. In the Kuskokwim area, the annual subsistence harvest of chums was larger than the commercial harvest until 1977 (Alaska Department of Fish and Game, 1979c). The same was true for the Yukon River until 1970.

Although not a prime target for sport fishermen in Alaska, thousands of chum salmon are taken by anglers every year.

II. SPECIFIC HABITAT RELATIONSHIPS/REQUIREMENTS

A. Upstream Spawning Migration

The habitat requirements of mature adult chum salmon migrating upstream to the spawning grounds are relatively broad. The time spent during this phase varies from less than a day for stocks which spawn in the tidal zone or within a few kilometers of the stream mouth, as is common in southeastern Alaska and Prince William Sound, to several weeks for stocks which spawn in tributaries of the larger rivers such as the Yukon.

I. Temperature

Manzer et al. (1965, cited by Bakkala, 1970) estimate that chum salmon at sea can probably tolerate temperatures of 1° to 15°C, but they prefer a range from 2 or 3°C to 11°C. Bell (1973) listed temperatures from 11.1 to 14.4°C as the preferred range for adult chums (he was probably referring to the freshwater phase only).

The temperature range during upstream migration of chums in some tributaries of the Kuskokwim River is 5.0 - 12.8°C (Alaska Department of Fish and Game, 1980a). The temperature range during the peak of the upstream migration in the Anvik River is 10.0 - 17.7°C (Trasky, 1974). The temperature in Traitors River ranges from 4.4 - 19.4°C during upstream migration; for the peak, the range is 8.9 - 14.4°C (Mattson and Hobart (1962)).

Hunter (1959) stated that adults entered Hooknose Creek in British Columbia to begin the upstream migration when the temperature ranged from 8°C to 14°C and that temperatures within this range did not seem to have any influence on the upstream migration.

II. SPECIFIC HABITAT RELATIONSHIPS/REQUIREMENTS

A. Upstream Spawning Migration

The habitat requirements of mature adult chum salmon migrating upstream to the spawning grounds are relatively broad. The time spent during this phase varies from less than a day for stocks which spawn in the tidal zone or within a few kilometers of the stream mouth, as is common in southeastern Alaska and Prince William Sound, to several weeks for stocks which spawn in tributaries of the larger rivers such as the Yukon.

1. Temperature

Manzer et al. (1965, cited by Bakkala, 1970) estimate that chum salmon at sea can probably tolerate temperatures of 1° to 15°C, but they prefer a range from 2 or 3°C to 11°C. Bell (1973) listed temperatures from 11.1 to 14.4°C as the preferred range for adult chums (he was probably referring to the freshwater phase only).

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For Japanese streams, Mihara et al.(1951, cited in Bakkala, 1970) reported that chum salmon start to enter the streams in the fall when the water temperature had declined to 15°C; most enter at temperatures of 10°C to 12°C. During the peak of the upstream migration, temperatures ranged from 7°C to 11°C. In northern Japan, stream temperatures during upstream migration can range from 0.1 to 20.0°C but, during the peak of migration, are generally around 7 to 11°C (Sano, 1966). Stream temperatures in the Memu River are 11 to 12°C (Sano and Nagasawa, 1958).

Levanidov (1954) stated that, while fall chum in the Amur River of Siberia rarely die before spawning, many summer chums died in certain years because of high water temperatures.

Bell (1973) suggests a water temperature criteria for successful upstream migration of chum salmon ranging from 8.3 to 15.6°C, with an optimum temperature of 10.1°C.

2. Stream Flow, Current Velocity, and Water Depth

One of the important parameters affecting upstream migration is stream flow. Of course, there are many reaches of streams that have potentially useable spawning grounds which are not available because of downstream barriers created by current velocities beyond the swimming capability of the adults, or other physical obstructions. However, in those streams that normally have spawning runs, the relative flow, whether the stream is in a high or low water stage, is an important factor. Water velocity, and possibly a heavy suspended sediment load, can be limiting to upstream migration during flooding, and water depth and elevated water temperatures can be limiting during low water stages.

There is little information available on the maximum sustained swimming velocity of which adult chum salmon are capable. Chum salmon have less ability to surmount rapids and waterfalls than other species of Pacific salmon (Scott and Crossman, 1973). Reiser and Bjornn (1979) state that water velocities of 3-4 m/sec are near the upper limit of the sustained swimming ability of Pacific salmon, although darting speeds can range up to about 6.7 m/sec (Bell, 1973). Thompson (1972, cited by Reiser and Bjornn, 1979) suggested that the maximum velocity for successful upstream migration of adult chum salmon was 2.44 m/sec and that the minimum water depth was 18 cm.

Adult chums have been observed traveling upstream in shallow riffles with the upper part of their bodies above water, but the distance that could be covered in this fashion is unknown. In southeastern Alaska, where the streams generally have low reservoir capacity and the flow is heavily dependent on rainfall, there have been several instances during dry periods when migrating chums have been unable or have had difficulty moving upstream. Similar situations have occurred in British Columbia (Wickett, 1958).

The timing of upstream migrations are often correlated with flow conditions. Lister and Walker (1966) have observed chum salmon delaying at the mouth of the Big Qualicum River in British Columbia during a period of extremely low discharge and then beginning a strong run upriver in a rapidly rising discharge. The amount of water discharged from power plants can also be a major factor controlling the timing of upstream migration (Mayama and Takahashi, 1975).

Kusnetzov (1928) noted that the run of fall chums in a Siberian river corresponded with the water level.

In Prince William Sound, Helle (1960, cited by Bakkala, 1970), observed that although chum salmon were spawning in certain streams, they were absent from a particular glacially fed stream until after a heavy flow and silt load had decreased. This is also the case in the Delta River where spawning chum do not enter the stream until after freeze up when glacial runoff has ended and the only source of water is upwelling groundwater. These fish spend enough time in shallow water in November to accumulate icicles on their backs (M. Geiger, personal communication).

3. Dissolved Oxygen

Reduced swimming performance by salmonids can result from levels of dissolved oxygen below air saturation (Reiser and Bjorn, 1979). This probably is seldom a limiting factor to the migration of chum salmon in Alaskan streams, but information is not available. Some small streams in Southeast Alaska may experience lowered oxygen levels caused by the decay of spawned-out salmon (J. Bailey, personal communication).

Winberg (1956, cited by Bakkala, 1970) found that the metabolic rate of adult chums swimming upstream an average of 115 km per day was seven to eight times greater than that of resting adults. In the Amur River of Siberia, the average daily use of energy was determined by Nikolskii (1954, cited by Bakkala, 1970), to be equivalent to 25,810 calories (25.8 Kcal) per kg bodyweight for adult males and 28,390 calories per kg bodyweight for females.

Oxygen consumption for adult chum salmon migrating upstream was $215 \text{ mm}^3\text{O}_2/\text{g body wt} - \text{hr}$ for males and $236 \text{ mm}^3\text{O}_2/\text{g body wt} - \text{hr}$ for females (Winberg, 1956 cited by Bakkala, 1970). Mature adults holding position used $71 \text{ mm}^3\text{O}_2/\text{g body wt} - \text{hr}$ (Awakura, 1963, cited by Bakkala, 1970).

4. Other Parameters

Adult chum salmon can tolerate an abrupt change from seawater to freshwater (Kashiwagi and Sato, 1970). In an experimental situation, the water content and the osmotic concentration of blood returned to normal about three days after such a transfer.

High suspended sediment loads could be inhibiting to adults attempting an upstream migration. Exposure can lead to tail rot and reduction of gas exchange across gills by physical damage, coating, or accumulation of mucous (Smith, 1978). The 96 hour LC_{50} values for juvenile chums from Puget Sound obtained by Smith are sediment concentrations of 15.8 to 54.9 g/l.

B. Spawning

Spawning grounds must consist of suitable substrate as well as suitable stream conditions. Many stocks of chum salmon, particularly fall chum, spawn in areas where there is a seepage of groundwater or springwater (Kobayashi, 1968; Kogl, 1965; Kusnetzov, 1928; Rukhlov, 1969b).

Chum redds have been measured ranging in area from 0.3 to 4.5 m. The average chum redd area in the upper intertidal zone of Olsen Creek in Prince William Sound ranged from 1.0 to 1.8 m^2 (Thorsteinson, 1965b). Burner (1951) found that chum redds in tributaries of the Columbia River averaged 2.3 m^2 in area.

Summer chum redds in an Asian stream averaged 1.3 m^2 (Vasilev, 1959, cited by Bakkala, 1970). Kusnetzov (1928) found that autumn chum redds ranged from 125 to 320 cm in length and from 106 to 213 cm in width in the Kamchatka and Amur areas. (This would equal a range in area from 1.3 to 6.8 m^2 if the shortest width was associated with the shortest length.) Chum redds on Sakhalin Island averaged 1.6 m^2 in area with a range from 0.3 to 4.5 m^2 (Kukhlov, 1969a). Summer chum redds in the Beshenaya River of Siberia were $1.0 - 2.3 \text{ m}^2$ in area and fall chum redds were $0.5 - 1.5 \text{ m}^2$ in area (Smirnov, 1947).

Measurements of the total area occupied by a spawning pair (total area of spawning grounds divided by number of spawning pairs) range from 0.3 to 10.1 m^2 . In Olsen Creek, this area ranged from about $1.5 - 10.0 \text{ m}^2$ (Thornsteinson, 1965b).

Burner (1951) suggested that a spawning pair of chum salmon requires an area of 9.2 m^2 . Wickett (1958) states that the optimum density of spawning chum varies with the permeability of the substrate (that is, the number of embryos and alevins a given area of gravel can support depends on the intragravel flow rate). In Nile Creek, B.C., Wickett found that there were $4.8 \text{ m}^2/\text{spawning pair}$. In McClinton Creek which has gravel of a higher permeability, there were $1.2 \text{ m}^2/\text{spawning pair}$. Semko (1954, cited by Sano, 1966) reported that the spawning area per female in a river on Kamchatka varied from 0.3 to 10.1 m^2 and Rukhlov (1969a) found $0.8 - 10.0 \text{ m}^2$ (average 1.7 m^2) per spawning pair on Sakhalin. Thorsteinson (1965b) reported that, on the average, 1.1 females used a square meter of the Olsen Creek spawning grounds and Bailey (1964), also at Olsen Creek, reported a cumulative density for the spawning season of 2.0 females m^2 . Schroder (1973) stated that the optimum density for maximum egg deposition is 1.7 to $2.4 \text{ m}^2/\text{female chum}$.

1. Temperature

Burner (1951) found chums spawning in tributaries of the Columbia River at water temperatures from 5.1 to 6.7°C. Chum salmon in British Columbia spawn at temperatures ranging from 4°C to 16°C (Neave, 1966). In Hooknose Creek, B.C., they spawn at a temperature of about 12°C (Hunter, 1959). McNeil (1969) reported a similar value for Sashin Creek in southeast Alaska where most chums spawn after the water temperature has dropped to 13°C or below. Chum salmon on Kodiak Island spawned at water temperatures ranging from 6.5 to 9.0°C in the Kizhuyak River and at 9.0 to 12.5°C in the Terror River (Wilson et al., 1981).

Stream temperatures of the Memu River in Japan during spawning range from 6 to 9°C (Sano and Nagasawa, 1958). Spawning of summer chum in the Amur River of Siberia occurs during August and September at water temperatures of 9 to 11°C while spawning of fall chum occurs during the period mid-September to the end of November at water temperatures of about 6°C (Sano, 1966). Ivankov and Andreyev (1971) report that most of the spawning of the South Kuril chum populations takes place when the water temperature is 5 to 6°C. On Sakhalin Island, spawning occurs at water temperatures of 1.8 to 8.2°C (Rukhlov, 1969a) and in the Iski River, it occurs at bottom water temperatures of 2 - 9°C (Smirnov, 1947).

Schroder (1973) noted that there was some inhibition of spawning by chum salmon in Washington at water temperatures below 2.5°C. About 98% of the females present spawned when the water temperature was around 7°C while only 82% spawned at temperatures around 2.5°C. Nest construction, spawning behavior, and egg deposition were all affected by the cold water.

Water temperatures recommended by Bell (1973) as criteria for spawning chum salmon range from 7.2 to 12.8°C. This is the same range which McNeil and Bailey (1975) state to be the preferred spawning temperature for Pacific salmon.

2. Current Velocity

Kogl (1965) measured surface current velocities during the spawning of chum salmon in the Chena River ranging from 0 to 60 cm/sec. He believed that surface current was of less importance to spawning chums than the presence of springs or groundwater. Sites where chum spawned in the Terror and Kizhuyak Rivers of Kodiak Island had current velocities ranging from 0 to 118.9 cm/sec (Wilson et al., 1981).

At chum salmon redds in Oregon, Thompson (1972, cited by Reiser and Bjornn, 1979) measured stream velocities of 46 to 97 cm/sec and Smith (1973), after sampling 214 redds, measured a mean velocity of 73 cm/sec. Collings (1974) measured velocities of 21 to 101 cm/sec at 12 cm above chum redds in Washington streams. In a spawning channel in Washington, Schroder (1973) measured stream velocities from 22.5 cm/sec to, at high tide, 0 cm/sec. These differences did not appear to disrupt normal spawning behavior.

Rukhlov (1969a) reported that chum spawning on Sakhalin most often takes place at current velocities from 10 to 90 cm/sec. Rukhlov also found that the average number of eggs deposited per redd decreased as the stream velocity over the redd increased. In the My River, chums have spawned where the stream velocity was 10 to 80 cm/sec (Soin, 1959) and 20 to 100 cm/sec (Strekalova, 1963). Spawning grounds in the Bolshaya River basin have current velocities of 10 to 30

cm/sec (Krokhin and Krugius, 1937, cited by Nicola et al., 1966).

Chum salmon have been reported spawning in the Memu River of Japan at stream velocities of 10 to 35 cm/sec (Sano and Nagasawa, 1958). Redds were most abundant in areas where the velocity was 15 to 20 cm/sec and least abundant where the velocity was less than 10 cm/sec or greater than 30 cm/sec. Sano (1967) states that chums will spawn in surface current velocities of less than 15 cm/sec if there is a good intragravel flow of groundwater.

Some recommended criteria for stream velocities at spawning areas are: 46 to 101 cm/sec for Oregon chums (Smith 1973) and 31 to 70 cm/sec for chums, chinooks, and cohos in the Wynoochee River of Washington (Deschamps et al., 1966, cited by Smith, 1973). A spawning channel at Jones Creek in British Columbia used by chum salmon was designed for a water velocity of 31 to 76 cm/sec (MacKinnon et al., 1961).

Tautz and Groot (1975) suggest that, in the selection of a spawning site, chum salmon prefer an area near a rock protruding above the substrate where there is an upwelling, accelerating current. A favorable current regime is also found at the boundary between pools and riffles. These irregularities are conducive to a good flow of intragravel water (Reiser and Bjornn, 1979).

The flow of a stream during spawning relative to the flow during the incubation period can be an important factor affecting survival. Eggs deposited in shallow water during high flow stages are subject to desiccation and/or freezing during low flow stages.

3. Water Depth

Water depths where chum salmon spawn fall within a certain range but pressure itself is probably not a factor limiting spawning. However, favorable combinations of current velocities, bottom configurations, and substrates (which are important factors) tend to occur together within a certain range of water depths.

Kogl (1965) found that chum salmon dug redds in the Chena River at water depths from 5 to 120 cm. Chums spawned at greater depths in areas of the Chena River where there were no springs or ground seepage. In certain areas of the main channel where the upwelling of groundwater was absent, the chums deposited their eggs at water depths greater than 100 cm. Eggs deposited in less than 100 cm of water were subject to winter freezing. Chums have been observed spawning in the Delta River at water depths up to 61 to 92 cm (Francisco, 1976). Water depths measured at sites where chum salmon spawned in the Terror and Kizhuyak rivers ranged from 7.6 to 106.7 cm (Wilson et al., 1981).

Burner (1951) measured water depths at chum salmon redds in tributaries of the Columbia River of 5.1 to 76.2 cm with a mean of 25 cm. Smith (1973) reported that the average water depth over chum redds in five Oregon streams was 30 cm. In Washington streams, Collings (1974) measured water depths of 15 to 53 cm.

In Hokkaido, water depths of 20 to 110 cm at chum spawning sites were measured by Sano (1959, cited by Bakkala, 1970). For the Memu River in Tokachi, Sano and Nagasawa (1958) reported that chum redds were most abundant where water depths were 20 to 30 cm and least abundant at water depths greater than 100 cm.

Soin (1954) in the My River of Siberia, measured water depths over redds of 30 to 100 cm. Kusnetzof (1928) reported that chums favor water depths of 60 to 100 cm for spawning.

Water depths recommended as criteria for chums by Deschamps et al. (1966, cited by Smith, 1973) for a Washington stream range from 23 to 46 cm. Smith (1973) suggested that the water depth for chums in Oregon be no less than 18 cm. Thompson (1972) uses the same figure. An artificial chum spawning channel at Jones Creek, B.C., was designed for a water depth of 31 to 61 cm (MacKinnon et al., 1961).

4. Substrate Composition

The suitability of stream substrates from the standpoint of successful reproduction is more related to its quality for incubation of eggs and alevins than to the ease of excavating redds by spawning females. Chums may deposit eggs in bottom materials where redds are fairly easily constructed but which are less than ideal for incubation, perhaps because of a high silt content or low porosity. Certain substrates in which it would be difficult or impossible to excavate a redd can be fairly good incubation substrates. An example is loose cobble and boulders over bedrock where the chums deposit their eggs and milt into existing crevices.

Rukhlov (1969b) reported that smaller chums on Sakhalin Island tend to have a higher percentage of sand in the redd. Rukhlov assumed that the weaker (smaller) females build their nests in less resistant gravel.

Different investigators have used different methods and definitions to present substrate composition information which makes comparisons difficult. In general, chum salmon excavate redds in gravel beds with a particle size of 2 to 3 cm diameter, but they will also construct redds in substrates with particles of a greater size and will even use bedrock covered with small boulders (Morrow, 1980; Scott and Crossman, 1973). Generally, substrates with a percentage of fines (particles less than 0.833 mm in diameter) greater than 13% are of poor quality because of reduced permeability (Thorsteinson, 1965). However, chum salmon often spawn in areas of upwelling ground water and may therefore be able to tolerate higher percentage of fines than would seem desirable if some of the fines are kept in suspension by the upwelling water (J. Helle, personal comment). Sano and Nagasawa (1958) reported that upwelling water washed away mud and fine sand from chum redds in a stream in Japan.

The spawning grounds of the Delta River are composed mostly of particles 1.3 to 12.7 cm in diameter with variable amounts of fines (Francisco, 1976). Sano (1959, cited by Bakkala, 1970) reported that chum salmon in Hokkaido spawn in a substrate of which 25% is 0.6 to 3.0 cm, and 30% is greater than 3.1 cm. Particles less than 0.5 cm comprise less than 20% of the composition and particles greater than 3.0 cm comprise 25 to 53% of chum spawning gravels in the Memu River (Sano and Nagasawa, 1958). The spawning beds of My River are composed of gravel mixed with sand and small quantities of silt (Soin, 1954). Substrate samples taken from chum redds on Sakhalin Island are mostly composed of particles 0.2 to 1.0 cm in diameter (Rukhlov, 1969a). Rukhlov (1969b) reported that a particle size analysis of 143 samples from chum redds on Sakhalin showed the average sand content to be about 12%; gravel content to be around

35%; shingle content to be around 45%; and fractions greater than 10 cm to be about 5%. Chum redds in tributaries of the Columbia River were found by Burner (1951) to have the following composition: mud, silt, and sand - 6.0%, medium and small particles greater than sand size but less than 15.2 cm 81.0%, and large gravel over 15.2 cm - 13.0%. Hunter (1959) reported that the spawning grounds of Hooknose Creek in British Columbia consisted of particles from 1.3 to 13.0 cm., "liberal" quantities of coarse sand, and "a certain amount" of fine sand and silt.

McNeil and Bailey (1975) suggested a substrate size range of 1.3 to 15.2 cm in diameter for the aquaculture of Pacific salmon. MacKinnon et al., (1961) used gravel ranging in size from 0.6 to 3.8 cm for a spawning channel for chum salmon in British Columbia. Bell (1973) recommended a size range of 1.3 to 10.2 cm for artificial spawning channels to be used for salmon, including chums.

Duker (1977), in an experimental situation in Washington, presented female chums with a choice between four sizes of spawning gravels. The females preferred the two substrates which consisted mainly of particles 0.7 to 7.6 cm in diameter, rather than a substrate with mostly smaller particles or substrate with mostly larger particles.

5. Salinity

Saline water can interfere with fertilization of the eggs of chum salmon spawning in or near the intertidal zone. Rockwell (1956) found that salinities of 18 parts per thousand (ppt) or greater inhibit fertilization of chum eggs, although a limited amount of fertilization could occur at salinities up to 30 ppt.

C. Intragravel Development of Embryos and Alevins

The intragravel period in the development of the chum salmon consists of two life history stages with differing habitat requirements, that of the fertilized eggs or embryos and that of the alevins. Further, the habitat requirements of each stage change with the state of development or age. However, most investigators have treated the intragravel period as a single stage from the standpoint of measurements of environmental parameters; that is how it is treated here. Wherever data are available, distinctions between the stages will be made. Mortality is generally higher for the embryo stage than for the alevin stage (Levanidov, 1954). Information on the density of chum eggs and alevins per square meter in Alaska has been given by several investigators (Bailey, 1964; Dangel and Jewell, 1975; Mattson and Rowland, 1963; Mattson et al., 1964; Roys, 1968; Thorsteinson, 1965b).

1. Temperature

Water temperature is an important variable to chum salmon during the gravel incubation period. The time to hatching and time to emergence are directly related to water temperature. Cold air temperatures, combined with a low stream flow or an insufficient ground water flow, can reduce intragravel water temperature to the point where embryos and alevins are killed by freezing. Temperature also influences other parameters such as the solubility of oxygen in water. The temperature of intragravel water is controlled by the temperature of the stream water and ground water and by the rate of exchange among these three reservoirs.

Stream water temperatures from slightly below 0° to about 15°C have been observed during the incubation period of chum

salmon (Koski, 1975; McNeil, 1966). A site in the Chena River had intragravel temperatures of 0.5 to 4.5°C (Kogi, 1965). Intragravel water temperatures at several chum spawning sites in the Noatak River ranged from about 6.1 to 10.0°C in early October to a low of 0.2 to 3.3°C in March (Merritt and Raymond, in prep.). Francisco (1977) measured intragravel temperatures of 0.6 to 6.7°C in the chum spawning areas of the Delta River during the incubation period. Intragravel temperatures in the Kizhuyak River during the month of April were about 3 - 5°C (Wilson et al., 1981). Bailey (1964) reported intragravel temperatures (probe 20.3 cm deep) in Olsen Creek of 4°C in October, near 0°C in December and January, and 1°C in mid-March just prior to fry emergence.

Sano and Nagasawa (1959) reported that the intragravel temperatures in the Memu River of Japan during incubation ranged from 7.0 to 11.0°C. Sano (1966) found that autumn chum in northern Japan chose to spawn in spring areas where the water temperature in the spawning bed did not become lower than 4°C. Semko (1954, cited by Sano, 1966) reported intragravel water temperatures in a river on the Kamchatka Peninsula of 3.9 to 4.9°C during chum egg incubation and 2.4 to 3.0°C during the alevin phase. Levanidov (1954) found water temperatures in chum redds in the River Khor of 3.3 and 6.0°C and, in the Bira River, intragravel temperatures during incubation ranged from 3.5 to 5.0°C (Disler, 1951).

The lower end of these temperature ranges may not be ideal for chum salmon in some areas. Koski (1975) found this to be the case for chum eggs in a Washington spawning bed and Schroder (1973), working in the same area, stated that temperatures below 4.4°C adversely affected chum eggs. Schroder et al. (1974, cited by Koski, 1975) reported that chums in Washington exposed to water temperatures below

1.5°C during the early stages of embryonic development experienced lower percent survival to emergence. At the chum salmon hatchery at Clear Air Force Station in interior Alaska, Raymond (1981) reported that the percent mortality (fertilization to emergence) for one year when incubation temperatures ranged from 2.0 to 4.2°C was 38%. The following year, incubation temperatures were raised about 1°C to 3.6 to 4.5°C and the percent mortality declined to 18%. It appeared that the increase in temperature was largely responsible for the decline in mortality. The lower water temperatures of the hatchery also caused a delay in emergence of about seven weeks beyond that of wild fry of the same stock in the Delta River which had incubated at about 3.9°C. Kirkwood (1962) stated that chum salmon eggs in Prince William Sound which had not hatched before the colder months of January and February did not survive. He found that chum eggs in the upper intertidal zone of a streambed had a higher survival rate than eggs above the influence of the tides and attributed this to the slightly warmer temperatures of the former areas.

For the water temperature range (stream water temperature not intragravel temperature) observed at Hooknose Creek, B.C. (0 to 14°C) Hunter (1959) could not demonstrate an effect of temperature on the percent survival (eggs in female to fry emergence) of chum salmon.

Stream temperatures very close to freezing may not pose any problem as long as there is a sufficient flow of slightly warmer springwater or groundwater through the incubation area.

Chum salmon, particularly fall chums, actively choose such areas (Kogl, 1965; Levanidov, 1954; Morrow, 1980; Sano, 1966). Springs in certain rivers of Kamchatka maintain

water temperatures in chum salmon spawning gravels of 1°C even though the air temperature may be as low as -50°C (Sano 1966). The same is true in the Chena River (Kogl, 1965) and the Delta River (Francisco, 1977).

McNeil and Bailey (1975) suggest that water temperature during aquaculture of Pacific salmon be kept above 4.4°C for at least 10 days after fertilization, and preferably for 20 to 30 days. After this period, the eggs can tolerate temperatures as low as 0°C as long as the water does not freeze. Exposure of salmonid embryos to water temperatures below 4.4°C prior to gastrulation and before closure of the blastopore can lead to high mortalities (Koski, 1975). Bell (1973) recommended an incubation temperature for chum salmon of 4.4 to 13.3°C.

The time to hatching of chum salmon eggs ranges from about 50 days at 7.0 to 15.0°C to about 130 days at 0.0 to 5.0°C (Bakkala, 1970).

Koski (1975) found that annual water temperature variations in a Washington stream significantly alters the timing to chum fry emergence from the substrate. During a three year period, the time to 50% emergence varied up to 30 days.

2. Stream Flow, Current Velocity, and Water Depth

The flow of water in the stream channel is important to incubating embryos in promoting an adequate intragravel flow and in protecting the substrate from freezing temperatures. Heavy mortality of embryos can occur during periods when there is a relatively high or a relatively small discharge. Flooding can cause high mortality by eroding eggs from the redds or by depositing fine sediment on the surface of the redds which can reduce permeability or entrap emerging fry

(Bailey, 1964; Dill and Northcote, 1970; McNeil, 1966; Rukhlov, 1969b; Strekolova, 1963; Thornsteinson, 1965b; Wickett, 1958).

Low discharge periods can lead to desiccation of eggs, low oxygen levels, high temperatures, or, during cold weather, freezing (Neave, 1953; Levanidov, 1954; McNeil, 1966; Sano, 1966; Wickett, 1958).

McNeil and Bailey (1975) recommend a stream gradient at the incubation area of 0.2 to 0.5%, a water depth greater than 15.2 cm, a current velocity in the surface water of 30.5 to 91.4 cm/sec and a flow of $0.16 \text{ m}^3/\text{sec}$ per linear meter of width for the aquaculture of Pacific salmon.

The water depths and current velocities given in the section for spawning adults apply in general to the intragravel life history stages as well, although both decline in many streams during the freezing months. Water depths over chum redds in some tributaries of the Columbia River ranged from 7.5 - 43.2 cm and had an average of 21.6 cm (Burner, 1951). Water depths over summer chum redds in the Beshenya River in Siberia ranged from 16 - 104 cm and over fall chum redds ranged from 3 - 34 cm (Smirnov, 1947).

Lister and Walker (1966) found an inverse relationship between chum salmon egg to fry percent survival and the peak daily discharge of the Big Qualicum River, British Columbia, during the incubation period. No relation between percent survival and the minimum discharge was apparent from their data. Wickett (1958) showed a direct relationship between an index of production (stock + 4 years divided by spawners times 100) and the discharge of Hooknose Creek, B.C., in November. Hunter (1959) could not demonstrate an effect of stream discharge of Hooknose Creek, B.C., on chum salmon

percent survival (eggs in female to fry emergence). On the Noatok River, low returns of adult chums appear to be correlated with high water levels (rainfall) during the brood year (Frank Bird, personal communication). Gallagher (1979) found a negative correlation between stream flows during the incubation period and brood year returns in the Puget Sound area over a fourteen-year period; low flows were correlated with good returns. Based on these seemingly contradictory results, it would appear that the effect of a varying discharge strongly depends upon the particular stream being examined.

3. Substrate Composition

Information on substrate size composition of chum spawning grounds was presented previously. The size and shape of substrate particles and the particle size distribution influence many parameters which are of importance to the successful incubation of embryos and alevins. Some of these parameters, several of them interrelated, are: permeability, porosity, flow of intragravel water, dissolved oxygen concentration, concentration of waste metabolites such as carbon dioxide and ammonia, the armoredness or resistance to abrasion of the substrate surface and the degree of imbeddedness of larger sized particles in the substrate surface.

Dill and Northcote (1970), using experimental containers, found a survival to emergence for chum salmon of approximately 100% in large gravel (5.1 to 10.2 cm) and 31% in small gravel (1.0 to 3.8 cm). They judged that the lower survival rate in the smaller particle did not result from a low dissolved oxygen content, but was probably a result of silt action or entrapment of fry. They found no significant effect of gravel size or egg burial depth (20.3 and 30.5 cm)

on the timing of emergence or on the condition of fry at emergence.

Koski (1975) showed that there was a highly significant inverse relationship between the percent sand content (fines less than 3.327 mm but greater than 0.105 mm) of substrate and the percent survival to emergence of chum salmon. An increasing sand content also resulted in an earlier emergence, increased the percentage of premature fry emerging from the substrate, lowered the percent yolk conversion efficiency, and tended to produce fry of a shorter length. Koski could not demonstrate a relationship between the percentage of silt (fines less than 0.105 mm) in the substrate and percent survival to emergence, primarily because the effect of silt, which ranged up to about 50%, was masked by a changing percentage of sand. However, silt contents of 45% or greater did have an adverse effect on percent survival.

Rukhlov (1969b), working on Sakhalin Island, also noted an increasing egg mortality rate with increasing sand content above 14%. He found that redds with a sand content of 22% or greater had a survival rate of 50% or lower. Rukhlov reported that average survival in the Tym' River was 85% where the sand content was 10% and 65% where the sand content was 18%. Kol'gaev (1962, cited by Kogl, 1965) noted a positive correlation between the duration of incubation and the particle size of the substrate when chum eggs were incubated in an experimental container with coarse sand. Thorsteinson (1965) stated that spawning grounds with percent fines (particles less than 0.833mm) greater than 12.7% are of poor quality for chums because of reduced water permeability.

In hatchery situations, the absence of a gravel substrate apparently leads to a less desirable habitat for Pacific salmon alevins (Bams, 1969; Emadi, 1973; McNeil and Bailey, 1975). Emadi (1973), in an experimental situation, discovered that chum alevins kept on smooth substrate had a higher percentage of malformed yolks (30%) than those kept on gravel of 2 to 3 cm diameter (0%) at a water velocity of 100 cm/hr and a temperature of 12°C.

Sedimentation during the incubation period can be a major source of egg mortality (Levanidov, 1954, Neave, 1953; McNeil, 1966; Rukholov, 1969b; Wickett, 1954). Siltation one year in the River Khor of Siberia killed 100% of the embryos in 42 chum redds (Levanidov, 1954).

4. Intragravel Flow and Permeability

The rate of flow of intragravel water is an important variable affecting the survival and fitness of embryos and alevins. Water flowing through the gravel supplies oxygen, removes waste metabolites such as carbon dioxide and ammonia, and is important in regulating temperature. The rate of intragravel flow is affected mainly by the rate of stream flow, stream gradient, bottom configuration, substrate surface irregularities, degree of substrate surface armoredness, and permeability of the substrate which depends strongly on the substrate particle size distribution (Sheridan, 1962; Vaux, 1962). Johnson (1980) showed experimentally that the permeability of spawning gravels decreases with an increasing percent of fines (particles less than 0.5 mm). Different methods of measurement of intragravel flow by different investigators has resulted in order of magnitude differences in results.

Reiser and Bjornn (1979) reported that the percent survival of chum to the migrant fry stage increased from about 2% to 15% as the permeability of the streambed gravel increased from about 30 to 155 cm/hr.

Wickett (1958) surveyed the gravel permeability of two streambeds in British Columbia over several years and found that chum salmon percent survival (egg in female to fry) in the streambed with an average permeability of 1914 cm/hr was 1.2%, while in the streambed with an average permeability of 4035 cm/hr, it was 7.6%.

Kol'gaev (1962, cited by Kogl, 1965) found that the survival of chum eggs in coarse sand in an experimental apparatus was directly related to the volume of flow through the sand.

Wickett (1957) stated that the minimum intragravel apparent velocity for the survival of pre-eyed eggs is 10 cm/hr; 50 cm/hr is desirable.

McNeil and Bailey (1975) recommended an intragravel apparent velocity of at least 200 cm/hr for the aquaculture of Pacific salmon.

5. Dissolved Oxygen

The supply of dissolved oxygen is of critical importance to eggs and alevins; a low supply of dissolved oxygen leads to an increased mortality or a decreased fitness (Alderdice et al., 1958; Koski, 1975; Wickett, 1954, 1957 and 1958). Apparently, a rate of supply of oxygen less than optimum for survival and fitness occurs frequently in nature. It is the rate of supply of dissolved oxygen which is important to the egg or alevin, not the actual concentration of dissolved

oxygen in the water (Daykin, 1965). The rate of supply to the embryos and alevins is influenced primarily by the dissolved oxygen (DO) concentration of the source water and the rate of water flow through the gravel. Because of a certain upper limit on possible velocities of intragravel flow, there is a certain minimum DO concentration below which it would be difficult to maintain an adequate rate of oxygen supply. There are also other biological and chemical oxygen demands within the gravel which compete for the available supply. The relationship of particle size and DO concentration was noted by Koski (1975) who found a significant inverse relationship between minimum observed DO concentration and maximum observed percent sand and silt in spawning gravels in Washington.

Water saturated with dissolved oxygen may be regarded as the optimum condition for eggs and alevins (Alderdice et al., 1958). The concentration of oxygen in oxygen-saturated fresh water depends mainly on the temperature.

Oxygen requirements vary considerably for different stages of development of eggs and alevins. Temperature also has a strong effect on the rate of oxygen consumption.

Often, the oxygen requirements can be met by a fairly low concentration of dissolved oxygen, about 2 mg/l, as long as the rate of flow of intragravel water is sufficient (Kogl, 1965; Levanidov, 1954). Wickett (1954) measured the apparent velocity of water 12 inches down in the gravel with a standpipe. He determined that a dissolved oxygen concentration of 4 p.p.m. at 8°C (50% saturation) would just maintain full metabolism of a pre-eyed chum egg providing intragravel water flow to the egg is sufficient.

Insufficient oxygen supply results in an increase in the mortality rate or decreased fitness in the surviving embryos or larvae which may be manifested as premature or delayed hatching or emergence, production of monstrosities, decreased length, or less efficient yolk conversion (Alderdice et al., 1958; Koski, 1975). As with many environmental parameters, the duration of the period of stressful levels of oxygen and the interaction of other stresses is important.

a. Oxygen consumption rate

Wickett (1954) measured the oxygen consumption of chum salmon eggs and found a rate of 0.0001 to 0.0003 mg/egg-hour for pre-eyed eggs 0 to 12 days old, (temperature 0.1 - 8.2°C), 0.0002 to 0.008 mg/egg-hour for faintly eyed eggs 67 to 85 days old (temperature 0.1 - 4.9°C), and 0.0002 mg/egg-hour for eyed eggs 103 days old (temperature 5.9 - 6.1°C).

Alderdice et al. (1958), using chum salmon eggs at four developmental stages at 10°C, reported oxygen consumption rates from 0.00093 mg/egg-hour for middle stages to 0.00521 mg/egg-hour for later stages. They also showed that, while the oxygen consumption per embryo increases with age because of increasing embryo mass, the actual rate of oxygen consumption per gram of embryo initially decreases and then more or less levels off with increasing age. An early developmental stage had a rate of about 0.006 mm³/g-min, mid-stages were about 0.040 mm³/g-min, and late stages were about 2.100 mm³/g-min.

Lukina (1973) measured oxygen consumption rates of 0.00015 to 0.00951 mg O₂/egg-hour at 3.5 to 4.5°C for chum embryos and 0.0132 mg O₂/larvae-hour at 5 to 6°C for chum larvae.

b. Effect on survival

Critical oxygen levels (the lowest concentration at which respiration is just satisfied) for chum salmon eggs have been found in laboratory experiments to range from 0.72 mg/l for early developmental stages to 7.19 mg/l for later developmental states at 8 to 10°C (Alderdice et al., 1958; Wickett, 1954). Whether or not these concentrations are sufficient to satisfy the oxygen demand of the eggs depends on the flow rate of the intragravel water. Alderdice et al. (1958) reported that the incipient median lethal level for dissolved oxygen ranged from about 0.4 mg/l for early developmental stages to 1.0 to 1.4 mg/l previous to hatching.

Levanidov (1954) stated that the fall chum of the River Khor in Siberia have an ability to adapt and to develop under a continuous oxygen deficiency. Oxygen concentration in one spawning gravel dropped to 4 mg/l (30% saturation) in March and the oxygen content of another area which had a strong outflow of ground water dropped to 2.5 to 3.0 mg/l (20 to 25% saturation) at the end of February. The rate of egg survival and fry development was high at both of these sites. A third site, where the survival rate of eggs was also good, had an oxygen concentration in mid-December of 2.0 mg/l. Experiments conducted

by Levanidov (1954) showed that fall chum eggs 10 to 15 days after fertilization can survive two hours exposure to water of zero oxygen content. Eggs which are a few days from hatching can survive (two hours?) exposure to water with an oxygen concentration of 0.45 to 0.50 mg/l. Larvae 24 hours after hatching can survive an oxygen concentration of 0.28 mg/l.

Disler (1951) stated that the DO concentration of some chum redds in the Bira River of Siberia does not exceed 3-4 mg/l. In Hokkaido streams, Kobayashi (1968) found oxygen saturation values of 31.3 to 73.9% in the intragravel waters. Intragravel DO concentration in the Chena River during incubation of chum eggs ranged from 0.6 to 6.5 mg/l (Kogl, 1965). There were low survival rates at the lower concentrations and high survival rates at the higher concentrations. Koski (1975) found that the rate of chum salmon survival to emergence at a site in Washington was significantly correlated with DO concentration and that survival decreased rapidly at DO concentrations below 3.0 mg/l. DO levels in the intragravel water of Indian Creek (Kasaan Bay) have an annual range from 0.0 to 12.7 mg/l (McNeil, 1962). Long dry periods in southeastern Alaska can lead to low intragravel DO levels as a result of reduced stream and intragravel flow. Such conditions in Traitors River one year led to an intragravel DO level of 1.77 mg/l which resulted in a high mortality rate of embryos (Mattson et al., 1964). In another situation, a low water permeability at one tide level in the intertidal spawning area of Olsen Creek led to a

low intragravel DO value (3.6 mg/l) and a low percent survival to emergence (Bailey, 1964).

Wickett (1954 and 1957) stated that chum salmon eggs, in the absence of other stresses, have a lethal limit of about 2 mg/l at 5°C. On the other hand, both Levanidov (1954) for the Amur River of Siberia and Kogl (1965) for the Chena River of Alaska reported good survival rates in gravel with DO concentrations of 2 mg/l as long as there was a strong flow of groundwater or springwater. Kogl (1965) was not able to demonstrate a relationship between egg survival and DO concentration at concentrations greater than 2 mg/l.

Cheyne (1941, cited by Nicola et al., 1966) reported that chum salmon eggs developed at about the same rate in waters with DO levels from 3.6 to 7.6 mg/l. Wickett (1957) stated that a DO level of 5 mg/l is low for chum eggs and that a level of 8 mg/l is desirable. Based on experimental studies, Lukina (1973) indicated that a DO concentration of 6 to 8 mg/l was the most favorable for the development period of chum embryos and larvae at a temperature of 4-8°C.

McNeil and Bailey (1975) suggest, for aquaculture of Pacific salmon, that alevins be provided water with DO concentration of at least 6 mg/l O₂. Chum salmon embryos and alevins in redds in the intertidal zone of streambeds may be exposed to a lowering of DO levels during high tide. At the 2.1 m tide level in Olsen Creek, the DO level in a redd dropped from about 7 mg/l at low tide to 4.5 mg/l at high tide (Thorsteinson 1965a).

c. Effect on fitness

Kogl (1965) reported that low DO concentration in the intragravel water of the Chena River affected the size of chum alevins. The dry weight of alevins decreased from about 2.3 mg at a site where the DO concentration had averaged 4.1 mg/l to about 0.1 mg at a site where the DO concentration had averaged 2.1 mg/l. Cheyne (1941, cited by Nicola et al., 1971) stated that chum eggs held at a DO level of 7.6 mg/l resulted in larger fry than those held at 3.6 mg/l. Conversely, Koski (1975) was able to show little, if any effect of DO concentrations less than 6.0 mg/l on mean fry lengths and weights at emergence. Alderdice et al. (1958) found that early developmental stages of chum salmon eggs (12 days after fertilization) could survive seven days exposure to a DO concentration of 0.3 mg/l but, upon hatching, had a high percentage of monstrosities (deformed alevins). The abnormality took the form of a shortening of the vertebral column posteriorly. Eggs at a later developmental stage (22 days after fertilization) did not tolerate seven days exposure to the same DO concentration (0.3 Mg/l) and exhibited 100% mortality.

Alderdice et al. (1958) further showed that seven days exposure to oxygen levels below saturation produced delays in the mean hatching rate of chum salmon eggs at 10°C. Early and middle developmental stages were most affected. Eggs of the most advanced developmental stage showed the opposite effect, premature hatching. Koski (1975)

found that the low dissolved oxygen (3.0 mg/l or less) during the incubation period appeared to delay the timing of chum fry emergence from the gravel of spawning beds in Washington. A delay in emergence could place the fry in an unfavorable situation with regard to feeding, predators, or temperature. Beall (1972), using the spawning channel at Big Beef Creek, Washington, incubated a group of chum eggs in a trough with gravel and another group in an open trough, with the result that the fry produced in the open trough were, on the average, shorter by 1 to 2 mm and lighter by 0.04 g. Beall found that the predation rate by coho salmon (Oncorhynchus kisutch) was significantly higher on the smaller group of fry.

6. Salinity

Seawater incursion on chum salmon embryos and alevins in gravel in or near the intertidal zone can have an adverse effect. Presumably, 100% freshwater is ideal for chum salmon embryos and alevins, but Rockwell (1956) suggested that, based on laboratory experiments, hatching of eggs may be slightly improved by a small percentage of seawater mixing with freshwater. He found that chum eggs and larvae survived for several days in seawater of up to 30 parts per thousand (ppt) salinity, that they could survive the higher salinities at lower temperatures, and that larvae withstood higher salinities than eggs. Important variables affecting survival at various salinity concentrations were time of exposure and temperature. For eggs in early developmental stages, exposure to 6 ppt salinity had no effect; however, exposure to 11.6 ppt significantly retarded development and led to a 67% mortality. Fully

developed eggs had a 50% survival rate at salinities of 6.0 to 8.5 ppt through hatching.

Data obtained by Kashiwagi and Sato (1969) indicated that percent survival of eggs to hatching was inversely related to percent seawater concentration. Eyed eggs had a 100% hatching rate in water of about 9 ppt salinity; this decreased to 75% for 18 ppt, 50% for 27 ppt, and 25% for 35 ppt. The time of incubation was increased from about 10 days in water of 0 to 18 ppt to about 14 days in water 27 to 35 ppt. However, almost all of the alevins which did hatch from eggs exposed to water of 9 to 35 ppt died within a few days. Alevins which were hatched in freshwater and then exposed to seawater mixtures could survive a salinity of 9 ppt, but died at higher salinities.

Shepard (1948) demonstrated that chum alevins, given a choice between two flows, showed a preference for stronger current velocities. Given a choice between a seawater flow and a freshwater flow, they chose the latter. Salinity was more important than current velocity in influencing the alevins.

In the intertidal area of streambeds of Olsen Creek (3.7 m tide) there is constant residual intragravel salinity of 3 ppt from the 2.1 m level on down (Thorsteinson, 1965a). Salinities up to 25 ppt have been observed at all levels. The salinity of the intragravel water fluctuates with the tide. At the 2.1 m level, there was a 7 ppt increase at high tide. The egg to fry survival of chum salmon was 40 - 50% in the upper section of the intertidal zone and 10 - 15% in the middle section. Chums do not use the lower section. The mortality rate is influenced by oxygen

and temperature differences as well as by salinity differences.

McNeil and Bailey (1975) suggest that Pacific salmon eggs can tolerate salinities of 0 to 9 or 11 ppt and that chum eggs can survive periodic inundations by water of 15 to 30 ppt as long as there is freshwater flushing in between the seawater inundations.

7. Chemical Parameters

There is a limited amount of data available on the desirable levels of soluble substances present in intragravel water, or on their effects on chum salmon embryos and alevins.

The pH of Chena River intragravel water at chum redds was 6.5 (Kogl, 1965); this is similar to the Amur River in Siberia (Levanidov, 1954) and a Hokkaido stream, which was pH 6.3 to 6.5 (Kobayashi, 1968). McNeil and Bailey (1975) suggest that pH 6.0 to 8.0 is a desirable range for Pacific salmon.

McNeil (1962) measured intragravel CO₂ levels in some streams of southeastern Alaska of 2 to 24 mg/l. Levanidov (1954) reported that the CO₂ content of groundwater in the Amur River was about 25 to 30 mg/l. He found that concentrations greater than 20 to 25 mg/l inhibited the development rate of chum salmon eggs. Alderdice and Wickett (1958) observed that CO₂ concentrations greater than about 10 mg/l decrease the percent survival to hatching. The uptake of oxygen is inhibited at CO₂ concentrations greater than 125 mg/l. Koski (1975) measured CO₂ concentrations of up to 48 mg/l in intragravel water in a Washington incubation

area, but the effect of this concentration on survival was not studied. Disler (1951) found CO_2 levels in the intragravel water of the Bira River of 16 to 20 mg/l and Kobayashi (1968) found levels of 17.8 to 25.2 mg/l in a Hokkaido stream. McNeil and Bailey (1975) recommended that the CO_2 concentration in Pacific salmon hatcheries be kept below 5 mg/l.

The alkalinity of intragravel water in chum salmon redds in the Chena River was 86 to 103 mg/l; iron content was 0.1 to 0.3 mg/l (Kogl, 1965). Good survival rates were noted at these sites.

Ammonia is a waste product of metabolism which could be highly toxic to embryos and alevins if not removed by intragravel flow. McNeil and Bailey (1975) recommend that Pacific salmon hatcheries keep ammonia levels below 0.002 mg/l.

Hydrogen sulfide (H_2S) is produced by sulfur-reducing bacteria in waters of low oxygen content and is highly toxic to embryos and alevins. Koski (1975) found H_2S levels in intragravel water of a spawning channel in Washington of 0.4 to 0.5 mg/l but did not measure the effect on chum embryos or alevins. McNeil and Bailey (1975) suggest that H_2S levels in Pacific salmon hatcheries be kept below 0.5 mg/l in acidic waters.

Springs often have higher levels of CO_2 and H_2S and lower levels of DO than stream water. In some areas, these substances may be at such levels that they are detrimental to the incubation of chum eggs and alevins.

8. Light

Disler (1953) stated that direct sunlight is fatal to chum salmon embryos. Indirect sunlight can retard the rate of development, affecting earlier stages more than later stages of development (Soin, 1954).

D. Emergence and Downstream Migration of Fry

This section will consider the period between the time of fry emergence from the gravel and the time the fry enter estuarine waters. Most chum fry begin the seaward migration shortly after emerging from the gravel in the spring and essentially all have left freshwater by mid-summer. Habitat requirements during this period center on favorable temperatures, cover from predators, availability of food, and eventually, availability of seawater.

Downstream migration occurs as a result of the response of the fry to physical and chemical parameters including light and photoperiod, current, temperature, salinity, and objects in the environment (Hoar, 1956 and 1957). The outmigration from streams in British Columbia results from a combination of active swimming and displacement at night when visual orientation is diminished. Streams in northern Alaska or Siberia have very little darkness during the time of outmigration. Response to the various environmental stimuli (phototaxis, rheotaxis) can change. An increase in temperature can change a positive rheotaxis to a negative rheotaxis. Mihara (1958, cited by Bakkala, 1970) found that chum fry in Hokkaido streams displayed a negative rheotaxis and moved downstream quickly when the temperature reached 15°C. This was interpreted as an adaptive response to avoid the high summer stream temperatures.

1. Temperature

Bams (1969) demonstrated a very close correspondence between water temperature and the numbers of chum fry emerging from the gravel in a laboratory in British Columbia. There were about eight fry emerging per hour at 5.3°C and about 48 per hour at 7.2°C.

Emergence and outmigration of chum fry from the Delta River has been observed at temperatures of 3.0 to 5.5°C, (Raymond, 1981). The temperature range observed during the peak of chum fry outmigration from the Salcha River was 5 - 7°C (Trasky, 1974).

Downstream migration of chum fry in Hokkaido begins in early April at water temperatures of 2.0 to 3.0°C but does not reach a peak until early to mid-May when water temperatures are 6.0 to 10.0°C (Sano, 1966). There are other factors as well, such as the rise in water level from melting snow in May. Semko (1954, cited by Sano, 1966) measured water temperatures of 4.6 to 5.5°C during the downstream migration of chum fry in April, May and June in the Bolshaia River.

Levanidov (1954) reported that chum salmon fry in the Amur River of Siberia can survive water temperatures up to about 15°C but that they prefer temperatures of 8° to 10°C.

Brett (1952) noted that young chum salmon (three to six months after hatching) in experimental tanks generally avoided temperatures above 15°C and preferred temperatures of 12 to 14°C. He found a lower lethal temperature for young chums of 0°C and an upper lethal temperature of 23.8°C. The young chums could acclimate to 23°C, but not to 24°C. In further experiments, Brett and Alderdice (1958) showed that the ultimate lower lethal temperature is 0.1°C.

Bell (1973) gives the migration temperature range of juvenile chum salmon as 6.7 to 13.3°C.

McNeil and Bailey (1975) state that Pacific salmon fry will grow in the temperature range 4.4 to 15.7°C, but that the ideal range is 10.1 to 12.9°C. Below 10.1°C, growth is slow and at 15.7°C and above, there are problems with diseases and other stresses. Fry can tolerate temperatures of 20° to 22°C for limited periods but prolonged periods at 18.5°C and above cause severe stress and prolonged periods at 21.3°C and above can cause mortality.

In experiments examining the culture of juvenile chums from Oregon in heated seawater, Kephshire (1976) found that growth was similar at 12.9, 15.7, and 18.5°C, but gross food conversion efficiency decreased with an increase in temperature. There was good survival at these temperatures, but not at 21.3°C.

Levanidov (1956, cited by Bakkala, 1970) found in the laboratory that the growth rate of Amur River chum fry was three percent of body weight per day at 8°C and five to six percent at 14 to 20°C. Temperature can also modify behavioral patterns. Keenleyside and Hoar (1955) found that most chum fry in an experimental situation exhibited a positive rheotaxis (swimming into the current) at 6 to 9°C and a negative rheotaxis (swimming with the current) at 10 to 13°C. A higher percentage exhibited negative rheotaxis at 17 to 19°C and an even higher percentage did so at 18 to 21°C.

2. Cover

Chum fry in short streams migrate mainly at night and seek cover in the substrate during the daytime if the journey is

not completed in one night (Neave, 1955). Observations by Hoar (1956) indicate that chum fry, after schooling, use the protection of the schools and no longer seek protection in the substrate. Saltwater increases the schooling tendency of the fry (Shelbourn, 1966).

Predation can be a major source of mortality (Hunter, 1959; Kirkwood, 1962). Hunter (1959) estimated that predation ranged from 23 to 85 percent in Hooknose Creek, B.C. Predators in Hooknose Creek include: coho salmon smolts, Aleutian sculpin, prickly sculpin, Dolly Varden char, cutthroat trout and steelhead trout. Kingfishers, mergansers, and certain mammals have also been mentioned as predators (Scott and Crossman, 1973).

3. Substrate

In addition to providing cover from predators, gravel substrate is apparently necessary to maintain orientation for those fry that still have a yolk sac upon emerging. In an experimental situation, Emadi (1973) found that chum alevins kept on a smooth substrate had a higher percentage of malformed yolks (30%) than another group kept on a gravel substrate of particles 2 to 3 cm in diameter (no malformed yolks), both in a current velocity of 100 cm/hr. McNeil and Bailey (1975) have also pointed out that when Pacific salmon are being artificially raised in hatcheries, the alevins and fry must be provided with a gravel substrate after emergence.

4. Food

In short streams where the outmigration is completed in a day or two, chum fry may feed very little, if at all. In longer streams and river systems they do feed and gain

weight during the course of their seaward migration. Fall chum fry of the Amur River may spend up to a month feeding in the spawning grounds (Levanidov, 1954). Chum fry from the Noatak River apparently feed in the lower 10 km or so until at least early August (Frank Bird, pers. comm.). This is also the case at the mouth of the Yukon River (W. Arvey, pers. comm.). Benthic organisms, mainly aquatic insects, are the dominant food species in freshwater. Prey species include chironomid larvae, nymphs of stoneflies and mayflies, caddisfly larvae, blackfly larvae, blackflies, mosquitoes, mites, and thrips, and other terrestrial insects.

Levanidov (1954) calculated that there was enough food in the River Khor to support 40 chum fry per square meter. He found that the food requirements of fall chum fry amounted to 8 to 10% of their body weight per day at 6 to 8°C and 17 to 20% of their body weight at 17 to 18.0°C. Levanidov also states that certain chum fry in freshwater with high food requirements would be unlikely to survive more than two or three weeks without food. Levanidov and Levanidova (1951) calculated that chum fry in Lake Teploe consumed about 27% of their body weight daily.

Volovik (1968) estimated that chum fry in the rivers of Sakhalin require 18.0 to 123.0 mg food per day, which was 5.2 to 9.0% of body weight.

5. Light

Chum fry exhibit responses to light (phototaxis) which aid them from streams in reaching the ocean during their outmigration. Loss of visual orientation at night leads to downstream displacement. An increasing daylength in the spring affects the thyroid system which increases salinity

tolerance and preference and the development of a capability for osmoregulation (Baggerman, 1960, Shelbourn, 1966). Hoar (1957) demonstrated that schools of fry show a preference for light, but exhibited no marked response to changing light intensity. Strong light is avoided (Neave, 1955).

6. Salinity

The preference of chum fry for higher salinities and their ability to osmoregulate in seawater increases with increasing age (Baggerman, 1960; Houston, 1961). At the onset of downstream migration, chum fry in an experimental situation preferred saltwater to freshwater (Baggerman, 1960).

Chum salmon fry that have absorbed their yolk sac can tolerate full strength seawater (Kashiwagi and Sano, 1969; McNeil and Bailey, 1975; Weisbart, 1968). Salinity tolerance increases with age after hatching and is related to an increasing capability for osmoregulation (Kashiwagi and Sano, 1969). Kashiwagi and Sano (1969) found that chum salmon 60 days after hatching and older can survive an abrupt transfer to 100% seawater (35 ppt). Conversely, Levandov (1952) found that fry captured during their seaward migration in the Khor River could survive transfer to water with salinities of 7.0 ppt and 17.1 ppt, but 8 out of 10 died in a salinity of 35.0 ppt. The period of acclimatization was characterized by an increase in the rate of respiration. Houston (1959) noted that an abrupt transfer of chum fry to seawater of 22 to 24 ppt. reduced their cruising speed to about 68% of the normal rate. After about 36 hours, the cruising speed was nearly back to normal, which ranged from about 19 cm/sec for 3.9 cm long fry to about 36 cm/sec for fry 4.9 cm long. Houston

suggested that this depression in cruising speed might be related to osmoregulatory adaptation.

Shepard (1948) conducted experimental studies on the interaction of current velocity and temperature in relation to salinity preferences of chum fry. The fry were initially presented with a choice between two flows. When one flow was freshwater and the other was seawater, they chose the seawater flow, regardless of relative strengths of the flows (flow difference of about 1.3 cm/sec). When both flows were freshwater and one was 10°C and the other 12.5°C, they chose the 10°C flow (they had been acclimated to 10°C). If the 12.5°C flow was seawater, they still initially preferred the 10°C freshwater flow, but gradually changed to the 12.5°C saline flow. These experiments demonstrated that no one parameter has a definitive effect and that the interaction of the three parameters plays an important role in governing the seaward migration of fry.

Chum salmon fry appear to have a physiological requirement for seawater within three or four months after emergence for normal development. This is not related to their need for access to the ocean for normal feeding. They have been raised experimentally to the adult stage in freshwater but this required especially careful handling (Hoar, 1976). Chum fry in natural systems whose access to the ocean was restricted would probably not survive.

7. Dissolved Oxygen

Levanidov (1954) stated that the threshold for the asphyxia of chum fry at 10°C occurs at a dissolved oxygen concentration of 1.5 mg/l. He found no change in the feeding intensity, assimilation, or growth rate of fry over the range 5 to 11 mg/l. Lukina (1973) reported that 8-9

mg/l was the most favorable concentration for chum fingerlings (temperature 8-10°C).

McNeil and Bailey (1975) suggest that the dissolved oxygen level for Pacific salmon fry in hatcheries be kept no lower than 6 mg/l.

The oxygen requirements of fry vary with the temperature. Chum fry used $188 \text{ mm}^3 \text{O}_2/\text{g}$ body weight-hour at 8.6 to 9.0°C, 228 mm^3 at 10.0°, and 445 mm^3 at 20°C and fingerlings used $144 \text{ mm}^3/\text{g}$ body weight-hour at 9.0 to 9.4°C (Awakura, 1963 and Levanidov, 1955; both cited by Bakkala, 1970). Volovik (1968) found that chum fry about 4 cm long used about 0.26 mg O_2/g live weight-hour (8.0°C) and fry about 5 cm long consumed around 0.61 mg O_2/g live weight-hour (7.3°C). Oxygen consumption varied during different hours of the day.

8. Stream Flow and Current Velocity

In experimental chambers in which chum salmon fry were presented with a choice between two channels with different "laminar" flows, MacKinnon and Hoar (1953) found that the fry preferred 350, 500, 600 and 700 ml/min flows to a flow of 200 ml/min; the greatest response was toward the 500 ml/min flow. In another experiment with "turbulent" water flow, the fry seemed to prefer flows of about 5,000 to 12,000 ml/min over either lesser or greater flows. They always exhibited a positive rheotaxis.

Levanidov (1954) stated that optimum stream velocities to support the feeding of fry in the Amur River are less than 20 cm/sec.

III. CONCEPTUAL MODEL OF HABITAT SUITABILITY

Suitability index curves in a conceptual form are presented for water temperature, stream depth, current velocity, dissolved oxygen concentration and salinity in Figures 2 through 5. The suitability index for each environmental parameter ranges from zero to one. An index of one indicates an optimum or preferred level of that particular parameter and an index of zero indicates a completely unsuitable level. These curves should not be construed as a graphical presentation of actual data. Rather, they are intended to be hypothetical models of the relationship between chum salmon and certain environmental parameters. As with any untested hypothesis, they must be tested and verified before being applied to any particular situation. The curves are based on published and unpublished data and on conversations with fishery biologists who have worked with chum salmon. Both experimental laboratory data and field measurements and observations were used. The published data base is summarized in Tables I through IV.

A problem encountered in constructing the curves is that much of the data in the literature concerning environmental parameters of chum salmon habitat does not relate various levels of the parameters to some measure of habitat suitability. Often, ranges of the parameter are given based on measurements taken throughout the area occupied by chums but there is no indication that one point on the range is any better or worse than any other point in terms of habitat suitability. A good example is stream velocity measurements in spawning areas. A measurement of spawner density is needed from throughout the range of stream velocities where spawners are found. This kind of information is rare in the literature. More useful data has been collected in the case of measurements of dissolved oxygen concentration of intragravel water, which are frequently linked with percent survival to emergence.

The curves are drawn using data from throughout the natural range of the chum salmon. Although there are differences in habitat

preferences and tolerances for different stocks in different geographical areas or even in different streams of the same geographical area, there is not enough data to support drawing separate curves at this time. However, one must be aware that any point on the curve, especially toward either extreme, may be more suitable or less suitable for a particular stock. It may even be that the extremes are completely unsuitable. How far the stock deviates from the curve must be determined by field measurements and experimentation with that particular stock.

A second precaution regarding use of the curves concerns the interaction of various parameters. A given level of one parameter can have a different effect on the fish as the level of another parameter varies. For example, a dissolved oxygen concentration of 5 mg/l may be suitable at a water temperature of 5°C, but unsuitable at a temperature of 20°C. Ideally, given enough data, a separate dissolved oxygen curve should be drawn for each of several different temperatures. The overall suitability of any particular habitat is a summation of interacting effects of many parameters.

A third precaution to consider is that the effect on the fish of less than optimum levels of any parameter depends strongly on the duration of exposure. Exposure to seawater may have little effect on chum embryos in the upper sections of the intertidal zone of a stream where they are exposed for short periods at high tide, whereas longer exposure to seawater in the lower sections of the intertidal zone may have a severe effect on the embryos.

Also, because different life stages have different requirements, information on embryos and alevins (Figure 4) should not be drawn as one curve. Because of insufficient data, it was drawn this way and, if nothing else, points out the need for more field measurements during these life stages. In fact, there should be different curves for different ages of embryos and for alevins of different ages after hatching. It has been shown that at least the oxygen requirements of

chum salmon embryos and alevins vary considerably for different ages (Alderdice et al., 1958).

Despite the fact that there is not enough known about the habitat needs of the chum salmon to construct accurate suitability index curves, the ones that are presented in this section do serve a useful purpose. Overall, they provide an indication of what would make a desirable chum habitat and what would make a less desirable habitat. Also, although they are general, they are probably specific enough to show that there are differences in habitat needs among chum salmon and the other species of Pacific salmon. Further, the process of constructing these curves is beneficial in defining those areas where more data is needed. Lastly, these curves can aid in the design of experiments and sampling programs. As more data becomes available, these hypothetical curves can be further refined. At the present, they are only conceptual models which synthesize available data in the form of graphs.

The overall suitability of a particular reach of a stream as habitat for chum salmon is a summation of all the suitability index curves for particular parameters and would include other parameters for which there was not enough information to construct curves. For example, the habitat suitability of a particular spawning substrate would be an aggregation of suitability index (SI) curves for all parameters during spawning and during incubation of embryos and alevins. The most likely aggregation function which would define a habitat suitability index (HSI) for chum salmon would be that of limiting factors. This aggregation function takes the form:

$$HSI = \text{minimum} (SI_1 + SI_2 + \dots + SI_n).$$

In other words, the habitat suitability index could not be any higher than the lowest suitability index value of the spawning substrate for any one parameter. If the dissolved oxygen regime of the intragravel water has a suitability index value of 0.5, then the HSI, or the

ability of the spawning substrate to support the successful production of chum salmon relative to other areas, could be no higher than 0.5 even if all other parameters (substrate size, water depth, temperature, and so on) had optimum values ($SI = 1.0$).

Different environmental parameters have different degrees of importance in contributing to the quality of chum salmon habitat. Parameters which were not drawn in the form of curves for the upstream migration phase of the life history because of insufficient information were: current velocity, water depth, physical obstructions, and turbidity. These four are all important factors and perhaps, in Alaska, are more important than water temperature (which is shown graphically), and should be included in any habitat suitability index which might be constructed.

During the spawning phase of the life history, one of the most important factors that determines the habitat quality of a particular reach of stream is the composition of the streambed. It was not possible to satisfactorily show the relationship between the particle size distribution of the streambed and habitat quality in a two-dimensional plot. Water depth, current velocity, and temperature are also important factors during spawning.

The development of embryos and alevins in the substrate is perhaps the most critical stage in the freshwater life history of the chum salmon. One of the most important factors during this stage is the permeability of the substrate or the amount of water flow through the substrate. This parameter has a strong influence on many other parameters such as intragravel temperature, oxygen supply, and concentration of waste metabolites. Unfortunately, there are few measurements of permeability or intragravel flow in chum spawning gravels and it was not possible to construct a curve. The particle size distribution of the substrate is the most important factor determining the permeability. Curves were not constructed for surface current velocity or stream depth. These two are of much less

importance than intragravel flow. Salinity, which was placed in the form of a curve, can be a major limiting factor in intertidal streambeds. Chemical parameters such as carbon dioxide concentration and pH, which were not graphed, can be limiting factors in some areas where upwelling ground water have values outside the limits preferred by chums.

Curves were constructed for temperature and salinity, which were graphed for the emergence and outmigration of fry stages. The amount and duration of daylight is important but is a given factor for this time of year. Stream flow is also important, but the appropriate discharge rate is unique to each stream.

In summary, more information is needed on several environmental factors before it will be possible to assign a habitat suitability index to any particular area. More detailed information on the deficiencies of the data base is provided in Section IV.

**CHUM SALMON
ADULTS**

See text for qualifications
for use of this curve.
(NOT RECOMMENDED FOR APPLICATION
TO SPECIFIC WATERSHEDS WITHOUT
FIELD VERIFICATION)

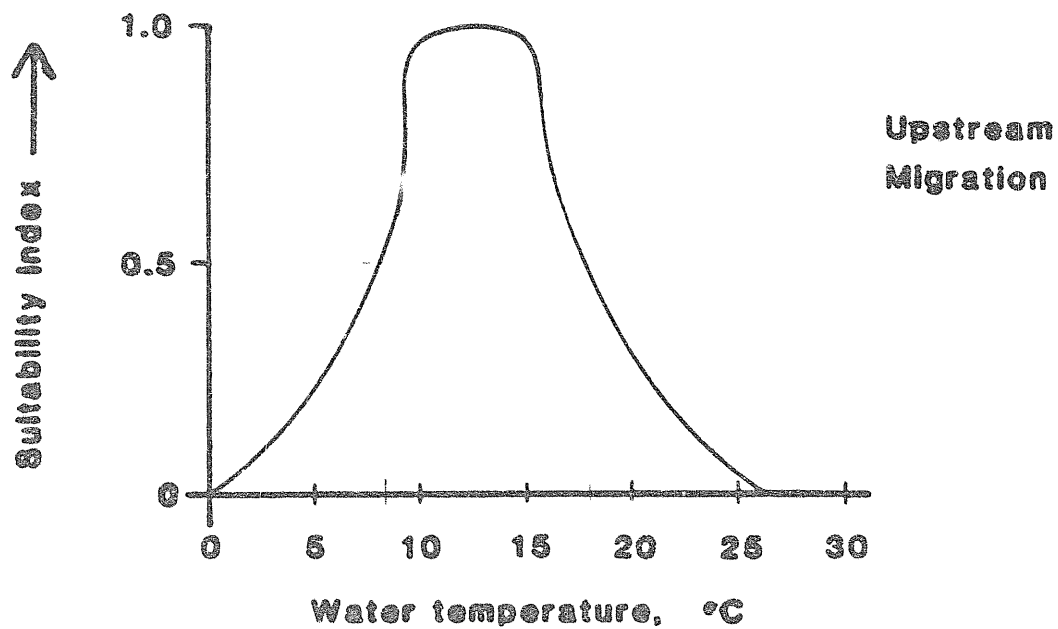


Figure 2. Conceptual model of relationship between adult Chum salmon and water temperature.

**CHUM SALMON
ADULTS**

SPAWNING

See text for qualifications
for use of these curves.
(NOT RECOMMENDED FOR
APPLICATION TO SPECIFIC
WATERSHEDS WITHOUT FIELD
VERIFICATION)

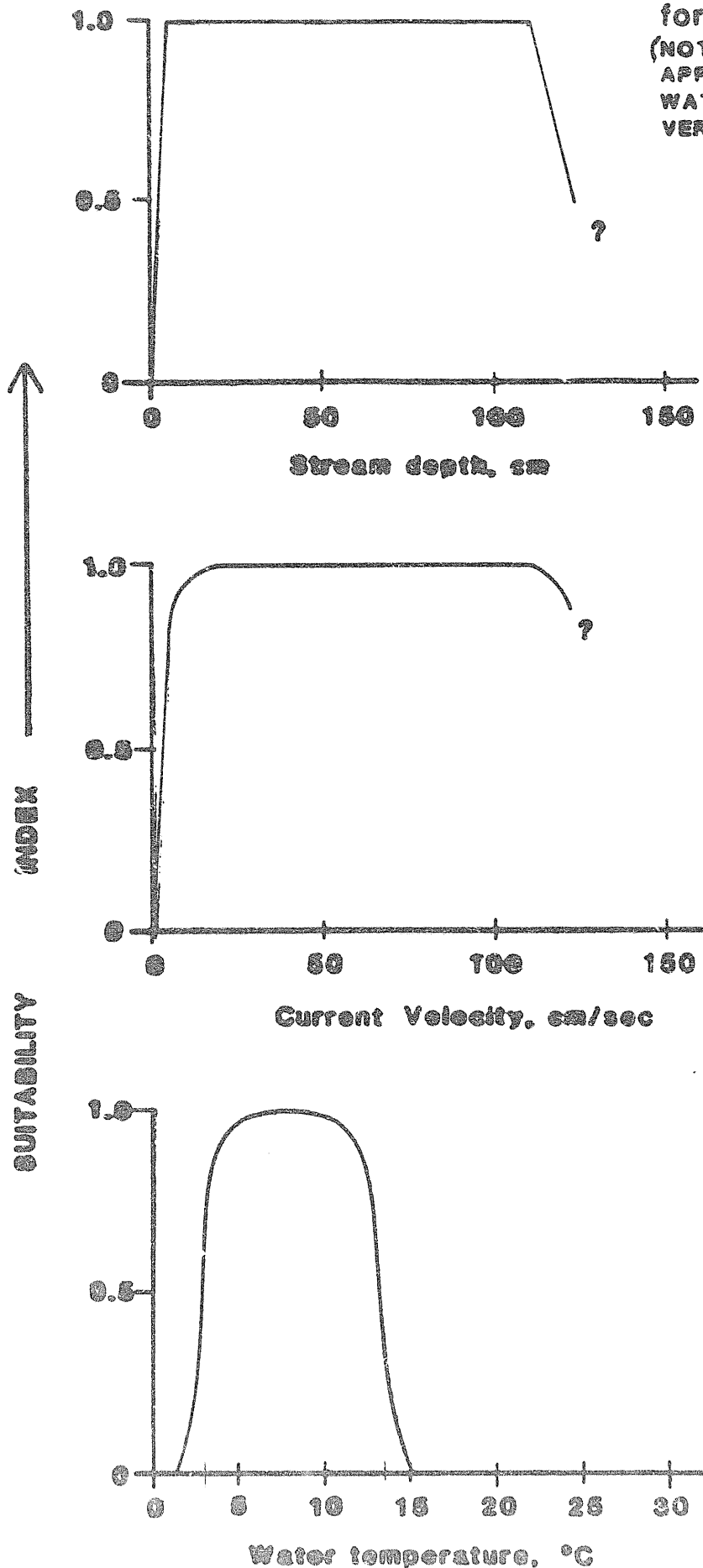


Figure 2. Conceptual model of relationship between adult Chum salmon and stream depth, velocity, and water temperature.

CHUM SALMON EMBRYOS AND ALEVINS

INCUBATION

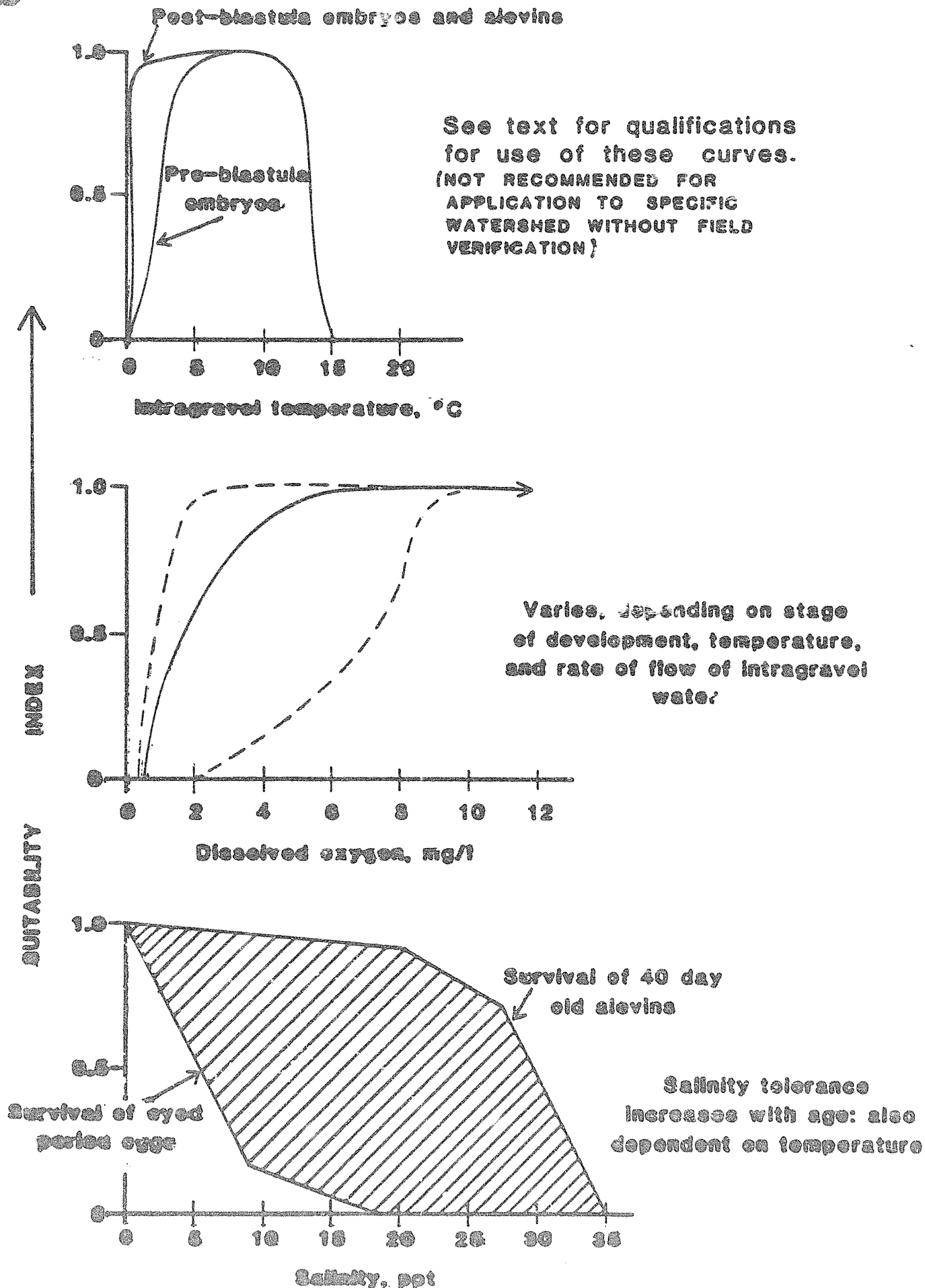


Figure 4. Conceptual model of relationship between Chum salmon embryos and alevins and intragravel temperature, dissolved oxygen concentration, and salinity.

CHUM SALMON
FRY

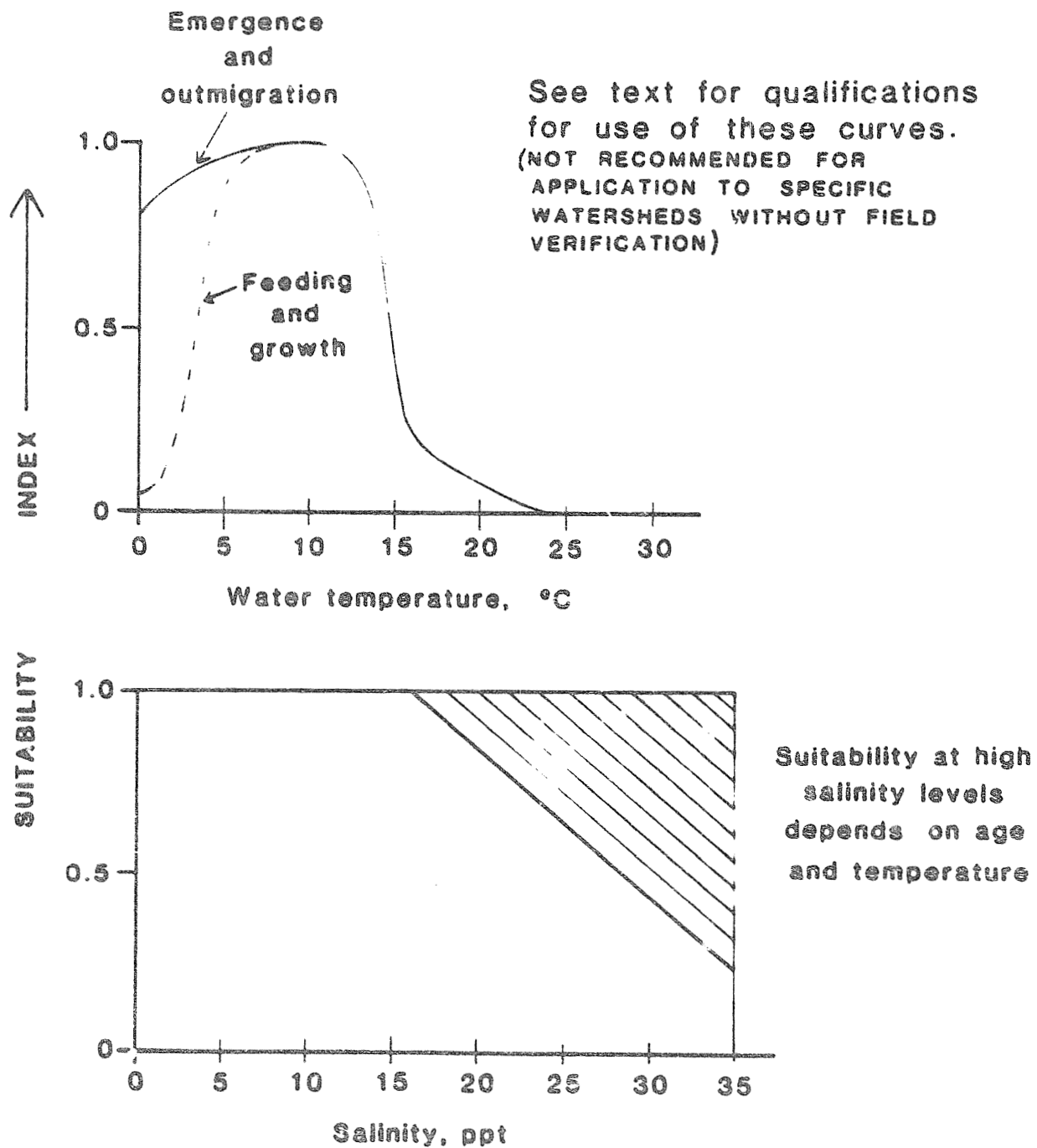


Figure 5. Conceptual model of relationship between Chum salmon fry and water temperature and salinity.

Table I.

CHUM SALMON

Adults - Upstream Migration

Parameter	Observed Values	Remarks	Location	Reference
Temperature °C	4.4 - 19.4	total range	Traitors River	Mattson and Hobart (1962)
	8.9 - 14.4	range during peak migration		
	5.0 - 12.8	range during upstream migration	Tribs. of Kuskokwim River	ADF&G (1980a)
	10.0 - 16.7	during peak of upstream migration	Anvik River	Trasky (1974)
	8 - 14		Hooknose Ck., B.C.	Hunter (1959)
	8.3 - 21.1	range for the species		Bell (1973)
	10.1	optimum value		
	0, 25.6	lower and upper lethal limit		
	0.1 - 20.0	total range	Northern Japan	Sano (1966)
	7 - 11	range during peak of migration		
	11 - 12		Memu River, Japan	Sano and Nagasawa (1958)

Table II.

CHUM SALMON

Adults - Spawning

Parameter	Observed Values	Remarks	Location	Reference
Temperature °C	6.5 - 12.5		Terror and Kizhuyak R.	Wilson et al. (1981)
	≤13	most spawning	Sashin Creek	McNeil (1964)
	ca. 12 4 - 16		Hooknose Creek, British Columbia	Hunter (1959) Neave (1966)
	2.5	inhibited spawning behavior	Big Beef Creek, Washington	Schroder (1973)
	<15		Big Beef Creek, Washington	Koski (1975)
	4.4 - 6.7	range during part of spawning season	tribs of lower Columbia	Burner (1951)
	7.2 - 12.9	suggested criteria for species		Bell (1973)
	1.8 - 8.2		Sakhalin, USSR	Rukhlov (1969a)
	5 - 6	most spawning	South Kuril Isl. USSR	Ivankov and Andreyev (1971)
	9.5 - 12.8	mean temperatures, summer chum	Amur River, USSR	Soin (1954)
	9 - 10	summer chum	Amur River, USSR	Sano (1966)
	ca. 6	autumn chum		
	2 - 9	bottom water	Iski River, USSR	Smirnov (1947)
	6 - 9		Memu River, Japan	Sano and Nagasawa

Table II Cont'd.

CHUM SALMON

Adults - Spawning

Parameter	Observed Value	Remarks	Location	Reference
Water depth, cm	61.0 - 91.5	partial range	Delta River	Francisco (1976)
	5 - 120		Chena River	Kogl (1965)
	7.6 - 106.7		Terror and Kizhuyak R.	Wilson et al. (1981)
	5.1 - 72.2 25.4	range mean	Tribs of lower Columbia River	Burner (1951)
	≥ 18		Oregon streams	Thompson (1972, cited by Reiser and Bjornn(1979)
	18	minimum depth	Oregon streams	Smith (1973)
	15 - 53	preferred depth	Western Washington	Collings (1974)
	23 - 46	recommended depth	Wynochee River, Wash.	Deschamps et al. (1966, cited by Smith, 1973)
	60 - 100	preferred depth	Amur River, Kamchatka, USSR	Kusnetzov (1928)
	30 - 100	summer chum	My River, USSR	Soin (1954)
	20 - 110		Northern Japan	Sano (1959, cited by Bakkala, 1970)
	<20 - 100+ 20 - 30 <100	range redds most abundant redds least abundant	Memu River, Japan	Sano and Nagasawa (1958)

Table II - Cont'd.

CHUM SALMON

Adults - Spawning

Parameter	Observed Values	Remarks	Location	Reference
Stream Velocity, cm/sec	0 - 60		Chena River	Kogl (1965)
	0.0 - 118.9		Terror and Kizhuyak Rivers	Wilson, et al. (1981)
	46 - 97		Oregon streams	Thompson (1972, cited by Rieser & Bjornn (1979)
	46 - 101	range, $\bar{V}$ 12.2 cm above bed	Oregon streams	Smith (1973)
	73	mean		
	21 - 101	$\bar{V}$ 12.2 cm above bed	Western Washington	Collings (1974)
	31 - 70	recommended range	Wynoochee R., Wash.	Deschamps et al. (1966, cited by Smith, 1973)
	10 - 80		My River, USSR	Scin (1954)
	20 - 100		My River, USSR	Strekalova (1963)
	10 - 90	most spawning	Sakhalin, USSR	Rukhlov (1969a)
	10 - 30	characteristic	Bolshava R. Basin USSR	Krokhin and Krogus (1937, cited by Nicola et al., 1966)
	<10 - 35	range	Memu R., Japan	Sano and Nagasawa (1958)
	15 - 20	redds most abundant		
	<10 & 30-35	fewer redds		

Table II - cont'd.

CHUM SALMON

Adults - Spawning

Parameter	Observed Values	Remarks	Location	Reference
Substrate Particle Size	gravel 2 - 3 cm in diam., also use coarser stones and even bedrock covered with small boulders		Alaska	Morrow (1980)
	gravel mostly 1.27-127.0 cm with variable amount of fines	spawning grounds	Delta River	Francisco (1976)
	stones 1.3-13.0 cm, coarse sand, fine sand and silt		Hooknose Creek, B.C.	Hunter (1959)
	gravel I > 2.69 cm (98%)	gravel sizes II and III selected by 75% of spawning females; gravel I selected by 20%, gravel IV selected by 5%	Big Beef Creek	Duker (1977,
	gravel II 1.35 - 7.61 cm (97%)			
	gravel III 0.67 - 2.69 cm (96%)			
	gravel IV 0.02 - 0.67 cm (96%)			
	1.3 - 10.2 cm	substrate size criteria for species		Bell (1973)

Table II - Cont'd

CHUM SALMON

Adults - Spawning

Parameter	Observed Values	Remarks	Location	Reference
Substrate Particle Size	gravel mixed with sand, small amount of silt		Amur River, USSR	Soin (1954)
	"sand" (0.8 - 52.8%, av. 12.0 - 12.7 %)	spawning grounds	Sakhalin	Rukhlov (1969b)
	"gravel" (10.0 - 50.1%, avg. 33.0 - 45.9%)			
	"shingle" (6.0 - 84.1%, avg. 41.4 - 44.4%)			
	>10 cm (0.0 - 73.9%, avg. 0.0 - 10.0%)			
	"sand" (14 - 22%)	decreased survival to emergence	Sakhalin	Rukhlov (1969b)
	0.5 cm (25%), 0.6 - 3.0 cm (45%), 3.1 cm (30%)		Northern Japan	Sano (1959, cited by Bakkala, 1970)
	particles 0.5 cm (always 20%)	spawning grounds	Memu River, Japan	Sano and Nagasawa (1958)
	particles 3.0 cm (25 - 53%)			

Table III CHUM SALMON

Embryos and Alevins - Intragravel Development

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	0.5 - 4.5		Chena River	Kogl (1965)
	2.0 - 4.2, 3.6 - 4.5	higher mortality at lower range	Clear hatchery	Raymond (1981)
	2.0 - 4.5	emergence delayed beyond that of wild fry incubated at 3.9°C		
	0.2 - 10.0		Noatak River	Merritt and Raymond (in prep.)
	0 - 4	probe 20.3 cm deep	Olsen Creek	Bailey (1964)
	0.4 - 6.7		Delta River	Francisco (1977)
	<1.5	during early development stages, leads to higher mortality	Big Beef Creek, Washington	Schroder et al., (1974, cited by Koski, 1975)
	4.4	lowest limit for good survival	Big Beef Creek, Washington	Schroder (1973)
	4.4 - 13.3	suggested criteria for species		Bell (1973)
	4.4	lowest temp. prior to closure of blastopore (Pacific salmon), then can go as low as 0°C and still have good survival		McNeil and Bailey (1975)
	3.5 - 5.0	range, fertilization to emergence	Bira River, USSR	Disler (1951)

Table III Cont'd.

CHUM SALMON

Embryos and Alevins - Intragravel Development

Parameter	Observed Values	Remarks	Location	Reference
Temp. Cont'd	3.9 - 4.9	egg stage	Bolshaia River, USSR	Semko (1954, cited by Sano, 1966)
	2.4 - 3.0	alevin stage		
	7.0 - 11.0		Memu River, Japan	Sano and Nagasawa (1958)
	4.0	lowest temp. in redd during winter	Northern Japan	Sano (1966)
Substrate Particle Size	finer <0.0833 cm (>12.7%)	poor quality substrate	Prince William Sound	Thorsteinson (1965)
	silt and sand (6%), <15cm (81%), >15 cm (13%)	redds	tributaries of lower Columbia River	Burner (1951)
	5.1 - 10.2 cm 1.0 - 3.8 cm	greater survival to emergence in larger gravel	Robertson Creek, British Columbia	Dill and Northcote (1970)
	sand, 0.0105-0.3327 cm (ca. 5 - 50%)	lower survival to emergence and smaller fry at higher percentages	Big Beef Creek, Washington	Koski (1975)
	mostly 0.2 - 1.0 cm, some particles >2.0 cm	redds - also, redd had less of the 0.025 - 0.1 cm fractions, but more sand and mud than spawning gravel	Sakhalin	Rukhlov (1969a)
	"sand" (1.8 - 30.0%, avg. 10.0 - 13.5%)	redds	Sakhalin	Rukhlov (1969b)
	"gravel" (13.4 - 60.0%, avg. 33.5 - 40.3%)			

Table III - Cont'd.

CHUM SALMON

Embryos and Alevins - Intragravel Development

Parameter	Observed Values	Remarks	Location	Reference
Substrate Cont'd	"shingle" (13.7 - 75.9%, avg. 39.2 - 53.0%) > 10 cm (0.0 - 50.0%, avg. 0.7 - 9.5%)			
Dissolved Oxygen, mg/l	> 2	good survival of eggs and alevins (strong flow of groundwater)	Chena River	Kogl (1965)
	0.6 - 3.0	low survival		
	2.8 - 6.5	high survival		
	2.1 - 4.1	smaller alevins produced at lower end of range		
	0.0 - 12.7	annual range	Twelvemile Creek	McNeil (1962)
	5.4 - 8.9	September and November	Indian Creek	
	1.77 - 6.80	July - September, lowest caused by long dry period	Traitors River	Mattson et al. (1964)
	3.6 - 8.3	upper intertidal area July - September, low percent survival at low end of range	Olsen Creek	Bailey (1964)
	<3.0	survival to emergence de- creases, emergence is delayed	Big Beef Creek, Washington	Koski (1975)
	3.6 - 7.6	same rate of egg development, but eggs held at the highest value produced the largest fry	Washington	Cheyne (1941, cited by Nicola et al., 1966)
	0.72 - 3.70	critical values for embryos 0-85 days old	British Columbia	Wickett (1954)
	2	lethal limit for hatching eggs and alevins at 5°C		

Table III - Cont'd.

CHUM SALMON

Embryos and Alevins - Intragravel Development

Parameter	Observed Values	Remarks	Location	Reference
Dissolved Oxygen, mg/l	0.72 - 7.19	critical values for eggs with temp. units (°F) from 4.0 - 452.4	British Columbia	Alderdice et al. (1958)
	2	lethal limit for eggs	British Columbia	Wickett (1957)
	5	low		
	8	desirable		
	> 2	good survival of eggs and alevins as long as there is a strong ground water outflow	Amur River, USSR	Levanidov (1954)
	6 - 8	most favorable level for entire development period of embryos and larvae at 4-8°C	N. Okhotsk, USSR	Lukina (1973)
	3 - 4	lowest value in redds	Bira River, USSR	Disler (1951)

Embryos and Alevins - Intragravel Development

Parameter	Observed Values	Remarks	Location	Reference
Water depth, cm	7.6 - 43.2	depth of redds, range	tributaries of lower Columbia River	Burner (1951)
	21.6	average depth of redds		
	16 - 104	summer chum		
	3 - 34	fall chum	Beshenaya River	Smirnov (1947)
Stream Velocity, cm/sec	0 - ?		Chena River	Kogl (1965)
Intragravel apparent velocity, cm/hr	10	minimum for survival	British Columbia	Wickett (1957)
	50	desirable level		
	200	minimum recommended for Pacific salmon hatcheries		
	ca. 25 - 150	percent survival to emergence increases as velocity increases		
				McNeil and Bailey (1975)
				Reiser and Bjornn (1979)

Embryos and Alevins - Intragravel Development

Parameter	Observed values	Remarks	Location	Reference
Salinity (ppt)	0 - 25	eggs and alevins exposed to lower levels had higher survival (temp. and oxygen level also factors)	Prince William Sound	Thorsteinson (1965)
	0 - 11	eggs can tolerate continuous exposure		McNeil and Bailey (1975)
	15 - 30	eggs can tolerate intermittent exposure		
	<6	no effect on early egg stages	Washington (laboratory)	Rockwell (1956)
	6 - 8.5	50% of fully developed can survive through hatching	Washington (laboratory)	
	>11.6	retarded egg development		
	9 - 35	rate of hatching for eyed period eggs declined from 100% at 9 ppt to 25% at 35 ppt; alevins hatched at higher salinities did not survive	Japan (laboratory)	Kashiwagi and Sato (1969)
	0 - 35	delay in hatching and decreasing survival as salinity increased		
	<9	good survival of alevins		

Table III Cont'd

CHUM SALMON

Embryos and Alevins - Intragravel Development

Parameter	Observed Values	Remarks	Location	Reference
ph	6.5	intragravel	Chena River	Kogl (1965)
	"slightly acidic"	intragravel	Amur River, USSR	Levanidov (1954)
	6.3 - 6.5	intragravel	Hokkaido, Japan	Kobayashi (1968)
CO ₂ , mg/l	> 10	percent survival to hatching decreases	British Columbia (laboratory)	Alderdice and Wickett (1958)
	48	high value in some sections of intragravel water	Big Beef Creek, Washington	Koski (1975)
	25 - 30	range for ground water	Amur River, USSR	Levanidov (1954)
	> 20	inhibitory to development rate of eggs		
	16 - 20	intragravel water	Bira River, USSR	Disler (1951)
	17.8 - 25.2	intragravel water	Hokkaido, Japan	Kobayashi (1968)

Table IV. CHUM SALMON

Fry - Emergence and Downstream Migration

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	3.0 - 5.5	emergence and outmigration	Delta River	Raymond (1981)
	5 - 7	range during peak of fry outmigration	Salcha River	Trasky (1974)
	5.3 - 7.2	greater rate of emergence at higher end of range	Port John, British Columbia	Bams (1969)
	12 - 14	preferred range, three months after hatching	British Columbia (laboratory)	Brett (1952)
	> 15	generally avoid		
	-0.1, 23.8	ultimate lower and upper lethal temperature	British Columbia (laboratory)	Brett & Alderdice (1958)
	12.9 - 18.5	good survival; growth rate similar over this range but gross food conversion efficiency decreases as temperature increases	Oregon (laboratory)	Kepshire (1976)
	21.3	survival is not good		
	6.7 - 13.3	preferred range for species		Bell (1973)
	8 - 10	preferred temp (over the range 5.2 - 19.0°C)	Amur River, USSR	Levanidov (1954)
	< 15	survive		
	4.5 - 5.5	outmigration	Bolshaia River, USSR	Semko (1954, cited by Sano, 1966)

Table IV - Cont'd.

CHUM SALMON

Fry - Emergence and Downstream Migration

Parameter	Observed Values	Remarks	Locations	Reference
Temp. Cont'd	2.0 - 3.0	fry become active when temp. reaches this level	Hokkaido, Japan	Sano (1966)
	6.0 - 10.0	peak of downstream migration		
Salinity, ppt	35	tolerated by fry that have absorbed yolk sac		McNeil and Bailey (1975)
	7.0, 17.1	tolerated by fry at least up to 30 hours	USSR (laboratory)	Levanidov (1952)
	35.0	8 out of 10 fry died		
	35	tolerated by fry 90 days from hatching and older	Japan (laboratory)	Kashiwagi and Sato (1960)

IV. DEFICIENCIES IN DATA BASE AND RECOMMENDATIONS

Chum salmon are the least studied of the five species of Pacific salmon found in North America (Merrell, 1970). There are only a few studies conducted in the laboratory on physiological tolerances of chum salmon to various physical and chemical parameters. Because of the interaction of the effects of several parameters in natural environments, it is important to isolate each parameter in the laboratory and expose the fish to a wide range of values for that parameter. This will provide an understanding of the true response of the fish and of the lethal limits. It is also important to examine the interaction of the effects of two or more parameters in a controlled situation. Much of the data in this report comes from field observations. It would be incorrect to refer to these as absolute requirements of the species because the extremes of the particular parameters may not have occurred at the time the field measurements were made.

Much of the actual data in this report comes from Japan or the Soviet Union. Another large block of data originated in Washington and British Columbia. Of all the published references taken as a source of data for generation of the curves in Section III, only four or five reported on work in Alaskan streams. This is the greatest deficiency in this document which is intended to focus on habitat conditions for chum salmon in Alaska. As a consequence, it is not possible to document differences in habitat preferences among different stocks or different geographical areas within the State, although many fishery biologists suspect that such differences exist. In fact, it was not possible to conclusively demonstrate differences in habitat preference between Alaskan chums and those from Washington or Hokkaido or Kamchatka.

Information on the timing and abundance of chum salmon during the upstream migration and, to a lesser extent, during the outmigration of fry is available in varying degrees of completeness from throughout

volume) is graphed versus particle size. Several different spawning gravels plotted in this fashion result in an envelope which describes the range. One further step is needed to make this method well suited to habitat evaluation and that is to outline those areas of the envelope that are optimum habitat and those areas that are less than optimum. This could be done quantitatively by using some measure of habitat quality such as the density of spawners or the number of eggs deposited per square meter or the percent survival to emergence per square meter. Presumably, the areas outside the envelope describe those substrates that are unsuitable for chum salmon.

The intragravel development of embryos and alevins is probably the period of the life history which has the greatest influence on production. Variation in one of several different parameters during this critical stage can dramatically influence the survival rate and can lead to strong or weak brood years. Yet, this stage of life history, occurring in winter, is the least studied in Alaska. Information is needed on virtually all the important environmental parameters during intragravel development. Intragravel temperature, dissolved oxygen concentration, flow, and substrate composition data are most needed. More information is needed on the differences in habitat tolerances and preferences that exist among different stages of development of embryos and alevins.

There is little information available on use of cover by fry during outmigration. Although chum fry do not overwinter in freshwater as do kings, cohos, and sockeyes, they do experience a high rate of mortality during their seaward migration.

In summary, much information is needed on habitat requirements, tolerances, and preferences of chum salmon during their entire freshwater life history in Alaska. A research program directed toward the intragravel period would greatly assist our understanding of the needs of chum salmon and also our understanding of the annual variation in their abundance.

the State. This information needs to be related to physical, chemical, and biological parameters of the environment in order to be useful for habitat evaluation.

No data were found on the swimming ability of adult chums during the upstream migration other than distance covered per day. Information on the maximum velocity possible over time and on their ability to overcome obstacles would be useful in determining whether certain streams are accessible to spawning chums.

Measurements of the current velocities and water depths in Alaskan streams during the upstream migration would be useful in establishing the range for those parameters. Daily stream temperature and discharge data from the time of breakup until after the upstream runs are completed, correlated with the number of spawners moving upstream, are needed to establish the optimum levels of those conditions when the peak run occurs.

Information is needed from Alaska on all parameters associated with spawning: water temperature, current velocity, water depth, and substrate composition.

Probably the greatest deficiency in the data base for the species throughout its range is information on the substrate used for spawning and for development of embryos and alevins. Much can be determined about the habitat quality of a particular reach of stream by the particle size distribution of the substrate. Much of the literature reviewed for this report described substrate in semi-quantitative terms such as "large" or "coarse" gravel. Methods used for describing substrates should be standardized in order to make comparisons with other areas more feasible. Some investigators use dry sieves, others use wet sieves. Some report on the percent passing each sieve size by volume, others use the percent passing by weight. A good method to use to describe spawning gravels would be that used by MacKinnon et al. (1961) where the cumulative percent sediment passing by weight (or

This report and the conceptual suitability index curves which were presented are based in part on a review of published and unpublished data which was collected by the original authors for purposes other than constructing such curves. The curves presented here need to be field tested. A research program is needed to check the accuracy of these curves, to further refine and narrow their ranges, and to determine differences in habitat relationships among different stocks.

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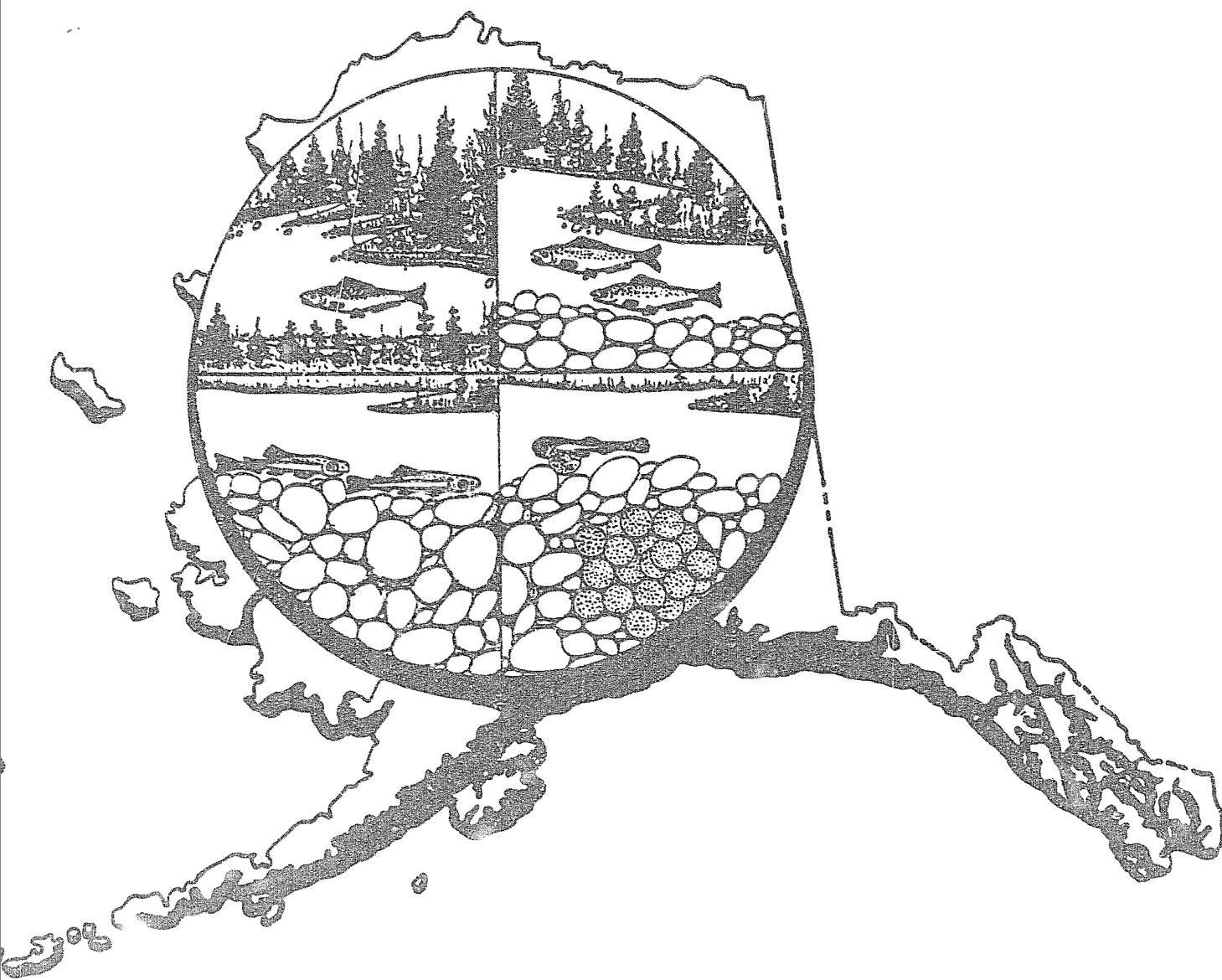
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FRESHWATER HABITAT RELATIONSHIPS

PINK SALMON - ONCORHYNCHUS GORBUSCHA



ALASKA DEPARTMENT OF FISH & GAME
HABITAT PROTECTION SECTION
RESOURCE ASSESSMENT BRANCH

APRIL, 1981

FRESHWATER HABITAT RELATIONSHIPS
PINK SALMON (ONCORHYNCHUS GORBUSCHA)

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I. INTRODUCTION

A. Purpose

The purpose of this project is to describe how selected physical and chemical features of lotic habitats within Alaska influence the survival and behavior of the freshwater life stages of pink salmon, Oncorhynchus gorbuscha (Walbaum).

Objectives of this project are:

- 1) To gather data from published and unpublished sources within Alaska, Canada, U.S.S.R., the Pacific Northwest, and Japan (with emphasis on Alaska), and from fishery biologists from Alaska and nearby areas concerning aquatic habitat - pink salmon relationships;
- 2) To develop an Alaskan data base composed of narrative and habitat suitability index (HSI) models following U.S. Fish and Wildlife Service techniques to better understand lotic habitat-pink salmon relationships; and,
- 3) To identify data gaps and recommend appropriate research to fill these gaps.

This report discusses the habitat relationships (with emphasis on the physical and chemical habitat components) of the fresh water life history stages of the pink salmon which include:

upstream spawning migration;
spawning;
egg, alevin development; and,
downstream fry migration.

B. Distribution

Pink salmon are the most abundant of the five species of Pacific salmon. They spawn in North American and Asian streams bordering the Pacific and Arctic Oceans and are more abundant in Asia than in North America (Scott and Crossman, 1973). In North America this fish ranges from northern California to northern Alaska and eastward to the Mackenzie River, Northwest Territories. Within Asia, the pink salmon is found from Korea and Hokkaido, Japan northward and westward to the Lena River, Siberia. Pink salmon have been introduced to and are maintaining populations in Lake Superior, Newfoundland, and northern Europe.

Pink salmon are widely distributed along coastal Alaska; major production areas include streams within the southern Alaska Peninsula area eastward to southeastern Alaska including the Chignik area, Kodiak Island, Cook Inlet, and Prince William Sound (Alaska Department of Fish and Game, 1978). More localized pink salmon production occurs in the lower Kuskokwim and Yukon River drainages and certain Norton and Kotzebue Sound streams. Pink salmon are found in the Yukon River drainage up to the Anvik River. Pink salmon abundance in streams above the Arctic Circle is relatively low, but they have been documented in limited numbers as far east as the mouth of the Mackenzie River.

C. Life History Summary

Pink salmon have the shortest life cycle of any Pacific salmon. They spend about 15 months in the sea and grow to about 1 to 3 kg (2.2 to 6.6 lbs), then migrate to coastal areas and usually ascend their natal streams to spawn and die. Explanations of timing and orientation of ocean migration by pink salmon are not thoroughly understood. Olfactory cues probably aid pink salmon in detecting their natal streams after the fish reach coastal

waters. However, pink salmon tend to stray more than the other species of Pacific salmon (Hasler, 1971; Morrow, 1980).

Pink salmon may enter Alaskan streams from June through October, but arrival and subsequent spawning times in a given stream are similar from year to year (Sheridan, 1962 b). Early, middle and late runs of pink salmon occur in southeast Alaska and Prince William Sound (Alaska Department of Fish and Game, 1978). The two year life cycle prevents consecutive, 'even' and 'odd' year stocks from interbreeding and produces genetically distinct 'even' and 'odd' year runs. The abundance of these runs often varies considerably.

Distance of from the estuary to spawning areas may influence the timing of upstream migration of pink salmon in large river systems. Pink salmon spawning in the upstream reaches of the Skeena River, northern British Columbia, traditionally arrive about two weeks earlier than fish that spawn in the lower reaches of the Skeena River (Neave, 1966).

The extent of upstream migration of pink salmon within streams is variable. They generally spawn within 40 miles of the ocean, but may ascend streams for considerable distances. Pink salmon have ascended the Yukon River as far as 160 km (100 mi), the Fraser and Skeena rivers up to 500 km (311 mi) and the Amur River. China up to 700 km (435 mi) (Scott and Crossman, 1973).

The relative abundance of fish can influence pink salmon distribution and the extent of upstream migration. During years of high abundance of pink salmon in various streams ('on' years), reaches of a stream or adjacent streams which normally support few, if any of these fish, may support substantial numbers of pink salmon (Neave, 1966).

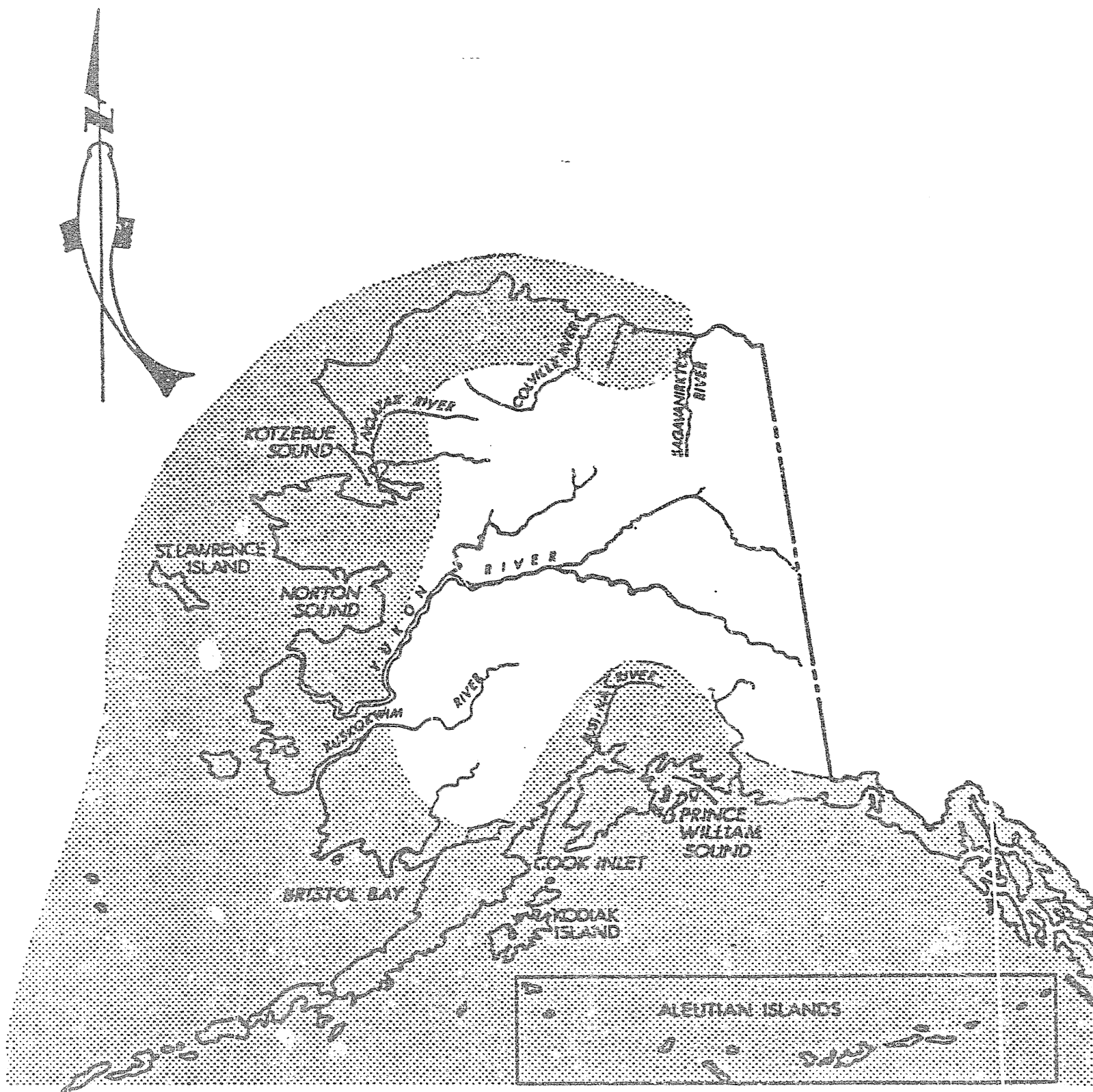


FIG.1. DISTRIBUTION OF PINK SALMON IN ALASKA
(ALASKA DEPT. OF FISH & GAME, 1978)

The spawning behavior of pink salmon is similar to other salmonids. The female is solely responsible for construction of the redd and the male defends the immediate redd area from other male pink salmon. The female excavates the redd by turning on her side and repeatedly flipping her caudal fin against the substrate, displacing silt, sand and gravels which are carried downstream. Some of the displaced substrate material forms a characteristic lip on the downstream end of the redd. Dimensions of the finished redd vary with the size of the female, current velocity, and substrate composition and imbeddedness. Redds can be as long as 91.5 cm (36 in) and up to 45.7 cm (18 in) deep. The spawning pair then descend into the center of the redd, with mouths agape and fins erect and release eggs and sperm. The fertilized eggs, 0.6 cm (0.24 in) in diameter, settle into interstices within the redd. Egg numbers may range from 800 to more than 2,000. The fecundity of pink salmon is variable and influenced by the size of the fish, the geographic area and the year (Scott and Crossman, 1973). After the pair completes spawning in the first redd, the female may begin construction of a new redd immediately upstream of the previous one. This activity displaces gravels into the first redd, covering the fertilized eggs. McNeil (1962) determined that pink salmon eggs within selected redds of several southeast Alaska streams were overlain by 0.08 to 0.41 m (0.25 to 1.33 ft) of gravel. This gravel layer protects the fertilized eggs from sunlight and predation, reduces mechanical disturbance by anchor ice and other objects, allows water to transport oxygen to and metabolic wastes from the developing eggs. The female guards the redd from disturbance by other females. A female may spawn with different males and both sexes die soon after spawning.

Streams used by pink salmon may range from extremely small, short coastal streams to large river systems like the Yukon River. Tidally and non-tidally influenced stream reaches are used for spawning. Intertidal spawning is especially characteristic of

pink salmon populations within Prince William Sound and southeast Alaska. (Helle, Williamson and Bailey, 1964).

Hatching of fertilized pink salmon eggs occurs in the spring. Hatching is followed by a period of alevin growth as the attached yolk sac gradually shrinks. Eggs and alevins remain in the redd gravels from 6 to 8 months.

Substantial mortality of pink salmon eggs and alevins (sometimes exceeding 75%, occasionally 90%) has been documented in selected reaches of various streams in Alaska and British Columbia (Wickett, 1952; Hunter, 1959; McNeil, 1962; Helle, Williamson and Bailey, 1964). McNeil (1962) determined greater mortality generally occurred during the egg than the alevin stage of development. Egg and alevin mortality appears to be the major limitation to production (McNeil, 1962; Bailey, 1969).

The fry emerge from the gravels in the spring (March to June) when development is complete. The newly emerged fry range from 3 to 4.5 cm (1.2 to 1.8 in) in length (Scott and Crossman, 1973). They immediately begin migrating downstream to the sea (Neave, 1966). Emergence and subsequent downstream movement of fry generally occurs shortly after dusk and ceases before dawn (Hoar, 1956; Godin, 1980). Pink salmon migrating down short coastal streams may reach the estuary within the first night of travel. Pink salmon fry migrating long distances downstream may cease migration during the day and conceal themselves in the substrate. They resume downstream movement at dusk. Limiting migration to dusk or dark probably minimizes predation (Neave, 1966). Pink salmon fry may migrate downstream during the day at flood flows, periods of high turbidity, or during the latter portion of fry emergence (Neave, 1966; MacDonald, 1960; Godin, 1980).

D. Ecological and Economic Importance

Pink salmon are extremely important to the commercial fishery, and to a lesser extent, to the recreational and subsistence fisheries. Although their relative value (price/pound) to commercial fishermen is lower than for most other Pacific salmon, their abundance makes them economically important. From 1962 through 1976, pink salmon contributed 30% of the income brought to commercial fishermen from all Pacific salmon caught in Alaskan waters. Their mean annual value to commercial fishermen during this period was nearly 16 million dollars. They are the 'bread and butter' commercial fish species within the southern Alaska Peninsula, Chignik area, Kodiak Island, Cook Inlet, Prince William Sound, and southeast Alaska, especially during years of abundance (Morrow, 1980; Alaska Department of Fish and Game, 1979). Pink salmon are harvested commercially by beach and purse seines, and drift and set gill nets. Pink salmon are also harvested by trolling, primarily in southeast Alaska (Alaska Department of Fish and Game, 1979). Pink salmon are usually canned, the roe is processed for exportation, and the remaining material used for fertilizer and pet food.

II. SPECIFIC HABITAT RELATIONSHIPS/REQUIREMENTS

A. Upstream Spawning Migration of Adults

1. Water temperature

Sheridan (1962b) observed pink salmon returning to and spawning in various streams at different times of the year. He determined that pink salmon spawned in colder streams earlier in the season than in warmer streams. Sheridan attributed variations in spawning times to adaptations of pink salmon to the water temperatures.

Upstream migration of pink salmon has been documented in streams with water temperatures ranging from 7.2 to 15.5°C (45 to 60°F) (Bell, 1973). Various researchers have not found significant positive correlations between upstream migration of pink salmon and water temperature (Neave, 1966). Upstream spawning migration may also be delayed by water temperatures exceeding 21°C (70°F) (Bell, 1973).

2. Stream discharge, current velocity and water depth

Stream discharge, current velocity, and water depth can influence the upstream spawning migration of pink salmon in a variety of ways.

High stream discharges with associated high current velocities can surpass the swimming capabilities of pink salmon and prevent upstream movement. If current velocities near constrictions or falls exceed the swimming capabilities of adult fish, the upstream migration will cease. Pink salmon can negotiate maximum current velocities of about 2.1 m/sec (6.6 ft/sec). Waterfalls that may block fish passage

at some flow conditions may not limit fish at other flows (Thompson, 1972).

Conversely, low flows with characteristic shallow water depths can also prohibit fish movement upstream, depending on the severity of dewatering (Neave, 1966; Reiser and Bjornn, 1979). Minimum water depths needed for upstream passage of adult pink salmon are about 0.18 m (0.6 ft) (Thompson, 1972). These values will vary with the size and condition of adult pink salmon and the length of stream reach with shallow water. Pink salmon have been observed passing over shallow riffles less than 0.09 m (0.3 ft) deep along the Kizhuyak and Terror Rivers (Wilson, Trihey, Baldrige, Evans, Thiele and Trudgen, 1981).

Davidson and Vaughan (1943) examined the relationship between adult pink salmon numbers and discharge rates in two streams in southeast Alaska and one in British Columbia. They found a positive correlation between discharge and numbers of ascending adult pink salmon in Sashin Creek, British Columbia. In this creek the fish reside in the bay near the stream when maturing, then enter the stream, usually during freshets. No positive correlation was found between numbers of ascending pink salmon and discharge rates in the other two streams. Differences in these findings may be attributed to the relatively shallow water of Sashin Creek and the relatively deep pools of the other two streams (Banks, 1968).

Hunter (1959) showed that flow conditions in Hooknose Creek, British Columbia, accounted for about 34% of the variation in upstream fish movement. However, only data from 1952 were presented.

Pritchard (1948) also found a significant positive correlation between numbers of adult pink salmon migrating in this stream and rainfall and discharge in McClinton Creek, British Columbia.

B. Spawning

1. Water temperature

Sheridan (1962b) observed pink salmon spawning in southeast Alaska streams at water temperatures from 7.2 to 18.40°C (45 to 65°F). Bailey (1971) reported that pink salmon spawning activity commenced in Grace Creek, near Ketchikan, Alaska in mid-August at maximum water temperatures of about 10°C (50°F). McNeil (1964) stated that pink salmon spawning in Sashin Creek generally occurs after water temperatures decline to 13°C (55.4°F) or below.

Pink salmon are reported to spawn in Hooknose Creek, British Columbia, in water temperatures cooler than 12°C (58°F) (Hunter, 1959). Webb (1978 a, b and 1980) reported pink salmon spawning in Buckland, Shaktoolik and Inglutalik Rivers in water temperatures of 16°C (61°F), 9°C (48°F) and 10°C (50°F), respectively. Bailey and McNeil (1975) stated "mature salmon generally ripen and spawn as water temperature declines from its summer maximum; the preferred range for spawning is 7.2°C to 12.8°C (45 to 55°F)." Bell (1973) also stated that the preferred spawning temperatures of pink salmon range from 7.2 to 12.8°C (45 to 55°F).

Relatively high stream water temperatures and low dissolved oxygen levels associated with drought conditions have apparently killed many ripe pink salmon in several southeast Alaska streams. Water temperatures exceeding 17°C and dissolved oxygen levels of 4 ppm or less were responsible

— for the mortality of several thousand adult pink salmon in Staney Creek, Alaska during mid-August, 1979 (personal communication, John Edgington, 1981).

2. Current velocity

Asian pink salmon spawn in a variety of current velocities, ranging from about 0.3 to 0.8 m/sec (1.0 to 2.6 ft/sec). They have also been observed spawning in areas of upwelling water with no current during years of abundance (Semko, 1939; Krohkin and Krugius, 1937; Dvinin, 1952).

Current velocities utilized by pink salmon in selected State of Washington streams are reported to be 0.21 to 0.99 m/sec (0.7 to 3.30 ft/sec) (Collings, 1974). These velocity measurements were taken 0.12 m (0.4 ft) above the substrate.

Hourston and MacKinnon (1957) described current velocity and water depth preferences of spawning pink salmon in the Jones Creek spawning channel on Vancouver Island, British Columbia. The 615 m (2,000 ft) long spawning channel was divided into 15 sections of equal length and three "complete depth-velocity cross sections were made in each section of the channel" at a discharge of about $7 \text{ m}^3/\text{sec}$ (246 cfs) prior to the arrival of the fish.

Current velocities within the channel apparently exceeded preferred velocities of spawning pink salmon. The first fish to enter the experimental channels usually chose the slowest velocities available in the channel. Only 400 pink salmon entered the channel in 1955; density conditions were extremely low with only one spawning female per 10.5 m^2 of channel.

Pink salmon spawning in Terror River, Alaska selected current velocities ranging from 0.19 to 0.66 m/sec (0.6 to 2.0 ft/sec) and within this range, they preferred velocities from 0.35 to 0.47 m/sec (1.1 to 1.5 ft/sec) (Wilson, Trihey, Baldridge, Evans, Thiele and Trudgen, 1981). All values are expressed as mean column velocities.

Pink salmon in the upper Skagit River, Washington spawned in areas with current velocities ranging from 0.10 to 1.32 m/sec (0.3 to 4.3 ft/sec) (Graybill, Burgner, Gislason, Huffman, Wyman, Gibbons, Kurlso, Stober, Iagnan, Stayman and Eggers, 1979). Eighty percent of the fish were observed in current velocities ranging from 0.37 to 1.0 m/sec (1.2 to 3.2 ft/sec). All measurements were taken 0.16 m (0.5 ft) above the substrate.

3. Water depth

Selection of water depths by spawning pink salmon is associated with current velocity, substrate type and spawner densities. Kuznetsov (1928) stated that pink salmon in the Amur River and streams of West Kamchatka spawn in depths ranging from 0.2 m (0.7 ft) in relatively fast current velocities to 0.3 m (1 ft) in slower currents. Dvinin (1952) observed pink salmon in streams of southern Sakhalin. He found that in uncrowded conditions the fish spawned in water depths of 0.5 m (1.7 ft) and in crowded conditions they utilized water depths from about 0.1 to 1.2 m (0.3 to 3.9 ft).

Water depth preferences of pink salmon in selected Washington State streams are about 0.15 to 0.53 m (0.5 to 1.75 ft) (Collings, 1974). Hourston et al. determined water depth preferences of spawning pink salmon in the Jones Creek spawning channel, using the transect method.

They observed that the first fish to enter the spawning areas chose mean water depths of 0.42 m (1.38 ft), and the subsequent 100 spawning fish occupied slightly shallower mean water depths of 0.39 m (1.28 ft) (Table 1). The mean water depth of the entire spawning channel was 0.37 m (1.20 ft). No fish utilized the relatively shallow depths (0.30 to 0.34 m, 1.0 to 1.1 ft) which also had rather high current velocities (0.73 to 0.98 m/sec, 2.4 to 3.2 ft/sec). Female pink salmon density within the channel was extremely low with one female per 10.5 m².

Spawning pink salmon in the Terror River, Alaska used water depths ranging from 0.09 to 1.2 m (0.3 to 3.8 ft) and demonstrated a preference for depths from 0.37 to 0.63 m (1.2 to 2.0 ft) (Wilson et al., 1981).

Spawning pink salmon in the Skagit River, Washington were observed at water depths ranging from 0.09 to 1.32 m (0.3 to 4.2 ft) and 80% of those fish were in water ranging in depth from 0.28 to 0.78 m (0.9 to 2.5 ft) (Graybill et al., 1979).

4. Substrate composition

Pink salmon spawn over a variety of substrate materials. The size, shape, density and imbeddedness of this material, current velocity, water depth and fish densities can influence substrate selection. Adult pink salmon usually spawn in small gravels, sometimes reaching 10 cm (4 in) in diameter. Pink salmon have also been observed spawning over much larger substrate in selected Prince William Sound streams during 'on' years (R. Nickerson, personal communication, 1980).

Houreston and Mac Kinnon (1957) examined substrate samples taken from 'good' pink salmon spawning areas along the Adams

and Okanagan Rivers and Jones Creek. They found that gravel from 0.6 to 3.8 cm diameter provided the best substrate for in artificial spawning channels. Lucas (1959) used substrate sizes from 2 to 10 cm diameter in spawning channels.

5. Spawner Densities

Redd superimposition influences egg survival when high densities of pink salmon spawn in streams with limited spawning habitat. Pink salmon redds may be partially or totally torn apart and reexcavated by newly arriving females. McNeil (1962) formulated a hypothetical model predicting the effects of pink salmon spawner density on egg survival in a selected reach of the Harris River. At a spawner density of 4.5 fish/9.3 m² (100 ft²) redd superimposition accounts for about 25% of total egg mortality. At a density of 10.6 fish/9.3 m² (100 ft²), egg mortality was predicted to be about 50%. Helle (1966) also recognized that redd superimposition increased pink salmon egg mortality in Olsen Creek, Prince William Sound.

C. Intragravel Development of Eggs and Alevins

1. Water temperature

Rates of egg development and hatching times are strongly controlled by temperature regimes and by the number of degree-days accumulated since egg deposition. A degree-day is the number of degrees above a base temperature (usually the freezing point) in the average temperature of one day. It has been estimated that at least 500 degree days (°C) are required for the hatching of pink salmon eggs (Scott and Crossman, 1973). This is equivalent to 50 days at 10°C or 71 days at 7°C. Abnormally warm or cold temperatures can

accelerate or depress development rates and cause premature or delayed salmon fry emergence.

There are upper and lower temperature limits for successful incubation of salmonid eggs. Pink salmon eggs are more sensitive to cold water (0°C, 32°F) at initial developmental stages than later stages. Combs and Burrows (1957) and Combs (1965) reported that hatchery pink salmon eggs could tolerate water temperatures as low as 0.5°C (33°F) provided temperatures exceeded 5.5°C (42°F) during the initial month of development. Bailey and Evans (1971) concluded from laboratory tests with pink salmon eggs from Grace Creek near Ketchikan, Alaska that water temperatures above 4.5°C (40°F) are necessary through the gastrula stage to ensure development.

Bailey and Evans (1971) found that egg mortality and the occurrence of spinal deformities in alevins were inversely related to increases in water temperatures between 2.0°C (36°F) and 8.5°C (47°F). Water temperatures of 4.5°C (40°F) and 3.0°C (37°F) caused substantial egg mortalities and spinal deformities among alevins. Complete mortality of eggs occurred at 2.0°C (35°F). No egg mortalities or alevin spinal deformities were found at 8.5°C (47°F). After pink salmon eggs reach the gastrula stage they can tolerate water temperatures close to freezing.

The upper and lower estimated threshold temperatures for pink salmon eggs are 13.3°C and 4.4°C (Bell, 1973). Mortality is expected to increase if these thresholds are exceeded. Eggs will survive and develop normally at lower temperatures than indicated, provided initial development of the embryo has progressed to a stage that is tolerant of colder water.

Timing of the downstream migration of pink salmon fry is probably correlated with habitat conditions in the estuary in late spring or early summer (Sheridan, 1962). Fry emerging earlier or later than normal could encounter suboptimal physical conditions and lower food availability in the estuary.

2. Stream discharge, current velocity and water depth

Discharge alterations can adversely affect developing pink salmon eggs and alevins. Spates can mechanically remove substrate material and developing fish (McNeil, 1966). McNeil (1966) observed damaged pink salmon redds and displaced pink salmon eggs and alevins in several southeastern Alaska streams after intense rains between October and December. He estimated that these floods destroyed about 50 to 90% of the developing pink salmon eggs and alevins within these streams. Pink salmon spawning areas within the mainstem Terror River have been scoured during storm flow conditions (Wilson, 1981). This phenomenon is probably more common in moderately high gradient streams used by spawning pink salmon.

Summer and winter low flows can adversely affect developing pink salmon eggs and alevins, depending on the severity of flow reduction, temperatures, and other factors. McNeil (1966) believed that significant mortality of chum and pink salmon eggs and alevins occurred in one of two study streams in southeastern Alaska during extremely cold weather and low flows. He noted that discharge in Indian Creek was considerably less than in Twelvemile Creek. Indian Creek is characterized by an extreme range of discharges (500 fold); in contrast, Twelvemile Creek exhibited only an 80 fold difference.

Pink salmon eggs deposited along the stream margins may be subjected to high mortality with winter low flows. This could cause redds to become exposed, desiccated, or frozen.

Summer drought conditions, and the attendant low flows and high temperatures, can cause reduced intra-gravel dissolved oxygen levels. McNeil (1966) attributed the high mortality of pink and chum salmon in several southeastern Alaska streams in 1957 to low flow, unseasonably warm summer temperatures and low dissolved oxygen levels.

3. Substrate composition

Substrate composition, particularly the percentage of small particles (called 'fines') can influence the intragravel environment and condition of developing eggs and alevins. Fines have been defined as materials less than 6.4 mm (0.26 in), 3.0 mm (0.12 in) and 0.833 mm (0.03 in) minimum diameter by McCuddin (1977), Phillips (1975) and McNeil and Ahnell (1964), respectively. Increased amounts of fines within the substrate interstices where eggs and alevins are developing, can reduce water permeability and intragravel flow rates (apparent velocity) (Wickett, 1962). This influences the rate at which oxygen is transported to and metabolic products from the developing eggs and alevins. McNeil and Ahnell (1964) classified the pink salmon production capability of six streams in southeastern Alaska by the permeability of their spawning areas. They concluded that the substrate of 'productive' streams generally contained less than 5% by volume of fines (0.833 mm) and had associated permeability rates of 24,000 cm/h (787 ft/h). Less productive pink salmon streams were characterized by 15% or more fines with associated permeability rates of less than 1,300 cm/h (43 ft/h). Wickett (1958) and Reiser and Bjornn (1979) reported 12% survival of pink and chum salmon

to emergence at permeability rates of 96,000 cm/h (3,150 ft/h) and 2% survival at rates of 1,800 cm/h (59 ft/h).

Pink salmon egg and alevin survival in relation to tidal influence (with associated sediment, salinity, dissolved oxygen and temperature conditions) has been examined by several researchers. Scud and Hanavan (1954) determined that pink salmon egg and alevin survival in tidally influenced reaches of Lover's Cove Creek were as high or higher than in upstream non-tidal influenced reaches. Kirkwood (1962) determined that egg and alevin survival decreased from higher to lower tidal levels in several Prince William Sound streams. Helle, Williamson and Bailey (1974) examined Olsen Creek in Prince William Sound. They reported decreased survival at lower intertidal reaches associated with increased proportions of fine sediments. Helle (1970) corroborated previous findings in Olsen Creek. He attributed greater egg and alevin mortality rates from higher to lower intertidal areas to increased fine sediments and salinity. Dissolved oxygen and temperature were additional factors influencing mortality.

Fines can influence emergence of alevins from the redd. Survival and emergence of chinook salmon and steelhead trout fry were adversely affected when fines (6.4 mm) exceeded 20% of the volume of the substrate in laboratory troughs (Bjornn, 1969; McCuddin, 1977). Koski (1966) documented that coho salmon fry were unable to emerge from natural redds with substantial accumulations of fines.

4. Dissolved Oxygen

Dissolved oxygen is supplied to developing eggs and alevins within the redd by intragravel flow. Dissolved oxygen levels within the redd are influenced by the dissolved

oxygen levels within the stream, rate of intragravel flow, biological oxygen demand of material within the redd such as detritus and dead eggs, water temperature, metabolic rates of the developing eggs and alevins, density of eggs and alevins, and other factors.

Oxygen consumption generally increases as embryo development progress (Bailey, Rice, Pella and Taylor, 1980). Bailey et al. (1980) planted various densities of fertilized, eyed pink salmon eggs (0; 1,600; 6,400; 12,800 and 25,600 eggs/0.015 m³) in experimental egg incubators. Dissolved oxygen content of inflow water was maintained at relatively constant levels during the test: 9.16 mg/l in December and 8.08 mg/l in April. Oxygen consumption rates measured at pre-hatching, post-hatching and pre-emergence progressively increased with time and developmental stage. For example, within the incubator containing 6,400 eggs, oxygen consumption rates increased from 0.003 to 0.010 mg/h per egg prior to and following hatching and reached a maximum of 0.027 mg/h per alevin immediately prior to fry emergence. Resultant dissolved oxygen levels within the various incubators reflected egg densities and oxygen consumption rates.

Dissolved oxygen levels generally decreased with time and were progressively lower within incubators containing more eggs or alevins (Bailey et al., 1980). For example, dissolved oxygen levels immediately prior to emergence of fry within incubators containing 1,600, 6,400 and 12,800 alevins were 7.0, 5.5 and 4.3 mg/l respectively. An exception occurred in the incubator containing 25,600 eggs where alevins emerged prematurely. Premature emergence was probably due to the combined effect of low dissolved oxygen and high ammonia levels. The dissolved oxygen concentration at emergence was only 6.2 mg/l.

Dissolved oxygen levels exceeding 6.0 mg/l are recommended for the successful development of pink salmon eggs and alevins (Bailey et al., 1980). Dissolved oxygen levels below 6.0 mg/l apparently caused premature emergence, decreased size and low survival of fry, especially at higher densities. Fifty percent of the fry in incubators containing 12,800 and 25,600 eggs emerged 7 and 82 days earlier, respectively, than fry in the incubator with 1,600 eggs. Emergent fry at the two highest densities also were shorter than fry from the other incubators. Survival was only 50% in the highest density incubator.

Coble (1961) and Phillips and Campbell (1961) determined that intragravel dissolved oxygen concentrations at or above 8 mg/l are necessary for high survival of steelhead trout and coho salmon eggs. McNeil (1962) attributed low survival of pink salmon eggs in 1957 in several southeast Alaska streams to low flows and associated low dissolved oxygen levels and, possibly, other factors. Reiser and Bjornn (1979) recommended dissolved oxygen levels near saturation with momentary reductions no lower than 5 mg/l (approximately 40-45% saturation) for eggs and alevins.

5 Salinity

Pink salmon commonly spawn in the intertidal regions of streams. Noerenberg (1963) estimated that over 50% of the pink salmon spawning activity in Prince William Sound occurs in tidally influenced areas. Fluctuations in salinity, dissolved oxygen, water temperature and fine sediment may influence pink salmon egg and alevin survival. Various researchers have recognized that pink salmon fry production within intertidal stream reaches is generally highest in the upper reaches, moderate in the intermediate reaches and low or non-existent in the lower reaches. Little research has

focused on the effect of just salinity on pink salmon egg and alevin survival (Hanovan and Skud, 1954; Kirkwood, 1962; Hell, Williamson and Baily, 1964; Helle, 1970).

Bailey (1966) conducted laboratory experiments to simulate salinity conditions of developing eggs and alevins at the 2.4 m (8 ft), 1.8 m (6 ft) and 1.2 m (4 ft) tide levels in Olsen Creek, Alaska. Test salinity conditions ranged from 12-30⁰/oo. He concluded that developing pink salmon eggs fertilized in fresh water showed no adverse affects to salinity conditions at the 2.4 m (8 ft) tide level. Pink salmon fry production was severely limited at the 1.8 m (6 ft) tide level and was extremely limited or nonexistent at the 1.2 m (4 ft) tide level.

D. Downstream Fry Migration

1. Cover

Pink salmon fry may reach the estuary along short coastal streams within the first night of travel, but fry migrating down relatively long streams need adequate cover during the day. Cover could be from gravel interstices, overhanging riparian vegetation or other instream cover.

2. Discharge

A wide range of discharges are suitable for successful downstream fry migration. Discharges must be high enough to maintain adequate water depths in the channel and to enhance the swimming of the fry.

3. Water temperature

Water temperatures encountered during downstream migration and in the estuaries can influence dissolved oxygen levels, swimming performances and growth rates of the fry, and the ability to capture and digest food (Reiser and Bjornn, 1979). Brett (1952) determined that the upper lethal temperatures for pink salmon fry (40 to 50 mm total length) were about 21, 22.5, 23 and 24°C at acclimation temperatures of 5, 10, 15 and 20°C, respectively. Preferred water temperatures were about 11, 13 and 17°C at acclimation temperatures of 10, 15 and 20°C, respectively. Low temperature tolerance limits of pink salmon fry were not determined.

III. CONCEPTUAL SUITABILITY INDEX CURVES

The habitat suitability curves presented in this section are derived primarily from threshold values reported in the literature. Avoidance behavior, abnormal development and increased mortality are expected to occur if the threshold points are exceeded. A major limitation of the suitability index curves is that they do not represent the increments of habitat quality between the two threshold points. Because of the paucity of data, particularly between the threshold points, the curves are simplistic and have limited application.

The conceptual habitat suitability curves depict the influence of certain physical and chemical lotic habitat components on the survival and behavior of different pink salmon life stages. Most lotic habitat components collectively influence all life stages. For example, water permeability within the redd influences the intra-gravel environment and the well-being of developing pink salmon eggs and alevins. Dissolved oxygen and water temperatures also affect intra-gravel water quality. Other lotic habitat components, such as current velocity, water depth and substrates collectively influence spawning site selection by female pink salmon.

The habitat suitability curves presented in this document do not account for interactive effects of chemical and physical parameters. For example, a dissolved oxygen concentration of 5 mg/l may be suitable at a water temperature of 5°C, but unsuitable at a temperature of 20°C. Ideally, a separate dissolved oxygen curve should be drawn for each of several different temperatures or dissolved oxygen levels represented as percent saturation.

Additionally, the effect on the fish of less than optimum conditions depends on the duration of exposure and on the particular life stage of the fish.

The conceptual habitat suitability curves are not constructed for application to specific watersheds. Field data collection techniques (when described) often varied. For example, three techniques for measuring current velocity preferences of spawning pink salmon were found in the literature: the mean column velocity, the current velocity 0.12 m above the redd and the current velocity 0.16 m above the redd. These values may vary significantly among techniques. In addition, field data were presented as means, ranges, frequencies of occurrence or the range of values utilized by a given percentage of the sample population. Certain suitability index curves were based upon laboratory tests, such as the water temperature--pre-gastrula curve.

The value of each habitat component which was regarded as 'ideal' was given a 1.0 rating on the Y-axis of the suitability index. The threshold points were connected by a solid line and dashed lines were used to delimit the known upper and lower threshold points.

Table 1 - AQUATIC HABITAT CRITERIA USED FOR CONCEPTUAL SUSTAINABILITY INDEX CURVES
REGARDING UPSTREAM PASSAGE OF PINK SALMON

<u>Parameter</u>	<u>Observed Values</u>	<u>Remarks</u>	<u>Location</u>	<u>Reference</u>
Water temperature	7.2-15.6°C	Preferred water temperatures for pink salmon		Bell (1973)
	21.1°C	May cause migration delay for pink salmon		Bell (1973)
Water depth	0.18 m	Minimum passage requirement for pink salmon. This value will change with actual size and condition of fish.	Oregon	Thompson (1972)
	0.09 m	Pink salmon passage noted along riffles of several streams on Kodiak Island less than 0.09 m (0.3 ft)	Alaska	Personal communication, Jean Baldrige (1981)

Table 2 - AQUATIC HABITAT CRITERIA USED FOR CONCEPTUAL SUITABILITY INDEX CURVES
REGARDING UPSTREAM PASSAGE OF PINK SALMON

<u>Parameter</u>	<u>Observed Values</u>	<u>Remarks</u>	<u>Location</u>	<u>Reference</u>
Water temperature	7.2 - 18°C	Southeast Alaskan stream temperatures at time of pink salmon spawning	Southeast Alaska	Sheridan (1962b)
	4.5°C	Minimum value for successful pink salmon egg development	Grace Crk. eggs subjected to controlled environmental conditions	Bailey & Evans (1971)
Current velocity	0.19-0.66 m/sec	Range of current velocities chosen by spawning pink salmon. Mean column velocity	Terror River, Alaska	Wilson, Trihey, Baldrige, Evans Thiele & Trudgen (1981)
	0.35-0.47 m/sec	Current velocities preferred by spawning pink salmon. Mean column velocity	Terror River Alaska	Wilson, Trihey, Baldrige, Evans Thiele & Trudgen (1981)
	0.10 m/sec to 1.32 m/sec	Range of current velocities chosen by spawning pink salmon. 0.16 m above substrate	Skagit River Washington	Graybill, Burgner Gislason, Huffman Wyman, Gibbons, Kurko, Stober, Fagnan, Stayman, and Eggers (1979)
	0.37 m/sec to 1.0 m/sec	Current velocities chosen by 80% of detected spawning pink salmon.	Skagit River Washington	Graybill, Burgner Gislason, Huffman Wyman, Gibbons, Kurko, Stober, Fagnan, Stayman and Eggers (1979)

Table 2 - AQUATIC HABITAT CRITERIA USED FOR CONCEPTUAL SUITABILITY INDEX CURVES
cont'd REGARDING UPSTREAM PASSAGE OF PINK SALMON

<u>Parameter</u>	<u>Observed Values</u>	<u>Remarks</u>	<u>Location</u>	<u>Reference</u>
	0.21-0.99 m/sec	Values measured 0.4 ft above substrate	Washington State	Collings (1974)
	0.3-0.8 m/sec	Assorted streams; method not stated	Sakhalin Peninsula USSR	Dvinin (1952)
	0.45-0.73 m/sec	Range occupied by first 100 fish in each channel section	Jones Creek, Brit. Columbia	Hourston and MacKinnon (1957)
	0.39-0.64 m/sec	Range occupied by first spawning pair	Jones Creek, Brit. Columbia	Hourston and MacKinnon (1957)
Substrate composition	0.6-3.8 cm in diameter	Jones Crk. spawning channel primarily pink salmon	Jones Creek, Brit. Columbia	Hourston and MacKinnon (1957)
	2-10 cm in diameter	Robertson Crk. spawning channel	Robertson Crk. Brit. Columbia	Lucas (1959)
	2-250 mm in diameter	Range of substrate diameter utilized by spawning pink salmon	Terror River, Alaska	Wilson et al. (1981)
Water depth	0.2-0.3 m	Values for relatively fast and slow current velocity, respectively	Amur River USSR	Kuznetsov (1928)
	0.5 m	Uncrowded conditions	Southern Sakhalin USSR	Dvinin (1952)
	0.1-1.2 m	Crowded conditions	Southern Sakhalin USSR	Dvinin (1952)

Table 2 - AQUATIC HABITAT CRITERIA USED FOR CONCEPTUAL SUITABILITY INDEX CURVES
cont'd REGARDING UPSTREAM PASSAGE OF PINK SALMON

<u>Parameter</u>	<u>Observed Values</u>	<u>Remarks</u>	<u>Location</u>	<u>Reference</u>
Water depth	0.15-0.53 m		various streams in Washington State	Collings (1974)
	0.42 m	Mean value for sites selected by first spawn- ing pink salmon in each of the 15 channel sections	Jones Creek spawning channel Vancouver Island Brit. Columbia	Thurston and Mackinnon
	0.39 m	Mean values for sites selected by first 100 within each of 15 channel sections	Jones Creek spawning channel	Thurston and Mackinnon
	0.09-1.20 m	Range of water depths utilized by spawning pink salmon	Terror River, Kodiak Island, Alaska	Wilson, Trihey, Baldrige, Evans, Thiele, Trudgen (1981)
	0.37-0.63 m	Preferred depths utilized by spawning pink salmon	Terror River, Kodiak Island, Alaska	Wilson, Trihey, Baldrige, Evans, Thiele, Trudgen (1981)
	0.09-1.32 m	Range of water depths utilized by spawning pink salmon	Skagit River, Washington	
	0.28-0.78 m	Water depths utilized by 80% of spawning pink	Skagit River, Washington	Graybill et al. (1979)

Table 3 - AQUATIC HABITAT CRITERIA USED FOR CONCEPTUAL SUITABILITY INDEX CURVES
REGARDING UPSTREAM PASSAGE OF PINK SALMON

<u>Parameter</u>	<u>Observed Values</u>	<u>Remarks</u>	<u>Location</u>	<u>Reference</u>
Water temperature	% Survival-Water Temperature 94-100% - Ambient 88-93% - 4.5°C 18-40% - 3.0°C 0% - 2.0°C	Laboratory controlled environment tests with pink salmon eggs - % survival to hatching stage. Completion of gastrula stage varied with water temperature - Ambient - 26th day, 4.5°C - 45th day, 3.0°C - 62nd day	Egg source - Grace Creek near Ketchikan, Alaska	Bailey & Evans (1971)
Dissolved oxygen	6 mg/l	Minimum value recommended for satisfactory development of pink salmon eggs and alevins	Laboratory tests using eggs from Sashin Creek, Alaska	Bailey, Rice, Pella & Taylor (1980)

See text for qualifications
for use of these curves.
(NOT RECOMMENDED FOR
APPLICATION TO SPECIFIC
WATERSHEDS WITHOUT FIELD
VERIFICATION)

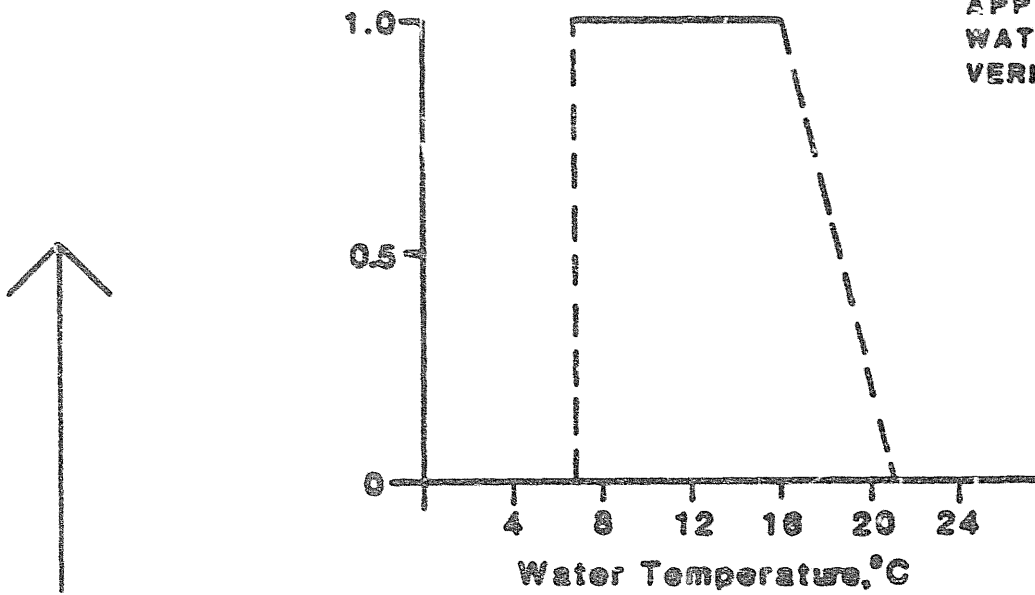


Figure 2 Water temperatures suitable for upstream migration.

SUITABILITY

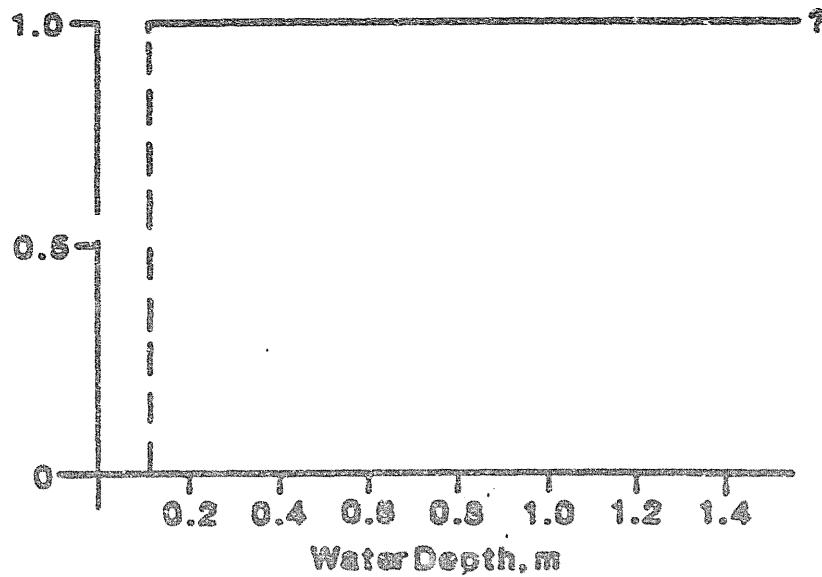
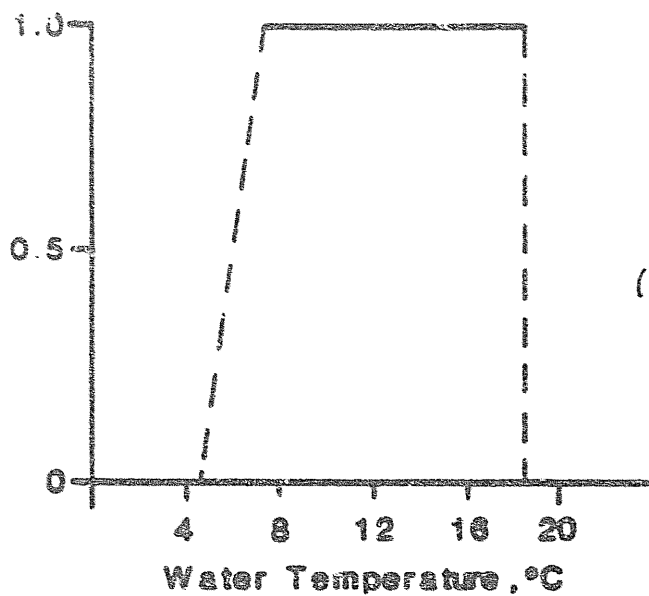


Figure 3 Suitable water depths for passage of Pink salmon.

↑
INDEX
SUITABILITY



See text for qualifications
for use of these curves.
(NOT RECOMMENDED FOR APPLICATION
TO SPECIFIC WATERSHEDS WITHOUT
FIELD VERIFICATION)

Figure 4 Water temperatures suitable for spawning Pink salmon.

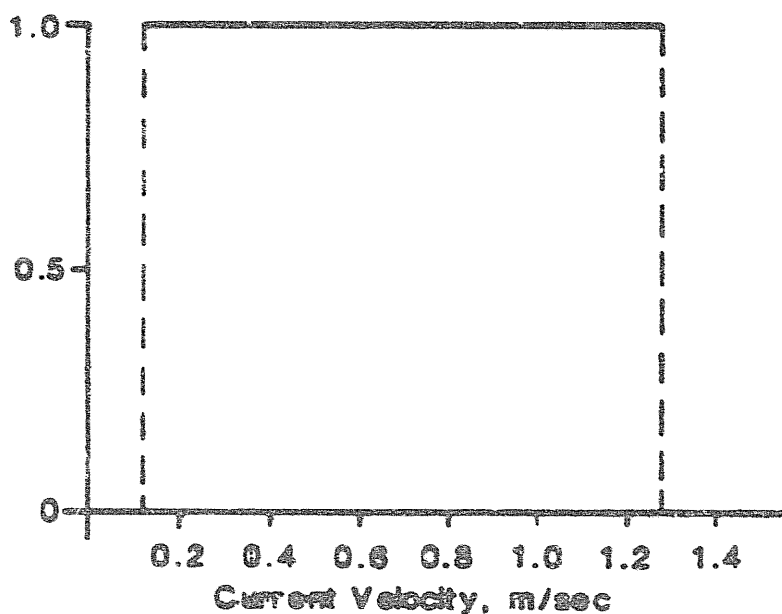


Figure 5 Current velocities suitable for spawning Pink salmon.

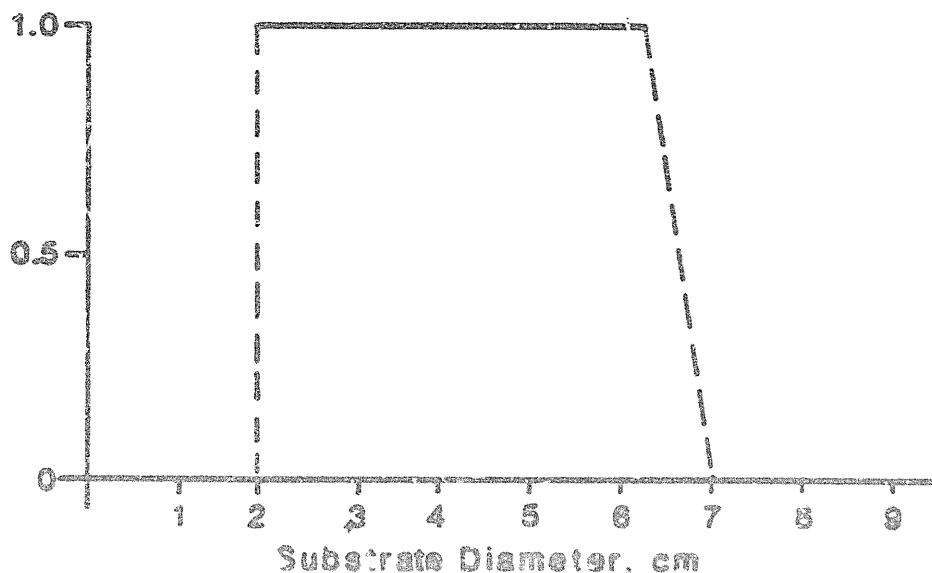


Figure 6 Substrate conditions suitable for Pink salmon spawning activity.

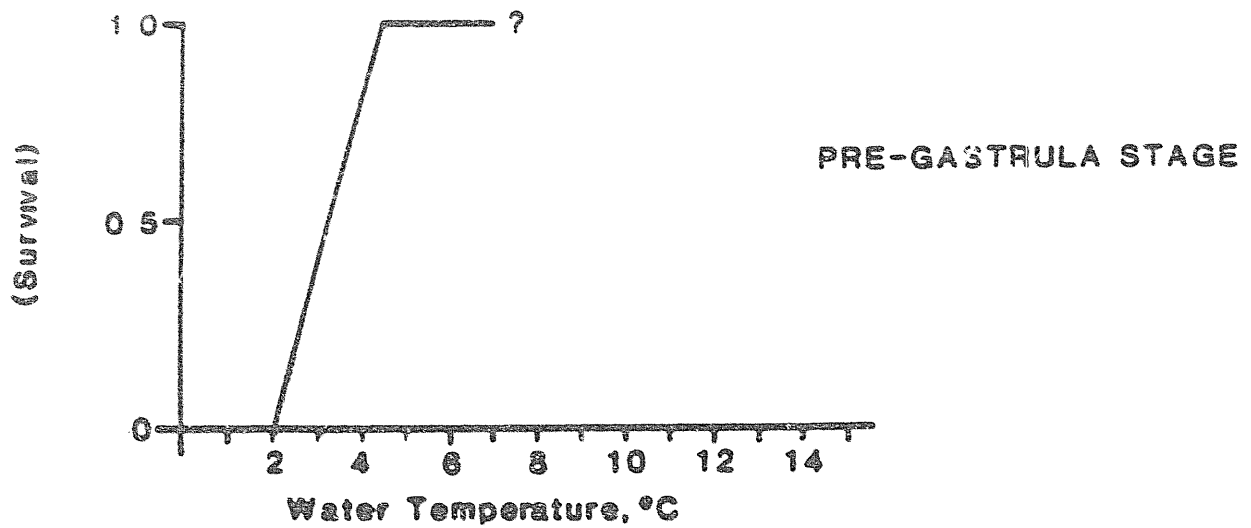


Figure 7 Effects of water temperature on Pink salmon egg survival based upon results of Bailey and Evans, 1971

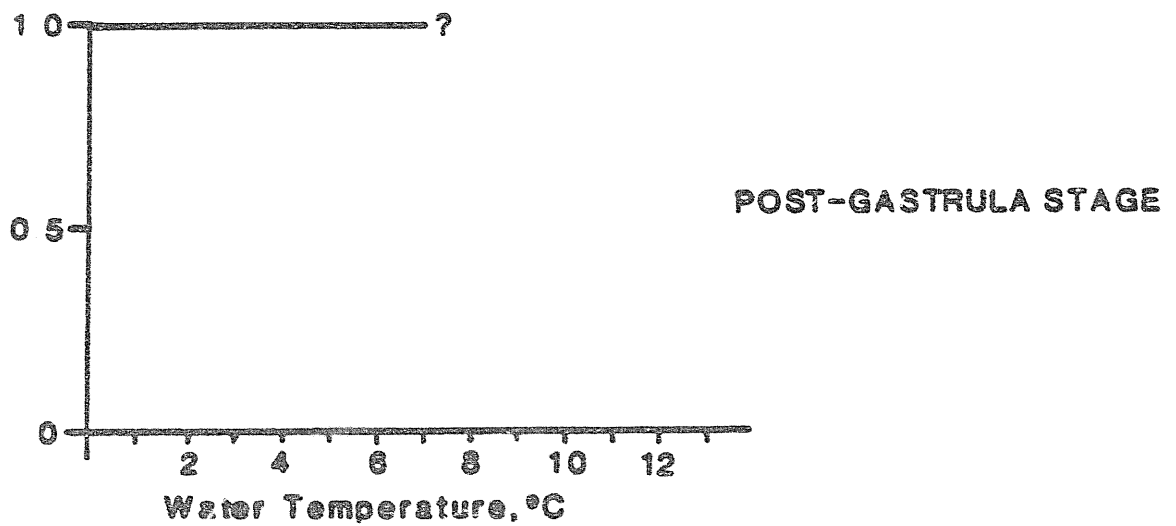


Figure 8 Effects of water temperature based on results of Bailey and Evans, 1971.

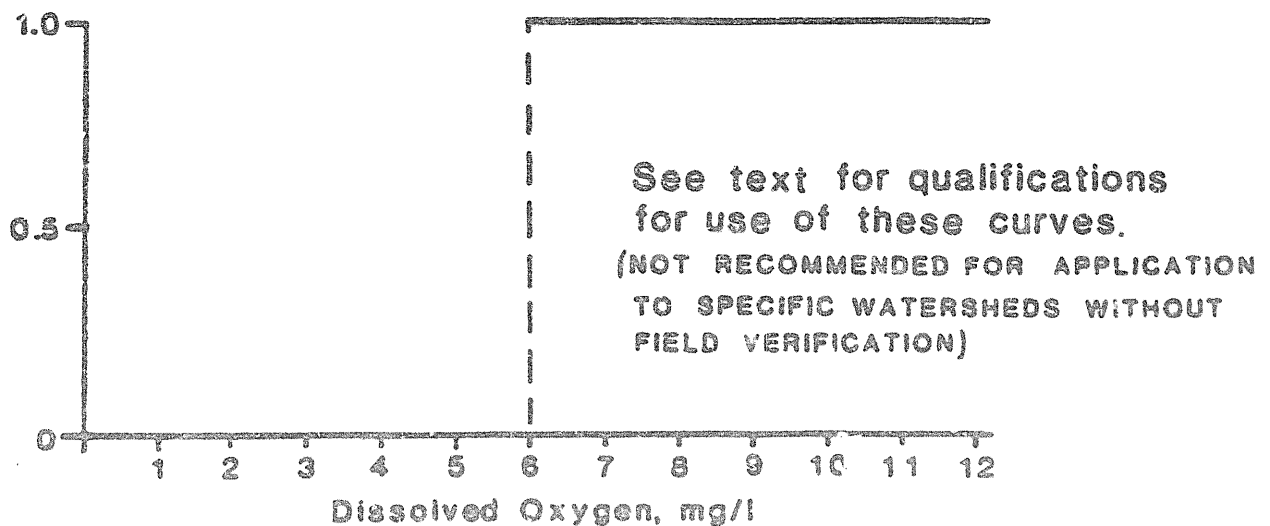


Figure 9 Recommended dissolved oxygen levels for satisfactory development and survival of Pink salmon eggs and alevins.

IV. DEFICIENCY IN DATA BASE

Many measurements of aquatic habitat parameters could not be adapted to habitat suitability curves. Most studies of current velocity, water depth and substrate selection by spawning pink salmon did not record the relative abundance (availability) of each habitat type. The availability of these habitats, which vary within and among streams, influences selection by spawning pink salmon.

Components of egg and alevin habitats were also usually not expressed in a form which was usable for habitat suitability curves. Intragravel flow, dissolved oxygen, substrate composition and other aquatic habitat components which influence the survival and fitness of pink salmon eggs and alevins are difficult to measure in the field. Most aquatic habitat evaluations are conducted with the objective of determining upper and lower thresholds. Few studies examine the relative growth rates, survival or overall habitat quality associated with incremental changes in chemical and physical parameters between threshold levels.

V. RECOMMENDATIONS AND FURTHER STUDIES

Current velocity, water depth and substrate conditions selected by female pink salmon for spawning should be measured and analyzed throughout Alaska using standardized techniques. Past studies have measured current velocity as mean column velocity or the velocity at 0.12 or 0.16 m above the redd. A focal point measurement (current velocity at the fish's snout) combined with mean column velocity at the redd site would more realistically represent actual current velocities.

There is a need for a standardized method of substrate classification which evaluates substrate composition, predominate particle size, shape, imbeddedness and angularity. Ideally the classification system should be objective and not overly time consuming. Commonly used methods for substrate analysis usually require considerable time and expense for collection, transportation and analysis.

Frequency analysis of pink salmon habitat preferences may be a useful tool for constructing suitability curves; a frequency distribution is comparable to a habitat suitability curve. Previously used frequency distributions reflected stream or stream-reach habitat availability (Wilson, Trihey, Baldrige, Evans, Thiele and Trudgen, 1981) rather than habitat preferences of the fish.

Pink salmon spawning habitat is a composite of available current velocity, water depth and substrate conditions. To better understand constituents of pink salmon spawning habitat within a stream all available habitat should be inventoried, whether it is utilized or not.

A variety of lotic systems from small, clearwater streams to larger clearwater and glacial streams should be examined in various geographical areas of Alaska to better determine aquatic habitat preferences of spawning pink salmon. These investigations, ideally,

should encompass both 'on' and 'off' stocks. Aquatic habitat-pink salmon relationships will be very different among different population densities.

Laboratory experiments investigating the effects of various substrate compositions on intragravel flow, dissolved oxygen and survival of pink salmon eggs and alevins should be initiated. Field studies should compliment laboratory research in assessing the influence of fines on pink salmon production. The contribution of fine substrate material to pink salmon spawning streams by various land use activities should be determined.

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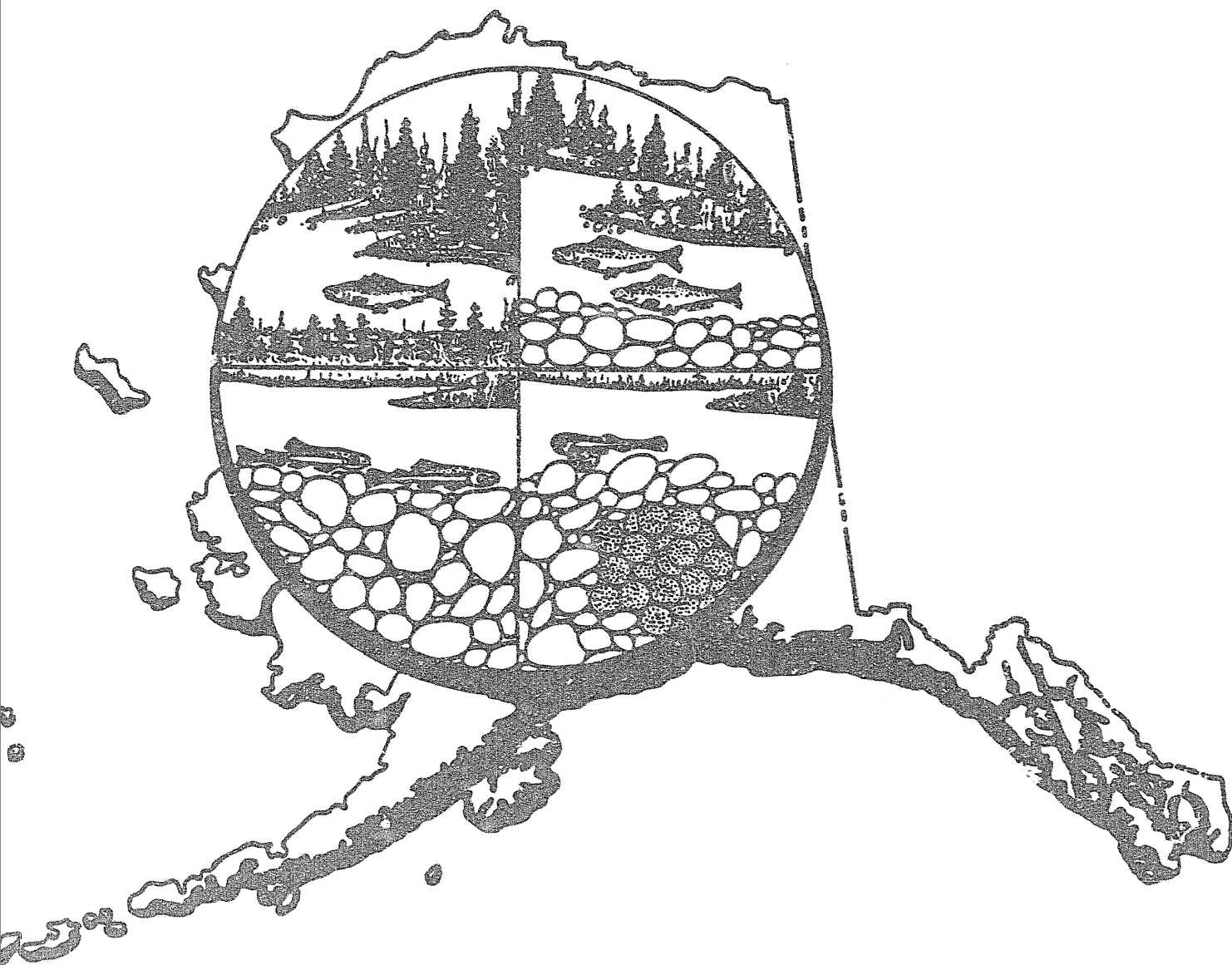
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FRESHWATER HABITAT RELATIONSHIPS

BROAD WHITEFISH - COREGONUS NASUS



ALASKA DEPARTMENT OF FISH & GAME
HABITAT PROTECTION SECTION
RESOURCE ASSESSMENT BRANCH

APRIL, 1981

FRESHWATER HABITAT RELATIONSHIPS
BROAD WHITEFISH - COREGONUS NASUS

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I. INTRODUCTION

A. Purpose

This report presents available information on the freshwater habitat requirements of the broad whitefish, Coregonus nasus (Pallas) and evaluates the habitat parameters which are most important to the species or are most often critical to survival or limiting to production.

Because the range of the species includes coastal brackish waters which are used as summer feeding areas or as overwintering areas, information from such areas was also considered.

The emphasis of this report is on habitat requirements, primarily those of a physical or chemical nature. Certain biological factors affecting the well-being of the population such as feeding, predation, competition, and disease are not comprehensively treated.

This report is intended to support habitat evaluation activities by presenting a data base for the species and by pointing out where more data are needed.

Although information has been examined from throughout the range of the species, emphasis is placed upon Alaska. While there appears to be wide differences in growth rates between different populations within the state, there is insufficient information to show that habitat requirements differ among the various populations. There are some problems with the taxonomy of the species. Information referring to Coregonus nasus (Pallas) sensu Svardson in Scandinavia was not used because that species evidently is different from the Coregonus nasus (Pallas) of Siberia, Alaska, and northwest Canada.

The life history of the broad whitefish, especially that of the early life stages, is not well known. Even less is known of habitat tolerances, preferences, and requirements. The broad whitefish appears to have fairly wide habitat tolerances. Several reports on the life histories of related species are presented in the Biology of Coregonid Fishes, edited by Lindsey and Woods (1970).

B. Distribution

The broad whitefish is a lacustrine-fluvial species, but is found more often in rivers than in lakes. It also occurs in brackish areas of coastal waters.

It is distributed in North America in Bering Sea and Arctic Ocean drainages from the Kuskokwim River system in Alaska north and east to the Perry River, Northwest Territories. In the USSR, it is distributed from the Pechora River near the Ural Mountains east in Arctic Ocean drainages and south in Bering Sea drainages to the Bay of Korf, and in the Penzhina River on the northeastern corner of the Sea of Okhotsk (Berg, 1948; McPhail and Lindsey, 1970; Scott and Crossman, 1973). The southern limit inland is approximately 60° N.

In Alaska, the broad whitefish is found in most drainages north of the Kuskokwim River system, where it is common, and the Alaska Range. (Figure 1). It occurs in the Yukon River system from the mouth to the headwaters in British Columbia (Morrow, 1980), including the Koyukuk River and Porcupine River drainages. It is common in the Minto Flats area of the Tanana River system but apparently uncommon further upstream. It is widespread in the drainages emptying into the Bering Sea (Kuskokwim River and north), Chukchi Sea, and Beaufort Sea. The Susitna River and the Copper River drainages have no broad whitefish (Alt, 1971).

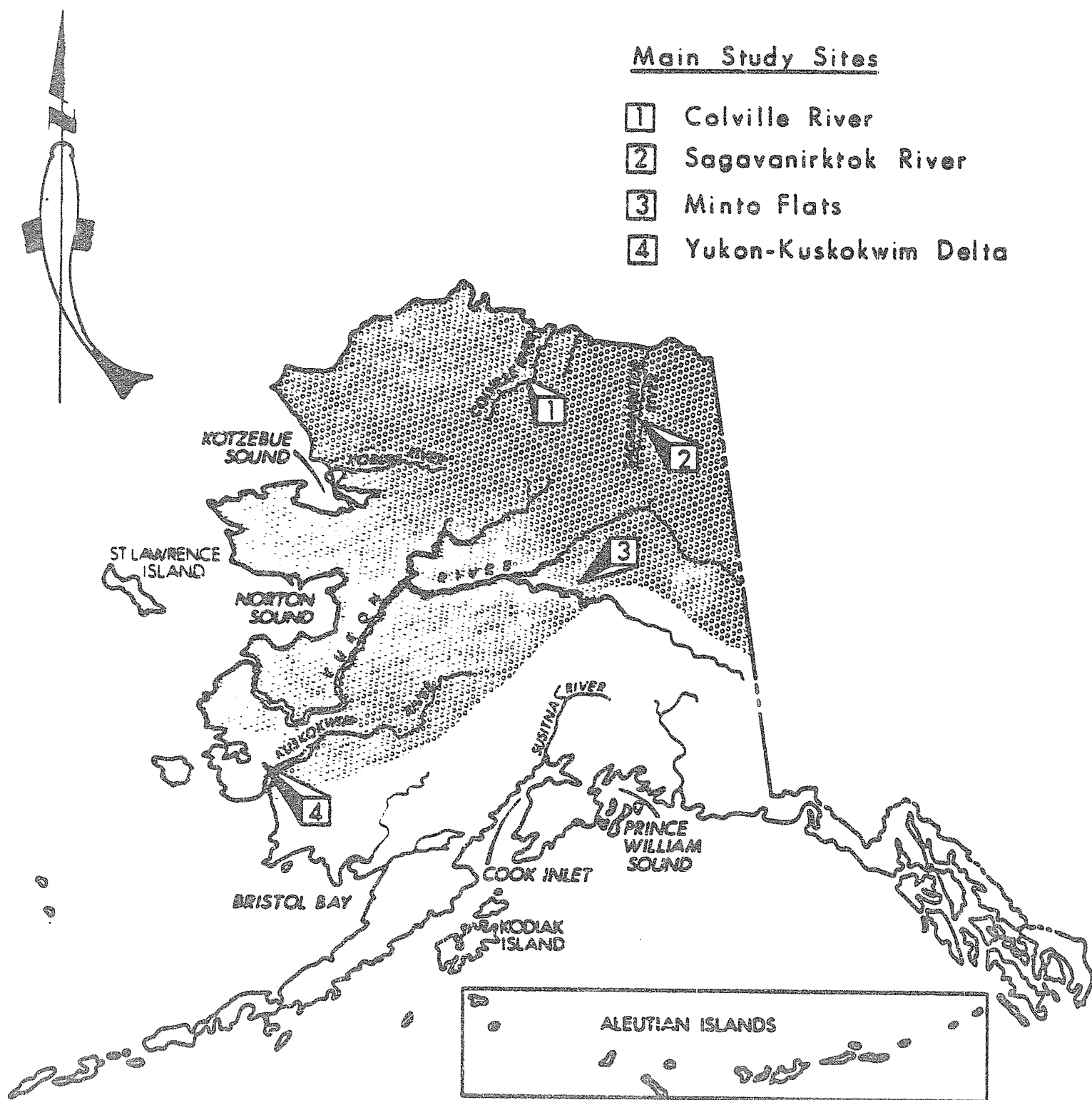


Figure 1 Distribution of broad whitefish in Alaska (R. Baxter, personal communication; Morrow, 1980) and main study sites.

C. Life History Summary

The life history of the broad whitefish is not well known. Migrations occur between summer feeding areas, spawning areas, and overwintering areas. In general, spawning migrations occur in the late summer and fall as the fish move out of summer feeding areas and move to spawning areas. Baxter (1973) has noted that, in the Kuskokwim River area, the ripening females move downstream out of the tundra lakes, ponds, and streams in August and September and begin a slow migration up the Kuskokwim River. They are followed by the sexually developing males in September and by the non-spawning adults of both sexes in late September through October. Immature fish leave the tundra in October through December. Broad whitefish apparently migrate downstream out of the Minto Flats into the Tanana River in August (Kepler, 1973; Townsend and Kepler, 1974). On the North Slope, fish that had been feeding in coastal areas enter the Sagavanirktok River in late August to migrate to the spawning areas (Bendock, 1977). A sizeable spawning run moves up the Colville River in August (Bendock, 1979). Alt and Kogl (1973) found that the Colville run is spread over several months and peaks in late July.

Wynne-Edwards (1952, cited by McPhail and Lindsey, 1970) stated that upstream spawning migration of broad whitefish occurred in the lower Mackenzie River in July and August. Evidently, the migration up the Mackenzie peaks in the inner delta during September and October (DeGraaf and Machniak, 1977). In the upper Yukon River, broad whitefish on spawning migrations have been observed entering small tributaries in September; ripe fish have been captured in the main river in early October (McPhail and Lindsey, 1970). Spawning in the Mackenzie River apparently takes place in back eddies during October (DeGraaf and Machniak, 1977). Spawning in the USSR takes place in October and November (Berg, 1948).

Morrow (1980) states that spawning of the broad whitefish in Alaska occurs in September and October and possibly into November. Baxter (1973) found that the spawning season in the lower Kuskokwim River lasts from October to early December. Adults do not spawn every year. Broad whitefish in the Colville River apparently spawn in September in the upper section of the river (Alt and Kogl, 1973). Cohen (1954) reported that broad whitefish (Coregonus nasus kennicotti) spawn in Ikroavik Lake near Barrow in July and possibly in June.

Spawning usually takes place in rivers. In Alaska, there are spawning populations of broad whitefish in Lake Minchumina (Baxter, 1973) and possibly also in the Killick Lakes of the North Slope (Terry Bendock, personal communication). Cohen (1954) reported a spawning population of broad whitefish in Ikroavik Lake. Kuz'min (1969) reported that an attempt to raise broad whitefish in lakes from spawn taken from rivers was not successful because the females did not come to sexual maturity. Kuz'min suggested that running water is a requirement for successful reproduction of these populations.

Broad whitefish broadcast their eggs over substrates ranging from mud and sand to gravel and cobble (Baxter, 1973; Kogl, 1971; Morrow, 1980). Little else is known about their spawning habitat needs.

The fecundity of a sample of 11 females from the Mackenzie River ranged from 26,922 to 65,798 eggs/female with a mean of 39,721 eggs/female (DeGraaf and Machniak, 1977). Three fish from the Kuskokwim River had fecundities ranging from an estimated 46,219 to 127,707 eggs/female (Baxter, 1973).

Apparently, in several stocks, there is a post-spawning downstream migration of adults to overwintering areas in deep sections of rivers or in brackish water areas or lakes (Baxter,

personal communication; Bendock, 1977; Berg, 1948; Morrow, 1980; Scott and Crossman, 1973). In the Mackenzie River, this downstream migration occurs in early November. Broad whitefish overwinter in the outer Mackenzie Delta and in lakes of the inner Delta (DeGraaf and Machniak, 1977).

In the lower Kuskokwim River, the population which overwinters in the main river migrates back to the summer feeding areas of the tundra system in late May or early June after spring runoff (Baxter, 1973). A similar migration occurs in the Minto Flats area. Broad whitefish move in June from the Tanana, Tolovana, and Chatanika Rivers to feed in the lakes and sloughs of the Flats (Kepler, 1973). On the North Slope, some broad whitefish migrate out of the larger rivers such as the Colville, Canning and Sagavanirktok when these rivers break up in early June and move into shallow bays and lagoons of the Beaufort Sea for summer feeding (Bendock, 1977). Other broad whitefish remain in the rivers throughout the summer.

Young broad whitefish hatch in the spring and apparently migrate to summer feeding areas which may include lakes (Baxter, 1973; Berg, 1948; Morrow, 1980). There is no information on whether or not the young-of-the-year fish have rearing areas separate from the immature and adult fish.

The broad whitefish is apparently a bottom feeder. The diet includes gastropods, pelecypods, chironomids including midge larvae and pupae, mosquito larvae, other dipteran larvae and adults, terrestrial insects, trichopterans, amphipods, mysids, copepods, and phytoplankton (Bendock, 1977 and 1979; Berg, 1948; Boughton and Clemens, 1966; DeGraaf and Machniak, 1977; Furniss, 1975; McPhail and Lindsey, 1970; Scott and Crossman, 1973). Apparently, little feeding, if any, occurs during overwintering. Stomachs of fish captured while overwintering in the Colville River (Bendock, personal communication; Kogl and Schell, 1975)

and the Sagavanirktok River (Bendock, 1977) have been empty. In the Kuskokwim River area, the fish do not feed from the time they leave the tundra system in the fall until the time they return to the tundra lakes and streams in the spring (Baxter, 1973). Stein et al. (1973, cited by DeGraaf and Machniak, 1977) collected broad whitefish from lakes in the Mackenzie Delta during the summer. They reported that a lower percentage of fish taken from lakes had empty stomachs than those taken from the Mackenzie River, indicating the importance of lakes as feeding areas.

Most broad whitefish reach sexual maturity at about age five to seven (Alt, 1976; Berg, 1948). At that time, they are around 35 - 50 cm fork length and weigh around 0.5-2 kg (Alt, 1976; Bendock, 1979; Berg, 1948). Specimens have been captured in Siberia weighing up to 12 kg and perhaps 16 kg; the longest fish reported was 86 cm long (Berg, 1948). The maximum age reported to date is 22 years (Craig and Haldorson, 1980).

The broad whitefish is the largest of the Alaskan whitefish (Morrow, 1980) except for the sheefish. The maximum length reported for most populations of Alaskan broad whitefish is around 65 cm fork length (Alt, 1976; Bendock, 1979; Kogl, 1971); the largest fish from the Kuskokwim River was 72.4 cm fork length and weighed 7.6 kg (R. Baxter, personal communication). Most Alaskan broad whitefish captured are between 25-60 cm fork length, between 0.5 - 2.5 kg in body weight, and are four to eight years of age (Alt, 1976; Bendock, 1979; Furniss, 1975). The average weight of fish in the commercial harvest in the lower Kuskokwim is 3.3 kg (R. Baxter, personal communication). There are considerable differences in growth rates and in size of broad whitefish among different geographical areas.

D. Ecological and Economic Importance

The broad whitefish is of excellent quality as a food fish and is important in commercial and subsistence fisheries. In Alaska, a limited commercial summer fishery on the Colville River delta takes about 3000 broad whitefish or about 7,000 kg per year (Alt and Kogl, 1973). The broad whitefish is the target species in the Nechehik Channel of the Colville (Kogl and Schell, 1975). Another small commercial fishery exists in the Yukon-Kuskokwim Delta area. The broad whitefish is widely used throughout its range in Alaska for subsistence food. In the Kuskokwim River delta area, it is second only to salmon in importance (Baxter, 1973). It is taken year round by gill nets; in the summer, fish fences and dip nets are also used. Small numbers are taken each year in Alaska by sportfishermen.

II. SPECIFIC HABITAT REQUIREMENTS

A. Adults

Broad whitefish have been captured in Alaska and northwest Canada in water temperatures ranging from 0 to 16°C (Bendock, 1977; Craig and Haldorson, 1980; Kogl, 1971; Muth, 1969). They may tolerate summer temperatures in shallow ponds of the Kuskokwim River delta up to about 20°C (R. Baxter, personal communication). There is no information on preferred temperatures, but fish from the Mackenzie River (0 to 15.5°C annual range) have a greater growth rate than Coppermine River fish (0 to 10.0°C annual range) which may suggest that summer temperatures above 10°C are more favorable for growth (Muth, 1969). The longer growing season and the greater food abundance in the Mackenzie could also be factors. Alt (1976) suggests that the slower growth rate of broad whitefish from the Sagavanirktok River and Imuruk Basin (Seward Peninsula) as compared to other populations within Alaska may be a result of the shorter ice-free period in those two areas.

Broad whitefish in Alaska generally occur in streams where the gradient is less than 0.75 m/km (Alaska Department of Fish and Game, unpublished manuscript; Kogl, 1971). Current velocities for several bodies of water on the North Slope where broad whitefish occur range from 0 to around 180 cm/sec. (Kogl, 1971).

The broad whitefish occurs in Alaska in tundra ponds where the pH can range down to pH 5.5 or 6.0 (K. Alt, personal communication; R. Baxter, personal communication). They also occur in lakes where the pH at the surface can range upward to 8.1 (Boughton and Clemens, 1966). However, the exact range that they can tolerate or that they prefer is unknown.

Broad whitefish have been caught in waters with salinities of: 11.4 to 40.8 parts per thousand (ppt) in April on the Colville River Delta (Kogl and Schell, 1975), 0-30 ppt in coastal areas of the North Slope (Craig and Haldorson, 1980), 4-28 ppt in Prudice Bay (Bendock, 1977), and occasionally in brackish water of 5-6 ppt in coastal areas of Siberia (Berg, 1948). Alt (1976) states that they are seldom taken in waters of greater than 20 ppt salinity. They have been caught in waters of the North Slope with turbidities of 2-146 NTU (Craig and Haldorson, 1980) and 5-10 ppm (Kogl, 1971).

1. Spawning Migration

In laboratory experiments at 12 - 13°C, Jones (197?) found that the critical velocity for broad whitefish with a fork length of about 35 cm was approximately 65 cm/sec. Jones projected that adult broad whitefish could move 100 m in 10 minutes against a current velocity of 40 cm/sec. Upstream migrations could be inhibited by higher current velocities or stream reaches longer than 100 m with velocities in the range of 40 cm/sec. However, the fish occur in the summer in streams of the North Slope which have current velocities of 80 to 180 cm/sec (Kogl, 1971).

2. Spawning

Broad whitefish spawn at water temperatures close to 0°C (K. Alt, personal communication; R. Baxter, personal communication; Berg, 1948). Spawning takes place at about the time of freezing of lakes and streams. The upper temperature limit is unknown.

Spawning takes place over substrates ranging from mud and sand to gravel, cobble, and boulders with perhaps fine

gravel being the most common substrate (Alt, personal communication; Baxter, personal communication; Kogl, 1971).

Running water prior to spawning may be a requirement of certain stocks of broad whitefish for successful sexual development of females (Kuz'min, 1969). However, there appear to be strictly lacustrine stocks. Examples in Alaska are the Lake Minchumina population which evidently spawns on gravel and cobble along the lake shore (R. Baxter, personal communication) and the Ikroavik Lake population (Cohen, 1954).

3. Overwintering

Broad whitefish overwinter at 0°C with no apparent ill effects (Baxter, 1973; Bendock, 1977). Kogl and Schell (1975) found broad whitefish in the Colville Delta in April where at dissolved oxygen concentrations were 2.3 to 7.8 mg/l and Bendock (1980) has found them overwintering in holes of the Colville River where dissolved oxygen levels were 1.4 to 4.6 mg/l. Fish found at the lower dissolved oxygen level appeared healthy. Baxter (1973) stated that 2 mg O₂/l is apparently the minimum oxygen level tolerable for Kuskokwim River broad whitefish.

B. Incubation of Embryos

Very little information is available for the embryonic stage of the broad whitefish. Because of their geographic location and time of spawning, must incubate at water temperatures close to 0°C. However, Cohen (1954) states that broad whitefish (Coregonus nasus kennicottii) spawn in Ikroavik Lake near Barrow in July; the eggs developed at 6-12°C and hatched in 30-60 days.

C. Juvenile Rearing

Young of the year and juveniles apparently mix with the adults. It is not presently known if there are differences in habitat requirements among these life stages.

III. SUITABILITY INDEX CURVES

No suitability index curves were drawn for the broad whitefish because there is not sufficient information to construct meaningful curves. The wide distribution of this species in habitats with differing ranges of habitat parameters further compounds the problem. Tables I and II provide a general overview of certain physical and chemical parameters.

BROAD WHITEFISH Table I. Adults

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	0	overwintering	Kuskokwim River area	Baxter (1973)
	0 - 1	overwintering	Colville and Sagavanirktok Rivers	Bendock (1977)
	0 - 15.5	annual range	Mackenzie River	Muth (1969)
	0 - 10.0	annual range	Coppermine River	Muth (1969)
	0 - 14	temperature at time of capture	North Slope	Craig and Haldorson (1980)
	14 - 16	summer range	North Slope	Kogl (1971)
	may go up to 20	tundra ponds	Yukon-Kuskowim Delta	R. Baxter (personal communication)
Dissolved Oxygen, mg/l	2.3 - 7.8	overwintering	Colville River Delta	Kogl and Schell (1975)
	1.4 - 4.6	overwintering	Colville River	Bendock (1980)
	2	minimum tolerable at 0°C	Kuskokwim River	Baxter (1973)
Salinity, ppt.	11.4 - 40.8	April	Colville River Delta	Kogl and Schell (1975)
	0 - 30		Coastal areas of North Slope	Craig and Haldorson (1980)
	4 - 28		Prudhoe Bay	Bendock (1977)
	5 - 6		Siberia	Berg (1948)

BROAD WHITEFISH Table II. Spawning

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	around 0		Kuskokwim River	R. Baxter (personal communication)
	close to 0		USSR	Berg (1948)
	0 - 4		Alaska	K. Alt (personal communication)

IV. DEFICIENCIES IN DATA BASE AND RECOMMENDATIONS

Because so little is known about the habitat tolerances, preferences, and needs of the broad whitefish, information is needed on almost all aspects. There is a need for basic descriptive life history studies, extensive measurements of habitat parameters, and physiological experiments in the laboratory.

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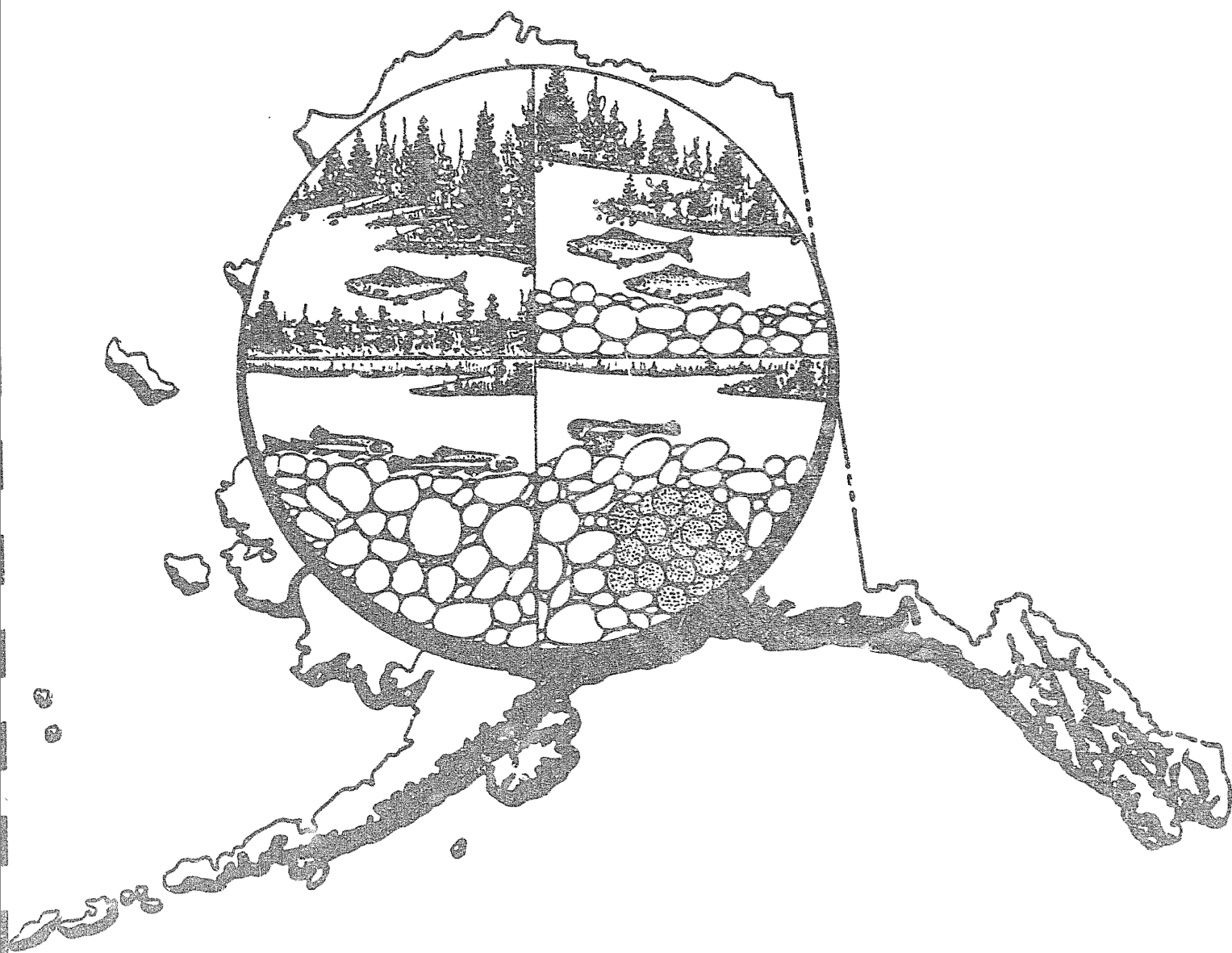
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FRESHWATER HABITAT RELATIONSHIPS

ROUND WHITEFISH—PROSOPIUM CYLINDRACEUM



ALASKA DEPARTMENT OF FISH & GAME
HABITAT PROTECTION SECTION
RESOURCE ASSESSMENT BRANCH

FRESHWATER HABITAT RELATIONSHIPS
ROUND WHITEFISH (PROSOPIUM CYLINDRACEUM)

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I. INTRODUCTION

A. Purpose

This report presents available information on the freshwater habitat requirements of the round whitefish, Prosopium cylindraceum (Pallas), and evaluates the habitat parameters which are most important to the species or are most often critical to survival or limiting to production. The emphasis of this report is on habitat requirements, primarily those of a physical or chemical nature. Certain biological factors affecting the well being of the population such as feeding, predation, competition, parasites, and disease are not comprehensively treated.

This report is intended to support habitat evaluation activities by presenting a data base for the species and by pointing out where more data are needed. Although information has been gained from throughout the range of the species, emphasis is placed upon Alaska. While there appears to be wide differences in growth rates between different populations within the State, there is insufficient information to show that habitat requirements differ among the various populations.

The life history of the round whitefish is not well known. It is one of the least studied coregonids (Jessop and Power, 1973). Several good papers on the life histories of related species are presented in Biology of Coregonid Fishes edited by Lindsey and Woods (1970). Most studies of round whitefish have dealt with age and length; little is known of habitat tolerances, preferences, and requirements. The round whitefish appears to have fairly wide habitat tolerances. They are widely distributed in Alaska, except for the Aleutian Islands and Southeast, and occur in a variety of habitats including lakes and rivers.

B. Distribution

The round whitefish is distributed widely in Siberia and the northern part of North America. It is one of the most widespread and common species of northern waters (McPhail and Lindsey, 1970). In Siberia, it occurs in Arctic Ocean drainages from the Yenisei River east to the Bering Sea, south to northern Kamchatka, and is also found in drainages on the north side of the Sea of Okhotsk. In North America, it occurs in New England, the Great Lakes (except for Lake Erie), in most of Canada (except for the southern part of the four western provinces and in the region of the Manitoba - Ontario boundary where there is a discontinuity) and in Alaska (McPhail and Lindsey, 1970; Scott and Crossman, 1973).

The round whitefish occurs throughout Alaska except for the Yukon - Kuskokwim delta, Aleutian Islands, Kodiak Island, and most of the southeast part of the State; although it does occur in the Chilkat, Alsek, and Taku drainages (R. Baxter, personal communication; McPhail and Lindsey, 1970; Morrow, 1980) (Figure 1.) It is most abundant in gravelly mountain streams and associated lakes (Alt, 1971; R. Baxter, personal communication; Berg, 1948; Krasikova, 1968; McCart et al., 1972).

C. Life History Summary

At least some populations of round whitefish apparently engage in spawning migrations but they are not as strong or directed as those of some of the other whitefish (Morrow, 1980). Movements have been observed in tributaries of the Sagavanirktok River in August and September prior to spawning season (McCart et al., 1972; Yoshirhara, 1972). In Newfound Lake, New Hampshire, fish move to the spawning area in the fall; the males usually arrive before the females (Norman, 1969). Craig and Wells (1975) reported aggregations of round whitefish in spring-fed sections

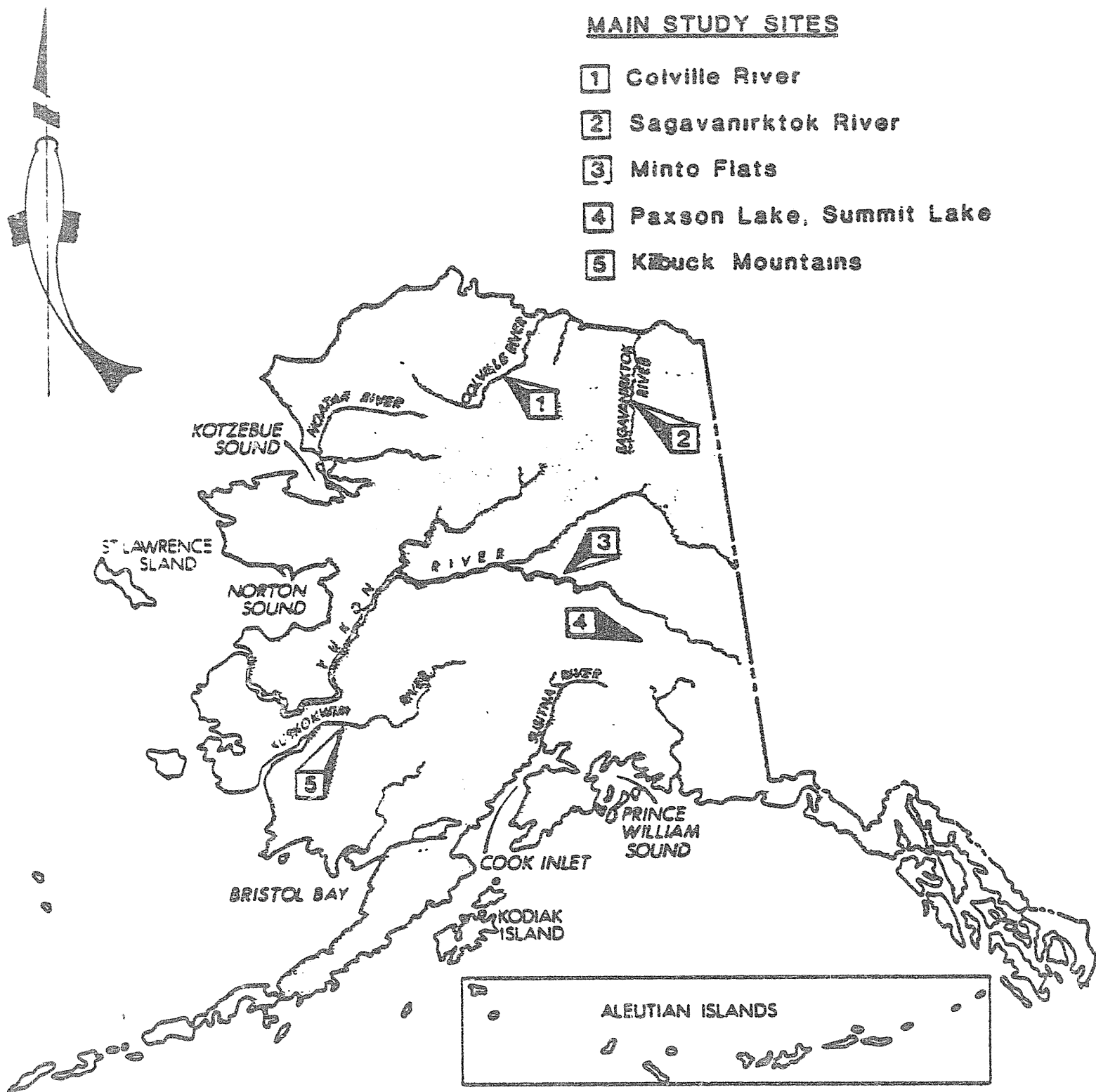


Figure 1. Distribution of Round whitefish in Alaska (R. Baxter, personal communication; Morrow, 1980) and main study sites

of the Chandalar River in the fall, which may indicate the existence of a spawning migration.

Spawning takes place in the fall in shallow, gravelled areas of lake shores or streams. Spawning in interior Alaska occurs in late September through October (Morrow, 1980). It may occur in northern Yukon Territory as early as late August (Bryan, 1973, cited by Bryan and Kato, 1975). November and December is the spawning season in the southern parts of the range (Scott and Crossman, 1973). Apparently there is little or no feeding during prespawning or spawning activities (Craig and Wells, 1975; Normandeau, 1969).

During spawning in Newfound Lake, males and females swim in pairs (Normandeau, 1969). Prior to spawning round whitefish on the spawning grounds in Aishihik Lake, Yukon Territory, slowly swam near the bottom in groups (Bryan and Kato, 1975). The eggs are broadcast over the substrate and settle into crevices in the gravel.

Fecundity ranges from about 2,000 - 14,000 eggs/female with large females producing up to 20,000 eggs; the average is around 5,000 - 10,000 eggs (Bailey, 1963; Craig and Wells, 1975; Furniss, 1974; Krasikova, 1968; McPhail and Lindsey, 1970; Normandeau, 1969). No parental care is provided for the eggs.

There are indications that in many areas, round whitefish, once mature, spawn every year (Craig and Wells, 1975; Krasikova, 1968; McCart et al., 1972); however, this is not the case in all areas (Jessop and Power, 1973).

In Newfound Lake, eggs incubate about 140 days (at 2.2°C) and hatch in April and May (Normandeau, 1969). The young hatch as sac fry and the yolk is absorbed in two or three weeks. The fry

remain upon the bottom after hatching and seek shelter in rubble and boulders. They evidently leave the spawning grounds within a month. In the northern Yukon Territory, fry have been found over gravel areas of streams soon after spring breakup (Bryan, 1973, cited by Bryan and Kato, 1975).

There is little information on whether the young fish have rearing areas separate from the adults. A survey of streams in the Sagavanirktok River basin showed that fry were abundant in the main river and lower Atigun River, but not in other areas where juveniles and adults were present (McCart et al., 1972). Kogl (1971) believed the Colville River delta to be an important rearing area as young age groups were captured there. Rearing also takes place in the summer in the tributaries of the Colville River (Alt and Kogl, 1973). Krasikova (1968) stated that in Siberia the young feed in the upper reaches of streams and along the shores of lakes. Bailey (1963) stated that there may be a segregation by age during the summer in the Isle Royale area of Lake Superior.

The adult round whitefish is usually found in deep lakes in the southern part of its range and more often in rivers and streams in the northern parts (Scott and Crossman, 1973). In the Great Lakes, it is considered to be a shallow water species. Koelz (1929, cited by Scott and Crossman, 1973) stated that it is found at water depths less than 45.7 m and Dryer (1966, cited by Scott and Crossman, 1973) found them to be most abundant in western Lake Superior at water depths less than 36.6 m. The greatest water depth at which Dryer caught fish was 71.9 m. Scott and Crossman (1973) state that a U.S. Fish and Wildlife Service vessel caught one specimen in a bottom gillnet set in eastern Lake Superior at 218.9 m. In the Kuskokwim River area, round whitefish occur in lakes at least as deep as the hypolimnion (R. Baxter, personal communication).

The round whitefish has been reported to occur in brackish waters along the coastline of Hudson Bay and off the mouths of the Coppermine and Mackenzie rivers (Scott and Crossman, 1973). Evidently, it does not occur in brackish water in Alaska (Alt, 1971); at least it has not yet been captured in such areas.

The round whitefish is a bottom feeder, consuming primarily benthic invertebrates in shallow areas of streams and inshore areas of lakes. Food items include: mayfly larvae, caddisfly larvae and adults, chironomid larvae and pupae, gastropod and pelecypod molluscs, fish eggs and small fish, immature Diptera including blackfly and mosquito larvae, stonefly nymphs, and cladocerans (Furniss, 1974; Krasikova, 1968; McCart et al., 1972; Morrow, 1980; Normandeau, 1969; Scott and Crossman, 1973). Krasikova (1968) found that the feeding rate of round whitefish in July and August is considerably higher in streams than in lakes. Movement of round whitefish into tributary streams of the Sagavanirktok River apparently are summer feeding excursions (McCart et al., 1972).

The maximum length, weight, and age reported for the species is 56.1 cm total length, 2.0 kg (perhaps 2.3 kg) and age 22 (Craig and Wells, 1975; Furniss, 1974; Morrow, 1980; Scott and Crossman, 1973). MacKay and Power (1968) stated that the ultimate size for the species was 40 - 50 cm fork length. Round whitefish in Alaskan waters are usually less than 40 cm fork length and usually weigh less than 0.5 kg although specimens up to 52 cm and 1.5 kg have been taken (K. Alt, personal communication; R. Baxter, personal communication).

The fish reach sexual maturity at about age 4 or 5 in the southern part of their range and at age 6, 7 or 8 in northern parts (McPhail and Lindsey, 1970; Morrow, 1980; Peck, 1964). Similar differences exist between fast and slow growing populations in Siberia (Krasikova, 1968).

Growth rates vary considerably throughout the range (Bailey, 1963; Craig and Wells, 1975; Falk and Dahlke, 1974; Jessop and Power, 1973; Mraz, 1964; Peck, 1964; Whye and Peck, 1968). Lake Michigan fish reach a total length of 50 cm in 7 years; fish from a lake in the Brooks Range take 12 years to reach this length (Morrow, 1980). Krasikova (1968) believed that the differences in growth rates among areas resulted from differences in food production.

D. Ecological and Economic Importance

The round whitefish plays a minor role in lake ecosystems as a predator on the eggs of other fish but it primarily consumes benthic invertebrates. The round whitefish is a prey item for other species of fish, including lake trout and pike.

The round whitefish is a high quality food fish. In past years, it has supported a commercial fishery in the Great Lakes up to about 180 metric tons annually (Scott and Crossman, 1973). It is of some commercial importance in the USSR. In Alaska, subsistence fishermen take limited numbers of round whitefish.

The fish is sought by sport fishermen in New Brunswick (Scott and Crossman, 1973) and a limited sport fishery exists in Alaska (Alt, 1971).

II. SPECIFIC HABITAT REQUIREMENTS

A. Spawning

Round whitefish in Aishihik Lake, Yukon Territory, spawned when water temperatures were around 1 - 2°C (Bryan and Kato, 1975). Krasikova (1968) found them spawning in the Rybnaya stream of the USSR in early October when the water temperature was around 0°C. Lake Superior fish spawned at 4.5°C (Scott and Crossman, 1973). Round whitefish spawn in both lakes and streams. At the outlet of Aishihik Lake, Bryan and Kato (1975) observed them spawning in current velocities ranging from less than 31 cm/sec to 63 cm/sec. A sampling grid in the spawning area revealed that eggs were most dense in the faster water. However, they also spawn in still water (Koelz, 1929, cited by Bryan and Kato, 1975; Normandeau, 1969).

Round whitefish spawned in the outlet of Aishihik Lake at water depths ranging from 0.7 to 2.5 m (Bryan and Kato, 1975). Eggs were most abundant at depths less than 1 m. In Newfound Lake, New Hampshire, they were observed spawning at water depths of 0.15 to 2.0 m or more (perhaps down to 3.66 m) although most eggs were found at depths between 0.15 and 0.60 m (Normandeau, 1969). Spawning in the Great Lakes takes place at water depths of 4 to 15 m (Koelz, 1929, cited by Scott and Crossman, 1973). The substrate chosen by round whitefish for spawning in Newfound Lake was a rocky reef covered with gravel and rubble and a few large boulders. The bottom was kept free of silt by wind driven waves. Sandy areas were not used for spawning (Normandeau, 1969). Bryan and Kato (1975) found that the round whitefish of Aishihik Lake spawned at the outlet over a variety of substrates ranging from mud to gravel and boulders but that the eggs were most dense over gravel (particle size 2-250 mm). Other investigators have reported them spawning over gravel and boulders (Koelz, 1929, cited by Bryan and Kato, 1975), over gravel (ADF&G, unpublished

MS), and over cobble and gravel in widened stretches of small streams (Krasikova, 1968).

B. Incubation

The water temperature of Newfound Lake was 2.3°C during the incubation period of round whitefish eggs (Normandeau, 1969). Given that round whitefish in Alaska spawn in the fall at water temperatures around 0°C, the eggs must incubate at temperatures close to 0°C. Eggs of round whitefish which spawned in lakes would probably incubate at slightly higher temperatures.

No information is available on dissolved oxygen levels required during incubation but the oxygen levels encountered must be fairly high, given that the eggs are located on the surface of substrate and incubate at low water temperatures.

C. Juvenile Rearing

Little information is available on any habitat requirements or preferences that juveniles may have which are different from adults. Baxter (personal communication) has found that Age I and II fish live in the same areas as adults but in shallower waters. Peck (1964) compared the growth rates of round whitefish in Paxson and Summit Lakes and found that the young-of-the-year fish in Paxson Lake have a greater growth rate. Peck suggested that this was a result of an earlier warming of the waters in the spring and a greater food productivity in Paxson Lake.

D. Adults

In the western part of the North Slope, round whitefish are found in the summer in streams where the water temperature ranges from 3 - 16°C (Kogl, 1971). Fall migrations in the Sagavanirktok River drainage have been observed at water temperatures ranging

from 0 - 13°C (McCart et al., 1972; Yoshihara, 1972). Round whitefish in Moosehead Lake, Maine, were distributed in August at water temperatures ranging from 13.9 - 17.5°C (Cooper and Fuller, 1945, cited by Ferguson, 1958). Round whitefish have been found overwintering in deep holes in the Colville, Kuparuk, and Sagavanirktok Rivers at water temperatures of 0 - 1°C (Bendock, 1977, 1979 and 1980).

Round whitefish in streams of the Kilbuck Mountains are generally found where the gradient is greater than 0.5 m/km (ADF&G, unpublished MS). They occur in North Slope streams where the gradient ranges from about 1 - 14 m/km and the current velocity ranges from about 24 - 274 cm/sec (Kogl, 1971). They may not actually be present in the higher current velocities, but do occur in streams which have these velocities. Berg (1948) and Krasikova (1968) stated that round whitefish in the USSR prefer swift currents.

Jones (197?) determined experimentally that the critical velocity for nine round whitefish with an average fork length of 30.4 cm was 42.5 cm/sec.

Round whitefish are found on the North Slope in the summer over substrates ranging from mud to cobble and boulders (Bendock, personal communication; Kogl, 1971). However, they seem to be found most commonly in streams with a gravel bottom (ADF&G, unpublished MS; Berg, 1948; Krasikova, 1968).

The turbidity of streams of the western North Slope where round whitefish are found in the summer ranges from clear to 15 ppm (Kogl, 1971). They apparently have a preference for clear streams (R. Baxter, personal communication; T. Bendock, personal communication; DeGraaf and Machniak, 1977).

In the Colville River, healthy appearing fish with food in their stomachs were taken from waters with dissolved oxygen concentrations ranging from 2.6 - 5.6 ppm (Bendock, 1980). In the Kuparuk and Sagavanirktok Rivers where round whitefish were taken, the dissolved oxygen saturation ranged from 49 - 100% (Bendock, 1977). Streams of the Kilbuck Mountains and Nulato Hills where they are found are well oxygenated throughout the year (ADF&G, unpublished MS).

III. SUITABILITY INDEX CURVES

No suitability index curves were drawn for the round whitefish because it was believed that there is not sufficient data to construct meaningful curves. The wide distribution of the species in a variety of habitats with broad ranges of habitat parameters further compounds the problem of describing optimum habitat. Tables I and II provide a general overview of certain parameters.

Table I: Round Whitefish Spawning

Parameter	Observed Values	Remarks	Location	Reference
Temperature °C	around 1 - 2		Aishihik Lake, Yukon Territory	Bryan and Kato, 1975
	around 0		Maya River, USSR	Krasikova, 1968
	4.5		Lake Superior	Scott and Crossman, 1973
Current Velocity, cm/sec	0		Great Lakes	Koelz, 1929 (cited by Bryan and Kato, 1975)
	0		Newfound Lake, N. H.	Normandeau, 1966
	<31 - 63	eggs most abundant in faster water	outlet of Aishihik Lake, Yukon Terr.	Bryan and Kato, 1975
Water Depth, m	0.7 - 2.5	eggs most abundant at water depths <1 m	outlet of Aishihik Lake, Yukon Terr.	Bryan and Kato, 1975
	0.15 - 2.0 +	range	Newfound Lake, N. H.	Normandeau, 1969
	0.15 - 0.60	most eggs		
	4 - 15	range	Great Lakes	Koelz, 1929 (cited by Scott and Crossman, 1973)

Table II: Round Whitefish, Adult

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	3 - 16	have been captured at these temperatures in the summer	Western North Slope	Kogl, 1971
	0 - 13	fall migrations	Happy Valley Crk. (trib. of Sagavanirktok R.)	McCart et al., 1972
	0 - 12	fall migrations	Lupine River (trib. of Sagavanirktok R.)	Yoshihara, 1972
	0 - 1	overwintering	Colville, Kuparuk and Sagavanirktok R.	Bendock, 1977 & 1980
	13.9 - 17.5	distribution in August	Moosehead Lake, Maine	Cooper and Fuller, 1945 (cited by Ferguson, 1958)
Dissolved Oxygen	2.6 - 5.6 mg/l	overwintering	Colville River	Bendock, 1980
	49 - 100% saturation	overwintering	Kuparuk and Sagavanirktok R.	Bendock, 1977

IV. DEFICIENCIES IN DATA BASE AND RECOMMENDATIONS

Because of the paucity of information, it is not possible to elaborate on specifics regarding the habitat tolerances, preferences and needs of the round whitefish. If the habitat of the round whitefish is to be adequately described in Alaska, more research is required. Studies needed range from basic descriptive life history studies to extensive measurements of habitat parameters to physiological experiments in the laboratory.

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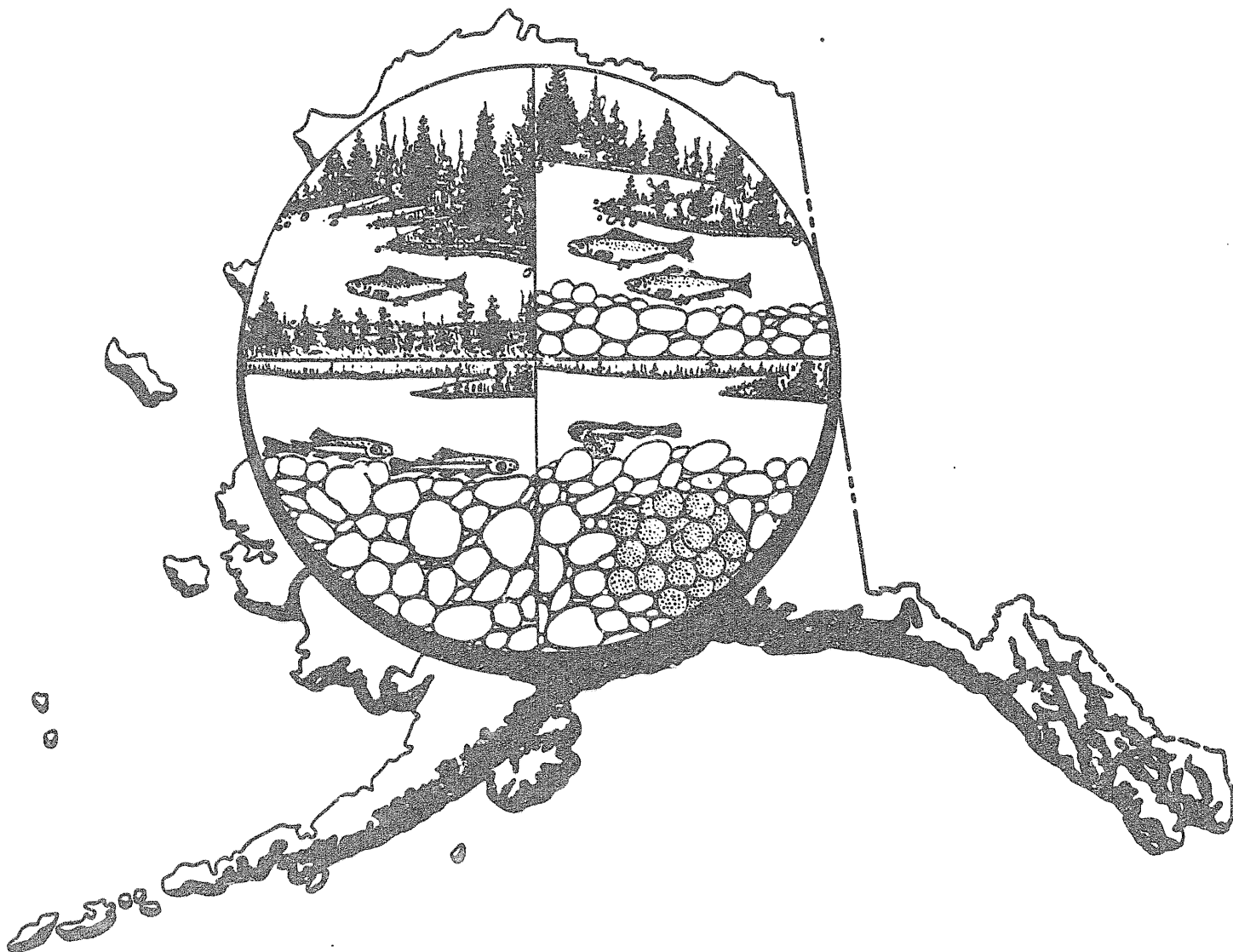
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FRESHWATER HABITAT RELATIONSHIPS

ARCTIC GRAYLING - THYMALLUS ARTICUS



ALASKA DEPARTMENT OF FISH & GAME
HABITAT PROTECTION SECTION
RESOURCE ASSESSMENT BRANCH

APRIL, 1981

FRESHWATER HABITAT RELATIONSHIPS
ARCTIC GRAYLING (THYMALLUS ARCTICUS)

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I. INTRODUCTION

A. Purpose

The purpose of this project is to describe how selected physical and chemical features of lotic habitat within Alaska influence the survival and behavior of the various life stages of Arctic grayling, Thymallus arcticus (Pallas).

Objectives of this project are:

- 1) To gather data from published and unpublished sources within Alaska, Canada and Montana and from conversations with fishery biologists from the above areas concerning the relationships between lotic aquatic habitat and Arctic grayling survival and behavior.
- 2) To develop an Alaska data base composed of narrative and tables of observed physical parameters to better understand habitat-Arctic grayling relationships; and
- 3) To identify areas where data are lacking and to recommend studies to fill gaps in the data.

The following "Life History Summary" and "Specific Habitat Relationships" sections will identify the lotic habitat relationships of the various life history and seasonal behavior stages of the Arctic grayling which include:

upstream spawning migration;
spawning;
post-spawning movements;
incubation;
summer rearing;

— migration to overwintering areas; and
winter rearing

B. Distribution

The Arctic grayling is a holarctic species of the genus Thymallus. Within North America it occurs from Hudson Bay west through northern Manitoba, Saskatchewan, Alberta and British Columbia, the Northwest Territories (excluding most islands of the Arctic archipelago), the Yukon and most of Alaska. In Eurasia it is found as far west as the Kara and Ob Rivers and south to Northern Mongolia and North Korea.

Several isolated, relict populations exist in North America. One is located in a fraction of its original range in the extreme headwaters of the Missouri River drainage in Montana (Nelson, 1953). Two other relict populations are found in Canada, one in southeast British Columbia and the other in southwest Alberta (Scott and Crossman, 1973).

An Arctic grayling population in the Great Lakes region was eliminated in the 1930s. Possible causes were log drives during the spawning season, intense angling effort and general habitat degradation (Creaser and Creaser, 1935). Attempts to restock these waters failed. Arctic grayling have been introduced to Colorado, Utah, Idaho and Vermont (Scott and Crossman, 1973). Arctic grayling are distributed over much of Alaska (Figure 1) (McClean and Delaney, 1978). Distribution of Arctic grayling within southeast Alaska is primarily limited to stocked lakes. Occasionally fish drift downstream in large stream systems, such as the Stikine River. These rivers often support substantial populations of grayling in their headwater reaches (McClean and Delaney, 1978).

Insert Figure 1

MAIN STUDY SITES

- 1 TANANA RIVER
- 2 KAVIK RIVER
- 3 GULKANA RIVER
- 4 TYEE LAKE
- 5 COLVILLE RIVER

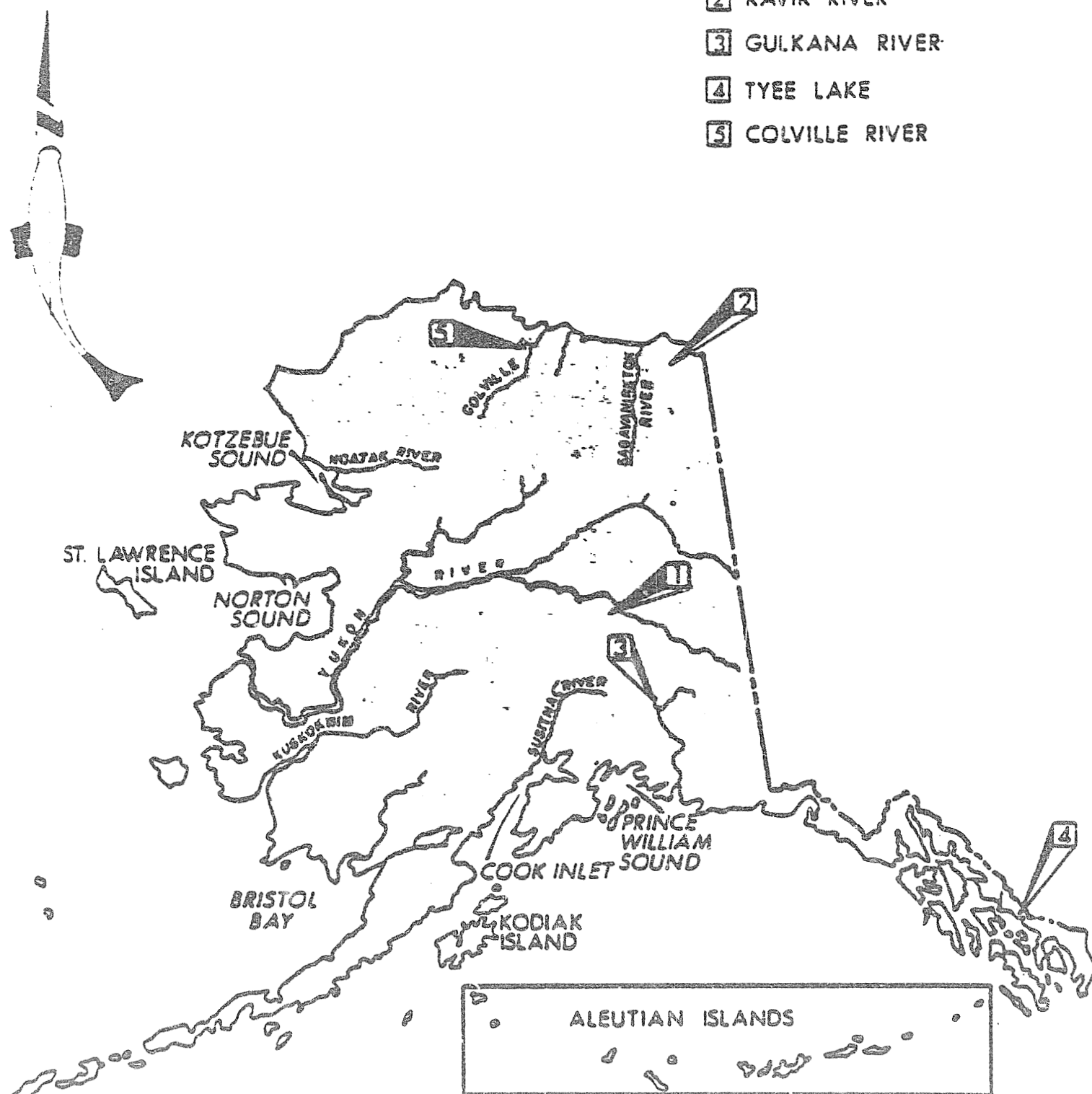


FIGURE 1. DISTRIBUTION OF ARCTIC GRAYLING IN ALASKA (FROM ALASKA DEPARTMENT OF FISH AND GAME, 1978) AND MAIN STUDY SITES.

Numerous clearwater tributaries and lakes within the upper Copper and Susitna River drainages contain Arctic grayling. Grayling are found in the Gulkana and Oshetna Rivers. Arctic grayling are extremely limited within the Prince William Sound area and lower Copper River drainage and somewhat limited within the lower Susitna River drainage. Both of these large rivers are glacial and support relatively small populations. However, a few clearwater tributaries of the lower Copper River and many clearwater tributaries of the lower Susitna River, such as the Talachulitna and Chunilna River, and Lake Creek contain Arctic grayling. Arctic grayling are not found on the west side of Cook Inlet south of Tyonek (McClearn and Delaney, 1978).

Numerous lakes within the Kenai Peninsula were stocked and now support reproducing populations of Arctic grayling. These include Crescent, Upper and Lower Paradise, Bench and Twin Lakes (McClearn and Delaney, 1978). Selected lakes on Kodiak and Afognak Islands contain Arctic grayling.

Grayling are also found in clear water streams of the Alaska Peninsula and Bristol Bay drainages. Especially large individuals are found in the Ugashik and Becharof Lake and Togiak River drainages (McClearn and Delaney, 1978).

Arctic grayling are widely distributed in the remaining Arctic and sub-Arctic areas of Alaska, with the exception of the Yukon-Kuskokwim River delta area (McClearn and Delaney, 1978).

(. Life History Summary

Arctic grayling usually migrate to spawning sites just prior to or during spring breakup. Several factors influence the upstream migration of this fish including distance separating overwintering and spawning sites, streamflow and water temperatures. Tack (1971) reported upstream movement of fish

within the ice covered Chena River about 2.5 weeks prior to breakup conditions. Tripp and McCart (1974) reported upstream movement of fish in the ice covered Mackenzie River to ice-free tributaries.

Fish passage can be prevented by ice jams, beaver dams or waterfalls. The swimming performances of adult and juvenile Arctic grayling are influenced by fish size, water temperature, current velocity and the size and extent of barriers. Sex and spawning condition also influence the migration of adult fish (MacPhee and Watts, 1976).

The importance of the spawning migration to juvenile fish is not clear. Tack (1980) related this phenomenon to homing. Juvenile fish may become imprinted on visual, olfactory or other conditions and recognize the spawning area upon maturation.

The establishment of male spawning territories may initiate spawning activity (Kruse, 1959; Bishop, 1971; Tack, 1971). Males select territorial sites for various physical conditions where spawning will eventually take place.

Grayling territories vary in size with respect to stream width, water depth, current velocity, channel configuration, spawner density and, possibly, other conditions. Kruse (1959) measured territories of 0.15 by 0.61 m (0.5 by 2.0 ft) in a 1.5 m (5 ft) wide reach of Northwest Creek, an inlet of Grebe Lake, Wyoming. However, in a wider (2.4-3.0 m, 8-10 ft) reach of the same stream, territory dimensions were approximately 1.2 by 1.2 m (4 by 4 ft). Tack (1971) noted that male fish territories in the outlet of Mineral Lake, Alaska were about 2.4 by 2.4 m (8 by 8 ft).

Ripe males establish spawning territories and vigorously defend them from other males. Short head-on thrusts usually repel

sub-adults. Adult males are repelled by lateral displays, sometimes followed by direct attacks (Tack, 1971).

Grayling spawn in areas with surface current velocities less than 1.4 m/sec (4.5 ft/sec), varying water depths and relatively small, unimbedded gravels about 2.5 cm (1 in) in diameter.

Fertilization occurs after the females leave their holding areas and pass through male territories. The females are pursued by several males who attempt to court her. The successful male places his dorsal fin over her back, initiating simultaneous body arching and vibrating. The male may drive the posterior third of the female's body into the substrate where eggs and sperm are released.

The fertilized eggs sink to the bottom of the stream and adhere to the substrate. No actual redd is constructed but the eggs may be covered by as much as 5 cm (2 in.) of dislodged substrate. There is no parental care of the eggs. After spawning, the female resumes her former resting position before possibly spawning again. Both sexes may spawn more than once with various partners. They are capable of spawning annually (Brown, 1938; Kruse, 1959; Bishop, 1971; Tack, 1971; Scott and Crossman, 1973). It is not known whether juvenile and adult Arctic grayling return to the same spawning stream.

The duration of Arctic grayling spawning activity may range from four days to two weeks (Warner, 1955; Tack, 1971; McCart, Craig and Bain, 1972; Tripp and McCart, 1974).

Age of maturity is variable and generally is greater in the northern reaches of this fish's range. Grayling have been found to reach sexual maturity at age 2 or 3 in Michigan (Creaser and Creaser, 1935) and in Montana (Kruse, 1959) streams. Most fish in the North Slope (of the Brooks Range, Alaska) and northern

Yukon and the Northwest Territories mature between ages four to nine (Bishop, 1971; McCart, Craig and Bain, 1972; deBruyn and McCart, 1974; Craig and Poulin, 1974). Fish in the lower Kuskowkwim River, Seward Peninsula and Tanana River, Alaska reach maturity at ages five to six (Alt, 1966 and 1978; Wojcik, 1955).

The life span of Arctic grayling is variable; northern populations generally live longer than southern populations. Maximum ages of Arctic grayling from Montana range from seven to eleven years (Brown, 1938; Nelson, 1953). Several fish from selected Beaufort Sea drainages in the Yukon Territories and the Chandalar River drainage in north-central Alaska ranged in age from 15 to 22 years (de Bruyn and McCart, 1974). Maximum ages of fish from various Tanana River, Alaska drainages are about 11 years (Tack, 1973). Regional differences in grayling life spans may result from varying environmental conditions over their range (Craig and Poulin, 1974) or from differences in aging techniques (scale versus otolith).

Female fecundity varies with fish size and stock. Brown (1938) reported egg fecundities ranging from 1,650 among Grebe Lake, Wyoming individuals (length and weight unknown) to over 12,900 eggs among large (0.91 kg (2 lb)) females from Georgetown Lake, Montana. Mean fecundity values among females from Grebe Lake varied from 1,900 eggs in individuals less than 280 mm (11 in) fork length (fl) to 2,800 in fish exceeding 305 mm (12 in) fl. Female fish ranging in fork length (fl) from 331 to 373 mm ($\bar{x}$ = 353 mm) from Weir Creek, a small tributary of the Kavik River, Alaska contained from 4,580 to 14,730 eggs ($\bar{x}$ = 8,482 eggs) (Craig and Poulin, 1974). Ten females (295 to 395 mm fl) from the upper Chandalar River, Alaska drainage contained 2,330 to 9,150 eggs ($\bar{x}$ = 4,937 eggs) (Craig and Wells, 1974).

Development of Arctic grayling eggs to hatching occurs very rapidly (13-32 days) and is influenced primarily by water

temperatures (Henshall, 1907; Ward, 1951; Bishop, 1971; Kratt and Smith, 1971; Tryon, 1974). The hatched fry, or alevins, with attached yolk sac, are about eight mm long (Scott and Crossman, 1973). The yolk sac is completely absorbed in one to two weeks.

Kruse (1959) examined survival of emergent grayling in Grebe Lake, Wyoming. He estimated that fish survival through the fry stage was about six percent in one of several inlet streams. Probable causes of this high mortality were egg dislodgment, predation and low fertilization. Water velocity could also influence egg and alevin survival. No redds were constructed during spawning and fertilized eggs may not have been covered with gravel.

Alevins hatching within the gravels probably have higher survival than those hatching on the exposed substrate (Kratt and Smith, 1977). The gravel provided cover, decreased the chances of dislodgement and lessened swimming stresses in the early stages.

Growth of Arctic grayling varies considerably over its range, but fish from northern regions generally grow more slowly than fish from southern areas (Craig and McCart, 1974b). The largest grayling recorded from Alaska weighed 2.13 kg (4 lb, 11 oz), and was 54.6 cm (21.5 in) long (Ugashik Narrows, Alaska Peninsula, 1975). The Canadian record grayling weighed 2.71 kg (5 lb, 7 oz) and measured 53.3 cm (21 in) (Northwest Territories, 1967).

Growth rates of young of the year (yoy) Arctic grayling can be extremely variable among drainages due to differences in length of open water (growing) seasons, temperatures and food supplies. For example, 49 fish within the outlet of Chick Lake (along the Donnelly River, a tributary of the Mackenzie River, Northwest Territories, Canada) attained a mean fork length (fl) of 49 mm $\pm$ 4 mm by 8 July, 1973. In contrast 38 individuals from a small inlet to Chick Lake were only 20 mm $\pm$ 4 mm by July (Tripp and

McCart, 1974). The Chick Lake inlet had lower water temperatures and lower benthic invertebrate standing crops than those of the Chick Lake outlet. Elliott (1980) noted substantial differences in growth rates among yoy Arctic grayling among small bog and mountain streams within Alaska. He ascribed those differences to food availability, water temperatures and durations of the growing seasons.

Arctic grayling are opportunistic feeders and consume more and larger prey as they grow. Young of the year fish have been observed feeding prior to total yolk sac absorption (Brown and Buck, 1939; Kruse, 1959). Fish inhabiting lakes may consume Daphnia and chironomid larvae and pupae. Elliott (1980) investigated the summer food habits of fish in selected spring, rapid-runoff and bog streams crossed by the Trans-Alaska Pipeline System (TAPS). Early yoy fish (less than 3.5 mm fl) consumed about three different aquatic and terrestrial invertebrate taxa whereas larger yoy fish (equal to or greater than 3.5 mm fl) consumed up to eight taxa. Immature chironomids were the most frequently eaten taxon.

Larger fish consume drifting immature and mature aquatic invertebrates, mature terrestrial invertebrates and occasionally leaches, fishes, fish eggs, shrews and lemmings (Rawson, 1950; Kruse, 1959; Bishop, 1971; Scott and Crossman, 1973). Mature fish apparently feed infrequently or not at all during the upstream spawning migration.

Arctic grayling may feed during the winter. Fish, captured by gillnet under the ice within pools of the Sagavanirktok and Colville Rivers, Alaska, contained ephemeropteran and plecopteran nymphs (Alt and Furniss, 1976; Bendock, 1980).

Predation on Arctic grayling eggs and alevins by other fishes could significantly reduce fish production. Tack (1971) reported

whitefish preying upon Arctic grayling eggs at the outlet of Mineral Lake, Alaska. Rainbow trout (Salmo gairdneri Richardson), Arctic char (Salvelinus alpinus (Linnaeus)), round whitefish (Prosopium cylindraceum (Pallus)), northern pike (Esox lucius Linnaeus), longnose suckers (Catostomus catostomus (Forster)), and other fishes may also consume Arctic grayling eggs and alevins (Bishop, 1971; MacPhee and Watts, 1976; Alt, 1977).

Spawned-out adult fish may remain within spawning areas or migrate considerable distances to summer feeding areas within lakes or streams. A spawned-out fish tagged in late June 1972 in a lake outlet entering the Mackenzie River near Norman Wells, Northwest Territories was recovered within a month in the Great Bear River, 159 km (99 mi) distant (Jessop et al., 1974). Tagged adults have been shown to leave Poplar Grove Creek, Alaska, a small bog stream, within several weeks after spawning and move to other areas for feeding (MacPhee and Watts, 1976; Williams and Morgan, 1974).

Movement of juvenile fish out of spawning streams can occur during or slightly after adult fish emigration. Decreased flows and lower food availability influence both adult and juvenile fish movements. Some juvenile fish may remain near spawning areas through the summer.

Studies examining the summer microhabitat selection by juvenile salmonids in various Pacific Northwest streams indicate that larger individuals progressively move to faster and deeper stream reaches for increased cover and food availability (Everest and Chapman, 1972; Lister and Genoe, 1970). Most of the larger juveniles were found in relatively fast water with some cover and areas of low current velocity. Everest and Chapman (1972) speculated that fish hold in areas of low current velocities and feed in areas of faster velocity with higher prey densities.

Fry (yoy) may remain within their natal streams or migrate to other systems where they feed and grow during the relatively short Arctic and sub-Arctic open water season (McCart and Bain, 1972; MacPhee and Watts, 1976). The movement of larger, older fish out of spawning streams may lessen competition among age classes. Rearing fish are segregated by size (age) with yoy fish generally occupying areas of lower current velocities, and more shallow water. Yearling and older fish generally occupy deeper, slightly faster areas (Chislett and Stuart, 1979). Larger fish have been observed in pools upstream of smaller fish; areas which probably contain higher densities of prey (Vascotto, 1971).

Fish appear to return to the same summer rearing areas. Many tagged individuals have been recovered the following year in the same areas (Tack, 1980).

Limited studies monitoring fish movements in small bog and mountain streams have detected a late summer to early fall out migration of juvenile and yoy fish (McCart, Craig and Bain, 1972; MacPhee and Watts, 1972). Downstream movement of juvenile fish generally occurs slightly before migration of yoy fish (Craig, McCart and Bain, 1972). Arctic grayling must migrate to their overwintering grounds before the streams become impassable from low flows or ice buildup. Decreasing water temperatures and flows associated with the onset of winter probably influence the timing of migration to overwintering areas.

The winter distribution of Arctic grayling is more restricted than the summer distribution. Most bog and many small mountain and lake inlet and outlet streams become dewatered or freeze solid during the fall and winter months. Fish overwinter in lakes, open pools, spring and glacial streams and in spring fed mountain streams. Fish have been found in pools of large interior Alaska mountain streams, such as the Chena River. Spring streams in the Tanana River drainage in interior Alaska

with seemingly suitable conditions for overwintering fish, do not appear to support overwintering of Arctic grayling (Reed, 1964; Pearse, 1964; Van Hyning, 1978). Spring fed streams along the north slope of the Brooks Range, Alaska, are often the only areas with flowing water and are important fish overwintering areas (Craig and Poulin, 1974).

D. Economic Importance

Arctic grayling are the basis of an important summer recreational fishery. The broad food habits of this fish allow anglers to use a variety of techniques, including fly casting.

Roadside angling is popular during the summer on streams and lakes along the Alaska, Steese, Elliot, Taylor, Glenn, Parks, Richardson and Nome-Taylor highways. Fly-in and float fishing trips are also popular during the summer.

II. SPECIFIC HABITAT REQUIREMENTS.

A. Lake Inlet/Outlets

1. Upstream Migration

a. Water Temperature

Water temperatures associated with the upstream migration of Arctic grayling to spawning areas within inlets and outlets of lakes may range from 0°C (32°F) to about 4°C (39.2°F). Warner (1955) stated that fish began entering a selected inlet of Fielding Lake as soon as there was flowing water. Water temperatures of the inlet during the initial phase of the migration were not given but water temperatures during the last two days of the migration were 0.6°C and 1.1°C (33°F and 35°F).

Many arctic streams may be impassable to Arctic grayling prior to spring breakup because of ice conditions or dewatering. Fish have been observed moving upstream through narrow furrows in anchor ice created by meltwater (Wojcik, 1955). However, maximum numbers of fish usually migrate within these streams at or near peak flow conditions (MacPhee and Watts, 1976; Tack, 1980). Ripe Arctic grayling have been detected moving upriver within ice-covered spawning streams such as Trail Creek, a tributary of the Mackenzie River, Northwest Territories, Canada (Jessop, Chang-Kue, Lilley and Percy, 1974). Arctic grayling may ascend rapid runoff and bog streams, and inlets and outlets of lakes as soon as flow conditions permit passage to spawning sites.

Tack (1972) reported Arctic grayling at the mouth of the Mineral Lake outlet approximately nine days after water temperature of the same outlet reached 1°C (33.8°F). The first large catch of fish at the same location occurred three days later, probably a function of the length of time required to move from their overwintering habitat.

Kruse (1959) noted that Arctic grayling in Grebe Lake, Wyoming, begin spawning migrations into four inlet streams and the outlet stream (the Gibbon River) when water temperatures range from 5.6° to 7.8°C (42°-46°F) and 2.2° to 4.6°C (36°-40°F), respectively. Average daily water temperatures at the conclusion of the spawning migrations in the inlet and outlet streams were 7.2° to 8.3°C (45°-47°F) and 2.2° to 8.9°C (36°-48°F). These temperatures are noticeably higher than those associated with spawning migrations in Fielding and Mineral Lakes.

Tack (1980) found no correlation between momentary temperature reductions below 1.0°C and upstream movement of fish in the Chena River. Diel water temperature patterns may influence upstream fish movement in other streams (Wojcik, 1954, Warner, 1955; MacPhee and Watts, 1976).

b. Current Velocity

Arctic grayling usually begin spawning migrations to inlets and outlets of lakes during breakup conditions. Wojcik (1954) first observed fish in one of several inlet streams of Fielding Lake, Alaska as it began flowing in mid-May, 1954. Warner (1955) observed the first fish in the mouth of the same stream the

following year shortly after open water appeared in early June. Tack (1972) reported Arctic grayling entering the outlet of Mineral Lake from the Tok River, via the little Tok River, during high flow conditions. Mature and immature individuals were captured by gillnet as they congregated near the lake's outlet.

2. Spawning

a. Water Temperature

Water temperature appears to significantly influence Arctic grayling spawning. Wojcik (1954) observed fish spawning in an inlet tributary of Fielding Lake in water temperatures of 3.3°C (38°F). Three to four days later, at the termination of spawning activity, water temperatures reached 7.8°C (46°F). Warner (1955) stated that fish spawning began in the same stream the following spring when maximum water temperatures approached 4.4°C (40°F).

Tack (1972) reported male fish establishing spawning territories in the outlet of Mineral Lake when water temperatures approached 4°C (39.2°F). Spawning ceased when water temperatures decreased and remained below 4°C (at 2°-3°C) for two days. Fish resumed spawning when water temperatures reached 4°C (39.2°F) and continued for four additional days as water temperatures ranged from 4° to 10°C (39.2°-50°F).

Grayling were reported spawning in southern tributaries of the Mackenzie River in water temperatures ranging from 8° to 16°C (46.4°-60.8°F) by Jessop, Chang-Kue, Lilley and Percy (1974).

Arctic grayling spawned in four inlet tributaries of Tyee Lake, near Ketchikan, Alaska during May and June of 1980 in water temperatures ranging from 6° to 11°C (42.8°-51.8°F) (Cuccarease, Floyd, Kelly and LaBella, 1980). Water temperatures of the streams during initial fish spawning were not reported.

Fish spawning occurred in four inlet streams of Grebe Lake, Wyoming in water temperatures ranging from 4.4°C to 10°C (40°-50°F). Water temperatures in the outlet stream during fish spawning ranged from 2.2 °C to 10°C (36°F-50°F) (Kruse, 1959).

Brown (1938) observed several fish spawning in a small, beaver dammed inlet tributary to Agnes Lake, Montana in water temperatures of 10°C (50°F).

b. Current Velocity

Arctic grayling spawn in a wide range of current velocities in inlets and outlets of lakes. Wojcik (1954) reported fish spawning in "slow, shallow backwaters, and not in riffles as had been supposed" in an inlet stream to Fielding Lake. The following spring the fish spawned in surface current velocities of about 1.2 m/sec (3.9 ft/sec) (Warner, 1955). Observations were limited by ice and snow cover during 1954 and 1955.

Surface current velocities in territories of 22 males along the outlet to Mineral Lake, Alaska ranged from 0.34 m/sec to 1.46 m/sec (1.1 ft/sec-4.8 ft/sec) with a mean value of 0.79 m/sec. (2.6 ft/sec) (Tack, 1971).

c. Substrate

Arctic grayling have been reported spawning over gravel substrates of inlets and outlets of lakes within Alaska and Montana. Warner (1955) observed fish spawning over fine (about 1 cm) gravel. Much of the stream was covered by ice and snow, therefore observations were made along an 0.18 km (200 yd) open reach near the mouth of the stream and in smaller open areas upstream. Tack (1971) described the spawning substrate in the outlet of Mineral Lake as being "pea size."

Fish spawning has been observed within riffles and runs of four inlet tributaries to Tyee Lake near Ketchikan, Alaska. Spawning substrate ranged from sand to small cobble. Coarse sand and gravel to about 2.5 cm (1 in) in diameter was commonly used by most fish (Cuccarease, Floyd, Kelly and LaBelle, 1980).

Arctic grayling were observed spawning over a sand-gravel substrate in an inlet stream to Agnes Lake, Montana by Brown (1938). He discussed the limited variety of substrate and other habitat conditions within the stream and the need to better determine the characteristics of optimum Arctic grayling spawning habitat in Montana streams.

Kruse (1959) ranked sand (.3 cm), gravel (.3-7 cm) and rubble (7.6-30.5 cm) in descending order as suitable substrate material for Arctic grayling spawning. Riffles were utilized more often than pools for spawning.

Fish were reported spawning over relatively fine gravel, not exceeding 3.8 cm (1.5 in) in diameter with

most material not exceeding 1.25 cm (0.5 in) in diameter, within the outlet of Bench Lake, Alaska (personal communications, Stephen Hammarstrom, 1981). Similar size substrate is used for spawning in the outlet of Crescent Lake, Alaska (personal communication, Ted McHenry, 1981).

d. Water Depth

Arctic grayling spawn in a range of water depths. Selection of spawning sites is more strongly influenced by current velocities and substrate conditions. Fish in an inlet to Fielding Lake spawned in "shallow back waters" (Wojcik, 1954) and in depths of 16 cm (6 in) (Warner, 1955).

Water depths measured in 22 fish territories in the Mineral Lake, Alaska outlet stream ranged from 0.18 to 0.73 m (0.6 to 2.4 ft) with a mean value of 0.30 m (1.0 ft.).

Cuccarese, Floyd, Kelly and LaBelle (1980) observed fish spawning in various inlet streams to Tyee Lake, Alaska in water depths ranging from 0.15 to 0.91 m (0.5-3.0 ft.) in the largest and most intensively utilized stream and from 0.05 to 0.46 m (0.17-1.5 ft) in several smaller, shallower streams with substantially fewer spawners.

e. Light

Grayling spawning occurs during daylight hours and probably stops during the evening (Scott and Crossman, 1973). Few observations of Arctic grayling spawning have been made during the evening (Kruse, 1959).

Netting at the Bench Lake outlet found few Arctic grayling spawning during evening and early morning hours (personal communication, Stephen Hammarstrom, 1981).

3. Post-Spawning Movements

Spawned-out Arctic grayling (fish having completed spawning) commonly vacate spawning sites within lake inlets and outlets and return to lakes or to other areas (Wojcik, 1954; Warner, 1955; Tack, 1980). Fish spawning within the outlet to Mineral Lake leave the stream upon completion of spawning and migrate downstream and then up to the Little Tok River or Trail Creek. Food availability probably influences post-spawning fish movement and distribution (Tack, 1980).

Small lake inlets may become dewatered by mid to late summer. Adult spawned-out fish typically leave these intermittent streams after spawning and enter lakes (Kruse, 1959).

4. Development of Eggs and Alevins

a. Water Temperature

Stream water temperatures influence Arctic grayling development rates within lake inlets and outlets. Kruse (1959) observed that eggs hatched 19 days after

fertilization in an inlet stream to Grebe Lake at water temperatures from 3.9° to 9.2°C (39.0°-48.5°F). Fertilized eggs from an inlet to Fielding Lake, Alaska required 18 days to hatch in water temperatures ranging from 6.1° to 9.4°C (43°-49°F) during the spring of 1954 and 1955. Fertilized eggs required only eight days to hatch in water temperatures of 15.5°C (60°F) at an Alaskan hatchery.

Henshall (1907) recommended minimum water temperatures of 5.5°C (42°F) for successful development of Arctic grayling in Montana hatcheries.

Water temperatures characteristically rise during the incubation period; therefore, eggs are not usually exposed to freezing. However, no upper or lower lethal temperature data for Arctic grayling eggs were found in the literature.

5. Summer Rearing

a. Current Velocity

Low flows during incubation could result in desiccation or freezing of developing eggs and alevins. Wojcik (1954) noted significant diel flow fluctuations along an inlet of Fielding Lake, Alaska and discussed the possibility of recently fertilized eggs becoming exposed, desiccated or frozen.

Downstream migration of yoy fish within inlets of lakes is probably a response to more suitable current velocities and an abundance of food items in lakes. Newly emerged yoy fish held positions in "quiet water coves and eddies" during the day along an inlet to

Grebe Lake, Wyoming (Kruse, 1959). At night the yoy fish vacated areas of low current velocities and actively migrated downstream to Grebe Lake.

Fry have also been found in shallow margins of Tyee Lake, Alaska and in small, shallow, pools in the delta area of inlet streams of Tyee Lake. High aquatic invertebrate production in littoral areas provided ample food (Cuccarese, Floyd, Kelly and LaBelle, 1980). Fry have not been observed in mainstem reaches of the inlet streams.

Arctic grayling fry within lake outlets typically occupy areas of low current velocities. Yoy fish have been observed in stream margins with shallow depths and low current velocities (personal communication, Stephen Hammarston and Ted McHenry, 1981).

b. Water Depth

Water depths occupied by yoy fish in lotic and lentic areas may vary considerably. Depths are probably selected for the associated current velocities and food availability. Fry within several inlets to Grebe Lake, Wyoming occupied shallow, slow habitats prior to migrating downstream to Grebe Lake (Kruse, 1959). Fry within Tyee Lake, Alaska occupy shallow littoral reaches ranging in depth from 2 to 46 cm (1-18 in). They also occupy shallow, quiet pools in delta regions of the inlet streams rather than the mainstem reaches (Cuccarese, Floyd, Kelly and LaBelle, 1980). Yoy fish have been observed in shallow margins of the outlets of Bench Lake and Crescent Lake, Alaska (personal communication, Stephen Hammarston and Ted McHenry, 1981).

6. Migration to Overwintering Areas

No information was found in the literature concerning movements of Arctic grayling within lake inlets and outlets to overwintering areas. Fish probably overwinter in lakes that are relatively deep and do not freeze to the bottom.

7. Overwintering

No information was available in the literature concerning overwintering habitat of fish within lakes. The winter ecology of Arctic grayling within lakes is poorly understood (personal communication, Fred Williams, 1981).

8. Bog Streams

1. Upstream Migration

a. Water Temperature

Adult grayling usually migrate upstream before juveniles. Water temperatures are lower at this time. Upstream migration of yearling, older juvenile and adult grayling within Poplar Grove Creek usually commenced when mean water temperatures ranged from 2° to 4°C (36°-39°F) during early to mid-May of 1973, 1974 and 1975. Upstream movement usually ceased when water temperatures approached 12° to 14°C (54-57°F) during late May to early June. Mean water temperatures during peak upstream migration of yearling fish (6°-12°C) were consistently higher than temperatures during adult upstream migration (3°-7°C). Diel variations in water temperatures never exceeded 2°C during May and June.

Mature 'green' (non-ripe) Arctic grayling entered Weir Creek, a tributary of the Kavik River, Alaska when water temperatures were about 5°C. The migration ceased when water temperatures approached 12°C (Craig and Poulin, 1974).

Upstream migration of adults in Weir Creek was similar: mature fish were first observed in water of about 4°C (39°F). Migration ceased when temperatures reached 15°C (60°F) (Craig and Poulin, 1974). Maximum water temperatures at the termination of the juvenile upstream fish migration reached 20°C (67°F).

b. Current Velocity and Discharge

The upstream migration of juvenile and adult Arctic grayling in bog streams usually coincides with high flows resulting from snow melt and surface run-off during spring breakup. The first mature 'green' fish were taken nine days after breakup in Weir Creek, Alaska during early June (Craig and Poulin, 1974). The time between initiation of flow in Weir Creek and arrival of fish was probably due to the distance from overwintering areas to the creek (probably the Shaviovik River, about 85 km distant). Wojcik (1954) captured mature 'green' fish at the mouth of Shaw Creek and Little Salcha Creek in the Tanana River, Alaska in early April 1953 and 1954 while the streams were frozen and impassable to fish. However, as melt water scoured furrows in the ice, the fish began migrating upstream. MacPhee and Watts (1976) trapped adult and juvenile fish in Poplar Grove Creek, a tributary of the Gulkana River, at peak and decreasing stream flows associated with spring breakup.

The upstream fish migration may span several weeks. Streamflow can be substantially reduced by the time the upstream migration of adult and juvenile fish is completed. For example, flows within Poplar Grove Creek, Alaska decreased during the upstream migration of adult and juvenile Arctic grayling during 1973, 1974 and 1975 (MacPhee and Watts, 1976). Adult and juvenile fish generally began moving upstream in mid-May during the initial stages of the open-water season. The relatively high discharge at this time ranged from about 1.3 to 4.0 m³/sec (46-141 cfs). However, the peak of the juvenile fish migration consistently occurred at lower flows, about five to ten days after the peak of the adult fish migration. Juvenile migration continued for several days after the adult migration. Discharge at the end of the adult and juvenile migrations were generally less than 1.1 m³/sec (38 cfs). The yearling fish lagged several days behind the older juvenile fish.

Upstream migration of juvenile and adult Arctic grayling in Weir Creek, a tributary of the Kavik River, Alaska, resembled migrations in Poplar Grove Creek (McCart, Craig and Bain, 1974). Adult fish migrated upstream in Weir Creek in 1971 between early and late June, 1971 as discharge decreased from 20 m³/sec to about 2 m³/sec. Juvenile fish moved upstream from mid to late June, about two weeks after the peak of the adult fish run.

Juvenile and adult Arctic grayling migrated upstream in Nota Creek, a tributary of the Mackenzie River, Northwest Territories, Canada, during spring breakup in May. During this time discharges decreased from

1.67 m³/sec to 0.38 m³/sec (58 to 13 cfs) (personal communication, Derrick Tripp, 1981).

Current velocities may influence the timing of juvenile and adult fish passage in bog streams. MacPhee and Watts (1976) demonstrated that large Arctic grayling could negotiate faster water than smaller fish. Decreasing flows may enhance the ability of juvenile fish to pass upstream and could be responsible for the lag between adult and juvenile fish. Other factors, such as increasing water temperatures, probably influence the timing of the upstream migration of juvenile and adult fish (MacPhee and Watts, 1976).

2. Spawning

The influences of current velocity, water depth and substrate on fish spawning in bog streams are not well documented. Flood stage flows and yellow or brown stained water limit observations.

Spawning data correlated to water temperature and flow conditions are available. Selected studies using weirs and seines noted the spawning condition of fish ('green', 'ripe' or 'spawned out'), water temperature, actual or relative flow conditions and direction of fish movement.

a. Water Temperature

Water temperatures of bog streams can be considerably higher than those of lake inlets and outlets during spawning. Minimum water temperatures may approach 4°C, the water temperature which apparently triggers spawning in lake inlets and outlets (Tack, 1980), and may approach or exceed 10°C (50.0°F). Arctic grayling

have spawned at the outlet of Tea Lake, Alaska in water temperatures of 7°C (44°F) (McCart, Craig and Bain, 1972). The Tea Lake system drains a flat, marshy area and is a bog stream.

Bishop (1971) reported that water temperatures of about 8° to 10°C (47°-50°F) appeared to stimulate fish spawning in Providence Creek, Northwest Territories.

Maximum water temperatures in Weir Creek during the Arctic grayling spawning period ranged from 4° to 16°C (39°-61°F) (Craig and Poulin, 1974). Maximum water temperatures in Nota Creek when Arctic grayling were "ripe" ranged from 3.5° to 11°C (38°-51°F). Maximum water temperatures at the peak of spawning ranged from 4.5° to 11°C (40°-52°F) (personal communication, Derrick Tripp, 1981).

Water temperatures in Happy Valley Creek during Arctic grayling spawning ranged from 4° to 12°C (39°-53°F) (McCart, Craig and Bain, 1972).

b. Current Velocity and Discharge

Observations of Arctic grayling spawning with respect to current velocities are limited. Several pairs of spawning fish were observed in shallow riffles along Mainline Spring Creek, Alaska (personal communication, George Elliott, 1980).

Flows within bog streams are typically high but usually decrease during the Arctic grayling spawning period. Flows in Happy Valley Creek, Alaska decreased substantially over the 10 day spawning period. Arctic grayling spawned in Weir Creek, Alaska for 10 days as

flows decreased. Arctic grayling in Poplar Grove Creek, Alaska spawned in late May to early June as streamflows decreased from peaks of about $1.1 \text{ m}^3/\text{sec}$ (23.2 cfs) in 1973 and $4.0 \text{ m}^3/\text{sec}$ (84.8 cfs) in 1971 (MacPhee and Watts, 1976). Bishop (1971) reported fish spawning in Providence Creek, tributary of the Mackenzie River, during breakup conditions.

c. Substrate

Arctic grayling appear to use a wide range of substrate sizes in bog streams for spawning. They spawned over gravel ranging from 2.5 to 3.75 cm (1-1½ in) diameter in Mainline Springs Creek near Atigun Pass, Alaska (personal communication, George Elliott, 1980). Spawning has also occurred in the outlet of Tea Lake, Alaska, near the Trans-Alaska Pipeline, over sand and fine gravel substrate, about 0.6 cm (¼ in.) in diameter (Craig, McCart and Bain, 1972).

Substrate used for spawning in Providence Creek, Northwest Territories, Canada was gravel mixed with sand. Fish did not spawn over pure mud, sand or clay (Bishop, 1971).

Fish spawned in organic detritus in Million Dollar Creek, Alaska, along the Trans-Alaska Pipeline (personal communication, George Elliott, 1980). The substrate in Million Dollar Creek is silt and fine sand overlain by organic muck (Elliott, 1980).

d. Water Depth

Observations of water depths used for spawning in bog streams are limited.

Several pairs of fish spawned in riffles 5 cm (2 in) deep in Mainline Spring Creek, Alaska (personal communication, George Elliott, 1980).

e. Light

Fish apparently spawn only during the day, as observed by Bishop (1971) in Providence Creek.

3. Post-Spawning Movements

Arctic grayling may migrate downstream immediately after spawning. In 1973, post-spawners left Weir Creek, Alaska within two weeks after spawning. Large juvenile Arctic grayling also emigrated within two weeks. Tagged adult fish from Weir Creek, Alaska were captured later in the Kavik River and the Shaviovik River (Craig and Poulin, 1974). Rapidly decreasing streamflows probably influenced fish movements.

Tagged adult post-spawners from Happy Valley Creek displayed similar downstream movement following spawning. No adult fish were found upstream of the weir (McCart, Craig and Bain, 1972).

An outmigration of adult and juvenile Arctic grayling occurred in Poplar Grove Creek during late May and early June after spawning and when streamflows were steadily declining. Emigration of spawned-out adults extended from

mid-May through mid-June 1973 as flows steadily declined from $1.4 \text{ m}^3/\text{sec}$ (49 cfs) to $0.3 \text{ m}^3/\text{sec}$ (11 cfs). Large juvenile Arctic grayling outmigrated after the adults during mid-June. Not all adult and large juvenile Arctic grayling left Poplar Grove Creek; of the 1,085 adults and 1,973 large juvenile fish found migrating upstream, only 779 and 937 were detected passing downstream. Many of these fish migrate to the Gulkana River drainage (Williams and Morgan, 1974; Williams, 1975 and 1976). Weir data suggest that adults may remain in Poplar Grove Creek until the stream freezes in fall.

Adult grayling ususally leave Nota Creek, a bog stream entering the Mackenzie River, Northwest Territories, Canada, within two weeks after spawning. Some spawned-out adults may return to food-rich Nota Lake for short periods of time. Emigration of large five and six year old juveniles was followed by younger, smaller individuals through early July. By mid-July young of the year Arctic grayling and some yearling and two year olds occupied Nota Creek (personal communication, Derrick Tripp, 1981). Decreased living space and food availability associated with low flows are probably important factors influencing fish movements.

Tack (1980) suggested that the outmigration of juvenile and spawned-out adult fish may allow yoy fish to rear and feed in natal streams without competition. Adult and juvenile fish may rear in other stream systems that are rich in food, such as spring streams.

4. Development of Eggs and Alevins

a. Water Temperature

Extremely limited information is available concerning egg incubation and water temperature relationships in bog streams. Bishop (1971) subjected fertilized eggs to a range of water temperatures. He determined that eggs hatched in approximately 14 days at a mean water temperature of 8.8°C (48°F).

Arctic grayling eggs required 18 to 21 days to hatch in Nota Creek in water temperatures ranging from 5.5° to 13°C (42°-55.5°F) and a mean water temperature of 9.6° to 10.3°C (49°-50.5°F) (personal communication, Derrick Tripp, 1981).

b. Current Velocity and Discharge

Spates could dislodge and destroy eggs and severely reduced flows could lead to desiccation.

Aquatic habitat selected by rearing yoy fish in bog streams may have current velocities of from 0 to 0.15 m/sec. Larger fish generally select faster water. Elliott (1980) measured mean column velocities at holding positions of 'early' yoy (≤ 35 mm fl) and 'late' yoy (> 35 mm fl) fish in selected bog streams during June and August 1980. The mean column current velocities associated with 'early' yoy fish were 0.02, 0.07 and 0.03 m/sec in Million Dollar Creek (n = 198), Pamplin's Potholes (n = 175), and the Tea Lake inlet, Alaska (n = 57), respectively.

Larger 'late' yoy fish were found in slightly faster mean current velocities: 0.08, 0.09, 0.14 and 0.1 m/sec. in Pamplin's Potholes (n = 87), Tea Lake inlet/outlet (n = 71), North Fork Fish Creek (n = 33), Mainline Spring Creek, Alaska (n = 18), respectively.

5. Summer Rearing

a. Current Velocity

Newly emerged yoy fry select protected stream areas where current velocities are extremely low (personal communication, George Elliott, 1980; de Bruyn and McCart, 1974; McCart, Craig and Bain, 1972). Typical emergent fry rearing areas include shallow backwaters and flooded stream margins and side channels.

Juvenile fish (age 1 and older, measuring 50-250 mm fl) have been observed in bog streams with slightly greater current velocities than yoy fish. The average mean current velocities occupied by juvenile fish in the Tea Lake inlet (n = 9) were 0.175 m/sec and in Mainline Springs Creek, Alaska (n = 16), 0.196 m/sec. Limited observations of adult Arctic grayling (250 mm fl) from bog streams showed adult fish holding in mean current velocities of 0.262 m/sec (Elliott, 1980).

b. Substrate

Rearing fish of all ages were associated with a variety of substrates including detritus, silt, sand, and gravels. Arctic grayling showed little movement in small bog streams during July and August following fish spawning and movement to summer rearing areas and before movement of fish to overwintering areas (McCart,

Craig and Bain, 1972; Craig and Paulin, 1974; MacPhee and Watts, 1976).

c. Water Depth

Water depths occupied by rearing fish vary considerably. Newly emerged yoy fish have been found in extremely shallow, slow water, flood channels and backwater sloughs (Personal communication, George Elliott; de Bruyn and McCart, 1974; McCart, Craig and Bain, 1972).

Early yoy fish occupied small bog streams with depths from about 0.09 to 0.85 m (0.3-2.8 ft). Late yoy occupied depths (within the same streams) ranging from 0.15 to 1.07 m (0.5-3.8 ft) (Elliott, 1980). Juvenile and adult fish in bog streams along the Trans-Alaska Pipeline System were found in water depths from 0.21 to 1.07 m (0.7-3.8 ft).

6. Migration to Overwintering Areas

Significant downstream movement of fish has been observed in bog streams during late summer, apparently in response to declining water temperatures and flows associated with the onset of winter. Emigration of yoy and juvenile fish may also occur during the summer.

a. Water Temperature

Decreasing water temperatures may influence the downstream movement of Arctic grayling. Significant numbers of yoy and juvenile fish moved downstream in Weir Creek, Alaska during September 1973. Minimum water temperatures during early, mid and late September were about 1°, 4° and 0°C, respectively. Downstream movement of juvenile fish occurred about one week before yoy fish in Weir Creek. No apparent relationship could be demonstrated between downstream movement of juvenile or yoy fish and water temperatures (Craig and Poulin, 1974).

Similar downstream movements of yoy fish occurred in Poplar Grove Creek, Alaska. Of the 65,536 yoy fish observed between July 17 and October 18, 1973, 96% (62,680) were observed in the lower reaches during October (MacPhee and Watts, 1976). In Poplar Grove Creek, downstream migration of yoy fish may be related to stream temperatures.

b. Current Velocity and Discharge

No relationship could be found between the downstream movement of juvenile or yoy fish and stream flows in Weir and Poplar Grove Creeks.

7. Winter Rearing

Winter rearing areas for Arctic grayling are limited in bog streams because they often become dewatered or freeze solid during the winter. Winter rearing areas such as deep lakes, deep pools of mountain streams or spring fed streams, may be quite distant from summer rearing areas. Fish overwintering

areas in the Shaviovik River and summer rearing habitat within Weir Creek are about 85 km (53 mi.) distant (Craig and Poulin, 1974).

C. Mountain Streams

1. Upstream Migration

a. Water Temperature

Low water temperatures are prevalent during the upstream migration of adult and juvenile Arctic grayling. Upstream migrants were taken in Vermillion Creek, Northwest Territory, Canada about one week after breakup when water temperatures ranged from 0° to 3°C (32°-37°F) (personal communication, Derrick Tripp, 1981). Tack (1980) also found that water temperatures of at least 1.0°C (34°F) stimulate upstream movement of Arctic grayling in large mountain streams like the Chena River near Fairbanks, Alaska.

b. Current Velocity and Discharge

Upstream migration of adult and juvenile Arctic grayling usually occurs during high flows at spring breakup. A weir placed in Vermillion Creek captured upstream migrating adult and juvenile Arctic grayling for ten days after peak flows in May of 1973 and 1975. The Mackenzie River was covered with ice for up to ten days after breakup occurred in Vermillion Creek during 1973 and 1975 (personal communication, Derrick Tripp, 1981), and observations of fish migration were not made.

Observations made under the ice along the Chena River indicate that Arctic grayling initiate upstream movement prior to breakup (Tack, 1980). The fish were probably moving to upstream reaches of the Chena River or its tributaries. The relative importance of streamflow and water temperature in relation to upstream fish migration is poorly understood.

2. Spawning

a. Water Temperature

Limited data is available concerning the relationship between Arctic grayling spawning and stream water temperatures. Spawning in the Chena River drainage has been observed in water temperatures of 5°C (Reed, 1964; personal communication, Jerome Hallberg). Tack (1980) discussed the possibility of the 4°C isotherm influencing the distribution of spawning fish in large streams like the Chena River.

b. Current Velocity and Discharge

Fish spawn in mountain streams in a wide range of current velocities. They have been observed spawning in an overflow slough in the Chena River, Alaska at relatively low current velocities (Reed, 1964) and in riffles of the East Fork Chena River, Alaska where surface current velocities approach 1.4 m/sec (4.5 ft/sec) (personal communication, Jerome Hallberg, 1981). Bendock (1979) reported spawning in pools of the Colville River, Alaska with negligible current.

Nelson (1954) observed fish spawning activity along Red Rock Creek, Montana in the ends of riffles. Fish

spawning occurred in similar low flow areas along the East Fork Chena River, Alaska (personal communication, Jerome Hallberg, 1981).

c. Substrate

Arctic grayling use a variety of substrates for spawning including mud, silt and gravel up to 4 cm (1.5 in) in diameter. Bendock (1979) observed fish spawning on silt overlaying gravel in the mainstem Colville River, Alaska and its tributaries. Spawning substrate used by Arctic grayling in the East Fork Chena River, Alaska consists of fine gravels from 0.75 to 4 cm (0.4-1.5 in) in diameter (personal communication, Jerome Hallberg, 1981). Spawning has also been observed in muddy sloughs along the Chena River (Reed, 1964).

Arctic grayling in Red Rock Creek, Montana spawned in gravel-rubble substrate of unknown size but not in pure silt or sand substrates.

3. Egg and Alevin Development

No information was found in the literature which discussed egg and alevin development in mountain streams.

4. Summer Rearing

a. Water Temperature

Results of standard, 96 hour bioassays (at test water temperatures of 5, 10, 15, 20 and 24.5 or 21.5°C) indicate that Arctic grayling can tolerate a wide range of temperatures. Fish from the Chena River near

Fairbanks, Alaska were used for this study. Results were expressed as median tolerance limit (TL_M), the temperature at which 50 percent of the individuals in a test die (LaPerrier and Carlson, 1973).

Results indicated that young of the year fish are apparently more tolerant of relatively high water temperatures than older fish. The TL_M of yoy fish exceeds 24.5°C, the highest test water temperature.

Individuals of 10 cm fl had TL_M values of 20.0 to 24.0°C and fish of 20 cm fl has TL_M values of 22.5 to 24.5°C. The small fish were acclimated at 4°C and the larger fish at 8°C.

Bioassay results indicate that water temperature differences of 2°C at relatively high water temperatures can cause very different survival rates of Arctic grayling. For example, survival of 20 cm fl fish was 100 percent at 22.5°C (72.5°F) and 0 percent at 24.5°C (75°F).

These bioassay results may not apply to actual stream conditions because fish could avoid warm water temperatures by moving to cooler areas.

b. Current Velocity and Discharge

Recently emerged yoy fry generally occupy areas with low current velocities. The small newly emerged fry (about 20 mm total length at 14 days) have limited swimming abilities. Chislett and Stuart (1979) noted that newly emerged fry clustered in shallow, protected reaches of flood channels, backwater sloughs and sidechannel pools of the Sekunka River, British

Columbia. These fish are found in similar habitats in the East Fork Chena River, Alaska (personal communication, Jerome Hallberg, 1981).

Nelson (1954) noted that recently emerged yoy fish were distributed in "backwaters and protected areas. . . , away from strong currents" within Red Rock Creek, Montana.

Older yoy fish occupy progressively faster waters. 'Early' yoy fish (≤ 35 mm fl) occupied a mean current velocity of about 0.07 m/sec (0.22 ft/sec) ($n = 183$) in selected headwater areas of the Gulkana River, Alaska in early July. Larger yoy fish (> 35 mm fl) inhabited slightly greater current velocities, 0.16 m/sec (0.52 ft/sec) ($n = 157$) (Elliot, 1980).

Chislett and Stuart (1979) found yoy fish (≤ 35 mm fl) occupying slow current areas of backwater and side channels in the Sekunka River and Martin Creek, British Columbia during July 1978. Side channels contained flowing water and were less ephemeral than backwater channels. All yoy fish were found in low current velocities.

Most of the backwater habitats dewatered during August low flows and yoy fish (> 35 mm fl) inhabited sidechannel riffle areas and margins of mainstem riffles.

By September and October yoy fish occupied sidechannel riffles and margins of mainstem riffles where current velocities approached 0.8 m/sec. Yoy fish at this time ranged from 50 to 96 mm fl (Chislett and Stuart, 1979).

Summer distributions of yearling and older fish were limited to mainstem and side channel pools in the Sekunka River, British Columbia. Older fish, age 4 to 8+ (oldest aged fish), occupied larger, deeper pools than the younger fish.

The distribution of juvenile and adult Arctic grayling in selected Alaskan mountain streams is similar to the the distribution in the Sekunka River, British Columbia where adult and juvenile fish are generally restricted to pools and sloughs (Alt, 1978; personal communication, Jerome Hallberg, Joe Webb, Terence Bendock, 1981).

Fish will move into shallower, faster riffle areas for more food, such as salmon and whiterfish eggs (Bendock, 1979; Alt, 1978).

c. Water Depth

Yoy fish generally occupy shallow lotic habitats with low current velocities. Fry in the Sekunka River, British Columbia selected shallow areas in sidechannels and backchannels (Chislett and Stuart, 1979). Yoy fish have been observed in backwater sloughs and shallow pockets of protected water in the East Fork Chena River, Alaska (personal communication, Steven Grabacki, Jerome Hallberg and Sandra Sonnichsen, 1981).

Older fish generally select deeper pools (Chislett et al.; personal communications, Steven Grabacki, Jerome Hallberg and Sandra Sonnichsen, 1981).

d. Cover

Recently emerged yoy fish seek various forms of instream cover when disturbed. Young (17-45 days old) fry in shallow, siltbottomed backchannels of the Sekunka River moved into deeper water with various types of instream cover. Similar aged yoy fish in sidechannels used substrate interstices and shadows of boulders for cover. Nelson (1954) noted that 14 to 21 day old fish in Red Rock Creek, Montana made little movement when disturbed and appeared to be "relatively helpless."

Older fish commonly use logs, boulders and turbulence for instream cover (personal communication, Jerome Hallberg, 1981).

5. Migration to Overwintering Areas

Little is known about Arctic grayling migration to overwintering areas. Tack (1980) observed a slow downstream movement of Arctic grayling in the Chena River, Alaska and compared it to the faster emigration of fish in North Slope mountain streams where winter conditions occur very early (Yoshihara, 1972). Yoshihara (1972) observed many fish moving downstream in the Lupine River immediately after water temperatures reached freezing. Age distribution of emigrants in the Lupine River is not known.

6. Winter Rearing

The distribution of overwintering Arctic grayling is more limited than the summer distribution. Streamflows are low, much or all of the stream is ice-covered and stream reaches

can be frozen solid during the harsh Arctic and sub-Arctic winters. Overwintering areas in mountain streams include pools of intermittent or flowing streams (such as Colville and Chena River, Alaska, respectively) or spring fed streams which remain open during winter months (the lower Shaviovik River, Alaska).

a. Current Velocity

Current velocities in overwintering sites are probably very low. Conventional current velocity meters do not function at air temperatures below freezing. Fish overwinter in intermittent pools of the Colville River where current velocity is negligible. In the Hulahula River overwintering sites had current velocities of 0.15 m/sec (0.5 ft/sec).

b. Water Depth

Fish have been observed under the ice in pools of at least 1.4 m (4.6 ft) depth in the Colville, Chena and East Fork Chena Rivers. Bendock (1980) found fish in intermittent pools deeper than 1.5 m (4.8 ft) in a reach of the Colville River, Alaska. Fish are restricted to pools in the East Fork Chena River and the mainstem Chena River, Alaska (Tack, 1980) during the winter months (Hallberg, personal communication, 1981).

Arctic grayling have been taken by Kaktovik, Alaska villagers in the Hulahula River in late April (Furniss, 1975) and through the ice in the East Fork Chandalar River near Arctic Village, Alaska (McCart, 1974). Maximum water depths were about 0.6 m (2 ft) in open water of the Hulahula River. Water depth of the East

Fork Chandalar River was 1.5 m (5 ft). These sites are thought to be important overwintering areas for Arctic grayling.

Spring fed mountain streams are often the only sites in the North Slope where water remains flowing throughout the winter. These streams are important overwintering sites for Arctic grayling. Alt and Furniss (1976) captured adult Arctic grayling in a spring fed pool in the Franklin Bluffs area of the Sagavanirktok River, Alaska on May 6, 1975. The approximate depth of the pool was about 1.2 m (3.9 ft).

c. Dissolved Oxygen

Bendock (1980) measured dissolved oxygen levels ranging from 0.6 to 4.6 mg/l in Arctic grayling overwintering sites in the Colville River. Dissolved oxygen levels were about 4.8 mg/l in the Sagavanirktok River at the Franklins Bluff site on April 10, 1975 (Alt and Furniss, 1976).

D. Spring Streams

1. Upstream Migration

Limited investigations indicate that Arctic grayling may enter springfed streams after spawning (Reed, 1964; Pearse, 1974; Tack, 1980).

2. Spawning

Arctic grayling apparently do not spawn in springfed streams where low water temperatures may adversely influence egg and alevin development (Van Hyning, 1978).

3. Summer Rearing

Arctic grayling rear in springfed streams. Reed (1964) reported that adult fish enter the Delta Clearwater River in early June and younger juvenile fish enter in late July. Pearse (1974) found similar trends in the Delta Clearwater in 1973; although adults tended to remain in the headwater reaches and immatures remained downstream.

4. Migration to Overwintering Areas

Reed (1964) stated that immature, catchable (by rod and reel) Arctic grayling moved downstream early in 1963 in the Delta Clearwater River. Larger adult fish remained in the river through most of September. Some tagged adult fish were found at the mouth of the Delta Clearwater River in late October.

5. Winter Rearing

Arctic grayling apparently do not rear in interior Alaska springfed streams (Van Hyning, 1978), but have been found in springfed streams in the North Slope (Craig and Poulin, 1974).

III. HABITAT-ARCTIC GRAYLING RELATIONSHIPS

Tables I through VI summarize the reported water temperature levels associated with various life stages and activities of Arctic grayling. Table VII lists the reported current velocities (or discharges) associated with different life history stages and Table VIII, the substrate types used for spawning.

Table I: Observed water temperatures associated with upstream migration of Arctic grayling to lake inlets/outlets.

Parameter	Observed Values	Remarks	Location	Reference
Water Temperature	0.6° - 1.1°C	Maximum water temperatures during last 2 day of fish migration	Inlet to Fielding Lake, Alaska	Warner (1955)
	1.0°C	First mature fish captured during fish migration	Outlet to Mineral Lake, Alaska	Tack (1972)
	5.6 - 7.8°C	Water temperatures of several inlets to Grebe Lk. during initial fish spawning migration activity 1953, 1954	Four inlets to Grebe Lake, Wyoming	Kruse (1959)
	2.2° - 4.4°C	Water temperatures of outlet (Gibbon R.) to Grebe Lake, Wyoming during initial fish spawning migration activity	Gibbon River, outlet to Grebe Lake, Wyoming	Kruse (1959)

Table II: Observed water temperatures associated with upstream migration of Arctic grayling within bog (tundra) streams.

Parameter	Observed Values	Remarks	Location	Reference
Water Temperature	5° - 12°C	Maximum water temperatures during early to late stage of adult fish spawning migration. Incomplete fish sampling due to high flows, 1973.	Weir Creek, Tributary to Kavik R., Alaska	Craig and Poulin (1974)
	3.9° - 15.6°C	Maximum water temperatures beginning and end of adult fish upstream migration, 1971. Weir placed in stream after fish migration began.	Happy Valley Crk, tributary to Sagavanerktok River, Alaska	McCart, Craig and Bain (1972)
	7.2° - 19.4°C	Maximum water temperatures from start to near termination of juvenile fish upstream migration, 1971.	Happy Valley Crk, Sagavanerktok River, Alaska	McCart, Craig and Bain (1972)
	2° - 4°C	Initial average water temperatures of Poplar Grove Creek during start of adult, sub-adult, juvenile fish upstream migration during May 1973-1975.	Poplar Grove Crk, tributary to Gulkana R., Alaska	MacPhee and Watts (1976)
	12° - 14°C	Average water temperatures at end of adult, sub-adult, juvenile fish migration in June 1973-1975.	Poplar Grove Crk, tributary to Gulkana R., Alaska	MacPhee and Watts (1976)

Table III: Observed water temperatures associated with Arctic grayling spawning in mountain streams.

Parameter	Observed Values	Remarks	Location	Reference
Water Temperature	5.6°C	Instantaneous water temperature of slough where fish were observed spawning	Slough along Chena River, Alaska	Reed (1964)
	5.0°C	Instantaneous water temperature during fish spawning activity	Riffle, E. Fork Chena River, Alaska	Hallberg (personal communication)
	5.0° - 9.0°C	Instantaneous water temperature during fish spawning activity	Seabee, Rainy, Fossil Crks, tributaries Colville R., Alaska	Bendock (1970)
	5°C	Instantaneous water temperature during fish spawning activity	Nuka River, tributary, Colville River, Alaska	Bendock (1979)
	4°C	Instantaneous water temperature during fish spawning activity	Aniak R, tributary, Kuskokwim River, Alaska	Alt (1977)

Table IV: Observed water temperatures associated with Arctic grayling spawning in lake inlets/outlets.

Parameter	Observed Values	Remarks	Location	Reference
Water Temperature	3.3°C	Initial fish spawning activity occurred	Inlet to Fielding Lake, Alaska	Wojcik (1954)
	7.8°C	Fish spawning activity was completed at this temperature 3-4 days after commencement of spawning activity.	Inlet to Fielding Lake, Alaska	Wojcik (1954)
	4°C	First spawning activity observed	Outlet to Mineral Lake, Alaska	Tack (1972)
	2° - 3°C	Fish spawning ceased as water temperature dropped below 4°C	Outlet to Mineral Lake, Alaska	Tack (1972)
	4° - 10°C	Fish spawning activity resumed and lasted 4 additional days	Outlet to Mineral Lake, Alaska	Tack (1972)
	6° - 11°C	Fish actively spawning	Several inlets to Tyea Lake, Alaska	Cuccarease, Floyd Kelly, LaBelle (1980)
	4° - 10°C	Fish actively spawning	Four inlets to Grebe Lk, Wyoming	Kruse (1959)
	2.2° - 10°C	Fish actively spawning	Outlet to Grebe Lake, Wyoming Gibson River	Kruse (1959)
	10°C	Fish actively spawning	Inlet to Agnes Lake, Montana	Brown (1938)

Table V: Observed water temperatures associated with spawning of Arctic grayling within bog streams.

Parameter	Observed Values	Remarks	Location	Reference
Water Temperature	6.7°C	Direct spawning observation, one temperature reading	Outlet Tyee Lk, Alaska	McCart, Craig and Bain (1972)
	8° - 10°C	Fish spawning activity seemed to be related to these water temperatures.	Providence Crk, tributary to Mackenzie River Northwest Territory	Bishop (1971)
	3.9° - 16°C	Maximum water temperatures based on occurrence of ripe and spawned-out Arctic grayling captured by weir	Weir Creek, Alaska	Craig and Poulin (1974)
	3.5° - 11°C	Maximum water temperatures during Arctic grayling spawning activity based on condition of fish in weir	Nota Creek, Alaska	Tripp (personal communication, 1981)

Table VI: Observed water temperatures associated with Arctic grayling egg and alevin development.

Parameter	Observed Values	Remarks	Location	Reference
Water Temperature	3.9°C - 9.2°C	Eggs hatched in 19 days	Inlet to Grebe Lake, Wyoming	Kruse (1959)
	6.1° - 9.4°C $\bar{x}$ = 7.7°C	Eggs hatched in 18 days in 1954 and 1955	Inlet to Fielding Lake, Alaska	Wojcik (1954); Warner (1955)
	15.5°C	Eggs at hatchery facility hatched in 8 days	Somewhere in Alaska	Wojcik (1954)

Table VII: Relationship of current velocity (or discharge)
to specific life history stages.

Activity	Current Rate or Flow	Reference
Spawning	slow, shallow backwater 1.2 m/s .34 m/s to 1.46 ($\bar{x}$ = .79) shallow riffles 1.1 m ³ /sec 4.0 m ³ /sec low flow and riffles of 1.4 m/s negligible	Wojcik, 1954 Warner, 1955 Tack, 1971 Elliott, 1980 MacPhee and Watts, 1976 MacPhee and Watts, 1976 Hallberg, 1981 Bendock, 1979
Early Development	.02, .07, .03 m/s shallow, protected areas	Elliott, 1980 Chislett and Stuart, 1979
Juvenile Rearing	shallow pools shallow pools .08 to .195 m/s .8 m/s	Cuccarese et al., 1980 Hammarston, 1981 Elliott, 1980 Chislett and Stuart, 1979
Adult Summer Habitat	.26 m/s	Elliott, 1980
Adult Winter Habitat	open areas	Chislett and Stuart, 1979
Upstream Migration	at breakup 1.3- 4 m ³ /s 2 m ³ /s → 20 m ³ /s 1.67 m ³ /s at breakup at breakup high flow	MacPhee and Watts, 1976 MacPhee and Watts, 1976 McCart et al., 1974 Tripp, 1981 Wojcik, 1954 Warner, 1955 Tack, 1972

Table VIII: Reported substrate types used for spawning.

Substrate	Reference
Fine gravel (1 cm)	Warner, 1955
"pea-size"	Tack, 1971
sand to small cobble	Cuccarease et al., 1980
sand - gravel	Brown, 1938
sand, gravel, rubble	Kruse, 1959
fine gravel (<3.8 cm)	Hammarstron, 1981
fine gravel	McHenry, 1981
gravel, 2.5 - 3.75 cm	Elliott, 1980
sand, fine gravel	Craig et al., 1972
sand, gravel	Bishop, 1971
organic detritus	Elliott, 1980
sand, muck	Elliott, 1980
mud, silt, gravel ($\leq$ 4 cm)	Bendock, 1979
gravel, .75 - 4 cm	Hallberg, 1981

IV. DEFICIENCIES IN DATA BASE

Factors influencing the migration of adult and juvenile Arctic grayling from overwintering areas to spawning streams is apparently influenced by flow and water temperature conditions. The timing of adult and juvenile fish migrations are not understood; the juvenile fish run lags several days to several weeks behind the adult fish in certain areas.

Information about selection of sites in mountain, lake inlet and outlet, bog and spring streams in relation to current velocity, water depth and substrate is limited. Most of the observations were made in lake inlets and outlets and mountain streams.

Habitat selection by spawning Arctic grayling is influenced by at least three variables - substrate, water depth and current velocity - which collectively determine the habitat quality. For example, Arctic grayling may be excluded from spawning areas by excessive current velocities despite acceptable substrates and water depths. There is limited information on the interaction of various physical parameters.

Factors influencing the survival and development of eggs and alevins are not well understood. Studies indicate that egg dislodgement by other spawning fish and spates may be a major cause of mortality. Minimum water temperatures required for successful egg development are not known; however, water temperatures above 6°C (42°F) have been recommended.

The movement of Arctic grayling to overwintering areas appears to be influenced by flow and water temperatures associated with the onset of winter. This emigration may be of short duration or extend over several weeks. There is very little information about Arctic grayling overwintering areas. Fish overwintering in the North Slope are limited to open water areas or to streams which do not completely freeze. Fish overwintering in interior Alaska and Canada may remain

in springfed and glacier streams. It is not known whether young of the year Arctic grayling burrow into interstices within cobble and rubble as water temperatures approach freezing.

The age structure of Arctic grayling populations during the open-water season may be significantly different among various lake inlet and outlet, bog, mountain and spring streams. Some streams appear to function as nursery areas for young of the year and older juvenile fish, and other streams may support only large juvenile and adult fish. Fish may be either sedentary or nomadic during the open-water rearing season. Explanations for fish emigration are speculative but living space and food availability are probably influential. Studies of juvenile and adult Arctic grayling habitats focused on water depth, current velocities and substrate in small bog and mountain streams.

Methods of describing water depth, current velocity and substrate characteristics varied among studies. Some investigators measured current velocity at the site of spawning Arctic grayling; others estimated surface current velocities. Substrate size classification systems also varied; few researchers evaluated substrate imbeddedness at spawning sites.

The effects of water temperatures and current velocities on a grayling's ability to ascend culverts has been studied for juvenile and adult fish. Relatively few tests were conducted with yearling grayling.

V. RECOMMENDATIONS AND FURTHER STUDIES

In depth investigations are needed to determine the relationships between specific chemical and physical features of aquatic habitats and grayling growth and behavior. For example, investigations should be designed and conducted to assess the factors which influence development and survival of Arctic grayling eggs and alevins in bog, lake inlet and outlet, spring and mountain streams. Investigations should consider egg dislodgement, predation, desiccation, and diel drift of emergent fry.

Water temperatures and ice conditions during grayling egg and alevin development may be easier to sample than the lower water temperatures and thicker ice cover characteristic of Pacific salmon and char incubation periods.

Laboratory studies should assess the effects of various durations of low water temperatures on the development and survival of eggs and alevins. Water temperatures at or below threshold levels could cause morphological deformities, slow development rates and high mortality among eggs and alevins. These investigations could explain the apparent avoidance of spring streams by spawning Arctic grayling.

Weirs could be used to sample grayling from bog, mountain, spring and lake inlet and outlet streams to relate residence time and migration to stream flow, water temperature and other physical and chemical stream factors.

Unique tags on upstream migrating adult and juvenile fish would provide specific migration data. Data from consecutive years could be used to determine Arctic grayling homing to specific spawning and rearing streams.

Arctic grayling spawning sites should be studied more extensively in northern latitudes. Characteristics of spawning habitat in terms of

water depths, current velocities and substrate conditions should be compared with habitat availability for specific stream systems. Water temperatures and fish spawning activities should be monitored to detect spawning activity cycles.

Internal radio transmitters could be used to monitor grayling movement to and within open-water rearing areas and overwintering sites. Radio telemetry could be used to study fish migration rates and patterns.

Surgical implantation of radio transmitters is probably the best method for spawned-out adult and large juvenile fish. Surgical implantation has less affect on fish equilibrium than esophageal insertion (Winter, Kvechle, Siniff and Tester, 1978). Rates of healing, condition of internal organs and the occurrence of infection among the fish should be determined for various water temperatures.

Criteria for radio transmitter selection should include size of transmitter and antennae, transmitter various temperatures, and signal receptions at various depths.

The feasibility of marking juvenile Arctic grayling with fluorescent pigment should also be determined. A variety of color combinations could be used to identify specific stream locations and dates of marking. Lack of scale development may prevent pigment retention by yoy Arctic grayling less than 1½ months old.

Comprehensive sampling of fry would determine movement of yoy Arctic grayling. Weirs of small mesh screen could be used to monitor yoy Arctic grayling movements. However smaller mesh size also necessitates more frequent cleaning of the weirs.

Weirs should remain within streams as long as possible prior to freeze-up to monitor Arctic grayling movements and physical and chemical habitat components. Weirs could remain in spring streams which remain ice-free to monitor the presence of fish.

Investigations should be conducted to determine open-water, lotic microhabitat selection by juvenile and adult Arctic grayling using techniques similar to those described by Everest and Chapman (1972). These investigations should describe water depths, current velocities, substrate, proximity to nearest fish and instream cover. Snorkeling, which has been used extensively in the Pacific Northwest and elsewhere, can be used where bank observations of fish are difficult.

Microhabitat investigations could complement fish movement data from weirs and radio telemetry studies. Microhabitat studies could also explain the apparent segregation of various age classes of Arctic grayling in certain rivers such as the Chena River.

Food availability and various physical and chemical habitat influence the summer, open-water distribution of Arctic grayling within streams. Drift and substrate sampling of invertebrates can be used to assess food availability and its relationship to the distribution of Arctic grayling.

Studies of juvenile and adult Arctic grayling overwintering habitat should continue. Gillnets, SCUBA and other techniques could be used to investigate these overwintering habitats.

Fish passage studies should be conducted to assess the ability of juvenile and adult Arctic grayling to ascend culverts and other high current velocity areas. MacPhee and Watts (1976) determined that the ability to ascend culverts was a function of culvert length and spawning condition. Studies of yoy and older juveniles would identify fish movement during the summer rearing season. The possibility that excessive current velocities associated with culverts prevent young grayling from reaching small rearing streams should be investigated.

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FRESHWATER HABITAT RELATIONSHIPS
DOLLY VARDEN CHAR (SALVELINUS MALMA (WALBAUM))

By

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I. INTRODUCTION

A. Purpose

The purpose of this project is to describe how selected physical and chemical features of lotic habitat within Alaska influence the survival and behavior of the various life stages of anadromous Dolly Varden char (Salvelinus malma (Walbaum)).

Objectives of this project are:

1. to gather data from published and unpublished sources within Alaska and from conversations with Alaskan fishery biologists concerning the relationships between lotic aquatic habitat and anadromous Dolly Varden survival and behavior.
2. to develop an Alaska data base for habitat-anadromous Dolly Varden char relationships. Because there are not sufficient data for the relationships between anadromous Dolly Varden char and conditions of the habitat, habitat suitability index relationships were not developed.
3. to identify data gaps and recommend appropriate projects to alleviate these gaps.

The following Life History Summary and Specific Habitat Relationships/Requirements sections will identify the lotic habitat relationships of the various life history and seasonal behavior stages of the anadromous Dolly Varden char which include:

upstream spawning migration,
spawning,
inmigrant migration to overwintering areas,

immigrant overwintering areas,
egg and alevin development,
summer juvenile rearing,
juvenile migration to overwintering areas,
juvenile overwintering areas,
juvenile migration to summer rearing areas,
immigrant migration to sea, and
smolt migration to sea

B. Distribution

The taxonomy of the Dolly Varden char, Salvelinus malma (Walbaum) is quite complex and a topic of debate. Morrow (1980) recognizes a northern and a southern form of Dolly Varden char, with the northern form equivalent to the anadromous Arctic char, Salvelinus alpinus (Linnaeus), and the southern form comprising the Dolly Varden char. Dolly Varden char is separate from the bull char, Salvelinus confluentus, which occurs in British Columbia, Washington, Oregon, Idaho and Montana (Behnke, 1980).

For purposes of this paper, Dolly Varden char are defined as those fish which occur south of the Arctic char and north of the bull char. Anadromous and non-anadromous Dolly Varden char are distributed within Alaska south of the Alaska Range.

C. Life History Summary

Migration of mature and immature Dolly Varden char from the ocean to southeastern Alaska may be concurrent and can extend from July through October. Immature individuals may stay in streams as long as spawners (two to three months) although non-spawning immature Dolly Varden char seldom remain more than one month prior to emigrating to other stream and lake systems, probably to overwinter. About 80% of the non-spawning immigrants left Hood Bay Creek, Alaska before the spawning fish (Armstrong and

Winslow, 1968). During 1966, tagged immature fish remained in Hood Bay Creek for 14 days (Armstrong, 1967), and mature fish for 85 days.

Age at maturity is variable; most Dolly Varden in southeast Alaska reach maturity by age four or five. Males may mature before females (Armstrong and Blackett, 1965).

Tagging studies in southeast Alaska (Armstrong, 1965a and 1974; Blackett, 1968; Heiser, 1966) indicated that mature, anadromous Dolly Varden char use their natal streams to spawn and lakes to overwinter. Immature fish originating in streams without lakes may enter several streams prior to finding a lake for overwintering. Immature fish of lake-stream origin probably re-enter the same system to overwinter. These tagging studies indicate that immature and spawned-out anadromous Dolly Varden char from numerous stream systems may use the same lake for overwintering.

The Dolly Varden, like other chars, usually spawns between September and November (Scott and Crossman, 1973). Blackett (1968) determined that the peak of spawning activity in Hood Bay Creek occurred between late October and early November. Spawning occurs in other southeastern Alaska streams from mid-September to mid-October (Blackett, 1968; Blackett and Armstrong, 1965). Both sexes display spawning coloration, although males are often scarlet on the ventral side and have black snouts.

Selection of spawning sites by anadromous Dolly Varden char appears to be influenced by various physical factors including current velocity, water depth and substrate composition. Fish have been reported spawning in sidechannel and mainstem riffle/run and pool reaches of streams on Kodiak Island and in southeast Alaska (Blackett, 1968; Wilson, Trihey, Baldrige, Evans, Thiele and Trudgen, 1981).

Limited observations indicate that the fish's spawning behavior is similar to other chars (Blackett, 1968; Scott and Crossman, 1973). Fish are usually paired, although more than one male may accompany a female (the largest male is usually dominant). The female is solely responsible for excavation of the redd (a depression in the stream substrate where fish spawn and deposit fertilized eggs). She forms the redd by turning on her side and thrashing the substrate with her caudal fin. The completed redd is typically oblong shaped. Dimensions of the redd vary with the size of the female and substrate and current velocities; redds are generally 30 to 61 cm (12-24 in) long and may be as deep as 30 cm (12 in). The male spawner actively defends the redd from male intruders and will nip and bite other males, sometimes grasping another male in the caudal peduncle for up to six seconds. Female spawners are not aggressive. (Blackett, 1968)

Fecundity of Dolly Varden char is variable among anadromous Alaska stocks and is greater with increasing female fish age and length (Blackett, 1968). For example, females about 300 mm fl (fork length) from Hood Bay Creek, Alaska contained less than 1000 eggs and females exceeding 450 mm fl supported at least 2000 eggs. Ripe eggs are usually 0.45 to 0.6 cm in diameter (Blackett, 1968).

The spawning pair descend into the redd and press against each other laterally. After the pair completes spawning the female may dig at the upstream end of the redd and displace gravel over the fertilized eggs. This gravel layer probably protects the eggs from sunlight and predation, reduces mechanical disturbance by ice and other objects while allowing water to transport oxygen to and metabolic wastes from the developing eggs.

Fish may spawn again with the same or a different partner and, unlike salmon, are capable in subsequent years. Males are less likely to survive spawning than females (Armstrong and Kissner,

1969). Armstrong and Kissner (1969) estimated that post-spawning mortality in Hood Bay Creek, Alaska was about 61% for male fish and 4% for female fish in 1967 and about 49% for male fish and 9% for female fish in 1968. This differential mortality is not understood, but the aggressive behavior of male spawners is probably a factor.

Emigration of spawned-out Dolly Varden char to the sea or to overwintering areas usually occurs within two weeks after completion of spawning. Fish surveys in Hood Bay Creek indicated that all spawned-out adults left the stream by late November (Armstrong and Winslow, 1968). These fish may have entered the ocean to feed for several months or moved to overwintering areas (Armstrong, 1974).

Longevity of Dolly Varden char is variable but fish in southeast Alaska may live nine to twelve years (Heiser, 1966; Armstrong, 1963).

Development of Dolly Varden eggs and alevins to the emergent fry stage requires about 210 days (Blackett, 1968). Hatching has been documented from 129 to 136 days at 8.5°C. The 1.5 to 2.0 cm long alevin typically remains in the gravel for an additional 60 to 70 days.

Limited research has focused on the survival of anadromous Dolly Varden eggs and alevins. Blackett (1968) estimated that egg to alevin survival within an area of Hood Bay Creek, Alaska was about 41 percent.

Intragravel flow, dissolved oxygen and sediment composition can influence the development and survival of salmonid eggs and alevins. Little work has focused on egg and alevin survival in relation to physical and chemical factors. Inferences can be made from work on other salmonid species. For example, transport

of dissolved oxygen to and metabolic wastes from developing eggs and alevins by intragravel flow is crucial for survival of salmonid eggs and alevins (Vaux, 1962; Wickett, 1958). Relatively low intragravel dissolved oxygen levels during the egg development stage of various salmonids may increase egg mortality, delay or hasten egg development or reduce the fitness of alevins (Alderdice, Wickett and Brett, 1958; Silver, Warren and Duodoroff, 1963). Coble (1961) and other investigators have determined that salmonid egg survival is enhanced by increased intragravel flow despite sufficient intragravel dissolved oxygen levels. Factors which could reduce the quantity or quality of intragravel water include reduced streamflow, sedimentation, and accumulation of organic debris (McNeil and Ahnell, 1964; Koski, 1966; Reiser and Bjornn, 1979).

Severe streamflow alterations can harm developing salmonid eggs and embryos. Mechanical scouring of the redd could dislodge substrate and destroy developing eggs and embryos. McNeil (1966) observed damaged pink and chum salmon redds and displaced eggs of both species in several southeastern Alaska streams following autumn spates. Koski (1966) reported low survival of coho salmon eggs subjected to freshets several days after redd construction.

Low flows and cold winter temperatures could cause redds to desiccate or to freeze. McNeil (1966) noted low survival of pink and chum salmon eggs in streams with low winter flows during harsh winter conditions in southeast Alaska.

Koski (1966) determined that significant accumulations of fine sediments within chum salmon redds can retard or prevent the emergence of fry. Deposition of fine sediments in anadromous Dolly Varden char spawning areas could retard or prevent fry from emerging.

Water temperature affects hatching rates of salmonid eggs; warmer than normal water temperatures can accelerate hatching and result in earlier than normal fry emergence (Sheridan, 1962). Blackett (1968) determined that Dolly Varden began hatching after 129 days in water with a mean temperature of 8.5°C. No upper or lower temperature tolerance limits of Dolly Varden char eggs or alevins were found in the literature.

Upon emergence, anadromous Dolly Varden char occupy relatively quiet stream reaches. Blackett (1968) and Armstrong and Elliot (1972) noted yoy fish in shallow stream margins of Hood Bay Creek, Alaska. Armstrong and Elliott also found yoy fish in rivulets along Hood Bay Creek during early summer. These stream margins were often only 1 m wide and 4 cm deep. No evidence of yoy fish entrapment by dewatering within these stream margins was detected in the literature. Yoy Dolly Varden, which feed primarily from the benthos, characteristically remain on or near the substrate, sometimes remaining motionless and occupying gravel interstices. Yoy coho salmon, however, feed primarily from the surface within these same areas (Blackett, 1968).

Earlier research indicates that juvenile salmonids occupy areas (Wickham, 1967) with relatively slow current velocities often adjacent to areas with faster current velocities and with higher densities of drifting invertebrates (Everest and Chapman, 1972). A fish moves periodically into the areas of greater food availability to forage and returns to resting positions in areas of slower current. This minimizes energy expenditures and maximizes feeding success (Chapman and Bjornn, 1969). As fish grow they often occupy deeper and faster areas of the stream (Everest and Chapman, 1972). This behavior probably applies to juvenile Dolly Varden char. Leggett (1969) suggested that the cylindrical body shape of bull char, which is morphologically similar to Dolly Varden, probably enables these fish to occupy

areas of faster current velocities than most other salmonids. Other salmonids typically have laterally compressed bodies.

Habitat selection by older pre-smolt Dolly Varden char is not well documented, although the char are distributed in deeper, sometimes faster habitat than yoy fish. Heiser (1966) noted that yearling and older pre-smolt Dolly Varden char occupied both still and flowing reaches of several inlet tributaries of Eva Lake. This lake was characterized by gravel and silt substrates with varying amounts of vegetation. Researchers studying Hook Bay Creek classified it into ten habitat types ranging from sloughs, undercut bank margins, pools and riffles. Baited minnow traps were placed in each habitat type, and length and frequency of pre-smolt coho salmon and Dolly Varden char were compared from each habitat type during July and August 1971. Pre-smolt Dolly Varden char and coho salmon were taken from all habitat types. The smallest Dolly Varden char (41-50 mm) were taken in sloughs and sidechannel undercut bank areas, and the largest Dolly Varden were found in riffles.

Yearling and older pre-smolt Dolly Varden char occupy "pools, quiet sidechannels and sloughs and tributaries off the mainstems of both. . ." the Terror and Kizhuyak Rivers, Alaska, although juvenile fish are occasionally found behind boulders in faster water (Wilson, Trihey, Baldrige, Thiele and Trudgen, 1981). Minnow traps were found to give a biased indication of habitat occupancy by fish because the bait may attract fish from a considerable distance. Habitat conditions where the fish are actually residing may be quite different from conditions immediately around the trap.

Reed and Armstrong (1971) noted that juvenile coho salmon and Dolly Varden char were capable of entering and exiting baited minnow traps fished for 24 hours. The placement of two lengths

of wire across the entrance to each trap resulted in a higher fish retention rate.

Distribution and abundance of pre-smolt Dolly Varden char may be influenced by intra and interspecific fish interactions. Observations of juvenile coho salmon, Oncorhynchus kisutch (Walbaum), and Dolly Varden char in Hood Bay Creek and in aquariums (Armstrong and Elliott, 1972) revealed that Dolly Varden fry are aggressive among themselves and in association with coho fry. Dolly Varden were frequently attacked by coho salmon fry but were never observed attacking coho fry. More Dolly Varden fry remained near the substrate when associated with coho fry than when they were alone. Coho fry occupied the upper half of the aquaria when alone and with Dolly Varden char fry.

Aquaria tests with older, pre-smolt Dolly Varden char and coho salmon indicated that Dolly Varden established and defended territories when alone and when with coho fingerlings. Dolly Varden fingerlings generally occupied positions within the aquaria at or near the bottom, but when alone, they occupied more mid and shallow depth positions. Coho fingerlings were consistently found in the upper strata of aquaria and seldom attacked Dolly Varden char fingerlings (Armstrong and Elliott, 1972).

Juvenile, anadromous Dolly Varden char grow relatively slowly during the three to four years prior to emigrating to the Pacific Ocean. Young of the year fish from Hood Bay Creek, Alaska grew about 10 mm between July 7 and October 1, 1965, reaching a mean fork length of about 38 mm (Blackett, 1968). Growth rates of pre-smolt fish may vary and length ranges of yoy and older age classes often overlap. Pre-smolt fish in Alaska generally grow 10 to 30 mm annually, primarily during the summer months (Armstrong, 1963; Heiser, 1966; Blackett, 1968).

The summer diet of stream rearing pre-smolt Dolly Varden char is influenced by food availability, fish size and stream habitat selection (Armstrong and Elliott, 1972). Gut analysis of pre-smolt fish from Hood Bay Creek during the summer rearing period (April to November) showed that substantial numbers of immature and adult aquatic insects were eaten throughout this period. Emergent and emigrant yoy salmon consumed invertebrates from April to June and salmon eggs from July to November. Relatively large pre-smolt Dolly Varden char ate more and larger food items than smaller fish. Pre-smolt fish occupying stream reaches characterized by overhanging vegetation and relatively low current velocities (such as sloughs and stream margins) generally consumed more terrestrial and surface floating insects than fish occupying mid-channel areas with moderate to fast current velocities and with greater invertebrate drift. No drift samples were taken to compare drift composition with fish gut contents. Pre-smolt Dolly Varden char occupy areas at or very near the substrate in streams with coho salmon. The char may browse along the substrate or consume drifting invertebrates (Armstrong and Elliott, 1972).

Land practices which result in removal of vegetation along stream margins and deposition of fine sediments in the stream channel could possibly reduce the abundance and fitness of pre-smolt Dolly Varden char (Armstrong and Elliott, 1972; Elliott and Dinneford, 1976).

The seasonal distribution of pre-smolt Dolly Varden char is apparently influenced by fluctuating flows and declining water temperatures during the late summer and fall. Fish appeared to be distributed evenly throughout Hood Bay Creek, Alaska from July through September. By November there were considerably fewer fish in the downstream reaches. Significantly more pre-smolt Dolly Varden char were captured in the upper stream reaches during this time. Fish were observed schooling in mid-stream in

October, behavior which had not been noted previously. Water temperatures during July through September ranged from 5° to 9°C (41°-48°F), and water temperatures during October and November were substantially lower (Blackett, 1968). Armstrong and Elliott (1972) found substantial numbers of pre-smolt Dolly Varden char in the upper reaches of Hood Bay Creek in late winter where water temperatures were consistently 6°C warmer than in downstream reaches. Armstrong and Elliott (1972) concluded that warm, ice-free reaches of Hood Bay Creek attract overwintering pre-smolt Dolly Varden char and that survival rates are higher in the warmer regions. Downstream reaches of Hood Bay Creek become frozen during the winter.

Elliott and Reed (1974) and Elliott (1975) determined that pre-smolt Dolly Varden char leave Starrigavan Creek, Southeast Alaska and enter spring-fed tributaries during autumn. The tributaries are characterized by relatively warm winter water temperatures and somewhat stable flows. Immigration of pre-smolt Dolly Varden char and coho salmon to overwintering areas usually commenced in September, peaked in early October, and ceased by December. Spates and decreasing water temperatures within Starrigavin Creek appeared to stimulate movement of fish into these streams.

Selection of lotic overwintering habitat by juvenile Dolly Varden char is not well documented.

Elliott and Reed (1974) noted that juvenile Dolly Varden char in Spring Pond Creek burrowed into logging slash and other debris when water temperatures decreased to 2°C. Fish reappeared when water temperatures rose above about 2°C.

Other researchers have noted movement of juvenile salmonids when stream water temperatures decrease in the autumn. As water temperatures decrease, fish activity levels and digestion rates

drop (Reimers, 1957; Chapman and Bjornn, 1969). Chapman (1966) stated that the distribution of winter rearing juvenile salmonids in the Pacific Northwest and other temperate areas is probably space related. Fish reduce feeding and seek overwintering areas when water temperatures decrease to or below 5°C. Winter stream conditions, including reduced flows, partial or complete ice-cover and water temperatures at or near freezing do not constitute suitable aquatic habitat for rearing salmonids. Juvenile salmonids reduce the risk of mechanical injury and displacement by avoiding shallow, cold stream reaches by moving to warmer and deeper stream reaches, burrowing into substrate interstices, or associating with submerged logs and root masses. Factors which could adversely affect the winter survival of juvenile (pre-smolt) anadromous Dolly Varden include freezing during streamflow reductions and displacement and injury from dislodged substrate material during spates. The movement of juvenile Dolly Varden to more suitable overwintering habitat in response to reduced winter streamflows has not been documented. Bustard (1973) reported the movement of yoy steelhead trout (Salmo gairdneri (Richardson)) to overwintering areas in response to altered flows in Carnation Creek, British Columbia. Bustard (1973) speculated that yoy steelhead trout overwintering within "small rubble, often less than 15 cm in diameter" could be susceptible to injury from substrate movement during spates in Carnation Creek, British Columbia. Hartmann (1968) found that stable submerged log jams provide excellent winter habitat for fish, although loose logging debris which is susceptible to displacement by floods is not suitable for salmonid overwintering habitat.

Removal of submerged logging debris, naturally occurring fallen trees and root masses, and destruction of bankside vegetation and associated submerged roots could significantly reduce the abundance of juvenile Dolly Varden char in streams where these materials are used for overwintering habitat. Bustard (1973)

emphasized the need to identify and preserve quality fish overwintering habitat, especially along small permanent and intermittent streams that may be overlooked as valuable fish habitat during timber harvest operations.

Food consumption by pre-smolt Dolly Varden char in overwintering areas is much reduced from summer levels (Armstrong and Elliott, 1972; Elliott and Reed, 1974). Armstrong and Elliott (1972) ascribed the difficulty in obtaining juvenile Dolly Varden char by baited minnow traps in the headwaters of Hood Bay Creek to the relatively low water temperatures, 5°C to 6.1°C, which influence fish activity.

Emigration of pre-smolt Dolly Varden char from winter to summer rearing areas appears to be influenced by water temperature and flow conditions (Elliott, 1975 and 1976). Rising water temperatures were associated with the emigration of pre-smolt Dolly Varden from Spring Pond Creek, Alaska. Fish emigrated from March or April through June. Floods appear to retard fish emigration within Spring Pond Creek.

Emigration of immature and mature anadromous Dolly Varden from lakes usually occurs after ice breakup in lakes. Factors, other than the breakup of ice, which could influence the timing of fish emigration from lakes include water temperature and streamflow (Armstrong, 1965b).

Behavioral and physiological changes, collectively termed smoltification, and subsequent seaward migration of age 2 to 4 and sometimes older juvenile anadromous Dolly Varden typically occurs in southeast Alaska streams from April to June. Non-lake systems may support an additional autumn smolt migration (Armstrong, 1965 and 1970; Armstrong and Kissner, 1969). Physiological changes for salinity tolerance, probably begin before seaward migration (Conte and Wagner, 1965). Factors

affecting timing of smoltification are speculative but fish size appears to be influential (Armstrong, 1965a). For example, Armstrong (1965) suggested that fish which reach migratory size several months after spring leave streams without lakes, such as Hood Bay Creek, and enter streams with lakes, such as Eva Creek, where they overwinter until the following spring. Fish have not been found to migrate seaward from lake-stream systems, such as Eva Lake during autumn. Armstrong (1965) speculated that fish that reach migratory size in lakes during the autumn probably overwinter and migrate seaward the following spring. Dolly Varden smolts may range in length from about 100 to 180 mm fork length (Heiser, 1966). Armstrong (1970) determined that spring smolts from Hood Bay Creek, $\bar{x}$ = 129-134 mm (fl) were considerably smaller than autumn smolts, $\bar{x}$ = 141-146 mm (fl) during 1967, 1968 and 1969.

D. Economic Importance

Anadromous Dolly Varden char are an important and sought after sport fish (Morrow, 1980).

II. SPECIFIC HABITAT REQUIREMENTS

A. Upstream Migration

Adult and immature anadromous Dolly Varden char leave the Pacific Ocean and enter various lake and non-lake stream systems from July through December. Various studies have indicated that lake and non-lake streams may support spawning anadromous Dolly Varden char although almost all fish (both spawning and non-spawning) entering non-lake streams such as Hood Bay Creek, Alaska, leave these streams and enter streams with lakes where they overwinter (Armstrong, 1963; Armstrong, 1965b; Armstrong and Winslow, 1968; Armstrong and Kissner, 1969). This section will discuss the upstream migration of anadromous fish in non-lake streams.

1. Stream Flow

Adult and immature anadromous Dolly Varden may migrate up non-lake streams for varying distances from July through November. Peak numbers of fish have been reported during spates in August and September in Hood Bay Creek (Armstrong, 1967; Armstrong and Winslow, 1968; Armstrong and Kissner, 1969).

Peak numbers of fish have been recorded entering selected streams during periods of high water in August and September (Armstrong and Winslow, 1968; Armstrong, 1969). Upstream fish migration may be hindered by high current velocities resulting from rapids and culverts. Low flows and shallow water depths could also prevent upstream fish passage.

2. Water Temperature

Water temperatures coinciding with the commencement, peak and termination of the immigration of anadromous Dolly

Varden in Hood Bay Creek, Alaska during 1967, 1968 and 1969 were about 4.4° to 12.6°C, 6.1° to 11.1°C and 3.3° to 4.4°C (Armstrong, 1967; Armstrong and Winslow, 1968; Armstrong and Kissner, 1969). Water temperatures at the end of the inmigration are slightly lower than those during the beginning.

3. Light

Most Dolly Varden move upstream in Hood Bay Creek at night (Armstrong and Kissner, 1969).

4. Current Velocity

No information regarding the upstream swimming ability of anadromous Dolly Varden was found in the literature.

B. Spawning

1. Current Velocity

There are only limited observations of anadromous Dolly Varden spawning habitat with respect to current velocity. Blackett (1968) reported fish spawning in a reach of Hood Bay Creek, Alaska which had current velocities ranging from 0.3 to 1.2 m/sec (1.0-3.8 ft/sec). Blackett and Armstrong (1965) noted fish (presumably spawning) in a reach of Rodman Creek, southeast Alaska, with a current velocity estimated to be about 0.63 m/sec (2 ft/sec).

2. Substrate

Anadromous Dolly Varden typically spawn in small gravels. Blackett (1968) found fish spawning primarily in small gravels, 6 to 50 mm in diameter in Hood Bay Creek. Blackett

and Armstrong (1965) observed what appeared to be fish spawning in Rodman Creek, southeast Alaska, in substrate composed of "25% sand and 75% rubble." No substrate classification scheme was presented. Spawning anadromous fish use gravels ranging from 2 to 32 mm in diameter in the Terror and Kizhuyak Rivers, Kodiak Island, Alaska (Wilson et al., 1981).

3. Water Depth

The relationship between spawning habitat and water depth is speculative. Blackett (1968) observed spawning fish at depths exceeding 0.3 m whereas Blackett and Armstrong (1965) noted probable spawning activity in a different southeastern Alaska stream in water depths of about 1.25 m.

4. Cover

There is little available information on the influence of stream cover on selection of spawning habitat, however, cover may be a requirement.

C. Inmigrant Migration to Overwintering Areas

Inmigrant, immature Dolly Varden in non-lake streams such as Hood Bay Creek, Alaska usually leave within several weeks; however, spawners may remain for up to three months (Armstrong, 1967). Periods of high water may enhance outmigration of immature and spawned-out Dolly Varden in Hood Bay Creek (Armstrong and Kissner, 1969).

Immature and spawned-out adult Dolly Varden inmigrate to overwintering areas of Eva Lake at different times. Immature individuals entered primarily during July, August and September, and spawned-out adults entered in late October and November

(Blackett and Armstrong, 1965). Most fish passed upstream during periods of darkness.

D. Inmigrant Overwintering Areas

Lakes, including turbid glacial lakes support overwintering populations of juvenile and adult Dolly Varden char (Armstrong, 1965b; Schmidt, Robards and McHugh, 1973). The char typically remain in Eva Lake from December through mid-March (Armstrong and Blackett, 1965). Their distribution within lakes may be quite restricted (Armstrong, 1965b; Schmidt et al., 1973).

E. Egg and Alevin Development

1. Water Temperature

Blackett (1968) determined that anadromous Dolly Varden eggs hatched in 129 days with 675 thermal units. Absorption of the yolk sac was completed about 65 days later when water temperatures were 2.2° to 2.8°C.

F. Summer Juvenile Rearing

1. Water Depth

Recently emerged Dolly Varden char typically occupy extremely shallow rivulets, tributaries or streamside margins (Blackett, 1968; Armstrong and Elliott, 1972). They may occupy deeper stream reaches as they grow (Armstrong and Elliot, 1972).

2. Current Velocity

Recently emerged Dolly Varden char may occupy extremely shallow, low current velocity stream reaches (Blackett,

1968; Armstrong and Elliot, 1972). Minnow traps captured juvenile, pre-smolt Dolly Varden char in Hood Bay Creek from a variety of lotic habitat types. The largest juvenile char, about 150 mm fork length, were captured in riffles (Armstrong and Elliott, 1972).

3. Instream Cover

Juvenile Dolly Varden have been observed in proximity to various forms of instream cover including root balls, trees and undercut banks (Armstrong and Elliott, 1972; Wilson, et al., 1981).

4. Substrate

Recently emerged fry have been found along stream margins with varying sizes of substrate, shallow depths and very low current velocities (Blackett, 1968; Armstrong and Elliott, 1972). Heiser (1966) noted juvenile Dolly Varden char occupying "gravel or muddy substrata" within tributaries of Eva Lake, Alaska.

Deposition of significant amounts of fine sediment in streams with limited flushing abilities could reduce the quality of juvenile anadromous Dolly Varden rearing habitat. Laboratory stream channels containing unimbedded rubble (0.30 m in diameter) consistently supported more juvenile steelhead trout, Salmo gairdneri (Richardson), and chinook salmon, Oncorhynchus tshawytscha (Walbaum), than stream channels containing imbedded rubble and with water temperatures exceeding 5°C (Bjornn, Brusven, Molnau, Milligan, Klampt, Chacho and Schaye, 1977). Bjornn et al. (1977) ascribed the reductions in fish abundance in the channels with imbedded rubble to loss of interstitial cover.

G. Juvenile Migration to Overwintering Areas

1. Water Temperature

Juvenile (pre-smolt) Dolly Varden char have been reported moving upstream in Starrigavin Creek when water temperatures decreased from about 7° to 4°C. The fish entered Spring Pond Creek, a spring-fed tributary characterized by more stable water temperatures and flows (Elliott and Reed, 1974; Elliott, 1975). No fish movement into Spring Pond Creek was noted after Starrigavin Creek water temperatures decreased below 4°C.

2. Stream Flow

Freshets within Starrigavin Creek, Alaska appeared to stimulate immigration of juvenile Dolly Varden char to Spring Pond Creek (Elliott and Reed, 1974; Elliott, 1975) until water temperatures decreased below 4°C.

H. Juvenile Overwintering Areas

1. Water Temperature

Fry overwintering areas in southeast Alaskan streams usually have relatively warm water temperatures. Spring Pond Creek, a tributary of Starrigavin Creek, supports overwintering Dolly Varden char. This stream usually has winter water temperatures at or above 1.0°C (Elliott and Reed, 1974; Elliott, 1975).

The headwater reaches of Hood Bay Creek also appear to support overwintering juvenile Dolly Varden char. Armstrong and Elliott (1972) found the greatest numbers of juvenile fish during March and April in headwater reaches of Hood Bay

Creek where water temperatures were 5° to 6.1°C. Downstream reaches were characterized by water temperatures of 3.9°C.

Elliott and Reed (1974) noted that Dolly Varden fry hid among substrate interstices as water temperatures in Spring Pond Creek decreased to 4°C to 2°C. When water temperatures rose above 2°C in March, fish began to move about the stream.

2. Stream Flow

Stable winter flow conditions such as those found in Spring Pond Creek, are probably very important to winter survival (Elliott and Reed, 1974; Elliott, 1975).

3. Substrate

Debris and large substrate material may enhance the quality of fish overwintering areas. Elliott and Reed (1974) noted juvenile Dolly Varden char burrowing into logging debris and slash when water temperatures declined to 4°C or below in Spring Pond Creek, Alaska.

Deposition of fine sediments in streams with limited sediment flushing capabilities could imbed substrate material and significantly reduce the available overwintering habitat for juvenile Dolly Varden char. Experiments of overwinter habitat selection by juvenile chinook and coho salmon and steelhead and cutthroat trout (Salmo clarki (Richardson)) at water temperatures less than 5°C indicate that substrate (15-30 cm in diameter) with interstices devoid of fine sediment consistently supported more fish than substrate imbedded with fine sediment (Bustard, 1973; Sjørn et al., 1977).

I. Juvenile Migration to Summer Rearing Areas

1. Water Temperature

Juvenile (pre-smolt) Dolly Varden char were found to emigrate from Spring Pond Creek, a spring-fed stream inhabited by overwintering juvenile and adult resident and anadromous Dolly Varden, to Starrigavin Creek when water temperatures rose to 4° to 5°C in April 1974 (Elliott, 1975).

2. Stream Flow

Elliott (1975) suggested that floods in Spring Pond Creek depressed the downstream movement of juvenile Dolly Varden. Fish emigration increased when flows decreased.

J. Inmigrant Migration to Sea

1. Water Temperature

Most immature and mature Dolly Varden char (not including smolts) emigrated from Eva Lake Creek, Alaska shortly after ice-breakup. Water temperatures ranged from 4.4° to 6.7°C (Armstrong, 1965b).

2. Stream Flow

Although ice-breakup in Eva Lake appeared to strongly influence fish migration to the sea, peak numbers of emigrants moved downstream during flood states (Armstrong, 1965b).

3. Light

Most Dolly Varden char emigrated from Eva Lake during darkness. During the height of the migration individuals were detected moving downstream during both night and day (Armstrong, 1965b).

K. Smolt Migration to Sea

1. Water Temperatures

Water temperatures coinciding with the initiation, peak and the near-end of the spring Dolly Varden smolt migration in Hood Bay Creek, Alaska were 3°, 5° and 6°C, respectively, during 1967, 1968 and 1969 (Armstrong, 1970).

Water temperatures at the beginning, peak and end of the smolt migration during 1962 and 1963 were 3°, 5° and 8°C in Eva Lake, and 6° and 10°C in Eva Creek (Armstrong, 1970). These values are somewhat similar to water temperatures during the spring smolt outmigration from Hood Bay Creek, Alaska.

Dolly Varden smolt stopped migration in mid-June 1957 in the Anchor River, Alaska when the water temperature reached 13.3°C (Allin, 1957).

The autumn smolt migration in Hood Bay Creek, Alaska began when water temperatures were 8°C and ended when water temperatures were 6°C during 1967, 1968 and 1969 (Armstrong, 1970).

2. Stream Flow

Floods apparently influenced the timing of the spring and autumn Dolly Varden char smolt migration in Hood Bay Creek, Alaska. Peak numbers of smolts migrated downstream during periods of high water (Armstrong, 1970). Smolts have also been noted emigrating from Mendenhall Lake (near Juneau) during the spring and early summer. Peak migrations often coincide with freshets (Bethers, 1974).

3. Light

Most smolt migrate downstream in Hood Bay and Eva Creeks during darkness, although the peak of smolt emigration in Eva Creek occurred during both night and day (Armstrong, 1970).

III. CONCEPTUAL SUITABILITY INDEX CURVES

Habitat suitability index curves were not constructed for anadromous Dolly Varden char. There were limited data relating the various Dolly Varden life stages to the physical and chemical characteristics of the habitats. When data were available, they were often not in a form which could be used to construct habitat suitability curves.

IV. DEFICIENCIES IN DATA BASE

A limited number of investigations indicate that juvenile anadromous Dolly Varden char move to spring-fed reaches of streams with relatively warm water temperatures during the fall and leave these areas the following spring, as evidenced by baited minnow trap samples from Hood Bay Creek (Blackett, 1968; Armstrong and Elliott, 1972) and by weir sampling in the Starrigavin Creek watershed (Elliott and Reed, 1974; Elliott, 1975, 1976 and 1977). The Starrigavin watershed was affected by timber harvest and deposition and removal of logging debris.

The relationships between upstream swimming capabilities of juvenile and adult anadromous Dolly Varden and current velocity, water temperature, water depth and stream gradient have not been sufficiently investigated. Excessive stream gradient and high current velocities associated with natural stream features or culverts could impede migration of juvenile and adult fish to summer and winter rearing and spawning areas. The upstream swimming performance of anadromous Dolly Varden is probably influenced by the above factors as well as fish size, spawning condition and, possibly, sex.

Lotic habitat selection by spawning anadromous Dolly Varden char is probably collectively influenced by current velocity, water depth, substrate composition and imbeddedness and instream and bankside vegetation. Few studies have objectively described the above lotic habitat conditions. If a specific area of a stream is characterized by one unfavorable spawning habitat feature, such as excessive current velocity or unsatisfactory substrate composition, that particular area of stream will not be selected by spawning fish despite other favorable habitat conditions.

Habitat conditions available for Dolly Varden spawning sites influence selection of spawning areas, although, methods of objectively describing this habitat have varied. For example, within a

hypothetical stream, stream reach A may support one pair of spawning fish and reach B, four pairs. These two reaches may contain equal amounts of "spawning habitat" as defined by current velocity, water depth and substrate composition and imbeddedness. The difference between the two reaches may be that "spawning habitat" within stream reach A was concentrated in one area and "spawning habitat" within stream reach B was scattered among relatively large substrate and fast water. The non-contiguous distribution of spawning habitat in stream reach B probably allows more fish to spawn because of increased cover and visual isolation. This example illustrates the need to examine entire stream reaches to better understand selection of spawning habitat.

The influence of dissolved oxygen levels, rates of intragravel flow, sediment compositions and water temperatures on the survival and development of anadromous Dolly Varden char is not understood. Numerous research focusing on the eggs and alevins of other salmonids indicate that the physical and chemical factors exert a substantial and often interactive influence on the survival and fitness on the development stages.

Adult and immature (post-smolt) Dolly Varden typically overwinter in lakes, although fish have been found in spring-fed reaches of streams in southeast Alaska. The importance of glacial or glacial-influenced lakes and streams has not been adequately examined. The relationships between overwintering habitat and water depth, current velocity, substrate composition, water temperature and other variables has not been determined. The distribution of overwintering Dolly Varden in selected lakes may be quite restricted, although physical and chemical factors which may limit the fish's distribution are not known.

Juvenile (pre-smolt) Dolly Varden have been documented moving to spring-fed tributaries and burrowing into logging debris when water temperatures approached 4°C. There were no references found in the literature of juvenile fish using mainstem reaches of rapid-runoff

streams for overwintering habitat. The apparent affinity of yoy and older juvenile fish to rapid run-off streams during the summer indicates that this type of area could be used for overwintering habitat.

There is little available information concerning the lotic summer micro-habitat selection by juvenile (pre-smolt) anadromous Dolly Varden char with respect to various physical and chemical lotic habitat variables, food availability and the presence of other fishes. Some investigators have attempted to describe juvenile fish habitat quantitatively by bankside observation, electro-shocking and baited minnow traps with varying degrees of success. Apparently snorkeling has not been used for fish observation in clearwater streams. Snorkeling has been shown to be a valuable fish observation technique in clearwater streams of the Pacific Northwest and the midwest (Everest and Chapman, 1972; Fausch, 1978).

Some work has focused on the feeding habits of juvenile (pre-smolt) fish occupying mainstem versus stream margins but no drift or benthos sampling was done to formulate "forage ratios." Few observations of the feeding behavior of juvenile Dolly Varden char have occurred in streams except for yoy fish in very shallow, low current velocity areas along stream margins.

Some observations of juvenile coho salmon and Dolly Varden char have occurred in aquariums and streams. The behavior of juvenile Dolly Varden char and other salmonids occurring in the same regions has not been studied adequately.

V. RECOMMENDATIONS AND FURTHER STUDIES

Studies should be designed and conducted to determine the survival, movements and behavior of all life stages of anadromous Dolly Varden char with respect to physical, chemical and biological habitat components within selected pristine Alaska drainages. The above relationships should be examined thoroughly both within the drainage and by supplemental laboratory and field studies prior to the occurrence of any land use activities which could modify the habitat. Several years of study could be required to meet this objective. Investigations should continue during and after land use activities to adequately monitor the fish life stage-habitat relationships. Such research and supplemental laboratory and field studies could provide land managers with needed information to protect and enhance anadromous Dolly Varden habitat.

Field and laboratory studies should be designed and conducted to determine the upstream swimming capability of immature (pre and post-smolts) and gravid and spawned-out adult anadromous Dolly Varden char in relation to current velocity, water depth, water temperature, stream gradient and length of potential migration barriers. Studies could be similar to those described by MacPhee and Watts (1976) for testing Arctic grayling swimming performance. Results of these tests could be used for determining the best methods for installing culverts to allow fish migration and to designs of culverts and other fish passage facilities.

Studies should be designed and conducted to evaluate the influence of water temperature, dissolved oxygen, rate of intragravel flow, substrate composition and possibly other physical and chemical habitat variables on the survival and development of anadromous Dolly Varden char eggs and alevins and the fitness and survival of emergent fry. Controlled environmental laboratory tests should complement field studies.

Standardized methods should be developed and evaluated to objectively describe current velocity, water depth, substrate composition and imbeddedness, instream and bankside cover and water temperatures at anadromous Dolly Varden spawning sites. The above lotic habitat data collected at a number of redds within a stream or stream reach could be examined by frequency analysis for each lotic habitat component. These frequency analyses would help describe lotic habitat selection by spawning fish, in relation to current velocity, water depth, substrate composition and imbeddedness and possibly other lotic habitat variables. The frequency analyses would not determine fish spawning habitat preferences because streams and stream reaches are characterized by a finite combination of acceptable habitat variables. Readers are urged to consult Appendix III of the Terror River, Alaska Instream Flow Report by Wilson et al. (1981) which discusses fish spawning habitat selection and the assumptions associated with habitat suitability curve construction.

Standardized methods should be developed and refined to evaluate current velocity, water depth, substrate composition and imbeddedness and instream and bankside cover at anadromous char spawning sites to better understand habitat selection within individual streams or stream reaches. For example, lotic habitat types could be characterized by current velocity, water depth, instream and bankside cover conditions within those ranges measured at redds. Measurements of substrate composition and imbeddedness which were not used for spawning habitat by anadromous Dolly varden char could help us to better understand spawning habitat selection of this fish in various streams.

Weirs should be used to monitor juvenile (pre-smolt) anadromous Dolly Varden char movements in relation to streamflow, water temperature and other physical and chemical habitat variables in small, intermittent and larger streams within a drainage. Snorkling and minnow trapping could supplement sampling with weirs.

Studies should be designed and conducted to describe summer habitat selection by juvenile (pre-smolt) anadromous Dolly Varden char with respect to a variety of physical and chemical habitat variables, food availability and the presence of other fish. Investigations using snorkling for fish observation should be conducted in clearwater streams using techniques similar to Everest and Chapman (1972) and Fausch (1978). Fish holding positions should be characterized by water depth, distance to streambed, lighting, substrate composition and imbeddedness, instream and bankside cover, current velocity and proximity to other fish, including char and other species. These investigations would complement fish movement studies along streams supporting weirs.

Studies of fish feeding behavior coupled with benthos and drift sampling and fish gut analysis should be conducted to better understand the feeding habits and apparent affinity of Dolly Varden char to the substrate.

More investigations should occur to detect and characterize overwintering habitat selection by various ages of juvenile (pre-smolt) anadromous Dolly Varden char with respect to water depth, current velocity, water temperature, overhanging vegetation, undercut banks, substrate material and proximity to stream margins. Identification of overwintering fish habitat is required for the protection of this fish species. Various land use activities could significantly reduce the quality of this habitat (Bustard, 1973). Habitat enhancement efforts should be formulated with an understanding of what constitutes good overwintering habitat for various ages of Dolly Varden char.

Laboratory and field tests, somewhat similar to those conducted by Bustard (1973), should be designed and conducted to complement studies of the distribution and behavior of overwintering anadromous Dolly Varden in selected streams. These tests should provide juvenile fish with a continuum of overwinter habitat types from no cover to total

riparian cover, unimbedded to totally imbedded substrate of sand to large cobble substrate and a variety of water temperatures. Juvenile fish of various ages should be tested because fish size may influence overwinter habitat selection.

Studies should be designed and conducted to determine the presence of overwintering immature (post-smolt) and adult anadromous Dolly Varden char in clearwater and glacial lakes and streams. The distribution of overwintering fish in lakes can be quite limited. Studies of lotic overwintering areas with respect to various physical and chemical habitat conditions should be conducted to explain habitat selection criteria and to predict fish overwintering areas by the character of the habitat.

Radio telemetry should be considered as a viable technique to monitor movements of immature and adult anadromous Dolly Varden char in overwintering areas which are difficult to sample by gillnet or other methods.

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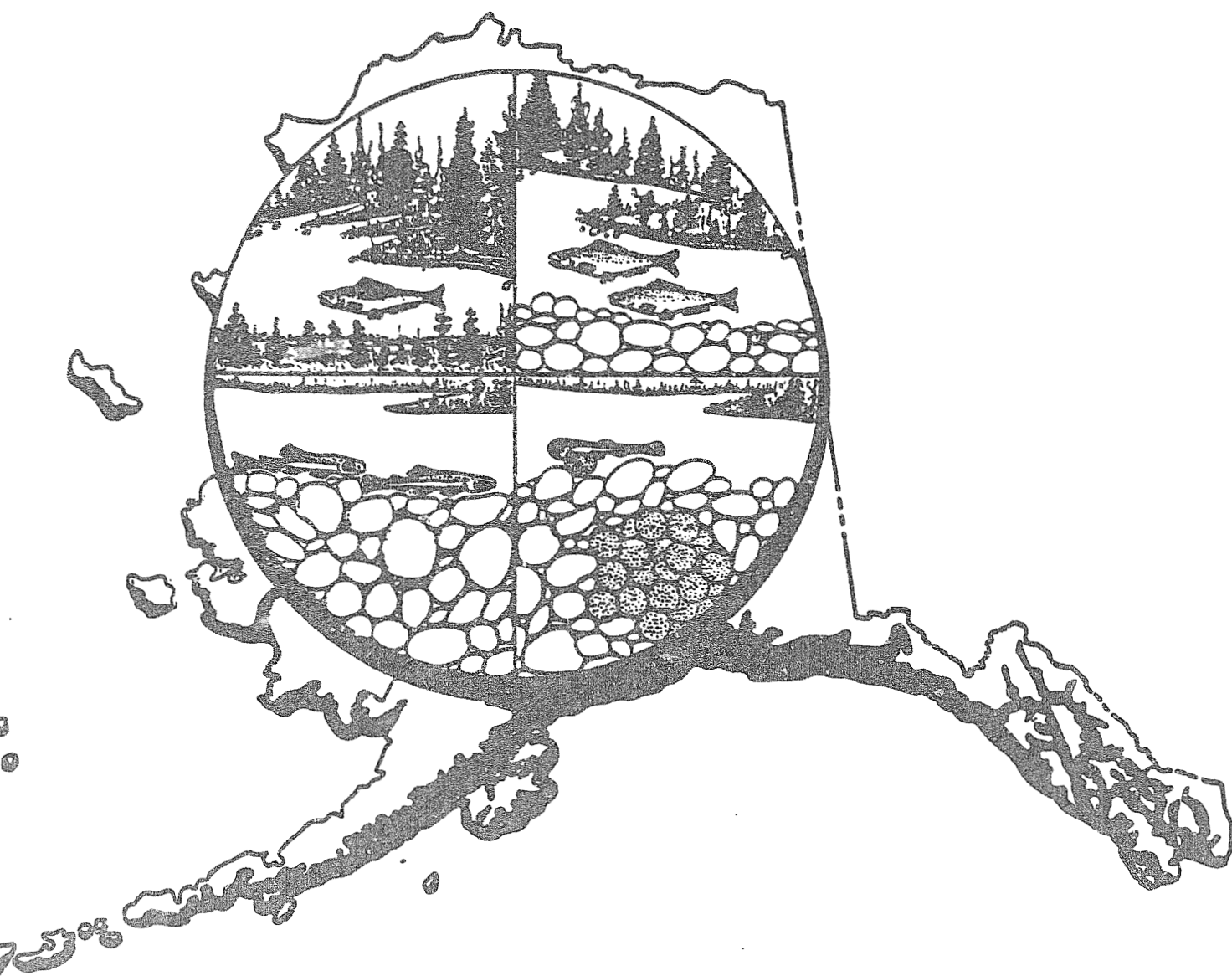
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FRESHWATER HABITAT RELATIONSHIPS

THREESPINE STICKLEBACK - GASTEROSTEUS ACULEATUS



ALASKA DEPARTMENT OF FISH & GAME
HABITAT PROTECTION SECTION
RESOURCE ASSESSMENT BRANCH

APRIL, 1981

FRESHWATER HABITAT RELATIONSHIPS
THREESPINE STICKLEBACK (GASTEROSTEUS ACULEATUS)

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I. INTRODUCTION

A. Purpose

This report compiles existing information on the freshwater habitat requirements, tolerances, and preferences of the threespine stickleback, Gasterosteus aculeatus (L.) and provides a data base for habitat evaluation procedures. The threespine stickleback is generally regarded as a hardy species, tolerant of a wide range of habitat conditions.

Information on physiological tolerances and requirements have been gathered from throughout the range of the species. However, observations on actual conditions observed in bodies of water where sticklebacks occur are generally restricted to Alaska. The threespine has been extensively used as a laboratory fish for behavioral and pollution studies. Much work has been done on the physiology of the species in Europe, but relatively little in North America. It is recognized that habitat requirements may differ for stocks from different geographic areas, but present data available from Alaska are insufficient to demonstrate this within the State.

Within the Gasterosteus aculeatus complex, three forms are generally recognized (McPhail and Lindsey, 1970). There is a partially plated freshwater form (called leiurus), a heavily plated marine form (called trachurus), and an intermediate form (semiarmatus). This report is restricted to the totally freshwater form (leiurus), even though the anadromous forms may use freshwater habitat during the breeding season.

This report emphasizes habitat requirements, primarily those of a physical and chemical nature. Certain biological factors affecting the well being of the population, such as feeding,

predation, competition, parasites, and disease, are not comprehensively treated.

B. Distribution

The threespine stickleback is widely distributed in the northern hemisphere in North America, Europe, and Asia. Except for Europe, it is not found more than a few hundred kilometers from the coast. On the Atlantic coast of North America, it ranges from Baffin Island and the Hudson Bay area down to Chesapeake Bay. On the Pacific coast of North America, it occurs from Alaska to Baja California. On the eastern coast of Asia, it ranges from the Bering Strait south to Japan and Korea (Scott and Crossman, 1973; Wootton, 1976).

In Alaska, the threespine stickleback occurs in all coastal areas from Dixon Entrance to the Alaska Peninsula, the Aleutian Islands and Bristol Bay (Morrow, 1980). It also occurs in the western tip of the Seward Peninsula and on St. Lawrence Island; however, the freshwater leiurus form is not thought to be present in the latter areas (McPhail and Lindsey, 1970; Wootton, 1976). (See Figure I.)

The leiurus form occurs in both lakes and streams.

C. Life History Summary

An excellent synthesis of threespine stickleback life history has been presented by Wootton (1976). Behavioral aspects of threespine stickleback life history regarding reproduction (spawning and incubation of eggs) have been extensively documented and will not be dealt with in this report. Section II, Specific Habitat Requirements, will examine data on tolerances and preferences for physical and chemical parameters

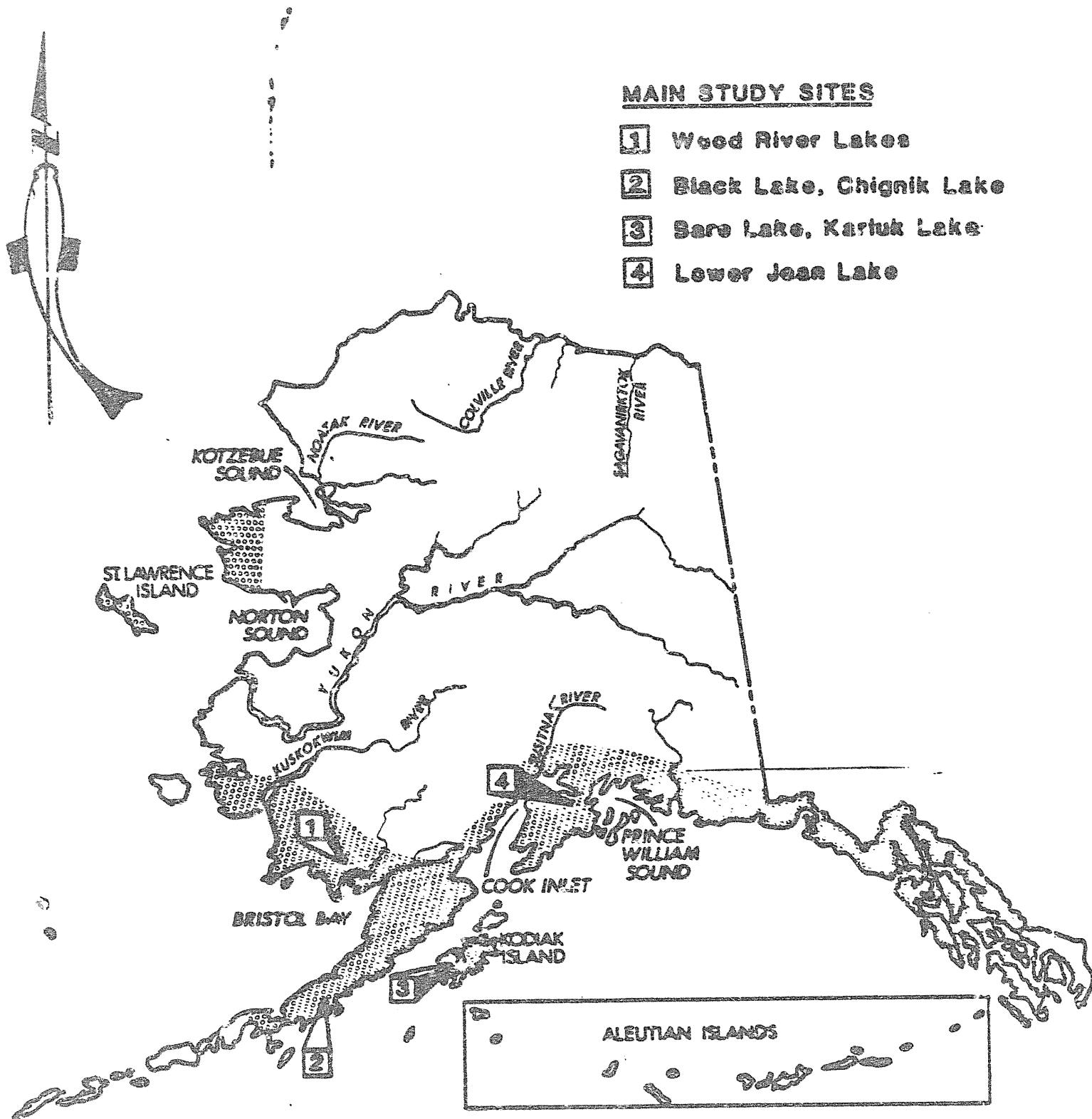


Figure 1. Distribution of Threespine stickleback in Alaska (Morrow, 1980) and main study sites.

history aspects other than reproductive behavior for juveniles and adults, emphasizing Alaskan studies. Much of this section has been provided by Cannon (1981), with permission of the author.

1. Size and Age

Cannon (1981) identified three discrete size classes of threespine sticklebacks in lower Jean Lake on the Kenai Peninsula. Standard lengths ranged from 22-71 mm. One size class ($\overline{SL}$ = 32-33 mm) was captured in surface tows in June and early July; weekly abundance for this size class in the catch decreased during this time. A smaller size class ($\overline{SL}$ = 28-29 mm) entered the catch in mid-June and rapidly dominated the catch by mid-July. During July and August, two size classes were distinguished in baited minnow traps fished on the lake bottom. Stickleback ($\overline{SL}$ = 38-40 mm) were taken in littoral areas; a larger size class ($\overline{SL}$ = 51-52 mm) was captured at depths of 19-20 m.

In Lake Nerka (Wood River lakes) Burgner (1958) observed a trimodality of size distributions which suggested the presence of three age groups in early summer. Stickleback fry did not appear in catches until August and were abundant in September. The maximum age was reached at three years or more and in adult fish, females were larger than males. The life history of populations inhabiting Karluk and Bare Lake on Kodiak Island was studied by Greenbank and Nelson (1959). Lifespan was determined to be 2+ years, some individuals probably lived past a third winter. Young of the year were first observed in collections made in early July; this size class was reported to be very abundant and soon dominated the catch. Mature females attained a somewhat larger size than did males. Narver (1968) described the general life history of threespine sticklebacks in the Chignik Lakes on

the Alaska Peninsula. Determination of age was accomplished by examination of length-frequency. An interpretation of size distribution for a September sample placed Age 0 fishes within the 20-30 mm fork length (F.L.) size range, Age 1+ within 40-45 mm range and Age 2+ within 55-65 mm range. Fry first appeared in tow net catches in early August; their density increased rapidly. Engel (1971) also identified three size classes in beach seine and minnow trap catches in Johnson, Scout, and Bear Lakes on the Kenai Peninsula. Length of life was estimated to be 2+ years, mean lengths for ripe males and females in Bear Lake were 50.5 mm (F.L.) and 49.5 mm respectively. These lengths correspond to those found by Greenbank and Nelson for Age 2 fish. The abundance and size of threespine found in Lake Aleknagik (Wood River lakes) were examined by Rogers (1972). Age groups were assigned on the basis of length frequency. Age 0 fish were approximately 10-20 mm ($\overline{SL}$) by the first week of August and initially appeared in beach seine hauls in mid-July. Age 1 were 30-35 mm, Age 2 were 40-50 mm, and Age 3 were 55-65 mm.

The variations in age and size structure found in these studies undoubtedly reflects differences in genetic and environmental influences between the respective populations. Direct comparisons are confounded by differences in sampling gear and measurement methods used. Rogers (1972) demonstrated that in years of unfavorable growth, major stickleback age groups showed distinctive length frequencies; but in years of good growth, the older year classes overlapped.

2. Maturity and Reproduction

Initial sexual maturity in the Lower Jean Lake stickleback population probably occurs during the second summer of life (Cannon, 1981). Fishes thought to be Age 1 which were captured in tows and minnow pots were sexually mature; a smaller size class, Age 0, was not mature. Only one age class at sexual maturity was reported by Greenbank and Nelson (1959) and McPhail and Lindsey (1970). Rogers (1968), Burgner (1958), and Narver (1968) suggested that threespines mature at Age 2. Carl (1953) and Jones and Hynes (1950) stated that breeding occurred during the first year of life (Age 0). Variation in these estimates cannot be explained with available information; however, differences in length of season, food availability and genetic character were probably influencing factors.

A decrease in Age 1 stickleback catch per unit effort for surface tows in Lower Jean Lake during the course of the summer and the presence of a similar size class in shallow shoreline areas suggested that there was a migration from pelagic to littoral habitats (Cannon, 1981). Because Age 1 fish were sexually mature and were strongly suspected of spawning in littoral areas during this time, the movement appeared to be associated with reproductive activity. Tinbergen (1952) and Narver (1968) described a spawning migration of schools of threespine stickleback into shallows. Males then left schools to establish territories. Baerends (1957) stated that when reproductive instinct in threespine is activated, adult fish begin to migrate. These migrations appeared to correspond with a reproductive stimulus that is only satisfied when the fish reach shallow, warm waters with abundant vegetation.

Although characteristic behavior associated with breeding was not observed by Cannon (1981) in Lower Jean Lake, the majority of the lake population apparently spawned in the lake. Spawning emigrations from the lake were not observed during the summer, however, they may have occurred prior to mid-May. Sticklebacks were not found in high densities milling near the inlet and outlet creek weirs nor attempting to pass through them. Greenbank and Nelson (1959) reported that in Karluk Lake, threespine in breeding condition were observed in the lake, but nesting was not witnessed.

Various authors have noted a variety of materials used in construction of nests. Tinbergen (1952) described nests constructed of small twigs, grass and other debris; Greenbank and Nelson (1959) and Vrat (1949) discovered nests formed from cemented sand grains.

Male sticklebacks apparently require the sight of aquatic vegetation for the initiation of nest building (Pelkewijk and Tinbergen, 1937, cited by Aronson, 1957). Narver (1968) noted that the occurrence of stickleback in spawning condition was greatest in areas where submergent flora was plentiful. Hagen (1967) observed sticklebacks nesting in still and standing backwaters near dense stands of aquatic vegetation. Male sticklebacks exhibiting breeding colors and females with distended abdomens were observed in or near thick patches of Chara sp. in Lower Jean Lake (Cannon, 1981).

Egg production in European populations has been estimated to be 100-200 eggs per spawning (Assen, 1967; Wootton, 1973 b). McPhail and Lindsey, 1970) reported that in populations from the Pacific Northwest, gravid females will often spawn several times per season and lay 50 to 200 eggs at a time. The number of eggs per spawning and the number of spawnings

per season have been shown to be positively correlated to the size of the female (Wootton, 1973 a). He suggested that population estimates which ignored the high potential of egg production and survival provided by the multi-seasonal spawning capacity of large females and the protective nesting behavior of males could grossly underestimate stickleback production and would incorrectly assess the importance of this species to the energetics of the freshwater community. Potapova et al. (1966) found that the quantity and viability of egg production is related to growth rate and lipid storage; large females exhibit higher fecundity.

The rigors of breeding evidently lead to increased mortality. This view is supported by detailed descriptions of the complex nature of stickleback reproductive behavior provided by Tinbergen (1952) and van Iersel (1953, cited by Wootton, 1976). High mortalities reported by Rogers in Lake Aleknagik may have resulted from a decreased resistance to high temperature due to the stress of spawning. Narver (1968) observed high death rates associated with spawning stress in the Chignik Lakes, Alaska. These high mortalities and the territorial spawning of sticklebacks were considered possible density-dependent population regulators. Hagen (1967) described post-reproductive mortality in the threespine population inhabiting the Little Campbell River, B.C. Many adults were found in extremely poor condition; fungus and other parasitic eruptions were noted. Sticklebacks in Karluk and Bare Lakes on Kodiak Island apparently incurred a high mortality after spawning and appeared nutritionally deprived (Greenbank and Nelson, 1959). Engel (1971) reported post-spawning mortality in study lakes on the Kenai Peninsula, Alaska.

3. Feeding and Competition

Feeding investigations of sticklebacks in North America have determined that their diet is composed mainly of zooplankton and insects. The fish are opportunistic and food sources are related to seasonal and regional availability. Carl (1953) found cladocera and copepods in the majority of stickleback stomachs collected in Cowichan Lake, B.C.; insects, ostracods, amphipods and algae were also observed. Greenbank and Nelson (1959) discussed the importance of chironomid larvae and pupae, copepods and cladocera in the feeding of sticklebacks in Karluk and Bare Lakes. Other items encountered occasionally were pea clams, ostracods, rotifers, snails, leaches, planarians, fish eggs and water mites. The importance of chironomids decreased over the summer. Most larger sticklebacks fed on ostracods and fish eggs; fewer of them fed on cladocera. Chironomid larvae and entomostraca were found to be primary food types in threespine sticklebacks in littoral areas of Lake Aleknagik with Entomostraca being their major prey in limnetic areas (Rogers, 1968). Sticklebacks inhabiting Black Lake, a shallow lake, fed predominately on insect larvae; threespines in Chignik Lake, which has only a small littoral zone, fed totally on zooplankton (Parr, 1972).

In Lower Jean Lake, feeding habits of threespines reflected differences in their distribution (Cannon, 1981) and seasonal availability. Fish utilizing bottom waters preyed on food species which were not caught in plankton hauls because most of these species live on or near the bottom. Threespines foraging in the limnetic surface zone preyed largely on planktonic invertebrates. Age 1 sticklebacks ($\overline{SL}$, 30-32 mm) fed predominately on copepods in mid-June; but for Age 0 sticklebacks ($\overline{SL}$, 28-30 mm) rotifers were dominate prey during July. The availability of prey species

in surface waters may have fluctuated during the summer, due to variations in their abundance or distribution. Surface and bottom feeding threespine sticklebacks in Lower Jean Lake were ecologically separated (Cannon, 1981). Distributional differences were considered a mechanism by which stickleback age classes minimized competitive stress and maximized the utilization of lake resources. The ability of threespines to utilize limnetic waters as well as bottom environments demonstrated their adaptability to use a wide range of conditions thus allowing exploitation of diverse aquatic niches. Separation of age classes between limnetic and bottom habitats were believed to be associated with spawning migrations. Exposure to a wide variety of habitat types was facilitated by these movements. Anatomical and physiological differences between age groups may have enforced separation.

Because spawning and early rearing occur in shallows, stickleback life history is closely associated with littoral habitats. The quantity of suitable littoral area potentially serves as an important stickleback population regulating factor (Narver, 1968). Ecological expansion would depend on the physical condition and the magnitude of co-actions (competition and predation) found in adjacent environs. For these reasons, the variety of potential niches accessible to sticklebacks and consequently their distributional patterns can be expected to vary seasonally and between systems.

Spatial differences exhibited between Age 0 and Age 2 sticklebacks and rearing sockeye salmon in Lower Jean Lake provided a mechanism to reduce interspecific competition (Cannon, 1981). Rearing sockeye were not caught in surface tows after mid-July; this decline occurred in conjunction with a large recruitment of Age 0 sticklebacks.

Feeding similarities between sticklebacks and rearing sockeye have been reported by Burgner (1958) in the Wood River Lakes, Alaska, Narver (1968) in the Chignik Lakes, Alaska, and Krokhin (1957) in the Kamchatka Lakes, USSR. Common prey preferences have suggested potential competition for food. In nature, many similar species appear to coexist while seemingly in competition; however, detailed observations have revealed differences in habitat and behavior that permit coexistence.

Rogers (1968) compared the food of sockeye salmon fry and threespine sticklebacks in the Wood River Lakes. In littoral areas, the benthos was used more by sticklebacks than sockeye fry; surface insects were utilized more by sockeye. In limnetic areas, winged insects were an important prey for sockeye, but were rarely ingested by sticklebacks. Parr (1972), who studied the feeding of juvenile sockeye and resident fish species including threespine in the Chignik Lakes, indicated that a dissimilarity existed between stickleback and sockeye feeding. Sockeye more frequently fed on winged and pupal insects. In Lower Jean Lake, a comparison of feeding between these species (although limited to only a five week period) found similar differences (Cannon, 1981). Sticklebacks and sockeye inhabiting surface waters during this period utilized similar prey, but sockeye appeared to prefer winged insect species more than sticklebacks.

Partitioning rations among sticklebacks and rearing sockeye in Lower Jean Lake appeared to be accomplished through differences in spatial distribution (Cannon, 1981). Age 2 threespine utilized bottom habitats. Age 1 sticklebacks and juvenile sockeye exhibited similar distribution patterns and feeding; however, spatial overlap and prey similarity are only prerequisites to potential competition. A significant

decrease in Age 1 threespines was observed during the summer in Lower Jean Lake. This reduction was believed to be associated with reproductive migrations which brought adult fish bottom environments. The rapid recruitment of Age 0 sticklebacks into the near surface waters during July may have influenced the apparent shift in vertical distribution of juvenile sockeye into deeper water strata and restricted the return of Age 1 sticklebacks into limnetic areas. The high preference of Age 0 sticklebacks for rotifers was not shared with sockeye or adult threespine, a small mouth size possibly was responsible for the apparent differences in feeding preference, although Age 1 threespine of approximately the same size fed predominately on copepods in June when rotifers were abundant in the net plankton. Temporal variations in the vertical distributions of prey species may have been involved. Rogers (1968) suggested that temporal as well as spatial differences in stickleback-sockeye feeding relationships could exist.

Narver (1968) developed a conceptual model of sockeye-stickleback co-actions for populations in the Chignik Lakes. He concluded that threespine sticklebacks which were ecologically a littoral species would be displaced from limnetic areas by rearing sockeye if the young salmon remained abundant. Parr (1972) determined that the abundance of Age 0 sockeye in the Chignik Lakes had an adverse effect on resident fish populations including threespine sticklebacks. Burgner (1958), Kerns (1965), and Rogers (1972) have suggested a similar population regulation of stickleback abundance by large Age 0 sockeye salmon recruitments in the Wood River Lakes. Reduced spawning escapement due to overharvest or environmental factors have resulted in periods of reduced sockeye fry abundance in the Wood River and Chignik Lakes. During these years,

sticklebacks were able to rapidly occupy vacant niches (Burgner, 1958; Narver, 1968).

The threespine stickleback is the dominant fish species inhabiting Lower Jean Lake (Cannon, 1981). Its dominance is favored by a prolonged spawning time, a substantial littoral spawning habitat with abundant submergent vegetation, an ability to utilize deep and shallow bottom habitats as well as pelagic areas for feeding, reduced intraspecific competition between age classes via differences in their spatial behavior and diurnal migrations, and an apparently low level of interspecific competition from rearing sockeye salmon in limnetic areas.

4. Distribution and Behavior

An apparent diel migration of threespines in surface waters of Lower Jean Lake was observed by Cannon (1981) during the summer. The abundance of sticklebacks in surface tow net samples collected in the Wood River Lakes by Burgner (1958) remained high throughout the day and night. Diel zooplankton migrations probably influenced stickleback distribution in Lower Jean Lake. Stomach analysis of threespine from different periods showed no significant decrease in numbers of whole undigested zooplankton. If feeding continued throughout the day and night, sticklebacks conceivably would concentrate at depths where prey density was high. Vertical migrations of limnetic zooplanktons commonly occurring in Alaska lakes have been observed (Rogers, 1974).

A reduction in interspecific competition between sticklebacks and sockeyes could result from seasonal variations in vertical distribution. Because threespine are more resistant to high temperature and illumination and

because they are equipped with a self-contained defense mechanism, near-surface water residence would be less ecologically intolerable for stickleback than for sockeye.

Outside of breeding season, stickleback feed in schools (Tinbergen 1952). Generally, schooling fish are the same size because fish of similar size swim at the same speed. Size in sticklebacks varies between sexes and schools comprised of all males or all females have been observed (Narver, 1968). Possible benefits attributed to schooling behavior have included increased feeding efficiency, predator detection and defense, increased ability to locate a mate, enhanced learning ability, and efficiency of movement (Eggers, 1975). Schooling was observed in sticklebacks in surface waters (juveniles) and in shallow littoral areas (adults) of lower Jean Lake (Cannon, 1981).

MacMahon (1946) described the threespine stickleback as the fiercest freshwater fish in Britain for its size. Its highly flexible fin motions are well suited to feeding in the dense vegetation and submerged debris of the littoral environment. Hagen (1967), who conducted dispersion studies of threespine, reported that sticklebacks (leiurus) were a sedentary fish. Recaptures of marked fish were never made beyond 200 m from the point of release. Sticklebacks in Lower Jean Lake generally exhibited a lethargic swimming activity (Cannon, 1981). Adult sticklebacks observed in schools feeding in algae beds and solitary fish which were probably spawning moved slowly through the water. Even pelagically feeding schools of Age 0 threespine swam sluggishly near the surface. Rapid swimming motions occurred during territorial defense and occasionally in pursuit of prey, but only for short distances.

D. Ecological and Economic Importance

The threespine stickleback is often abundant where it is found and plays a significant role as a predator, competitor, and prey species in many lake ecosystems. There has been concern regarding the stickleback as a potential competitor with sockeye salmon (Oncorhynchus nerka) fry but recent studies (Cannon, 1981; Manzer, 1976; Rogers, 1972; Wootton, 1976) have indicated that competition to the detriment of the sockeye fry does not often occur. (See also discussion in Section I.C., Life History Summary.) In artificial situations, such as the reclamation and re-stocking of lakes with rainbow trout (Salmo gairdneri), the presence of threespine sticklebacks may be detrimental to the trout population (Engel, 1971). In many areas, sticklebacks are an important prey species for predaceous fish such as trout, salmon, and northern pike (McPhail and Lindsey, 1970; Wootton 1976) and for fish-eating birds (Scott and Crossman, 1973).

The threespine stickleback has been harvested only to a minor extent. They have been used for oil, meal, fertilizer, and animal food, including sled dog food (Wootton, 1976).

Because the threespine stickleback is hardy, easy to keep, and widely distributed, it has proven to be an important laboratory fish. It has been extensively used for behavioral studies and for studies on the effect of water pollution (Wootton, 1976).

II. SPECIFIC HABITAT REQUIREMENTS

A. Spawning

1. Temperature

The surface water temperature during the breeding season in Lower Jean Lake ranged from about 12 to 18°C (Cannon, 1981). In a stream of southern British Columbia, the average temperature during the breeding season was 16°C (Hagen, 1967) and a stream in England during the spawning season had temperatures ranging from 16 to 19°C (Lindsey, 1962).

Greenbank and Nelson (1959) stated that the water temperature in two lakes on Kodiak Island may influence the time of spawning. Threespine sticklebacks spawned earlier in Bare Lake (surface water temperatures from mid-May to end of July were 4.4-22.8°C) than in the deeper Karluk Lake (3.3-13.9°C). Baggerman (1957, cited by Wootton, 1976) found that increased temperatures (about 20°C), given a sufficiently long daylength, accelerate the maturation process.

2. Water Depth

Male threespine sticklebacks build their nests in streams or in shallow areas of lake shores. Hagen (1967) found that the average depth of nests in Little Campbell River, B.C., was 24 cm; some nests were built in water as shallow as 4 cm.

3. Substrate

The nests are constructed of small twigs, plant material, and sand. Some nests may be constructed mostly of sand grains (Greenbank and Nelson, 1959; McPhail and Lindsey, 1970).

Nests in the River Wear, England, were built on a "muddy" bottom (Wootton, 1976). The same substrate was used by the leiurus form in Little Campbell River, B.C. (Hagen, 1967). Hagen gave male sticklebacks a choice between "sand" and "mud" substrates in the laboratory and found that they demonstrated a strong preference to build their nests on the mud. The leiurus form in Mayer Lake, B.C. also occurred on a soft mud bottom (Moodie, 1972). Scott and Crossman (1973) state that threespines prefer sandy areas for nest building (form not mentioned).

4. Aquatic Vegetation

Stickleback nests are usually found in or near aquatic vegetation.

Hagen (1967) observed stickleback (leiurus) nests in the Little Campbell River, B. C. near dense stands of aquatic vegetation such as Oenanthe, Potamogeton, Nuphar, Carex, Myosotis, Glyceria, Typha, Lemna, and green algae. The fish always nested among broadleaved vegetation.

In the laboratory, Hagen (1967) presented males of the leiurus form with a choice between Oenanthe (a plant found in the headwaters) and Elodea (a lower river plant) and found a strong preference for the former. In a survey of streams on Vancouver Island, during breeding season, Hagen found leiurus plentiful only in areas with dense aquatic

vegetation. The leiurus form in Mayer Lake, B. C., occurs only among the thick vegetation of inlet stream margins and stream mouths and apparently does not occur in open water (Moodie, 1972). The littoral zone of Mayer Lake is densely covered with Sphagnum and emergent grasses.

Narver (1966) reported that spawning sticklebacks in the Chignik Lakes were most abundant where aquatic vegetation was plentiful. However, Karluk and Bare lakes on Kodiak Island, which have good populations of sticklebacks, have only sparse aquatic vegetation (Greenbank and Nelson, 1959).

5. Light

Gonad maturation of threespine sticklebacks in the spring is dependent on both an adequate light intensity and on an adequate daylength (Baggerman, 1957, cited by McInerney and Evans, 1970). Baggerman found that high temperature (20°C) by itself is not effective in inducing sexual maturation, long photoperiods are also required. Baggerman also showed that sticklebacks exposed to 269-323 lux (25-30 ft-candles) matured slightly more rapidly than those exposed to 161 lux (15 ft-candles). McInerney and Evans (1970) reported that sticklebacks (presumably the trachurus form) exposed to an energy level of 370 ergs/cm²-sec in the laboratory had maturation rates comparable to those of wild fish. This energy level is equivalent to illuminance levels ranging from 230 lux (at the green wavelength) to 5 lux (at the purple wavelength). McInerney and Evans also tested the effect of light quality (wavelength) by exposing fish to four segments of the visible spectrum ranging from 388-653 millimicrons (long ultraviolet to short red). They found no major differences among the four in affecting the rate of gonad maturation.

6. Size of Territory

Wootton (1976) states that the maximum density of threespine stickleback nests is $4-5/m^2$ and that the minimum distance between nests is 30-50 cm. The average distance between nests in the River Wear, England, ranged from 143-237 cm (Wootton, 1976).

B. Incubation of Embryos

1. Temperature

The time to hatching is directly dependent on temperature. Wootton (1976) plotted the data of several investigators and found that the time to hatching varies from about 5 days at 25°C to about 15-43 days at 8°C. At 18-19°C, hatching occurs in about 8 days and the yolk sac is absorbed in another 4 days. Studies in Alaska have reported hatching times of 14 days at a water temperature ranging from 9-16°C (Kodiak Island; Greenbank and Nelson, 1959) and 5 days at a water temperature varying from 21.1-22.8°C (Kenai Peninsula; Engel, 1971). Neither of these studies was in situ.

Heuts (1947), in laboratory studies in Belgium, found that the best survival of eggs incubated in freshwater occurred at water temperatures of 16-26°C. Heuts showed that the eggs are adapted to a narrow range of temperatures. Lindsey (1962) reared the freshwater form in the laboratory at temperatures ranging from 10-28°C. No eggs were successfully reared in freshwater at 10°, 12°, 14°, or 28°C, and survival at 16° and 18°C was less than optimum. However, there may have been factors present other than temperature which lowered the survival rate. Lindsey also found that fish reared at higher temperatures (22°C and greater) had a higher proportion of females than fish reared

at 20°C and below. Lindsey further showed that eggs from females with few lateral plates have a higher optimum development temperature than eggs from females with more plates. The approximate optima were: 26°C (2 maternal plates), 20-27°C (4 or 5 maternal plates), 20- 22°C (6 maternal plates), and 16°C (7 maternal plates).

Wootton (1976), citing the work of Swarup (1958, 1959), stated that abnormal development occurs when newly fertilized eggs are exposed to very low (0°C) or very high (33°C) temperatures for a duration as short as 1.5-3.0 hours. One of the abnormalities was the production of fish with a triploid number of chromosomes. These fish developed and grew at the same rate as normal (diploid) fish, but were misshapen.

Hagen (1967) measured water temperatures ranging from 16 to 23°C during the nesting of sticklebacks in Little Campbell River, B.C. Some approximate surface water temperatures for various lakes in Alaska measured at the approximate time incubation occurs are: Bare Lake, 6? - 23°C, and Karluk Lake, 4? - 15°C (Greenbank and Nelson, 1959); Lower Jean Lake, 13 - 18°C (Cannon, 1981); Johnson and Scout Lakes on the western Kenai Peninsula, 12 - 18°C, and Bear Lake in the Kenai Mountains, 7 - 15°C (Engel, 1971); Wood River Lakes, 10 - 14°C (Rogers, 1968); Lake Nerka, 9 - 18°C (Burgner, 1958); Black Lake, 12 - 15°C, and Chignik Lake, 9 - 13°C (Parr, 1972).

2. Dissolved Oxygen

Given the fact that sticklebacks nest in shallow areas with adequate light penetration and aquatic vegetation, dissolved oxygen levels in the water near the nests are probably rarely a limiting factor. However, the eggs are placed inside covered nests, often on muddy bottoms containing much dead organic matter, and often in areas of little or no current, so circulation of water through the nest to replace the oxygen used by the embryos is necessary and is accomplished by the fanning of the male. In the absence of fanning, van Iersel (1953, cited by Wootton, 1976) noted that eggs became moldy and died. The rate of fanning reaches a peak shortly before hatching; presumably, this is when the oxygen requirement of the embryos is highest. When van Iersel ran water low in dissolved oxygen and high in carbon dioxide through a nest in the laboratory, the amount of fanning by the male increased.

C. Juvenile Rearing

After leaving their nests, young sticklebacks form schools, which may be an adaptation for cover, and eventually join the adults. There is little information to suggest that young of the year have habitat tolerances, preferences, or requirements different from those of adults.

D. Adult Life

1. Temperature

The adult threespine stickleback is usually regarded as a eurythermal fish (Wootton, 1976). Jordan and Garside (1972) studied the upper lethal temperature of threespine sticklebacks (probably the trachurus form) from the harbor

of Halifax, Nova Scotia (where the salinity ranges from 20-30 ppt) which had been acclimated to various combinations of temperature and salinity. The highest upper lethal temperature (28.8°C) was noted for fish acclimated to 20°C and 30 ppt salinity, tested at 12 ppt, and the lowest upper lethal temperature (21.6°C) was shown by fish acclimated to 10°C and a salinity of 0 ppt, tested at 30 ppt. Fish which had been acclimated to freshwater at 20°C, and tested in freshwater, had an upper lethal temperature of 27.2°C. There were no significant differences in survival among the different sized fish (total lengths ranged from 30-80 mm) tested. Coad and Power (1973), citing Bertin (1955) state that the threespine can tolerate temperatures around 25°C and is also tolerant of temperature changes. Heuts (1947) found with the leiurus form collected at 0°C and placed into water at 25 - 28°C that fish with fewer lateral plates survived longer than fish with more lateral plates. Mean survival time was around 40 hours. Heuts also stated that the freshwater form will not tolerate 'low' temperatures.

The threespine stickleback is found in Alaskan lakes with late spring to early fall temperature ranges of anywhere from 0° to 23°C (Burgner, 1958; Cannon, 1981; Engel, 1971; Greenbank and Nelson, 1959; Parr, 1972; Rogers, 1968 and 1972). The stickleback may not be found at the extremes of this range if they have a choice of more moderate temperatures. Little information is available on temperature preferences or on temperature distribution during late fall, winter, and early spring. In the summer, sticklebacks move into warmer, shallower, water but this is probably more a function of reproductive and feeding requirements than a demonstration of temperature preferences.

Temperature influences the rate of growth. Wootton (1976), citing the work of Cole, reported that the mean growth efficiency increases from 5.9% at 7.0°C to 11.3% at 20.0°C. Beukema (1968, cited by Wootton, 1976) found that the feeding rate also depends on temperature, the rate of stomach evacuation ranging from about 16 hours at 11-12°C to "one night" at 18-20°C.

2. Water Depth

The depth distribution of threespine sticklebacks in lakes results from temperature preferences, feeding migrations, reproduction requirements, predation and competition. They are generally a shallow water fish, particularly in the summer when they move into the shoals along the shore. During the summer they range from the surface to the bottom in lower Jean Lake (21.3m) (Cannon, 1981) and Johnson (4.0 m), Scout (6.1 m), and Bear (18.3 m) lakes (Engel, 1971) on the Kenai Peninsula. In Karluk Lake on Kodiak Island, they have been caught from the surface down to 24.4 m, but none were caught in attempts at 38.4 m or at 61.0 m (Greenbank and Nelson, 1959). Very few fish were caught below surface waters in Lake Nerka during the summer; the deepest stickleback was caught at 7.3 m (Burgner, 1958).

3. Current Velocity

Although threespine sticklebacks commonly occur in streams, they prefer areas with little or no current (Hagen, 1967). Hagen conducted a thorough study in Little Campbell River, B.C., and determined that swift waters are an unfavorable habitat. The average current velocity in a section of the stream where the leiurus form was plentiful was 3 cm/sec (gradient about 1.5 m/km). A section with an average velocity of 23 cm/sec had only a few sticklebacks of the

leiurus form and a riffle section with an average velocity of 74 cm/sec had none. When Hagen transplanted the fish from the low current area into an area of fast current, they migrated into areas of slower current. When Hagen gave males a choice between standing water and moving water in an aquarium, they demonstrated a strong preference for nesting in the standing water. Hagen also reported that some fish successfully passed through a 70 m long culvert with a current velocity of 92 cm/sec, although this was not a common occurrence.

4. Dissolved Oxygen

Krokhin (1957) calculated that the oxygen consumption of threespine sticklebacks in Kamchatka lakes where the temperature ranges from 2.0 to 14.3°C would range from 0.127 - 0.365 mg O₂/hr-g live weight. He found that fish in the laboratory at a temperature range of 0.5 - 19.5°C used oxygen at a rate ranging from 0.12 - 0.55 mg O₂/hr-g live weight. Threespine sticklebacks from some English streams had an oxygen consumption rate ranging from 1.0 microliters O₂/hr-mg dry weight (1 microliter = 1.43 micrograms) for 500 mg dry weight fish to about 2.5 microliters/hr-mg dry weight for 70 mg dry weight fish (temperature not given; Lewis et al., 1972).

Jones (1948 and 1952, cited by Wootton, 1976) stated that the minimum dissolved oxygen (DO) level at which threespine sticklebacks can exist is about 0.25 - 0.50 mg/l. Jones found that the avoidance response of sticklebacks is triggered when the fish are exposed to water with a DO level of 0.3 mg/l at low temperatures. At 20°C, the response occurs at 2.0 mg/l, indicating the fish have a lower tolerance for low DO conditions at higher temperatures. In a survey of some English streams, Lewis et al. (1972) found

that threespine sticklebacks were most abundant in waters with 8 - 12 mg O₂/l, less abundant in waters with 6 - 8 mg O₂/l, and absent from waters with 2 - 5 mg O₂/l.

In Lower Jean Lake, sticklebacks were caught near the lake bottom during the summer where DO levels ranged from 3.0 - 6.5 mg/l (Cannon, 1981). These levels apparently had no effect on feeding activity. Dissolved oxygen levels above the thermocline ranged from 10.1 - 14.0 mg/l. Greenbank and Nelson (1959) reported that the stickleback population in Karluk and Bare Lakes are in waters where there is an "abundance" of dissolved oxygen at all depths during the summer. They also stated that the threespine stickleback "is known to survive over winter in shallow lakes in northern temperate and subarctic zones, where.... dissolved oxygen sinks to a trace....".

5. Chemical Parameters

Threespine sticklebacks have been reported to occur in waters with a pH range of: 7.0 - 8.7 in Karluk and Bare Lakes (Greenbank and Nelson, 1959); 6.3 - 7.0 in three Kenai Peninsula lakes (Engel, 1971); and 6.8 in Little Campbell River, B.C. (Hagen, 1967). Jones (1948, cited by Wootton, 1976) tested the tolerance of the fish to a wide pH range and reported that they avoided a pH of less than 5.6 or greater than 11.4.

A survey of some English streams conducted by Lewis et al. (1972) showed that the threespine did not occur in waters which smelled of hydrogen sulfide and rotting vegetation.

6. Feeding

Krokhin (1957) calculated that threespine sticklebacks in some Kamchatka lakes, where the annual temperature range is $2.0 - 14.3^{\circ}\text{C}$, consume daily between 0.08 g/fish in winter and 0.23 g/fish in August. This represents 1.8 - 5.1% of body weight. The monthly food consumption ranged from 2.70 - 6.77 g/fish, for an annual total of 42.49 g, which is equivalent to 8 or 9 times the average weight of an adult (4.5 g). In Lake Dal'neye, Krokhin (1970) calculated that the monthly food consumption ranged from 0.80^2 g/g live weight in January to 2.185 g/g live weight in August.

Manzer (1976) reported that the daily ration of threespine stickleback in Great Central Lake on Vancouver Island, B.C., was 6.6% of the body weight in July and 7.8% in October. Wootton (1976) states that, to support a population of threespine sticklebacks, an area must produce suitable food --- on the order of $10 - 100 \text{ g/m}^2\text{-yr}$.

III. CONCEPTUAL SUITABILITY INDEX CURVES

Conceptual suitability index curves are presented for water temperature, current velocity, water depth, dissolved oxygen concentration, and pH in Figures 2 through 4. Data to support the curves is included in Tables I, II, and III. These curves should not be construed as a graphical presentation of actual data. Rather, they are intended to be hypothetical models of the relationship between threespine sticklebacks and certain environmental parameters. As with any hypothesis, they must be tested and verified before being applied to any particular situation.

The curves are based on published and unpublished data and on conversations with fishery biologists who have worked with threespine sticklebacks. Both experimental laboratory data and field measurements and observations were used. The suitability index for each environmental parameter ranges from zero to one. An index of one indicates an optimum or preferred level of that particular parameter and an index of zero indicates a completely unsuitable level.

Data from laboratory physiological studies in European populations of threespine sticklebacks indicates that the optimum temperature during incubation of embryos is 8 or 9°C higher than the average surface water temperature during the presumed incubation period in several Alaskan lakes (Figure 2). Until the temperature tolerance of Alaskan sticklebacks has been studied in physiological laboratory studies, it must be assumed that the optimum temperature for European sticklebacks (about 22°C) does not apply in Alaskan waters which rarely reach 22°C. A problem encountered in constructing the curves is that much of the data in the literature concerning environmental parameters of threespine stickleback habitat does not relate various levels of the parameters to some measure of habitat suitability. Often, ranges of the parameter are given based on measurements taken throughout the area occupied by threespines but there is no indication that one point

on the range is any better or worse than any other point in terms of habitat suitability.

The curves are drawn using data from throughout the natural range of the threespine stickleback. Although there probably are differences in habitat preferences and tolerances for different geographical areas or even in different streams of the same geographical area, there is not enough data to support drawing separate curves at this time. However, one must be aware that any point on the curve, especially toward either extreme, may be unsuitable for a particular stock. How far the stock deviates from the curve must be determined by field measurements and experimentation with that particular stock.

A second precaution regarding the curves concerns the interaction of various parameters. A given level of one parameter can have a different effect on the fish as the level of another parameter varies. For example, a dissolved oxygen concentration of 3 mg/l may be suitable at a water temperature of 5°C, but unsuitable at a temperature of 20°C. Ideally, given enough data, a separate dissolved oxygen curve should be drawn for each of several different temperatures. The overall suitability of any particular habitat is a summation of the interacting effects of many parameters.

A third precaution to consider is that the effect of less than optimum levels of any parameter on the fish depends strongly on the duration of exposure. Stickleback embryos exposed to a water temperature of 33°C for 1.5 - 3.0 hours experience an abnormal development (Swarup, 1958 and 1959, cited by Wotton, 1976), but survive. Embryos exposed to 33°C for a longer period of time would die.

Also, different ages within a life stage probably have different habitat requirements. For example, the oxygen requirement of embryos is highest just prior to hatching. However, because of insufficient data, it is not possible to draw separate curves for different ages.

Overall, the suitability index curves presented in this report provide an indication of conditions which make a desirable threespine habitat and conditions which make a less desirable habitat. Also, although the curves are general, they can show differences in habitat needs among threespines and other species. Further, the process of constructing these curves is beneficial in defining areas where more data is needed. Lastly, these curves can aid in the design of experiments and sampling programs. As more data becomes available, these hypothetical curves can be further refined.

Table I.

THREESPINE STICKLEBACK

Adult - Spawning

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	ca. 12 - 18	surface water temperature during breeding season	Lower Jean Lake	Cannon (1981)
	5.6 - 22.8 3.3 - 13.9	surface water temperatures during June and July	Bare Lake Karluk Lake	Greenbank and Nelson (1959)
	16	average during breeding season	Little Campbell River, B.C.	Hagen (1967)
	16 - 19	during spawning season	Hobson's Brook, England	Lindsey (1962)
Water depth, cm	4	shallowest nest	Little Campbell River, B.C.	Hagen (1967)
	24	average depth for nests		

Table II.

THREESPINE STICKLEBACK

Incubation of Embryos

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	16 - 26	best survival rate	Belgium (laboratory)	Heuts (1947)
	10 - 14	no eggs successfully reared	England (laboratory)	Lindsey (1962)
	16 - 18	survival less than optimum		
	20 - 26	best survival		
	28	no eggs successfully reared		
	> 22	lower male:female ratio than fish reared at $\leq 20^{\circ}\text{C}$		
	16 - 26	optimum development temperatures; the fish with fewer maternal plates having higher optimum temperatures		
	0, 33	exposure to these temperatures for 1.5 - 3.0 hours causes abnormal development	England ? (laboratory)	Swarur (1958 and 1959, cited by Wootton, 1976)
	8	time to hatching is 15 - 43 days	various	Wootton (1976)
	5	time to hatching is 5 days		
	25	time to hatching is 5 days		
	13 - 18	approximate surface water temp. during incubation period	Lower Jean Lake	Cannon (1981)
	12 - 18	approximate surface water temp. during incubation period	Johnson Lake	Engel (1971)

Table II. Cont'd THREESPINE STICKLEBACK

Incubation of Embryos

Parameter	Observed Values	Remarks	Location	Reference
Temperature °C	12 - 13	approximate surface water temp. during incubation period	Scout Lake	
	7 - 15	approximate surface water temp. during incubation period	Bear Lake	
	6? - 23	approximate surface water temp. during incubation period	Bare Lake	Greenbank and Nelson (1959)
	4? - 15	approximate surface water temp. during incubation period	Karluk Lake	
	10 - 14	approximate surface water temp. during incubation period	Wood River lakes	Rogers (1968)
	9 - 18	approximate surface water temp. during incubation period	Lake Nerka	Burgner (1958)
	12 - 15	approximate surface water temp. during incubation period	Black Lake	Parr (1972)
	9 - 13	approximate surface water temp. during incubation period	Chignik Lake	

Table III.

THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	27.2	Upper lethal temperature for the <u>trachurus</u> (?) form acclimated to 20°C in freshwater	Halifax, Nova Scotia (laboratory)	Jordan and Garside (1972)
	25	tolerable	general	Bertin (1925, cited by Coad and Power, 1973)
	25 - 28	The <u>leiurus</u> form collected at 0° and placed into water with these temperatures died after an average of 40 hours; fish with fewer lateral plates survived longer than fish with more plates	Belgium (laboratory)	Heuts (1947)
	7.0	mean growth efficiency of 5.9%	?	Cole (unpublished, cited by Wootton, 1976)
	20.0	mean growth efficiency of 11.3%		
	11 - 12	rate of stomach evacuation was 16 hours	?	Beukema (1968, cited by Wootton, 1976)
	18 - 20	rate of stomach evacuation was "one night"		

Table III. Cont'd

THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	6.9 - 17.7	early June-mid-July; observed water temp. fish present	Lower Jean Lake	Cannon (1981)
	3.9 - 15.0	Jun 1 - Sep.15; observed water temp. fish present	Johnson and Scout lakes	Engel (1971)
	8.9 - 18.3	Jun 1 - Sep.15; observed water temp. fish present	Bear Lake	
	4.4 - 22.8	mid May - mid Sept.; observed water temp. fish present	Bare Lake	Greenbank and Nelson (1959)
	3.3 - 15.0	mid May - mid Sep.; observed water temp. fish present	Karluk Lake	
	6.7 - 14.2	Aug., observed water temp. fish present	Wood River lakes	Rogers (1968)
	0.0 - 20.0	Jun - Sep; 6 yrs; observed water temp. fish present	Lake Nerka	Burgner (1958)
	11.5 - 15.0	early Jul - early Sep.; observed water temp fish present	Black Lake	Parr (1972)
	9.0 - 13.0	late Jun - early Sep.; observed water temp fish present	Chignik Lake	

Table III. Cont'd

THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Water Depth, m	0 - 21.3 (bottom)	summer	Lower Jean Lake	Cannon (1981)
	0 - 4.0 (bottom)	summer	Johnson Lake	Engel (1971)
	0 - 6.1 (bottom)	summer	Scout Lake	
	0 - 18.3 (bottom)	summer	Bear Lake	
	0 - 24.4	summer	Karluk Lake	Greenbank and Nelson (1959)
	38.4, 61.0	none caught; summer		
	7.3	greatest depth at which fish were caught; summer	Lake Nerka	Burgner (1958)
	0 - 10	Jun - Sept.	Kamchatka Lakes, USSR	Krokhin (1957)
	50 - 60	Dec., Jan., Feb.		
Current Velocity, cm/sec (stream population)	3	average in <u>leiurus</u> habitat	Little Campbell River, B.C.	Hagen (1967)
	23	marginal habitat		
	74	poor habitat		
	92	fish were able to negotiate a 70 m culvert with this velocity		

Adults

Parameter	Observed Values	Remarks	Location	Reference
Dissolved Oxygen mg/l	0.25 - 0.50	minimum level tolerable	Great Britain	Jones (1948 and
	0.3	level at which avoidance response is triggered at low temps.	(laboratory)	1952, cited by Wootton, 1976)
	2.0	level at which avoidance response is triggered at 20°C		
	8 - 12	fish most abundant in reaches with this level	England	Lewis et al., (1972)
	6 - 8	fish less abundant in reaches with this level		
	2 - 5	fish absent from reaches with this level		
	3.0 - 6.5	healthy fish caught near lake bottom at this level; summer	Lower Jean Lake	Cannon (1981)
pH	10.1 - 14.0	level above thermocline, summer		
	< 5.6 or > 11.4	avoided by fish	Great Britain (laboratory)	Jones (1948, cited by Wootton, 1976)
	6.8	measured value	Little Campbell River, B.C.	Hagen (1967)
	6.3 - 7.0	measured value	Kenai Peninsula lakes	Engel (1971)
	7.0 - 8.7	measured value	Karluk and Bare lakes	Greenbank and Nelson (1959)

THREESPINE
STICKLEBACK

INCUBATION

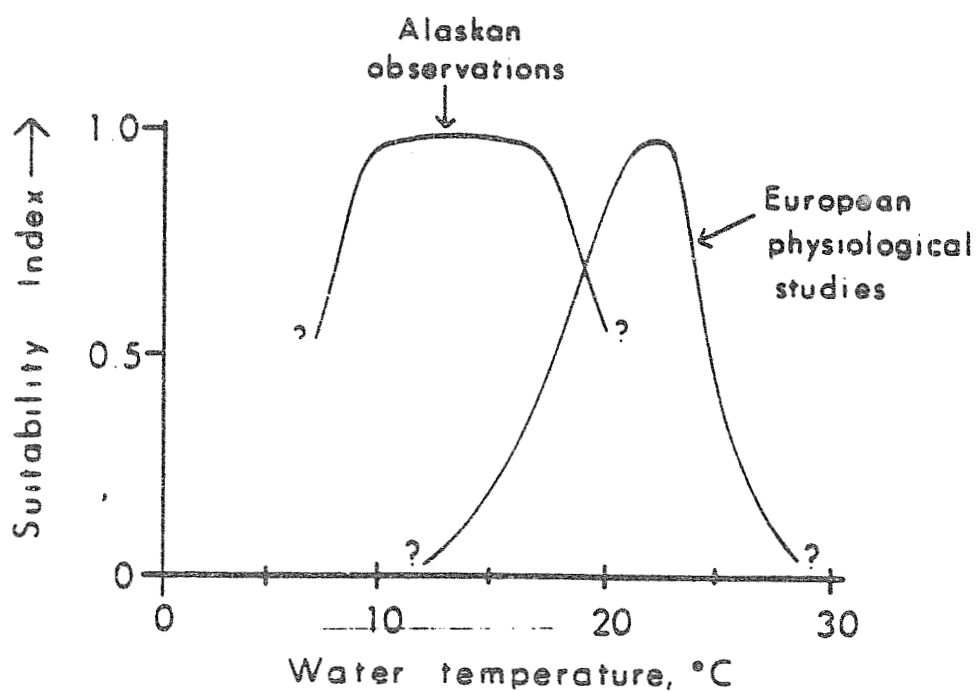


Figure 2. Conceptual model of relationship between Threespine stickleback embryos and temperature.

See text for qualifications for use of this curve
(NOT RECOMMENDED FOR APPLICATION TO SPECIFIC WATERSHEDS
WITHOUT FIELD VERIFICATION)

THREESPIKE
STICKLEBACK

ADULTS

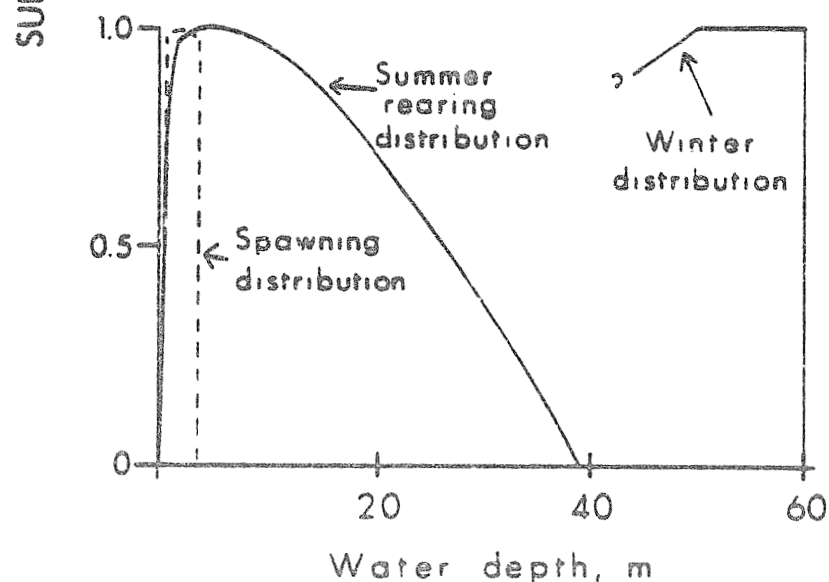
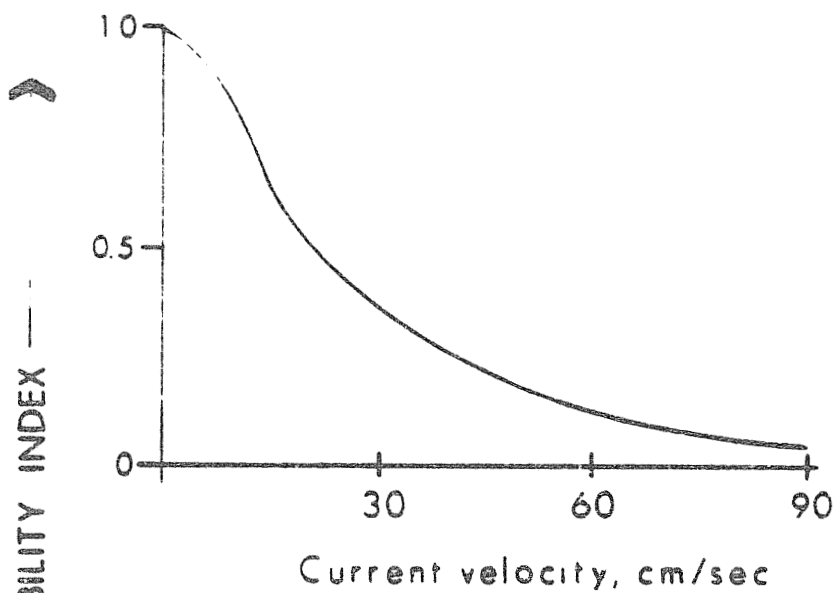
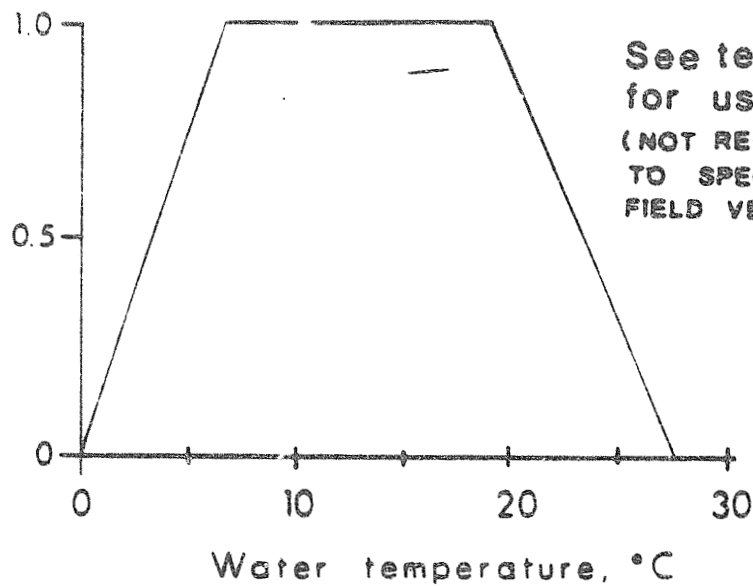


Figure 3. Conceptual model of relationship between Threespine stickleback adults and water temperature, current velocity (stream populations only), and water depth

THREESPINE
STICKLEBACK

See text for qualifications
for use of these curves
(NOT RECOMMENDED FOR APPLICATION
TO SPECIFIC WATERSHEDS WITHOUT
FIELD VERIFICATION)

ADULTS

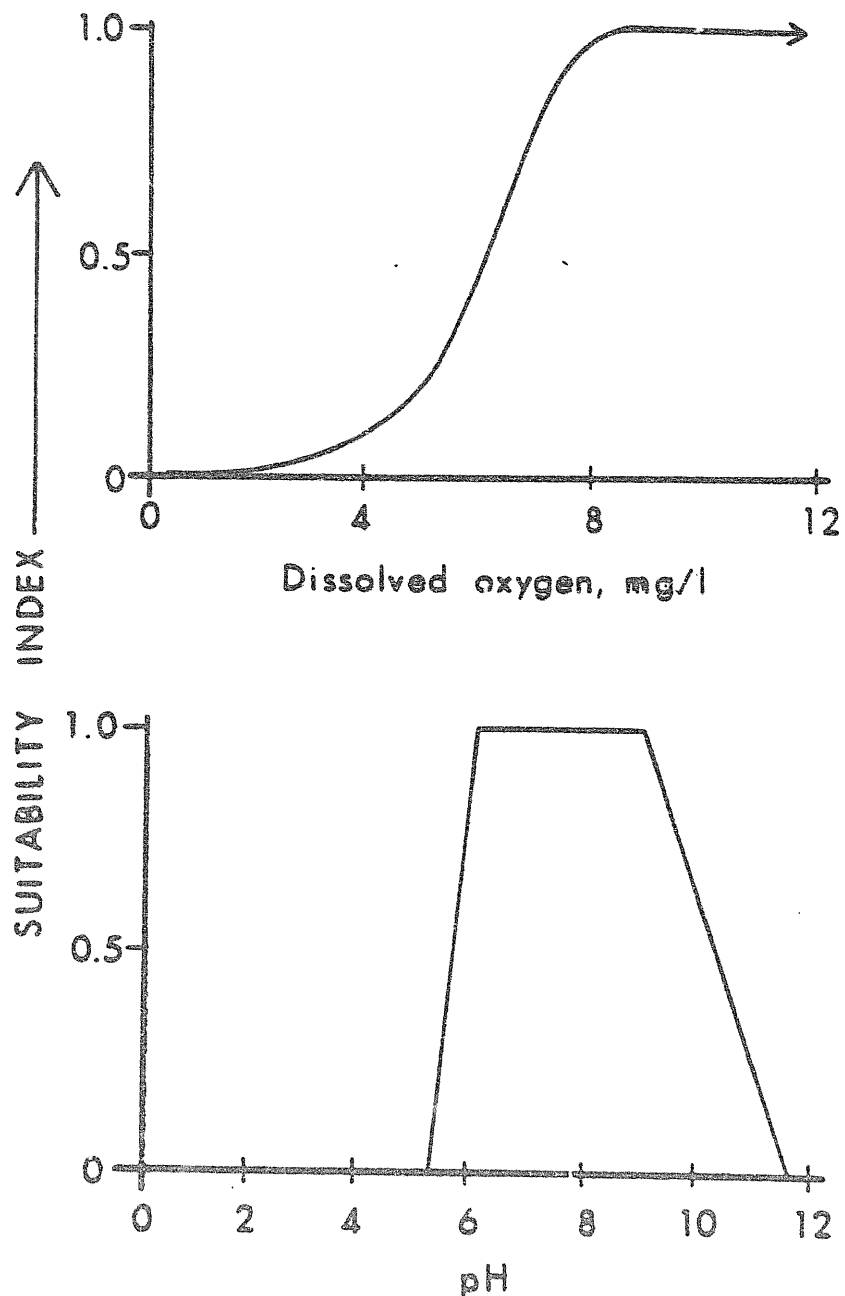


Figure 4. Conceptual model of relationship between Threespine stickleback adults and dissolved oxygen concentration and pH.

IV. DEFICIENCIES IN DATA BASE AND RECOMMENDATIONS

Although extensively used in behavioral and pollution studies elsewhere, the interest in the threespine stickleback in Alaska has centered mainly on its supposed role as a competitor with rearing sockeye salmon and rainbow trout. These Alaskan studies, therefore, have naturally concentrated on the distribution and feeding of sticklebacks.

Physiological studies on Alaskan populations are needed to define the tolerances to environmental parameters such as temperature and dissolved oxygen concentration. This need is dramatically shown by the difference between European physiological studies of temperature tolerance and the known temperature regime existing in Alaskan lakes where the sticklebacks are present (Fig. 2).

Information is needed on stream populations of threespine sticklebacks within the State. To date, Statewide investigations have concentrated on lake populations.

More data from Southeast Alaska is needed to describe regional differences within the State. The Southeast populations may be more similar to the populations described in British Columbia than they are to the Bristol Bay populations. Additionally, there is some indication that sticklebacks in the Kenai Peninsula area are exposed to and adapted to higher temperature regimes than sticklebacks in the Bristol Bay area.

A study in Alaska of differences in habitat requirements among the three forms of Gasterosteus aculeatus (leiurus, trachurus, and semiarmatus) would be beneficial as strong differences have been demonstrated elsewhere; for example, Hagen's (1967) work in British Columbia. Virtually nothing is known of the populations on the Seward Peninsula and Saint Lawrence Island (presumably trachurus). Because these populations are on the edge of the species range, studies of

these fish may provide interesting information about the environmental limits of the species.

Very little information is available on the habitat needs of the threespine stickleback during the stage immediately after hatching but prior to leaving the nests. During this period, they are still under the parental care of the male. There are also many questions about their life history between leaving the nest until they first begin to show up in minnow traps and fyke nets as young of the year. In Alaska, few observations have ever been made of actual nests.

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