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LITERATURE REVIEWS OF THE LIFE HISTORY, HABITAT REQUIREMENTS AND MITIGATION/COMPENSATION STRATEGIES FOR THIRTEEN SPORT FISH SPECIES IN THE PEACE, LIARD AND COLUMBIA RIVER DRAINAGES OF BRITISH COLUMBIA

by

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Under the *Fisheries Act* the Canadian Department of Fisheries and Oceans has the responsibility of conducting screening of proposed developments that may affect fish and fish habitat. This responsibility now extends to evaluating potential impacts of development proposals in watersheds which have historically been managed by the British Columbia provincial government, including the Peace, Liard, and Columbia drainages. This report collates and reviews life history and habitat use information for thirteen species of sport fish in the drainages; kokanee (*Oncorhynchus nerka*), rainbow trout (*O. mykiss*), westslope cutthroat trout (*O. clarki lewisi*), brook trout (*Salvelinus fontinalis*), bull trout (*S. confluentus*), lake trout (*S. namaycush*), Arctic grayling (*Thymallus arcticus*), walleye (*Stizostedion vitreum*), mountain whitefish (*Prosopium williamsoni*), lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota*), northern pike (*Esox lucius*), and white sturgeon (*Acipenser transmontanus*).

RÉSUMÉ

Ford, B.S., P.S. Higgins, A.F. Lewis, K.L. Cooper, T.A. Watson, C.M. Gee, G.L. Ennis et R.L. Sweeting. 1995. Literature reviews of the life history, habitat requirements and mitigation/compensation strategies for thirteen sport fish species in the Peace, Liard and Columbia River drainages of British Columbia. Can. Manuscr. Rep. Fish. Aquat. Sci. 2321: xxiv+342 p.

Conformément à la *Loi sur les pêches*, le ministére canadien des Pêches et des Océans est tenu d'évaluer les aménagement proposés qui pourraient avoir un impact sur le poisson et son habitat. Cette responsabilité s'étand maintenant a l'évaluation de l'impact possible des propositions d'aménagement qui touchent les bassins hydrographiques qui, jusqu'à présent, avaient été gérés par le gouvernement provincial de la Colombie-Britannique, (notamment les bassins des rivières Peace et Liard et du fleuve Colombia). Ce rapport est une synthèse des renseignements concernant le cycle biologique et l'habitat de treize espèces de poissons pêches sportivement dans ces bassins hydrographiques: saumon kokanee (*Oncorhynchus nerka*), truite arc-en-ciel (*O. mykiss*), truite fardée de Yellowstone (*O. clarki lewisi*), omble de fontaine (*Salvelinus fontinalis*), omble à tête plate (*S. confluentus*), touladi (*S. namaycush*), ombre arctique (*Thymallus arcticus*), doré (*Stizostedion vitreum*), ménomini de montagnes (*Prosopium williamsoni*), grand corégone (*Coregonus clupeaformis*), lotte de rivière (*Lota lota*), grand brochet (*Esox lucius*), et esturgeon blanc (*Acipenser transmontanus*).

EXECUTIVE SUMMARY

In 1990, the Department of Fisheries and Oceans (DFO) established the Eastern British Columbia Unit of the Habitat Management Division. The Unit (now the Eastern B.C. Habitat Unit of the Habitat and Enhancement Branch) was formed in response to the need for reviewing and screening proposed projects in the Peace, Liard, and Columbia river drainages as part of the federal responsibilities under the *Fisheries Act* and what was then the Environmental Assessment Review Process (EARP) and is now the *Canadian Environmental Assessment Act* (*CEAA*). Historically, fisheries resources of these drainages were managed solely by the British Columbia provincial government.

The Peace, Liard, and Columbia drainages support a valuable salmonid and non-salmonid sport fishing industry. Furthermore, the drainages provide considerable opportunities for industrial development, in particular hydroelectric, coal and base metal mining, pulp and paper projects, oil and gas development and forestry. Given these circumstances, concern was expressed that applications for proposed developments could proceed more rapidly than could effective environmental review as was specified under EARP (now *CEAA*). A principal factor limiting effective review was felt to be the paucity of current and relevant information on fish life histories, their responses to habitat disruption, and the methodologies for and effectiveness of mitigation and compensation measures used to offset development impacts. Hence, literature reviews addressing these issues were essential.

A total of thirteen sport fish species were initially identified as being of sufficient importance that literature reviews of their life history and habitat requirements should be conducted. The reviews were also to include a treatment of mitigation/compensation efforts conducted for offsetting the adverse impacts of development on fish and fish habitat.

The following species were reviewed:

Kokanee	*Oncorhynchus nerka*
Rainbow trout	*Oncorhynchus mykiss*
Westslope cutthroat trout	*Oncorhynchus clarki lewisi*
Brook trout	*Salvelinus fontinalis*
Bull trout	*Salvelinus confluentus*
Lake trout	*Salvelinus namaycush*
Arctic grayling	*Thymallus arcticus*
Walleye	*Stizostedion vitreum*
Mountain whitefish	*Prosopium williamsoni*
Lake whitefish	*Coregonus clupeaformis*
Burbot	*Lota lota*
Northern pike	*Esox lucius*
White sturgeon	*Acipenser transmontanus*

This document is intended to provide habitat and fisheries managers and other stakeholders a bench mark from which proposed projects can be more effectively screened and reviewed under *CEAA*. To be effective, the reviews must adequately present the state of knowledge in the scientific literature as well as a reasonably comprehensive treatment of mitigation and compensation measures employed to offset adverse impacts of development on fish and habitat.

The true utility of these reviews to facilitate effective review and screening of development proposals is dependant on the inclusion of fisheries information directly pertinent to the study drainages. This type of information is often contained in "grey" or unpublished literature (e.g. unpublished reports, office memoranda) which can be difficult to locate.

The methods for gathering information included on-line searches of computerized databases, correspondence and interviews with government agency personnel and fisheries consultants, and reviews of citation lists in publications received for review. The two principal databases searched were AQUAREF (Canadian water resource references) and

ASFA (Aquatic Sciences and Fisheries Abstracts). The resulting extensive list of publications in turn provided additional citations as well as the names of researchers involved in habitat assessment and evaluation of mitigation and compensation projects. Researchers and other personnel with expertise and/or information relevant to specific areas of interest were contacted by telephone or mail or interview personally.

These procedures yielded considerable grey literature and underscored the importance of such information in developing timely, comprehensive and defensible reviews of this nature. However, difficulties occurred in obtaining grey literature, particularly from government personnel. Understaffing, large work loads and responsibility over large geographic areas limit the ability of these staff in providing relevant information. This must be taken into consideration should updates of these reviews be undertaken. Even accepting that some information may be missing, the reviews are considered to be adequately comprehensive for their intended purpose.

As information was gathered it was screened for relevance, analyzed for technical merit and summarized. Particular attention was paid to identifying specific case histories where mitigation and compensation techniques were employed. Studies which included the results of follow-up monitoring were highlighted in order to gauge the effectiveness of such measures.

The challenges facing fisheries and habitat managers in evaluating proposed projects is due in great part to the diversity of habitat requirements and life cycle timing of the fish species present. Many of the rivers, lakes and reservoirs in the drainages support a mix of most of the thirteen species. This, of course, significantly increases the complexity of managing the resource since the benefits of mitigation and compensation for the potential impacts of a proposed project must be balanced among all the species present.

Observed habitat use and spawning characteristics for the thirteen fish species are presented in Table 1 and summarized below.

Table 1. Summary of habitat and spawning parameters for thirteen Species of British Columbia sport fish.

Species	Life Stage	Observed Habitat Use					Spawning			
		Temperature (°C)	Dissolved Oxygen (mg/L)	Velocity (m/s)	Depth (m)	Substrate	Time	Age (years)	Depth (m)	Velocity (m/s)
Kokanee	Eggs	2.0 - 15.0	9.75	high	-	-	-	-	-	-
	Juvenile	6.7 - 24.4	> 7.88	none	variable	gravel/cobble	-	-	-	-
	Adult	6.7 - 24.4	> 7.88	none	variable	none	September - November	2 - 5	> 0.06	0.15 - 0.85
Rainbow Trout	Eggs	2.0 - 20.0	> 5.3	0.02, intergravel	-	-	-	-	-	-
	Juvenile	0.0 - 24.0	> 7.0	0.08 - 0.20	0.3 - 6.0	cobble/rubble	-	-	-	-
	Adult	0.0 - 28.0	> 7.0	0.20 - 0.30	variable	cobble/boulders	March - August	1 - 4	0.15 - 2.5	0.30 - 0.90
Westslope Cutthroat Trout	Eggs	6.0 - 12.0	6.0 - 8.2	0.20 - 0.55	0.17 - 0.20	< 5 % fines, & 2 - 64 mm gravel	-	-	-	-
	Juvenile	0.0 - 22.0	9.0 - 11.0	0.07 - 0.125	< 0.40	gravel/cobble	-	-	-	-
	Adult	0.0 - 22.0	9.0	0.10 - 0.14	0.50 in streams	-	May - August	2 - 6	0.06 - 0.40	0.30 - 0.60
Brook Trout	Eggs	0.0 - 12.0	8.8	> 0.0001, intergravel	-	-	-	-	-	-
	Juvenile	0.0 - 24.0	> 7.0	0.087	0.42	cobble/gravel	-	-	-	-
	Adult	0.0 - 25.0	> 7.0	0.084 - 0.11	< 0.70	cobble/gravel	Late Summer - Late Fall	2 - 3	> 0.09	0.03 - 0.42
Bull Trout	Eggs	0.0 - 8.0	9.5	< scour velocity	-	-	-	-	-	-
	Juvenile	0.0 - 18.0	7.75	0.1 - 0.5	< 0.10	cobble/boulders	-	-	-	-
	Adult	0.0 -12.8	7.75	none	variable	NA	Fall	6	0.15 - 0.84	0.25 - 0.65
Lake Trout	Eggs	0.3 - 10.0	> 6.0	none	-	-	-	-	-	-
	Juvenile	-0.8 - 23.5	9.75	none	variable	cobble/rubble	-	-	-	-
	Adult	0.0 - 23.8	>7.75	none	variable	none	Fall	M = 5-13, F = 6-14	5 - 10	none
Arctic Grayling	Eggs	2.0 - 16.0	NA	< 0.3	0.02 - 0.03	gravel, < 20 % sand	-	-	-	-
	Juvenile	2.0 - 24.5	NA	< 0.5	< 0.50	gravel/cobble/sand	-	-	-	-
	Adult	1.0 - 20.0	NA	0.2 - 0.8	< 10	gravel/rocks/boulders	Mid-May - Mid-June	3 - 9	variable	0.3 - 1.5
Walleye	Eggs	6.0 - 19.0	> 5.0	0.73 - 0.91	-	interstices of gravel	-	-	-	-
	Juvenile	15.0 - 34.0	> 5.0	NA	variable	NA	-	-	-	-
	Adult	0.0 - 29/35	> 3.0	slight currents	variable	gravel/cobble	February - June	2 - 6	several cm - several m	0.73 - 1.5
Mountain Whitefish	Eggs	0.0 - 12.0	> 8.0	< scour velocity	-	-	-	-	-	-
	Juvenile	0.0 - 20.6	> 5.63	slow - moderate	< 3.0	sand/gravel	-	-	-	-
	Adult	0.0 - 20.6	7.75	moderate - fast	< 3.0	gravel/cobble	Late Fall - Early Winter	2 - 4	0.10 - 1.0	0.89 - 1.02
Lake Whitefish	Eggs	0.5 - 12.0	> 8.0	< scour velocity	-	-	-	-	-	-
	Juvenile	0.0 - 26.6	7.75	none	seasonal variation	gravel/cobble/boulders	-	-	-	-
	Adult	8.0 - 14.0	7.75	none	10 - 100+	none	October - November	M = 2-13, F = 3-13	0.1 (rivers) - 30 (lakes)	none
Burbot	Eggs	1.0 - 7.0	6.5	< 0.08	-	interstices of sand/gravel	-	-	-	-
	Juvenile	8.0 - 23.3	> 7.25	NA	Temp. dependent	gravel/rock/cobble	-	-	-	-
	Adult	0.6 - 23.3	> 7.25	< 0.3	Temp. dependent	gravel/rock/cobble	November - May	2 - 8	0.3 -3.0	< 1.22
Northern Pike	Eggs	3.0 - 24.2	> 3.0	none	-	aquatic vegetation	-	-	-	-
	Juvenile	5.8 - 33.0	> 3.0	none	< 2.0	mud/silt with vegetation	-	-	-	-
	Adult	1.0 - 29.4	> 5.63	none	shallow	mud/silt with vegetation	Spring - Early Summer	M = 2-6, F = 3-7	< 0.25	none
White Sturgeon	Eggs	? - 20	NA	1.2 - 2.8	3.0 - 21.3	gravel/cobble/boulders	-	-	-	-
	Juvenile	NA	7.5	NA	10.0 - 11.0	sand/fines	-	-	-	-
	Adult	0.0 - 25.0	NA	0.19	5.0 - 54.0	variable	April - July	M= 11-12, F= 11-13	13.0	0.9 - 1.6

With the exception of walleye and northern pike, the upper limit of the observed temperature range is not greater than 27°C. Pike and walleye are able to tolerate temperatures as high as 33 and 34°C respectively. Generally speaking, the juveniles and adults of all species are found in a wider range and higher temperatures as compared with eggs.

Dissolved oxygen requirements for eggs of the nine salmonid species are greater than those observed for walleye and pike. The range of observed or preferred dissolved oxygen levels for salmonid eggs is from greater than 5.3 mg/L for rainbow trout to 9.75 mg/L for kokanee whereas walleye and pike eggs can be found in water at levels of 5 and 3 mg/L respectively. These lower requirements undoubtedly reflect adaptation to higher water temperatures, which limits the amount of dissolved oxygen. No information was available for Arctic grayling, but since it is a salmonid, the species' requirements are inferred to be similar to those described for other fish in the same family. Although no specific data were reported for white sturgeon, oxygen requirements for eggs are likely to be similar to salmonids since they also prefer cooler waters. The species is, however, more lethargic as compared with salmonids and, consequently, the attendant dissolved oxygen preference may not be as stringent.

Most juveniles and adults of the salmonid species studied prefer oxygen levels of greater than 6 mg/L. Juvenile westslope cutthroat trout prefer oxygen levels between 9 and 11 mg/L, which were the highest of all species and age classes of fish reviewed. Predictably, oxygen requirements for juvenile and adult walleye and pike are lower than salmonids with these fish observed in concentrations as low as 3 mg/L. Of the two species, walleye seem to prefer slightly greater concentrations.

With the exception of lake trout, all adult salmonids prefer some current. This can range from low intergravel velocities of 0.0001 m/s as for brook trout eggs to near scour velocities observed for whitefish and bull trout. As for lake trout, juvenile and adult lake whitefish and kokanee have no velocity preference nor do adult bull trout. The only other species to show no preference for velocity is northern pike.

With the exception of lake trout, lake whitefish and northern pike, velocities for spawning adults are greater than those for juveniles and adults.

Depth and substrate preferences vary widely among the species. Eggs of most salmonids are found in reasonably shallow waters whereas eggs of whitefish, sturgeon and burbot may be found at variable depth. Spawning substrate varies from aquatic vegetation (pike), to interstices within sand (burbot) to gravel and cobble (salmonids). Juveniles of almost all of the thirteen species prefer gravel, cobble and boulder habitats. Juvenile pike, however, prefer a substrate of mud and silt with aquatic vegetation and juvenile sturgeon tend to prefer fine substrate. Adult substrate preferences range from mud, silt and aquatic vegetation (pike) to gravel, cobble and boulders (most other species) to pelagic (kokanee, lake trout and lake whitefish). Substrate for adult white sturgeon is variable, ranging from backwater silty/sandy sloughs to faster flowing cobble streams. Occurrence in one habitat type or another varies and depends on food availability and general type of habitat (riverine or lacustrine).

Timing of spawning varies among species and there is no period in the year where spawning does not occur. April and May appear to be the most critical months; eight of the thirteen species may spawn during this period. April and May are even more significant, from a management point of view, given that these eight species include salmonids, burbot, walleye, pike and sturgeon. October and November are also important; six of the thirteen species may spawn at this time. (Burbot display the widest spawning period which can occur from November until May).

Of the nine salmonid species, there are five that typically spawn in fall and winter (kokanee, bull trout, lake trout, mountain whitefish and lake whitefish) and three that spawn in spring and summer (rainbow trout, westslope cutthroat trout, and Arctic grayling). Brook trout spawn in late summer to early fall.

It is apparent that effective fisheries and habitat resource management and review of proposed development projects will need to take into consideration the diversity and complexity of the life cycles and habitat preferences of the sport fish in the Peace, Liard and Columbia river drainages. This requirement will, of course, complicate the review process but, at the same time, it underscores the need to deal with this diversity and complexity in order for DFO to meet its obligations and responsibilities under *CEAA*.

The underlying philosophy by which DFO conducts reviews of proposed developments is driven by the provisions of the *Fisheries Act*, which was expanded in the Ministerial statement entitled "Policy for the Management of Fish Habitat" (DFO 1986). The policy's overall long term objective is to achieve an overall 'net gain' of the productive capacity of fish habitats. Achieving this objective will require conservation of current productive capacities of habitats, the restoration of habitat, and the improvement and development of new habitat. If a proposed project may potentially affect fish habitats and the fisheries resource they support, the following DFO hierarchy of preferences is to be used as a guide for achieving 'no net less' of productivity:

(1) Maintain without disruption the natural productive capacity of the habitat(s) in question by avoiding any loss or harmful alteration at the site of the proposed development or activity (i.e. alternate siting and/or design mitigation).

(2) If it is impossible or impractical to maintain the same level of productive capacity, consideration will be given to the development of compensatory options. The prime focus is to develop `like for like' options. A secondary option (after more preferred alternatives have been eliminated) is moving off site to develop replacement habitat or increasing capacity of existing habitat.

(3) In rare cases where damage cannot be avoided or the habitat cannot be compensated for, proposals would be considered for artificial production.

The preferred compensatory measure is to replace lost habitat with like habitat at or near the site. Where this is impractical, consideration would be given to providing like for like habitat off-site as well as to increasing the productive capacity of existing habitat at the site or in a nearby area. Artificial production is rarely considered but may be for cases where other habitat replacement options are not possible.

Habitat replacement measures for some species such as salmon and trout are reasonably well developed given the amount of available information on their specific habitat requirements. Depending on species, manuals for constructing spawning and other types of habitat are available. Unfortunately, for many of the species in this review, there are still significant gaps regarding specific habitat requirements. Consequently, there are no manuals as yet developed for these species which would assist fisheries and habitat managers in their reviews of projects. This review will hopefully represent a significant step forward in developing such manuals.

Where adequate information exists regarding habitat requirements, compensation of lost habitat is to be provided in a 1:1 ratio. This may be suitable for species such as kokanee, rainbow trout, cutthroat trout and bull trout but other species, particularly Arctic grayling, whitefish, burbot and sturgeon, lack adequate data to even develop appropriate habitat replacement options. In these cases, DFO may require that habitat be augmented beyond a 1:1 ratio until such time as more specific and relevant data are collected to ensure the effectiveness of the mitigation/compensation measures. There is, therefore, an implicit requirement to design and carry out monitoring programs that will adequately evaluate the effectiveness of such measures. These programs must be diligently followed and continuously evaluated otherwise progress towards the development of effective site and species specific mitigation measures will not occur.

Review of the literature indicated that, although there was widespread use of mitigation/compensation programs, few organizations have initiated studies to quantify their success or failure. This is primarily due to the general absence of appropriate monitoring programs and the lack of follow-up evaluation on those that do exist.

The range of common mitigation/compensation measures can be categorized as follows:

(1) Mitigation Measures

(a) Adjustments in Water Levels and Flow

Widespread use is made of water releases to provide minimum flow requirements downstream of dams which store water for power generation, irrigation, public and industrial water supplies, and flood control. Downstream temperature control and the provision of flushing flows have also been used where capabilities exist.

The ability to regulate reservoir water levels has also proven to be beneficial to fish residing upstream of dams. Depending on the species and time of year, water levels can be adjusted to optimize access to spawning grounds in the reservoir and its tributaries as well as provide adequate depth for incubating eggs, rearing fry, and juveniles. This may be done in conjunction with shoreline revegetation thus optimizing habitat enhancement. Destratification of reservoirs has also been conducted to provide oxygen at depth, which provides additional habitat in previously oxygen-poor environments and hence mitigates against, for example, winter-kill.

(b) Upstream Fish Passage/Downstream Entrainment

Obstructions to fish movements have resulted from development activities such as dam construction and water diversions, improperly engineered or constructed culverts, and the (inadvertent) creation of velocity barriers. Entrainment of fish in hydroelectric turbines and other water intake/release structures has also had adverse effects.

Mitigating obstructions to fish passage has been accomplished by construction of fish passage structures, proper installation of culverts, and maintaining flows which do not create velocity barriers. Entrainment can be mitigated by construction of fish screens and bypasses. These techniques have proven to be very successful, particularly for some salmon and trout species. They may be applicable to non-salmonid species but there is little literature regarding this subject.

(c) Maintenance of Water Quality

Water quality may be compromised as a result of in-stream or near-stream construction activities, reservoir formation, gas supersaturation, and contaminant discharges. The principal impact on fish and habitat during construction is typically increased suspended sediment. This is mitigated through the use of settling basins, ditching and re-channelling to avoid discharge, and placement of instream silt traps and filters. Impacts can be further mitigated by minimizing upslope clearing, implementing bank erosion control measures such as revegetation and hydro seeding and by employing erosion control measures such as cross drains, ditch plugs and water bars.

Water treatment measures have been employed to remove contaminants prior to discharge. Some discharges may not include contaminants but may require adjustments in pH prior to release.

(2) Habitat Compensation Measures

Among the measures which can be undertaken to compensate, replace or improve habitat are: Streambank and shoreline stabilization such as rip rap, gabions, or revegetation; placement of current deflectors and shelters; streamside plantings to improve shading, cover and food supply; stream complexing using large organic debris (LOD), boulder placement, log structures and gabions; obstruction removal and access improvement; gravel cleaning, placement and construction of spawning platforms; mainstem spawning, off channel rearing and overwintering habitat creation. In some instances, fertilization of lakes or streams in spring may be appropriate to increase production.

The use and application of these and other mitigation/compensation measures is discussed in the report for each of the species where information is available. Where possible, relevant case history examples of application and resulting effectiveness as determined through monitoring programs are provided.

Based on the literature reviews conducted for this report, it is apparent that additional information needs to be gathered on the specific habitat requirements of these sport fish. The need to fulfil these requirements is central to the development of effective mitigation/compensation measures to minimize development impacts. In addition, the obvious lack of the development, continuity, and analysis of monitoring programs indicate that these areas require immediate and ongoing attention.

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◆ Duane Jesson, Prince George	Brook trout
◆ Bob Lindsay, Nelson	Bull trout
◆ Eric Parkinson, Vancouver	Kokanee and rainbow trout
◆ Marvin Rosenau, Surrey	White sturgeon
◆ Bill Westover, Cranbrook	Westslope cutthroat trout

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1.0 INTRODUCTION

1.1 Background

There have been recent advancements in the area of environmental assessment of resource developments that impact on fish and fish habitat. The federal Department of Fisheries and Oceans (DFO) now reviews projects proposed for development in watersheds that have, in the past, been managed solely by the British Columbia provincial government. In response to these changes, the Eastern B.C. Habitat Unit of the Habitat and Enhancement Branch of DFO is currently charged with the responsibility for applying the habitat provisions of the *Fisheries Act*, and for carrying out the environmental screening under the *Canadian Environmental Assessment Act* (*CEAA*), of projects that have the potential to impact fish and fish habitat in the Peace, Liard and Columbia River drainages.

The primary purpose of this literature review is to provide fisheries and habitat managers and other stakeholders with current information regarding thirteen sport fish species found in the Peace/Liard and Columbia/Kootenay drainages of British Columbia. This information will assist the above parties when assessing impacts from various development proposals. On a species-specific basis, this review documents and summarizes the timing of significant life history events, the habitat requirements of each life stage, and mitigation or compensation techniques and their success in off-setting the impacts of industrial development. The species reviewed are:

Kokanee	*Oncorhynchus nerka*
Rainbow trout	*Oncorhynchus mykiss*
Westslope cutthroat trout	*Oncorhynchus clarki lewisi*
Brook trout	*Salvelinus fontinalis*
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Northern pike	*Esox lucius*
White sturgeon	*Acipenser transmontanus*

1.2 Methods

The literature reviewed to prepare this document was gathered through a number of sources. Relevant key words were used in carrying out a computerized search of abstracts in the AQUAREF (Environment Canada water resources references) and ASFA (Aquatic Sciences and Fisheries Abstracts) databases. The resultant output provided an extensive citation list as well as names of researchers that were currently involved in habitat assessment and evaluation of mitigation and compensation efforts. Those individuals with expertise relevant to the areas of interest were contacted directly. The study team also contacted provincial and state fisheries biologists and fisheries consultants in order to collect and/or discuss unpublished ("grey") literature.

The most challenging aspect of this study was in documenting projects in which mitigation or compensation for habitat loss had been evaluated with respect to their effectiveness in maintaining or enhancing specific fish populations or minimizing the loss of fish habitat. For some species that have not been well researched, such as mountain whitefish, burbot, and walleye, there is little information on the type of habitat manipulations that can or have been used to offset habitat losses. For species more commonly studied, such as rainbow, cutthroat, and lake trout, many mitigation and compensation techniques have been identified and widely accepted as being effective. However, for all thirteen species there are only a few instances where there have been any ongoing studies to quantify the effectiveness of habitat compensation or mitigation initiatives.

The literature on each species has been summarized in a standard format in the chapters that follow. Table 1 in the executive summary provides a species by species synopsis of selected life history events and habitat requirements.

2.0 KOKANEE

(***Oncorhynchus nerka***)

2.1 Introduction

Kokanee salmon (*Oncorhynchus nerka*, subfamily Salmoninae, family Salmonidae) are a landlocked form of anadromous sockeye salmon and the only Pacific salmon species in North America to form natural populations living their entire life cycle in freshwater. Kokanee are generally accepted to have evolved independently from anadromous populations of sockeye on a number of different occasions (Ricker 1940; Nelson 1968; Foote et al. 1989). The pattern of genetic differentiation between sockeye and kokanee also suggests that the two types have diverged sympatrically on numerous and independent occasions (Foote et al. 1989). In some lakes, the forms still remain sympatric and spawn in the same location at the same time (Foote and Larkin 1988). Kokanee usually mature at smaller sizes than sockeye, and where the two forms occur together, they exhibit other morphological differences such as gill raker number, male secondary sexual characteristics and colouration (Nelson 1968).

Kokanee are abundant and widely distributed throughout British Columbia. An important sport fish, they are second only to rainbow trout (*Oncorhynchus mykiss*) as the species most frequently captured by anglers in British Columbia. Of the more than nine million sport fish caught in 1985, kokanee accounted for 14.5% of the total freshwater sport fish catch with approximately 80% retained as food (Stone 1988).

Contrary to their usual life history patterns, kokanee and sockeye have the potential to become anadromous and remain in freshwater respectively (Nelson 1968; Foerster 1968). Therefore, the range of naturally occurring populations of true kokanee is difficult to determine because of the presence of residual non-reproducing anadromous sockeye (Ricker 1940).

2.2 Distribution

The geographic distribution of indigenous kokanee is believed to be a result of landform changes (i.e. coastal uplift) or drainage changes that have isolated anadromous populations of sockeye salmon (Ricker 1940). Kokanee are indigenous to the Pacific drainages of North America and northeastern Asia. In North America, kokanee occur naturally in Alaska, the Yukon, British Columbia, Washington, Oregon, and Idaho (Nelson 1968). In northeastern Asia, they occur naturally in Japan and the U.S.S.R. (Scott and Crossman 1973).

Kokanee have been introduced widely in the United States in Maine, California, Montana, Colorado, Connecticut, New York (Webster and Flick 1960), Pennsylvania, Vermont, North Dakota, Nevada (Cordone et al. 1971), Utah and Wyoming (Buss 1957; Scott and Crossman 1973). In Canada, they have been introduced into lakes in British Columbia, Alberta, Saskatchewan, Manitoba and Ontario (Collins 1971; Scott and Crossman 1973).

In British Columbia kokanee are found throughout the Fraser, Columbia, Kootenay, and Okanagan systems (Scott and Crossman 1973; Ash et al. 1981; Facchin and King 1983). They have also been captured in Arctic Lake, at the headwaters of the Parsnip River above Williston Reservoir, and in very low numbers in the reservoir (McPhail and Lindsey 1970; Barrett and Halsey 1977). Their range has been expanding recently through natural expansion and planting of hatchery fish (E. Parkinson, Fish and Wildlife Branch, B.C. Environment, University of British Columbia, Vancouver, pers. comm. 1992). Figures 1 and 2 show kokanee distribution in the Columbia and Peace River drainages respectively.

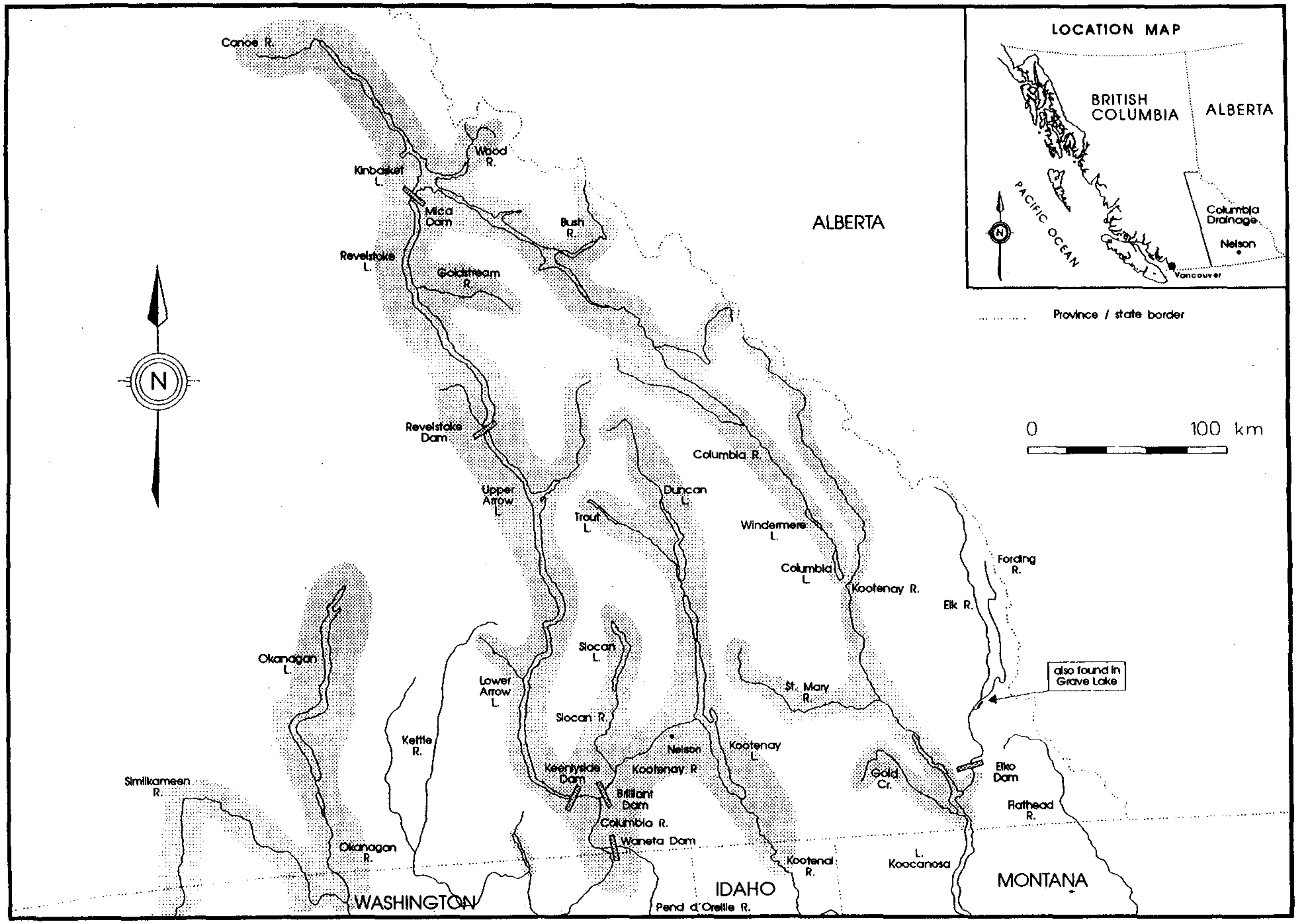

Figure 1: Kokanee Distribution in the Columbia Drainage, British Columbia

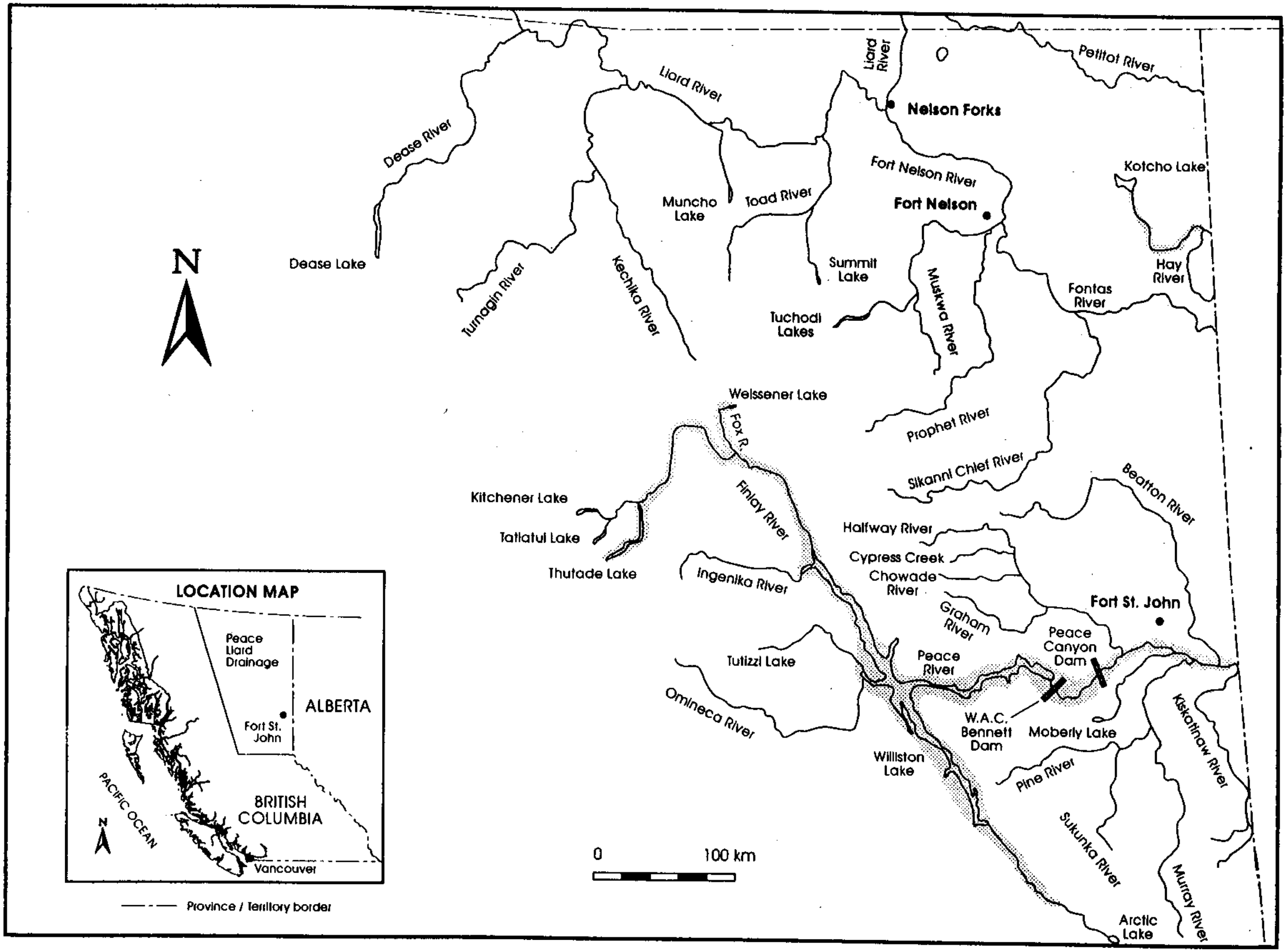

Figure 2: Kokanee Distribution in the Peace and Liard Drainages, British Columbia

2.3 Life History and Habitat Requirements

2.3.1 General

Various aspects of kokanee life history have been well studied but the details of other aspects of their biology have not yet been established. The morphology and behaviour of juvenile kokanee and sockeye salmon (0+ and 1+) are essentially identical, with positive identification of sympatric kokanee and sockeye being dependant on genetic analyses as they can not always be differentiated by electrophoretic examination (Foote et al. 1989). Given the difficultly in discriminating between young kokanee and sockeye, most of the current understanding about kokanee developmental biology, fry movement and juvenile ecology is derived from studies focusing on sockeye (Foerster 1968). Differences between kokanee and sockeye in later stages of life are more easily recognized; sockeye smolts leave the lake and return with a much larger size-at-maturity. This has facilitated more investigation of the reproductive biology and feeding ecology of kokanee. The information presented here focuses on kokanee but, where information regarding the juvenile stage is lacking, the information is based on sockeye.

In the early fall, kokanee eggs are deposited in the gravels of inlet streams to nursery lakes or in the gravels of lake beaches. The eggs develop over the fall and winter and fry emerge in spring to disperse. The fry either move directly from the lakeshore to the pelagic environment or temporarily reside in the littoral zone, near the delta of the spawning stream or beach spawning area, after which as juveniles they move offshore, grow and mature for a period of two to five years. Kokanee feed primarily on zooplankton and to a limited extent use benthic invertebrate food resources during certain stages of their life (Vernon 1957; Chapman et al. 1967; Finnell and Reed 1969; Scott and Crossman 1973; Rieman and Bowler 1980; Beattie et al. 1990). Growth rate and survival of emergent fry, underyearling, and yearling kokanee is highly variable and is related to lake productivity and to the intensity of intraspecific and interspecific competition.

Sexually mature adults migrate to the spawning grounds in the fall to deposit eggs. The coloration of spawning kokanee can be spectacular, varying from drab green to bright reddish orange. Kokanee are semelparous and usually die a few days to a few weeks after spawning. In extreme cases, they may live through most of the winter after spawning (Fallis 1970). Kokanee life history is illustrated in Figure 3. Observed habitat use and selected biological characteristics of kokanee are presented in Table 2 and discussed throughout the text.

2.3.2 Eggs and Incubation

There is limited information regarding the habitat requirements of kokanee eggs and larvae. Intragravel flows (apparent velocity), substrate composition (size and relative amount of fines), water quality (temperature, pH, dissolved oxygen concentration, and biological oxygen demand) are considered the primary factors determining the successful development of salmonid eggs (Reiser and Bjornn 1979).

Intragravel flow supplies the eggs and larvae with dissolved oxygen and removes metabolic wastes. Specific apparent velocity of intragravel flows past kokanee eggs is not known. Reiser and Bjornn (1979) suggested that, for salmonids, no less than 1300 cm/h is required to ensure survival. Substrate particles must be small enough to retain the eggs and larvae and large enough to ensure free flow in intragravel water. The effect of substrate gravel composition on the survival of kokanee eggs was investigated by Irving and Bjornn (1984). Experimentally they determined that survival rate decreased with increased relative amount of fines (diameter less than 0.85 mm) but was not related to the percentage of particles between 0.85 mm and 9.5 mm. Where there was a high percentage of fines, emergence occurred earlier than where fines were less abundant.

Temperature regulates the rate of development and can affect the survival of eggs and larvae. Acara (1977) estimated that approximately 600 accumulated thermal units (ATU) are required to develop fertilized eggs to the eyed stage, 1000 ATU to hatch eggs and an additional 600 ATU's to achieve emergence. Thus, when approximately 2200 ATU's

FIGURE 3 - KOKANEE SALMON LIFE HISTORY

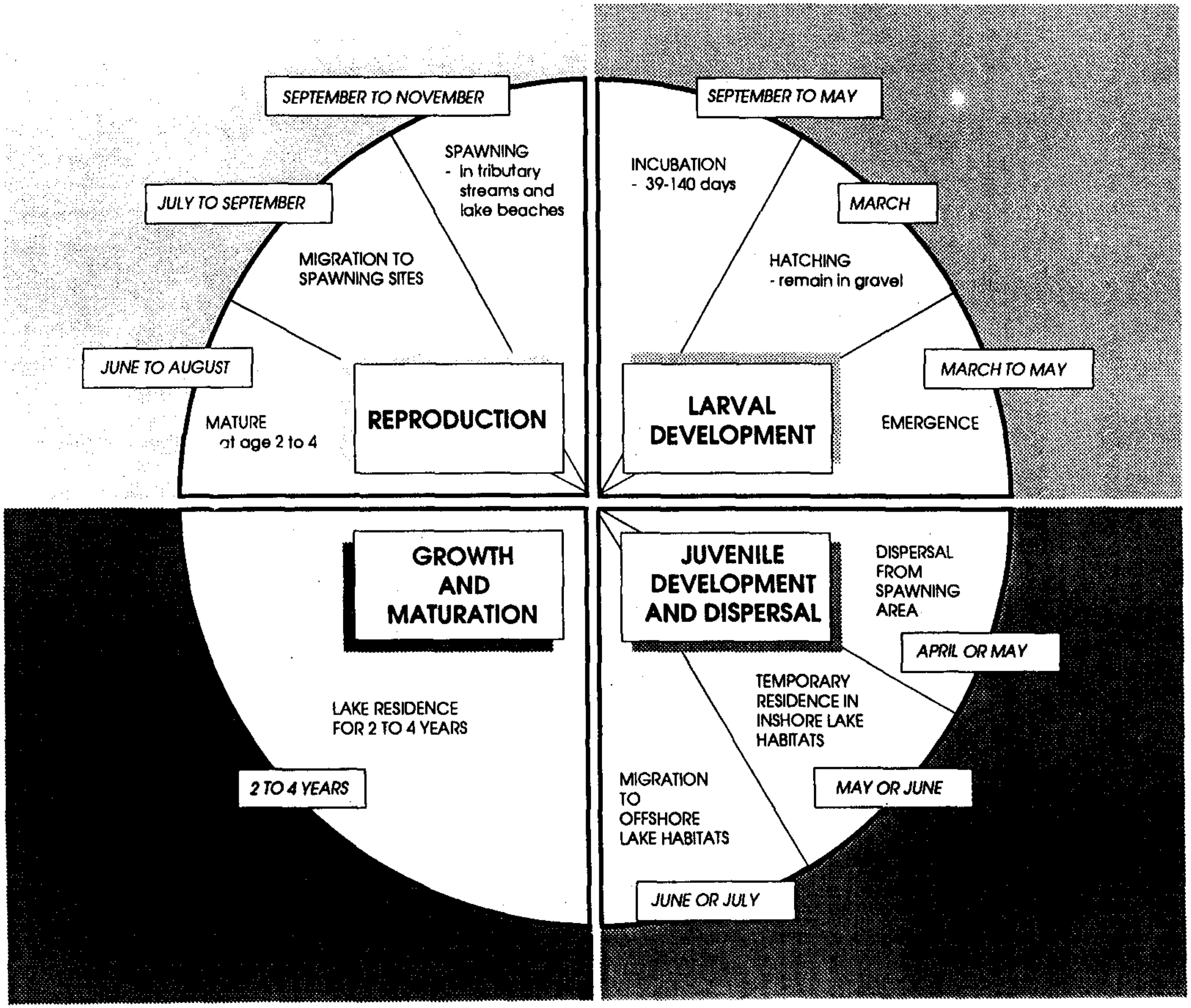

Table 2. **Observed habitat use and selected biological characteristics by life stage for kokanee.** (for sources refer to text, NA- data are not available)

Eggs

Temperature tolerance range	2°C to 15°C
Optimum incubation temperature	6.0°C
Recommended and optimum oxygen concentration	6.5 and 9.75 mg/L
Lower lethal oxygen concentration	3.98 mg/L
Range of incubation time	39 - 140 days
Incubation time at optimum temperature	90 days
Lower lethal pH	4.5 to 5.0
Recommended current velocity	high, with stable spawning materials
Intergravel flow requirements	>1300 cm/h

Juveniles

Temperature tolerance range	(for sockeye) 6.7°C to 24.4°C
Optimum temperature for growth	15°C
Recommended oxygen concentration	> 7.88 mg/L
Lower lethal oxygen concentration	4.16 mg/L
Habitat type preference	lake
Depth preference	variable, diel vertical migration
Preferred current velocity	none
Substrate (during migration from spawning to nursery areas)	gravel/cobble
Cover (during migration from spawning to nursery areas)	cutbanks/woody debris
Recommended maximum turbidity	<10 mg/l
Primary food category	plankton
Secondary food taxa	benthic invertebrates

Adults

Temperature tolerance range	6.7°C to 24.4°C
Optimum temperature for growth	15°C
Recommended oxygen concentration	>7.88 mg/L
Lower lethal oxygen concentration	4.16 mg/L
Habitat type preference	lake
Depth preference	variable, diel vertical migration
Substrate	none
Cover	darkness
Preferred current velocity	none
Turbidity tolerance	<10 mg/L
Primary food type	plankton
Secondary food type	benthic invertebrates
Form of reproduction	semelparous
Nest construction	yes, by stream spawners
Spawning habitat type	lake tributaries or lake beaches
Preferred spawning temperature	4.0 °C - 15.0 °C
Preferred spawning water depth	> 6 cm to at least 0.46 m
Preferred spawning substrate	gravel/cobble
Preferred spawning current velocity	0.15 to 0.85 m/s
Range of first age-at-maturity	age 2 - age 5
Range of fecundity	<200 - 1500 eggs/female

have been accumulated, fry emerge from the gravels, become free swimming and move towards nursery habitats. The time required for hatching and emergence are major selective forces that influence the time of spawning. Incubation times for kokanee eggs under different temperatures are presented below:

Source	Incubation Temperature (°C)	Incubation Time (d)	Accumulated Thermal Units (ATU) (°C·d)
Rucker (1937)	14.3	39	557.7
Rucker (1937)	10.9	53	577.7
Rucker (1937)	10.7	59	631.3
Rucker (1937)	8.2	73	525.6
Murray et al. (1989)	14.3	45	643.5
Murray et al. (1989)	10.9	57	621.3
Murray et al. (1989)	10.8	58	626.4
Murray et al. (1989)	8.2	73	598.6
Fallis (1970)	15.0	48	720.0
Fallis (1970)	4.0	140	560.0

These studies indicate that there is variability in egg development time among different populations of kokanee and that development time is inversely related to temperature. These differences have possibly evolved to maximize survival under the prevailing environmental conditions.

Murray et al. (1989) experimentally determined that the highest survival rates from fertilization to emergence occurred at 6°C (97.4%) and the lowest at 2°C (61.1%) for Hill and MacKenzie Creek stocks from Upper Arrow Lake. Temperature during the fertilization to hatching period had the most significant effect on survival; low incubation temperatures generally produced larger alevins and juveniles. In addition, they found that high temperature experienced during the incubation period could cause an increased rate of egg development and early emergence. Early emergence may result in migration to nursery areas at a time that would not provide optimum conditions for further growth and development. On the other hand, cooler temperatures may retard the developmental rate and the larvae may remain in the gravels for an extended period thereby causing excessive depletion of energy reserves resulting in poorer condition at emergence. Late emergence may also cause the fry to miss critical windows coinciding with plankton production or predator abundance or absence. Poor fry condition may give rise to smaller fry, reduced viability, lower temperature tolerance (Brett 1971), poor swimming performance, and increased vulnerability to predators (Bams 1967).

There are no experimental data regarding the lower lethal oxygen concentration for kokanee eggs or incubating larvae. Davis (1975) reviewed the literature on the effects of dissolved oxygen on aquatic organisms and suggested that the lower lethal concentration of oxygen for salmonid eggs and larvae is 3.98 mg/L, with the optimum concentration being greater than 9.75 mg/L. This agrees with Canadian Council of Resource and Environment Ministers (CCREM) (1987) guidelines of 9.5 mg/L for salmonid incubation habitats. Similarly, there are no data on the effects of suspended sediments on kokanee eggs, thus CCREM (1987) guidelines recommend a level of <10 mg/L.

Kokanee eggs and alevins are sensitive to pH (Parker and McKeown 1987). The most sensitive stages of development during chronic or episodic exposure to low pH are early embryonic development and newly hatched alevins. Lethal pH values were reported in this study to be 4.5 to 5.0, but pH of less than 7.1 was found to have sublethal effects including lower survival, delayed hatching, an increased rate of alevin mortality, and reduced efficiency of yolk sac energy conversion to tissue (Parker and McKeown 1987). These effects are more pronounced when the eggs are fertilized in a low pH environment. These data agree with Rombough's (1983) experiments on the effects of low pH on eyed embryos and alevins for sockeye and the other four species of Pacific salmon.

2.3.3 Rearing, Food and Growth

The timing of fry emergence and subsequent dispersal varies among systems but usually coincides with the onset of annual increases in plankton production. Fry dispersal is a critical period for kokanee. Emergent fry generally do not school until reaching the nursery habitat and therefore are vulnerable to predation. In streams with relatively constant temperature throughout the winter (i.e. just above freezing) spawning occurs in the early fall, hatching occurs in December and January and emergence may not occur until March or May. Emergent fry begin feeding immediately upon arrival at the nursery habitat and while the fry are resident in inshore waters they feed upon benthic invertebrates and planktonic organisms, depending on food availability (Jaenicke et al. 1987). At this time the small fry weigh approximately 0.1 g, and rely on the availability of suitably sized food organisms.

The availability of appropriate food resources at the time of fry dispersal is an important factor determining the survival of kokanee. Foerster (1968) suggested that the mortality of emergent fry is high when the appropriate sized food is not available. Hurley and Brannon (1969) have shown that inadequate supplies of food immediately following yolk sac absorption may lead to delayed growth later on, but does not lead directly to mortality through starvation. Rieman and Bowler (1980) indicated that the survival of kokanee fry in Pend Oreille Lake, Idaho is significantly affected by the presence or absence of small cladocerans during the May and June emergence period. LeBrasseur et al. (1978) demonstrated that survival of sockeye from egg to fall fry is correlated to spring zooplankton biomass, indicating that the abundance of food, as well as the available types and size classes of the zooplankton, is an important factor in determining year class strength.

Stream flow is important to emergent fry as it determines the length of time required to reach the nursery lake. The migration to nursery habitat is rapid and aided by stream flow. Low flows decrease the cross sectional area of the stream and increases stream velocity and the probability that fry will encounter a predator. Fraley and Clancey (1988) found that kokanee fry take advantage of current to aid in migrations. In sections where current was swift, fry moved at the same velocity as the current, however, in slow sections of the river, fry moved almost two times the current velocity. Using current in this way the fry were able to move approximately 100 km in 20 h. However, in most cases total downstream migration distance is short, usually ranging between 0.1 km and 5 km, taking less than one night of downstream migration. Cover provides fry refuge from predators during daylight hours. Illumination affects predator efficiency; low light intensity provided by shade reduces the visibility of fry and hence mortality of migrating fry.

Emergent fry are negatively phototatic and seek cover provided by aquatic vegetation and organic debris during daylight hours (Hartman et al. 1962; Acara and Smith 1971). Fry migration to nursery habitats is nocturnal and occurs during April, May, and June. Peak migrations generally occur between dusk and midnight (Lorz and Northcote 1965; Hartman et al. 1962; Acara and Smith 1971). These migrations are surface oriented with fry being evenly distributed across the width of the stream (Hartman et al. 1962). Reviewing the available data for sockeye, Foerster (1968) suggested that sockeye fry undergo genetically controlled directional migration from natal streams and fry that emerge from the redds in each spawning area exhibit unique direction and rheotactic preferences that enable the fry to move to the available nursery habitats.

Dispersal patterns into the nursery lake vary among systems and stocks. Brannon (1972) and Woodey (1972) observed that sockeye fry from Cultus Lake and Cedar River beach spawning stocks disperse immediately into the limnetic zone and form aggregated schools. In some Alaskan populations, pronounced sequential feeding by juvenile sockeye in littoral areas occurs for several weeks (Burgner 1962; Pella 1968). The duration of temporary littoral zone residence is dependent on local conditions and is related to the abundance of food, cover and piscivorous predators. However, northern populations tend to spend a longer period remaining inshore before assuming a pelagic existence.

Kokanee compete intraspecifically (i.e with sockeye and different age classes) as well as interspecifically (with threespine stickleback, lake whitefish, rainbow trout, and others) for the available food resources (Foerster 1968). Food habits of all age classes of kokanee are similar, with the exception being that kokanee fry consume more, smaller zooplankton.

After underyearling sockeye and kokanee move to offshore areas of thermally stratified lakes they typically show a pattern of diel crepuscular (i.e. active in the twilight) vertical migration. They move from cold, food-poor hypolimnetic strata where reduction or complete cessation of feeding occurs in full darkness and daylight (Foerster 1968), into warmer, food-rich metalimnetic and epilimnetic strata at dawn and dusk (Finnell and Reed 1969; Narver 1970; Levy 1990). During the daylight hours it is believed that sockeye and kokanee seek the cooler and darker waters to increase bioenergetic efficiency and to find a refuge from predators which are more common in the epilimnetic and metalimnetic waters (Levy 1987). As twilight approaches the fish ascend through the thermocline for a period of intensive feeding that lasts for approximately two hours (Narver 1970). At dawn, the fry rise to the upper portion of the thermocline for a second, less intensive feeding period followed by a retreat to depth as the daylight penetrates the epilimnion. This pattern gradually diminishes as surface waters cool in the fall. When lake turnover occurs, bringing uniform water temperatures to the water column, vertical migration ceases. Crepuscular feeding persists through the entire lake residence period of kokanee (Foerster 1968; Finnell and Reed 1969; Rieman and Bowler 1980; Levy 1987). Levy (1990) suggests that there is an ontogenetic shift in the vertical migratory behaviour of kokanee within Okanagan Lake. Kokanee fry migrate vertically in a similar fashion to juvenile sockeye. The pattern and extent of these vertical migrations varies between lakes and differences in temperature, the availability of food, relative light intensity, and predator abundance appear to stimulate the migrations. Later in life and after surpassing a threshold size (related to predation) kokanee may alter this behaviour and remain in relatively shallow water during daylight hours, presumably to feed on epilimnetic zooplankton. This behaviour is found in some lakes, including Nicola Lake (Northcote et al. 1964), Babine Lake (McDonald and Scarsbroek 1969), Pend Oreille Lake (Rieman and Bowler 1980) and Okanagan Lake (Levy 1990). Ontogenetic shifts in mysid utilization were noted in Kootenay Lake by Northcote (1973) and in Pend Oreille Lake by Rieman and Bowler (1980).

Crustacean zooplankters are the primary food organism utilized by juvenile kokanee, the species being consumed depending on seasonal changes in the zooplankton community. Finnell and Reed (1969) used 24 hour hydroacoustic surveys to show that during summer, kokanee in the Gransby Reservoir, Colorado fed diurnally on zooplankton in the epilimnion, descended below the metalimnion in early evening to rest and assimilate food and ascended to surface waters at dawn to resume feeding. *Daphnia pulex* was the primary food organism consumed. Rieman and Bowler (1980) observed that kokanee in Pend Oreille Lake, Idaho feed almost exclusively on crustacean zooplankton, with some terrestrial insects and midge larvae also consumed when available. In winter *Cyclops* sp. is consumed most frequently and in summer *Bosmina* sp. is the predominant food item. *Daphnia* sp. was the most preferred item in all seasons when it was available. Mysids were consumed by kokanee but did not contribute significantly to the diet.

Beacham and McDonald (1982) found no difference in the food of juvenile and adult kokanee in Babine Lake. Chapman et al. (1967) set gill nets on the bottom of Elk Lake, Oregon and found that during periods of darkness *Chironomus* sp. was the primary food organism for adult kokanee. They concluded that feeding does not stop during periods of darkness and that kokanee use benthic food resources at night to supplement daytime planktivorous feeding. Northcote and Lorz (1966) investigated the feeding habits of adult kokanee in Nicola Lake, British Columbia and found that for fish in their third (3+) and fourth (4+) summers crustacean zooplankton were most important in the fall and spring. Dipteran larvae derived from the benthos are consumed in the summer. They also documented that feeding increases with the onset of the fall spawning period. However, there was no significant feeding during spawning migration. Beattie et al. (1990) found that the kokanee in the Flathead system of Montana follow the same general pattern, with crustacean zooplankton forming the primary dietary component with minor changes occurring with the seasonal progression of zooplankton.

Growth of age 0+ and 1+ kokanee is influenced by water temperature, the type and quantity of appropriate food, and to a lesser extent, by fish density. Brett et al. (1969) found that when food is not limiting, optimum growth of juvenile sockeye occurs at 15°C, and growth shifts progressively lower with lower rations. Bowler and Rieman(1981) found that the maximum growth rate of kokanee in the first six months of life was 6.7% per day. Brett et al. (1969) determined that the maximum growth rate of juvenile sockeye five to seven months old was 2.6% per day and this decreased to 1.6% per day for fish seven to twelve months of age. No growth occurs for temperatures greater than 23°C. Bowler and

Rieman (1981) found that initial growth of swim-up kokanee fry was strongly correlated to zooplankton abundance and temperature. Biette and Geen (1980) found that at low levels of food abundance, increasing temperature caused a reduction in growth efficiency of juvenile sockeye. As food density increases, however, higher temperatures and the potential for fish to experience cyclic temperature regimes through vertical migration may contribute to increased growth efficiency (Biette and Geen 1980).

A number of studies have shown that growth rates and maximum sizes of sockeye produced in lakes are influenced by the quantity and size distribution of zooplankton (Brocksen et al. 1970). Physical factors such as lake morphology, edaphic characteristics of the lake basin and seasonal weather patterns each affect primary production, which regulates the production of zooplankton, the main food source of juvenile and adult kokanee. The concentration and ratios of limiting nutrients in the lake, such as phosphorous and nitrogen, will also be important in determining the composition and size distribution of phytoplankton, which in turn, determine the structure of the zooplankton community which are the primary food source for kokanee (Stockner and Shortreed 1984; Hyatt and Stockner 1985).

Rieman (1981) collected data on zooplankton abundance and kokanee growth in Payette, Spirit, Coeur d'Alene and Pend Oreille Lakes to investigate the effect of lake productivity and food availability on lake carrying capacity. He found that growth of age 0 + and 1+ individuals was influenced by lake productivity and availability of suitable food organisms, but the growth of age 2+ and 3+ kokanee was influenced by fish density. Declines in zooplankton abundance were generally accompanied by declines in kokanee growth, suggesting a strong relationship between the biomass of zooplankton and the instantaneous growth rate of kokanee. However, in some lakes, such as Great Central Lake, British Columbia, there is no significant correlation between zooplankton abundance and growth of sockeye to age 1 (LeBrasseur et al. 1978), but there is significant correlation for age 2+ smolts.

Additional factors that affect kokanee growth and maturation in the lake environment are temperature, light intensity and water turbidity, oxygen concentration, food availability, and predator abundance. Temperature and relative light intensity are primary factors that determine the juvenile and sub-adult kokanee habitat. Temperature is important because it determines areas of fish aggregation, influences the production of plankton, and is directly related to growth and development of the fish, as temperature affects growth rate and food conversion efficiency. Lake temperature and thermal stratification affect diel and seasonal movements, feeding behaviour, and depth preferences of stocks in different lakes. Feeding experiments over a constant temperature range revealed that optimum growth occurs at 15°C and optimum food conversion efficiency is maximum at 11.5°C (Brett 1971). Lower temperatures suppress growth rate, food conversion efficiency, ration size, digestion rate, and habitat selection. However, different stocks have become racially acclimated to different ranges of water temperature. Brett (1971) demonstrated that the upper lethal temperature for juvenile sockeye is 24.4°C and that the lower lethal temperature is 6.7°C. Sockeye are intolerant of low temperature exposure for extended periods even when acclimated to low temperature.

With respect to light intensity, Finnell and Reed (1969) found that during periods of darkness adults aggregated at 9 m to 18 m depths in temperature ranges between 10°C and 13°C in the Gransby Reservoir, Colorado. During daylight, fish were found above 9 m. Light intensity appeared to be correlated to the initiation of upward migrations at dusk. Lake turbidity is also an important habitat characteristic, as it can have both direct and indirect effects on habitat selection. The clarity of lake water influences the depth to which light will penetrate and thus the volume of water that is suitable for production of phytoplankton and zooplankton. Transparency will affect the ability of kokanee to capture food and the risk of being captured by predators. Siltation in the inshore areas of turbid lakes may reduce the productivity of submerged aquatic vegetation, smother spawning grounds and impair feeding. The effect of turbidity on the physiology or feeding efficiency has not been documented for kokanee in the literature, but CCREM (1987) guidelines suggests a level of <10 mg/L.

Oxygen concentration will limit the penetration and dispersal of fish in a lake. There are no data regarding the lowest concentration that will be tolerated by kokanee. However, Davis (1975) provided criteria for salmonid populations, suggesting that fish avoid depth strata where oxygen concentrations are below 3.96 mg/L, and for optimum conditions should be exposed to oxygen concentrations greater than 7.88 mg/L.

Sub-adult and adult kokanee remain in open water habitats of the lake until sexual maturation. Adult kokanee are known to undergo vertical, as well as inshore-offshore movements, both with a diel periodicity (Northcote et al. 1964; Lorz and Northcote 1965). Vertical and horizontal migration varies seasonally, and again are affected by temperature and food abundance. In spring and fall, adult kokanee inhabit all depths of the water column, but show pronounced seasonal differences in vertical distribution which many investigators have attributed to temperature preferences (Finnell and Reed 1969). Kokanee usually are found in the epilimnion and metalimnion and move into the cooler hypolimnion as summer water temperature increases. During summer, kokanee exhibit extensive vertical and onshore-offshore movements associated with temperature, the availability of food and the abundance of predators (Levy 1987).

There are few data to identify the oxygen concentration and turbidity tolerances of adult kokanee. CCREM (1987) recommend for salmonid spawning habitats in general that the water column dissolved oxygen concentration should be at least 9.5 mg/L, so that the interstitial concentration is 6.5 mg/L. Davis (1975) recommended that a minimum 7.75 mg/L is suitable for populations of freshwater fish that contain salmonids. Therefore, the dissolved oxygen concentration for spawning areas should be no less than 9.5 mg/L and greater than 7.75 mg/L for other habitats.

Kokanee are preyed upon during all stages of their life, and in some lakes, such as Okanagan Lake and Arrow Lakes, are considered to be a major forage species for trophy sport fish such as Girard rainbow trout (Andrusak and Parkinson 1984; Harris 1984). During downstream migration fry are consumed by coho salmon (*O. kisutch*), sculpins (*Cottus* spp.), cutthroat trout (*O. clarki*), Dolly Varden char (*Salvelinus malma*) and rainbow trout. During their lake residence, juvenile and adult kokanee are consumed by lake trout (*S. namaycush*), squawfish (*Ptychocheilus oregonensis*), bull trout (*S. confluentus*) and rainbow trout (Ricker 1940; Hartman et al. 1962; Scott and Crossman 1973).

2.3.4 Maturity, Adult Migration and Spawning

Age and size at maturity vary within and among stocks of kokanee. Scott and Crossman (1973) reported that kokanee generally live to age three to five years with most fish reaching sexual maturity at age four. Vernon (1957) found that 2+ spawners were predominant in the south and west arm stocks of Kootenay Lake, with 3+ spawners being predominantly north arm stock. Spawners from the west arm stocks were the largest (240 mm to 365 mm), north arm stocks intermediate (215 mm to 220 mm), and south arm stocks the smallest (185 mm to 201 mm). Korman et al. (1990) examined historical trends in size-at-maturity for Kootenay Lake and demonstrated that a decline had occurred since the mid 1970's and had been at historical lows for the last five years. Although many factors could influence this decline, they hypothesized that low food availability was the cause.

Within the Okanagan Lake chain (Vaseux, Wood, Skaha, Okanagan, Osoyoos, and Kalamalka) 2+ spawners were exclusively found by Northcote et al. (1972), with size ranging between 200 and 340 mm. Nicola Lake kokanee also mature as 2+ and 3+ fish with a size range between 225 mm and 277 mm (Lorz and Northcote 1965). Similar findings are documented from the Flathead system in Montana (McMullin 1981), Odell Lake in Oregon (Lewis 1977), Pend Oreille and Couer d'Alene lakes in Idaho (Bowler and Rieman 1981) and Lake Tahoe in California (Cordone et al. 1971).

In late summer as the spawning season approaches, sexually mature kokanee begin migration towards their natal spawning area. Spawning generally occurs during September, October, and November. Inshore movement and entry of spawners into inlet streams occurs at night, is timed to coincide with low light intensity, and is unrelated to stream temperature. There is likely strong natural selection for kokanee to enter spawning streams during dusk or darkness to minimize the risk of predation from aquatic, terrestrial, and aerial predators. In some lakes, high quality spawning habitat is provided by beach spawning areas with subsurface flow and suitable substrate as large as rubble/cobble (Harris 1984). Female kokanee dig relatively small nests in pea-sized (one-half to one inch) gravels. Adults of both sexes are present in approximately equal numbers on the spawning grounds and actively defend the nest prior to spawning and immediately following egg deposition in the gravels. The number of eggs deposited primarily depends on the abundance of spawners, their age composition, size and fecundity. Fecundity of female kokanee depends on racial characteristics and body size, and ranges from less than 200 eggs to 1500 eggs (Vernon 1957; Lorz and Northcote 1965; Scott and Crossman 1973; Acara 1977; Murray et al. 1989). Average fecundity of the Meadow Creek kokanee stock was estimated to be approximately 300 eggs (Acara 1977). In Arrow Lake kokanee stocks (MacKenzie and Hill Creeks), fecundity averages around 210 eggs. For these stocks Murray et al. (1989) hypothesized that lower fecundities are compensated by higher egg-to-fry survival rates. Bowles et al. (1989) reported that female kokanee from Sullivan Springs, a tributary stream to Pend Oreille Lake, on average produced 430 eggs. Paetz and Nelson (1970) stated that kokanee produce an average of 500 eggs per female. Thus, there is a large variation in the reported average fecundity of kokanee, but this is likely related to stock specific size-at-maturity.

Smith (1973), in a study of kokanee redds in three Oregon streams, found that the spawning sites had velocities of 0.15 to 0.73 m/s and depths of 6 cm or greater. Thompson (1972) reported mean velocities of 0.24 to 0.64 m/s in water depths of 0.09 to 0.46 m. Delisle (1962) reported that kokanee did not spawn in velocities greater than 0.64 m/s. Acara (1977) reported that kokanee in the Meadow Creek and Lardeau River, on average, selected spawning sites with a mean depth of 35.1 cm and velocity of 0.2 m/s. Parsons and Hubert (1988) investigated spawning in streams larger than those mentioned above and found that kokanee spawned in faster water and deeper areas than previously reported; modal velocities ranged from 0.67 to 0.85 m/s and modal depths from 0.18 to 0.37 m. Redds were generally found on outside bends of the river or in riffles just downstream of pools.

The absolute temperature range tolerated by spawning kokanee is not known; however, there are a range of observed spawning temperatures. Lorz and Northcote (1965) observed that kokanee moved into spawning tributaries of Nicola Lake when temperatures were between 9°C and 11°C. Parsons and Hubert (1988) observed that temperature in the Green River and Sheep Creek in the Flathead Lake system of Montana declined during the spawning period and ranged between 7°C and 4°C, and 15°C and 7°C respectively. Average temperature during spawning of Meadow Creek and Lardeau River kokanee was 9.0°C (Acara 1977). Reiser and Bjornn (1979) stated that a sudden change from standard temperature regimes during spawning may cause reduced nest building activity and inhibit egg deposition.

2.4 Mitigation and Compensation Strategies

As discussed above, kokanee live the greatest proportion of their lives in lakes and use tributary streams and lake beaches for spawning. Many potential impacts can be mitigated through relocation of a proposed development and related activities to areas of lower sensitivity, but if residual impacts remain, compensation will be required. Compensation strategies are limited to improving spawning habitat, improving access to underutilized habitat, adding nutrients to lakes to enhance the pelagic food chain, and removing potential predator and competitor species.

Reservoirs and diversion projects for hydroelectric development or irrigation water storage are likely to have the greatest impacts on kokanee populations. River impoundments change the upstream environment from riverine to lacustrine. Dams that create storage reservoirs or are run of the river facilities can alter flow regimes, change temperature and nutrient patterns and water quality in downstream flows, and block migration routes for spawning fish and for juveniles moving to rearing habitats. The operation of reservoirs for power generation can have additional impacts such as mortality resulting from impingement on fish screens and entrainment in turbines. Drawdown in reservoirs or reduced streamflows may render some spawning habitat inaccessible, isolated, or dewatered thereby desiccating or freezing eggs or forcing spawning where egg survival is reduced. Fraley et al. (1986) found a strong relationship between kokanee year class strength and river flow in the Flathead River, Montana. Because kokanee spawning sites were located in relatively shallow waters, the operation of the Hungry Horse Dam caused dewatering of kokanee spawning beds and high winter incubation mortality.

Impoundment and fluctuating water levels (flooding and dewatering) can also cause shoreline instability resulting in erosion and sedimentation, which may have detrimental effects on spawning areas and affect the feeding of emergent fry. Flooding can cause scouring of the redds and dislodgement or burying of incubating eggs (Stober et al. 1978; Thorne and Ames 1987). Although it is preferable to have swift currents over the redds, current velocities should be below that which will scour the redds or displace spawning bed materials.

Mitigation of the impacts of hydroelectric facilities may take the form of installation of fish screens to prevent entrainment or fish guidance systems to direct fish away from intakes. Managing the reservoir drawdown regime to maximize lake productivity may also mitigate impacts on kokanee if lake productivity limits their body size and/or population abundance. Where it is not possible to restore the productive capacity of the habitat or to increase the amount of natural spawning habitat by the removal of obstructions to upstream migration, it may be necessary to compensate for habitat loss through the use of spawning channels, lake stocking programs, or exploiting underutilized spawning habitat. For example, it has been proposed by British Columbia's Fish and Wildlife Branch that a fish passage facility be constructed on the Inonoaklin River to augment sport fish production in the Lower Arrow Lake and Columbia River below the Hugh Keenleyside Dam. If fish passage can be achieved, this would give access to approximately 32 km of high quality spawning habitat (H. Andrusak, Fish and Wildlife Branch, B.C. Environment, Victoria, pers. comm. 1991), enough spawning habitat for an additional 1,000,000 kokanee spawners.

In Okanagan Lake, stream spawning kokanee face loss of spawning habitat through domestic and irrigation water demands, stream channelling and flood protection (Harris

1984). These impacts can be compensated for by regulation of flows and by improvement of spawning gravels. However, studies have focused on the feasibility of enhancing shore spawning areas which are subject to fewer impacts than streams, allowing for more effective enhancement. Incubation mortality can be reduced by maintaining constant water levels during the egg stage, then manipulating water levels after mid-February when the alevins are mobile to allow them to escape desiccation (Matthews and Bull unpubl. in Harris 1984). On Okanagan Lake, previously underutilized shore areas were enhanced by the placement of 10 to 30 cm angular cobble at one site and 5 cm minus gravel at another. Kokanee spawned at both sites, but showed a preference for the gravel substrate. The data suggest that upwelling was not required for kokanee to select the area for spawning as long as there was suitable wave action. In addition, kokanee preferred sites adjacent to previously used spawning areas.

Forest harvesting can alter streamflows, fish migrations, structural habitat, water temperatures, nutrient cycles, patterns of erosion and deposition of sediment and create the potential for exposure to toxic substances. Mining-related activities can also degrade water quality and destroy or isolate kokanee habitats. Metal or coal mining operations may introduce heavy metals or acids into adjoining surface waters and impact kokanee at all ages and their food organisms. Metals can also bioaccumulate and present hazards to those consuming the fish. Construction of recycling or settling ponds may isolate spawning or rearing habitat. Instream sediment loading may also increase as a result of forest harvesting and mining through erosion of haul roads, run-off from tailing ponds and washout from settling ponds. Additional sedimentation related effects (McLeay et al. 1987), although only temporary, can be caused by destruction of aquatic and riparian habitat resulting from mining in streams and lake bottoms.

In shoreline areas of Coeur D'Alene Lake, Idaho, that have been altered by road construction activity, kokanee spawn in water as deep as 20 m, well beyond the preferred spawning depth (Hassemer and Rieman 1981). The substrate in these areas consisted of angular road-fill material that was too large for fish to excavate during redd construction. Spawning appeared to be more "broadcast" in nature on the road fill substrate rather than the typical redd construction noted for Pacific salmon. These observations suggest that kokanee can spawn successfully below the zone of water level fluctuations and that artificial spawning habitat for shoreline spawning stocks of kokanee can be created to compensate for the loss of spawning habitat.

Urban development can affect kokanee habitat by changing shoreline structure, removing riparian cover, channelling, or polluting the water from point and nonpoint sources such as petroleum products, heavy metals and pesticides.

Although it is not feasible to improve the structural characteristics of juvenile kokanee rearing habitat, it is feasible to improve the availability of food in these environments. Controlled additions of inorganic nutrients to increase primary and secondary production have been successfully used to improve growth and survival of sockeye salmon in lakes (Stockner and Hyatt 1984). Stockner and Northcote (1974) assessed the impact of the unregulated anthropogenic nutrient addition on fish stocks in Skaha Lake. Zooplankton biomass increased six-fold and the kokanee growth rate was significantly greater in 1971 than in 1948. Nutrients in sewage discharged to Kootenay Lake increased zooplankton two- to three-fold over pre-1950 biomass estimates, and kokanee in the west arm grew faster (Zyblut 1970; Northcote 1972). In the less eutrophic north arm and more turbid south arm kokanee growth rates did not differ significantly from pre-1950 estimates. In both cases positive consequences (increased zooplankton and fish biomass) and negative consequences (excessive algal blooms) of nutrient addition were observed. More recently, a decrease in nutrient addition because of the closure of a fertilizer plant, better sewage treatment, and upstream impoundment has resulted in reduced concentrations of phytoplankton nutrients and reduced productivity of kokanee stocks.

Korman et al. (1990) suggested that restoring the nutrient balance is a practical method for increasing fish productivity. However, in run of the river reservoirs, such as Revelstoke Reservoir and Dinosaur Lake (between W.A.C. Bennett and Peace Canyon Dams), this may not be an effective strategy because nutrients are flushed through the system too rapidly to be fully utilized. For example, the Revelstoke Reservoir has an estimated flushing rate of 4.2 times per year (Smith 1989). This will not only limit natural productivity of the lake but also reduce the efficacy and cost effectiveness of adding nutrients.

Another strategy to alleviate the effects of food limitation on the growth and survival of kokanee has been to introduce alternate food sources. In British Columbia there have been several attempts to introduce *Mysis relicata* to provide kokanee and other planktivorous fish species with larger food organisms. Lasenby et al. (1986) summarized the effects of mysid introductions on the zooplankton and fish communities of 21 British Columbia lakes between 1949 and 1979. Generally, cladoceran abundance declined, kokanee size increased and kokanee abundance declined after the introductions. In Idaho and Montana lakes where mysids were introduced, similar declines in kokanee abundance have been observed (Rieman and Bowler 1980; Rieman and Falter 1981; Beattie et al. 1990). Because there is little evidence that introductions yield positive long-term benefits and at present there are no methods known to remove a mysid population from a lake once they have become established, introduction of mysids are not a recommended method for enhancing kokanee populations (Lasenby et al. 1986).

Spawning channels have been successfully used in several areas of British Columbia. In 1967, a 3.3 km long spawning channel was constructed on Meadow Creek to enhance Kootenay Lake kokanee stocks to compensate for the loss of access to natural spawning grounds caused by the construction of the Duncan Dam on the Duncan River. Survival of fry in Meadow Creek was on average approximately 6% whereas in the channel fry survival was 16% in the 1970's (Acara 1977) and is anticipated to be about 30% now (E. Parkinson, pers. comm. 1992). The quality of fry produced in the natural and artificial spawning grounds was similar, thus overall the spawning channel was an effective compensatory method. However, further assessments of the spawning channel indicated very low survival rates. Success varies with the quality of the gravel and this has led to the replacement of gravels in the channel in an effort to improve egg to fry survival rates (J. Hammond, Fish and Wildlife Branch, B. C. Environment, Nelson, pers. comm. 1991).

Similarly, a spawning channel with fry survivals of 40 to 50% was constructed on Hill Creek to mitigate the effects of the Revelstoke Dam on Arrow Lake kokanee. Initially the channel was successful, but mean and maximum size-at-maturity and fecundity have declined since the late 1970's and have remained at historical lows for the last five years. The abundance of spawning fish has also decreased from 800,000 to 300,000 between 1985 and 1989. Food deficiency has been cited as one of the primary factors causing this decrease in productivity (Korman et al. 1990; G. Ennis, Department of Fisheries and Oceans, Vancouver, B.C., pers. comm. 1991). This case history points out that successful compensation requires a detailed understanding of the carrying capacity of the habitats and their potential productivity. Furthermore, temporal shifts in habitat productivity that occur naturally or as a result of anthropogenic activities can affect overall success of a compensation or mitigation plan.

Some lakes have been stocked with hatchery raised juvenile kokanee to increase the population and harvestable surplus. Size and time of release of hatchery-reared kokanee can be important factors determining future survival rates. As with other enhancement strategies, stocking success depends upon the abundance of suitable food resources (Vinyard et al. 1982) but will also depend on the availability of spawning habitats.

Lewis (1977) found that the size at time of release was an important factor determining survival and return of hatchery fish to the recreational fishery of Odell Lake, Idaho. Releasing kokanee of 2.3 to 5.4 g generally provided better returns than releases of smaller individuals. More kokanee returned from June and July releases than from May, August, or September releases, suggesting that zooplankton abundance at the time of release was the key to increased growth and survival. His evaluation of stocking programs at Odell Lake also included an analysis of the success of outplanting stocks of different racial origin. Generally there were differences in the age-at-maturity and time of spawning and this affected harvest patterns. However, there was no significant difference in the total return to the fishery. He recommended releasing fry greater than 70 mm during the period of increasing nursery lake zooplankton abundance (usually June and July) as well as releasing a mixture of early and late maturing races so that a longer harvest season could be established.

Rieman (1981) found that growth of fry in open water net pens exceeded the growth of fry held in a hatchery, allowing for their earlier release. This confers a survival advantage since the fry have the potential to grow early in the season and have an open water release which avoids shoreline predation. Open water releases may result in economic benefits from both increased production and decreased cost, as long term rearing in a hatchery may not be necessary.

Parkinson (1986) found that size and time of release were not significant factors in determining the survival of hatchery kokanee fry released into Skaha Lake. In his study, fry and fingerlings weighing 1.4 to 5.5 g were released during the period May 1 to July 30. Although hatchery fry were approximately 18 times larger than the wild fry in the spring of their first year, he found that hatchery fish lost this size advantage and were essentially the same size as wild fish of the same age at the end of their third summer of growth. He found some evidence that groups released early had better survival, but the relationship was weak.

The overall effectiveness of enhancing kokanee through restoration of natural spawning sites, construction of artificial spawning areas, or hatchery rearing is also dependent on the productivity of the nursery lake. The carrying capacity of kokanee nursery lakes is difficult to determine because the interaction between lake productivity, food availability, fish density and the resulting influence on kokanee growth and survival is not well understood. It is likely that the abundance of the more important prey species will be reduced to a greater extent in less productive lakes than in more productive lakes, and this cropping is an important mechanism in the density dependent response (Goodlad et al. 1974). A more productive lake may have a greater carrying capacity and allow more successful stocking programs and this should be considered before mitigation or compensation projects are undertaken.

Enhancement strategies that consider utilizing brood stock from other than native sources must consider the potential for the introduction of diseases and parasites. Infectious hematopoietic necrosis is a viral disease of alevins, fry and early sockeye salmon juveniles that can affect a much larger size range of all salmonids. Kokanee managers in British Columbia have realized this and now resist the development of kokanee hatcheries (B. Ludwig, Fish and Wildlife Branch, B. C. Environment, Victoria, pers. comm. 1991).

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3.0 RAINBOW TROUT

(Oncorhynchus mykiss)

3.1 Introduction

The rainbow trout has recently undergone a name change from *Salmo gairdneri* to *Oncorhynchus mykiss*. In June 1988, the American Fisheries Society (AFS) changed the genus of native "*Salmo*" trout of the Pacific Ocean drainages to "*Oncorhynchus*". The decision was based on recent consensus of the AFS that the Pacific coast *Salmo sp*. were more closely related to the Pacific salmon (*Oncorhynchus)* species than to the Atlantic and Eurasian *Salmo* species (Smith and Stearley 1989). With respect to the species name, taxonomists have speculated for some time that the North American rainbow trout and the Asian Kamchatka trout (originally *Salmo mykiss*) were the same species. Smith and Stearley (1989) cite a number of studies from the 1970's that further support this speculation. According to the rules of nomenclature, when two species are determined to be one, the older name, i.e *mykiss* takes precedence. Therefore, rainbow trout have been reclassified from *Salmo gairdneri* to *Oncorhynchus mykiss*.

Apart from the recent name change, the species and subspecies taxonomy for rainbow trout is confusing. Other species and subspecies names that have been used include *kamloops*, *whitehousei*, *irideus*, *rivularis*, *pupuratus*, *stellatus* and *argentatus* (Scott and Crossman 1973). Because of the variability in the different species and subspecies, it has become common for all North American and now Asian forms to be classed as *Oncorhynchus mykiss*. Anadromous forms are commonly referred to as steelhead, or steelhead trout, while the non-anadromous forms are usually called rainbow or Kamloops trout. (Gerrard stock in Kootenay Lake are considered a distinct strain from other, smaller forms in the lake (Hartman 1969)).

Rainbow trout are a popular fish and the species most frequently caught by anglers in British Columbia (Stone 1988). Scott and Crossman (1973) summed up the popularity of this beautiful fish in the quote:

> "It may simply be said that this species is one of the top five sport fish in North America and the most important west of the Rocky Mountains."
> (p 190)

3.2 Distribution

The natural distribution of rainbow trout ranges from Mexico to Bristol Bay, Alaska, including rivers and lakes west of the Rocky Mountains. Rainbow trout are also native to the Peace and Athabasca Rivers. Varieties have been widely introduced throughout North America (as well as other parts of the globe) to the extent that they are now found in most suitable waters of central and eastern North America at elevations ranging from sea-level to 4500 metres (MacCrimmon 1971).

In British Columbia, anadromous forms can be found in most of the larger streams along the coast and extending into the upper Fraser and Thompson Rivers. The natural distribution of non-anadromous populations includes coastal streams, the Fraser system, most of the Columbia drainage (except for the Moyie, Elk, and upper Kootenay Rivers), and the Peace River (Carl et al. 1967). Figures 4 and 5 show rainbow trout distribution in the Columbia, and Peace and Liard drainages, respectively. McPhail and Lindsey (1970) report that specimens taken from the upper Peace River have some red pigment in the hyoid grooves beneath the lower jaw, a characteristic typical of cutthroat trout which are found further south.

Stocking programs since the early 1900's have introduced rainbow trout to areas where they did not naturally occur. Since the Libby reservoir (Lake Koocanusa) was stocked, rainbow trout have moved into tributaries of the Kootenay River including the Elk and St. Mary rivers and Gold Creek. In some areas small residual populations have become

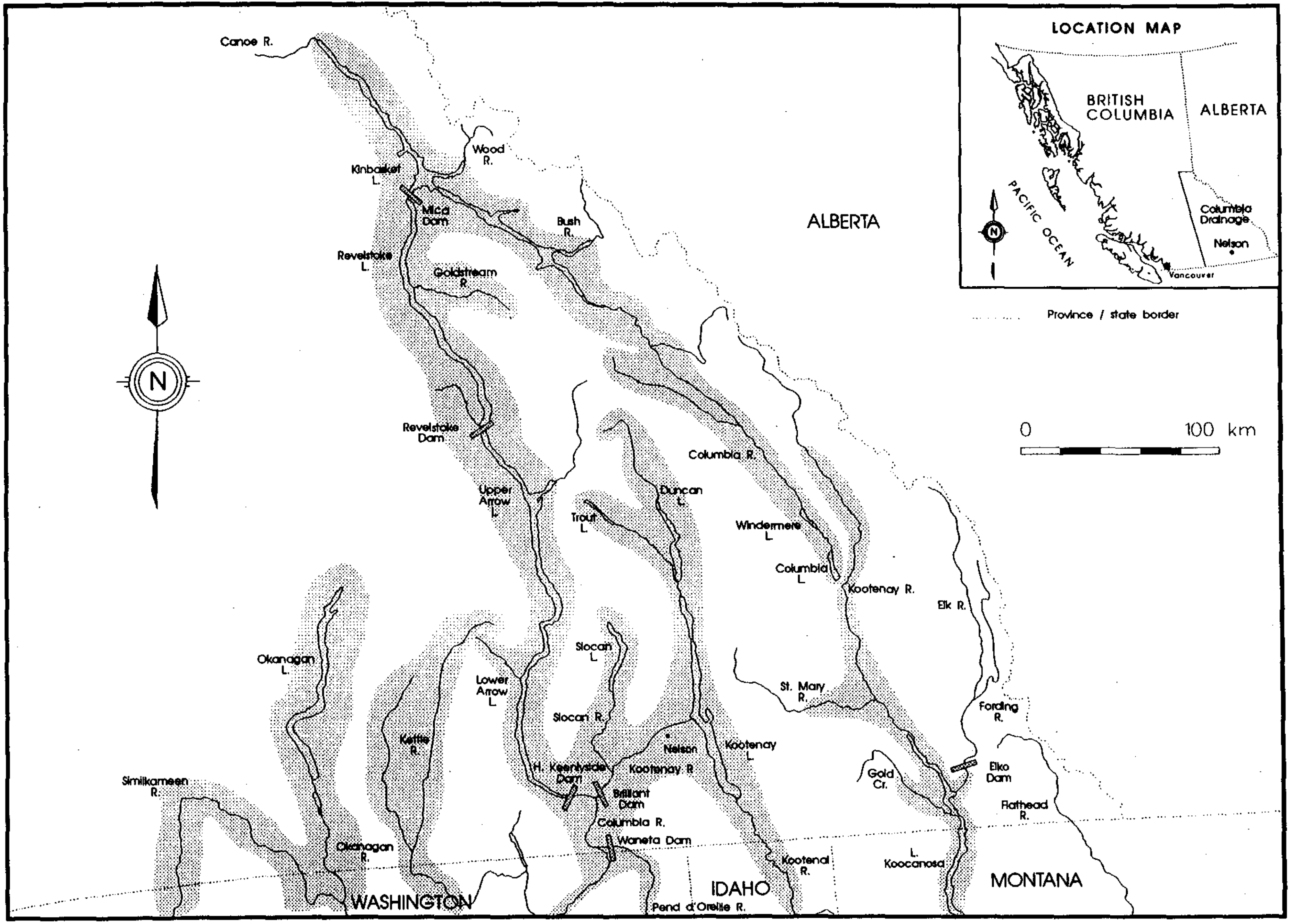


Figure 4: Rainbow Trout Distribution in the Columbia Drainage, British Columbia

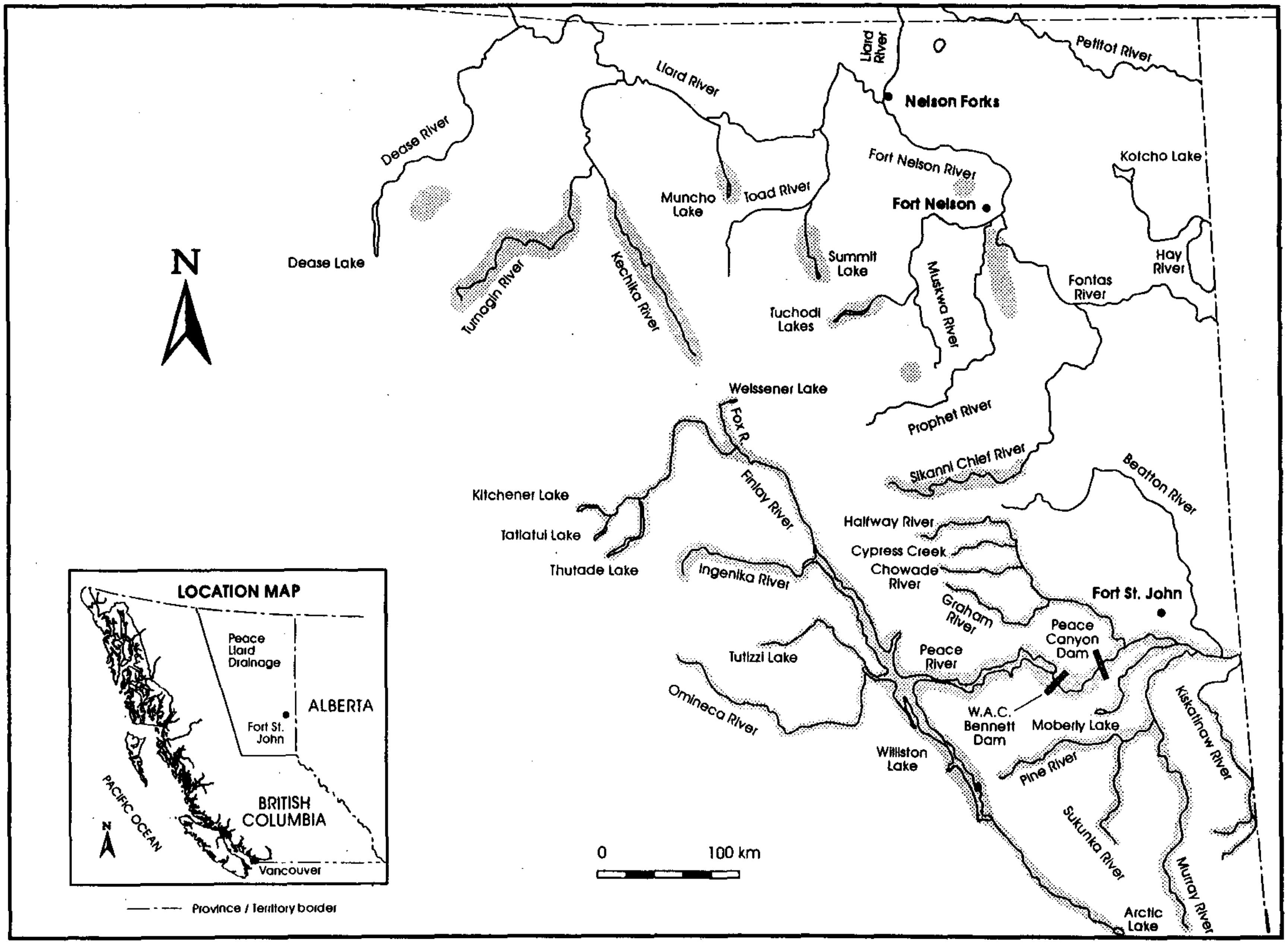


Figure 5: Rainbow Trout Distribution in the Peace and Liard Drainages, British Columbia

established as year-round stream dwellers rather than migrating back to the reservoir to mature. Unsanctioned stocking of rainbow trout has also occurred throughout British Columbia.

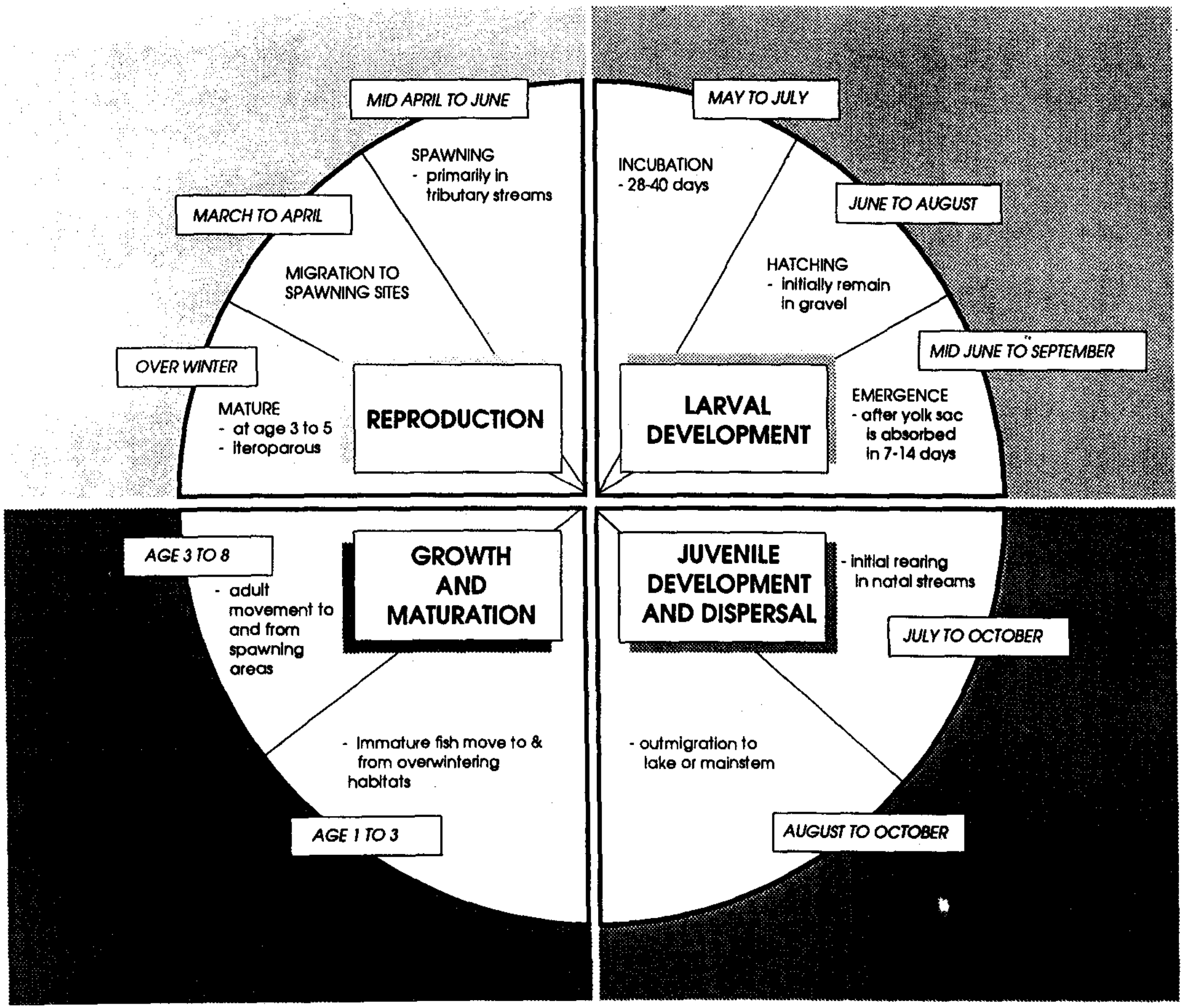
3.3 Life History and Habitat Requirements

3.3.1 General

Inland populations of rainbow trout exhibit several different life history strategies with considerable variation depending on geographic location and habitat. However, there are three basic strategies that have evolved: populations that live their entire life in small streams, those that spawn in small streams and migrate to rivers to rear and mature, and those that spawn in small streams and move into lakes to rear and mature. Within lakes, rainbow trout exhibit two basic strategies based upon lake size. In large lakes such as Kootenay, Okanagan, Shuswap and Quesnel, adults are large and piscivorous with kokanee as the predominant prey. In smaller lakes, the rainbow trout mature at a much smaller size (i.e. 30 - 50 centimetres) and feed mostly on insects. (E. Parkinson, Fish and Wildlife Branch, B.C. Environment, University of British Columbia (UBC), Vancouver, pers. comm. 1992). Rainbow trout life history is illustrated in Figure 6.

Rainbow trout generally spawn in the spring with migration into spawning streams before ice break-up. Females construct redds in the gravel into which the eggs are deposited. Young emerge from the gravel in the summer and usually migrate into rearing areas of streams or lakes in the first year. However, juveniles of lake dwelling populations that spawn in outlet streams may remain in the natal stream over the first winter. Normally the fish remain in the rearing lake or river until they reach maturity in 2 to 4 years, before moving back to the natal streams for spawning. Rainbow trout exhibit a wide range of growth rates depending on habitat, food type and availability, and life history strategy.

FIGURE 6 - RAINBOW TROUT LIFE HISTORY



While geographical location can account for differences in growth rates, local conditions tend to have a greater influence on growth and size, often masking general geographic variability. Generally the growth of rainbow trout is slower in streams than in lakes and greatest in the marine environment (Carlander 1969). The diet is dependent on the season and the size of the fish. Prey can be categorized into four groups; zooplankton, benthic invertebrates, terrestrial insects, and fish (Andrusak and Parkinson 1984).

Rainbow trout exhibit seasonal movements to access suitable habitat for feeding or overwintering. Such movements can take place within a small section of a tributary stream or within several kilometres in larger systems.

Basic habitat requirements for riverine rainbow trout were characterized by Raleigh et al. (1984) as being stream and river habitat with a pool-to-riffle ratio of 1:1; relatively stable flows and temperature regimes; clear, silt free, and cold water; rocky substrate; and vegetated stream banks. Most lakes supporting rainbow trout are mesotrophic while some are eutrophic. However, lakes that support important populations of rainbow trout are generally oligotrophic and have inlet or outlet streams that contain suitable spawning gravels. Lake resident Kamloops trout require adequate shallows and vegetation for good food production (Scott and Crossman 1973). Nilsson and Northcote (1981) reported that in coastal lakes, rainbow trout will use most areas, i.e. shallow littoral, mid-lake and surface areas provided there is no competition from other species such as cutthroat trout. The key limiting factors for lake populations include low dissolved oxygen concentrations in winter giving rise to winter kill, summer temperatures greater than 20-25 °C with inadequate oxygen concentrations, competition from other species, and inadequate spawning and rearing streams (E. Parkinson, pers. comm. 1992). Observed habitat use and selected biological characteristics of rainbow trout are presented in Table 3 and discussed throughout the text.

Table 3. Observed habitat use and selected biological characteristics by life stage for rainbow trout (for sources refer to text, NA- data are not available).

Eggs	
Temperature tolerance range	2 - 20°C
Optimum incubation temperature	11°C
Recommended oxygen concentration	> 5.3 mg/L
Lower lethal oxygen concentration	4.3 mg/L
Range of incubation time	18 - 102 days
Incubation time at optimum temperature	28 - 49 days
Lower lethal pH	5.3
Recommended intergravel current velocity	(yields 50% mort @ 5.3 mg/L DO) 2 cm/s
Optimal depth	NA
Substrate	gravel with < 5% fines
Juveniles	
Temperature tolerance range	0-24°C
Optimum temperature for growth	10-14°C
Recommended oxygen concentration	> 7 mg/L
Lower lethal oxygen concentration	3 mg/L
Habitat type preference	margins of lakes or streams
Depth preference	3 to 6 m in lakes, 0.3 - 1.2 m in streams
Preferred current velocity	8 - 20 cm/s
Substrate	cobble/boulder and rubble
Cover	cobble, woody debris
Turbidity tolerance	NA
Primary food category	benthic invertebrates and terrestrial insect larvae
Secondary food taxa	zooplankton, adult insects
Adults	
Temperature tolerance range	0-28°C
Optimum temperature for growth	10-14°C
Recommended oxygen concentration	>7 mg/L if<15°C,>9 mg/L if >15°C
Lower lethal oxygen concentration	3 mg/L
Habitat type preference	lakes and streams
Depth preference	variable, based on water temperature
Preferred current velocity	20 - 30 cm/s
Substrate	cobble to boulder
Cover	light intensity, debris, boulders
Turbidity tolerance	NA
Primary food type	terrestrial insect larvae, benthic invertebrates
Secondary food type	fish
Form of reproduction	iteroparous
Nest construction	yes
Spawning habitat type	small streams
Preferred spawning temperature	7.2-13.3°C
Preferred spawning depth	0.15 - 2.5 m
Preferred spawning substrate	typically 4 - 100 mm
Preferred spawning current velocity	30 - 90 cm/s
Range of first age-at-maturity	1 - 4 yrs
Range of fecundity	200-13,000 eggs/kg

3.3.2 Eggs and Incubation

Incubation time is dependent upon water temperature. Laboratory studies by Murray (1980) reported that at 14°C it took 32 days for 50% of the fry to emerge, at 5°C 102 days and at 2°C eggs did not survive.

Sowden and Power (1985) reported that there was no survival of pre-emergent rainbow trout if mean oxygen concentrations were less than 4.3 mg/L. Generally, the mean oxygen concentration should be above 5.3 mg/L and even then the survival rate is dependent on the rate the water passes through the redds. Sowden and Power (1985) found that at mean oxygen concentrations of 5.3 mg/L survival is negligible if the water velocity is near zero, while at a velocity of 2 cm/s survival is about 50%.

The source of oxygenated water passing through redds has a bearing on the substrate required for successful development of the eggs. In streams where the oxygenation of water passing through the substrate comes from exchange with surface water, substrate size and permeability will affect the rate at which dissolved oxygen reaches developing eggs. In streambeds that receive water from groundwater sources, substrate size and composition has less influence on the transport of dissolved oxygen to developing eggs (Sowden and Power 1985). Therefore, the percentage of fines in the spawning gravel will have less impact on egg survival if the spawning area is fed by groundwater. However, the ability of fines to entrap alevins also affects survival. Witzel and MacCrimmon (1981), in a laboratory setting, studied the survival and emergence of rainbow trout fry from different gravel substrates. They found that there was a significant correlation among survival to emergence, time of emergence, condition at emergence, and gravel size. In substrates of the 2 - 8 mm size categories there were high egg mortality rates (70-100%). Decreasing gravel sizes below 16 mm increasingly entrapped alevins during emergence and in gravels less than 5 mm alevins had to displace gravel to emerge. For optimal egg survival and emergence of alevins the gravel should contain less than 5% fines. If fines exceed 30% of the substrate composition, egg survival is greatly reduced and emergence of alevins is compromised (Raleigh et al. 1984). Optimal substrate for incubation is between 3 and 100 mm with the average size between 15 to 100 mm in diameter.

Gunn and Keller (1980) reported that rainbow trout eggs and alevins are sensitive to low pH conditions. At a pH of approximately 5.3, the survival rates of eggs were higher than that of the alevins, however, the egg to alevin mortality rate exceeded 98%. There was no specific indication of an upper limit of pH tolerance for eggs or alevins.

3.3.3 Rearing, Food, and Growth

Fry generally emerge from the gravel 45-75 days after spawning with approximately 639 accumulated thermal units (ATU) i.e. degree days above 0°C (Carlander 1969). Scott and Crossman (1973) reported that incubation takes 28-40 days and alevins take an additional 7-14 days to absorb the yolk and emerge from the gravel. Thus fry usually appear from mid-June to mid-August.

Carlander's (1969) summary of survival rates documented a range of 42-92% survival from eggs to fry while only 4 to 11% of the fry survived to emigrate downstream.

As fry emerge from the spawning gravels they move into riffle areas where they remain for most of the summer. Out-migration from tributary streams to Kootenay Lake generally occurs between the end of July and the beginning of September (Northcote and Hartman 1988). Fry of stream dwelling populations move into pools in the fall and winter (McPhail and Lindsey 1970). Fry from lake and river dwelling populations usually migrate to the lake or mainstem sometime in their first summer or fall. McPhail and Lindsey (1970) report that in some cases fry will overwinter in the natal stream. This behaviour is particularly common for fry in outlet streams; they often do not migrate upstream to the lake until the following spring.

Kelso and Northcote's (1981) study of inlet and outlet spawning stocks of rainbow trout indicated that fry from each strain showed different responses to water currents. Each strain exhibited the appropriate response to promote movement of fry toward the lake from their respective natal streams, i.e. outlet spawners tended to swim upstream or hold position in currents, while inlet spawners moved downstream. Kelso and Northcote (1981) postulated that this behaviour may be genetically controlled. The study found little difference in movement patterns between conditions of light and dark.

Recently emerged fry that spend time rearing in streams are found in water velocities of less than 30 cm/s and prefer velocities less than 8 cm/s. Fry will move to deeper, faster water as they grow, using interstices between rocks, debris piles, and aquatic vegetation for cover. The optimal temperature for fry is between 10 and 14°C. The upper lethal temperature is dependent on acclimation but is approximately 24°C .

As mentioned above, diet is dependent on season and fish size and can be catagorized as zooplankton, benthic invertebrates, terrestrial insects, and fish. The dominant zooplankton consumed are larger species such as *Daphnia* spp., *Gammarus* spp., leeches, mollusks, and larvae of aquatic insects are common benthic food organisms consumed. In areas where forage fish are present they do not become a common prey item until rainbow trout reach 25 to 30 cm. Fry of introduced rainbow trout in southeastern Ontario fed primarily on larval forms of ephemeropterans, trichopterans and dipterans followed by adult insects (Rose 1986).

In Kootenay Lake, rainbow trout do not feed extensively on bottom invertebrates or zooplankton. All sizes of rainbow trout consume terrestrial insects with the larger fish also preying on kokanee (Parkinson et al. 1989). Renewable Resources (1979) reported that resident fish in Farrell Creek, a tributary to the Peace River, fed on adult coleoptera as the most abundant food organism. Ephemeroptera nymphs where found in the largest percentage of stomachs, and sculpins were the only fish found.

Northcote and Hartman (1988) observed rainbow trout in streams tributary to Kootenay Lake and found that in streams with falls that form natural barriers, fry upstream tended to be smaller than fry downstream of the falls. This was attributed to both genetic factors and the higher productivity and macroinvertebrate drift in stream sections below falls.

Anderson (1978) reported that Kamloops trout in Pend Oreille Lake grew rapidly once they reached their fourth year and were approximately 43 cm, at which time kokanee became the dominant food item.

The table below summarizes some of the observations made and underscores the variability in the growth pattern of this species:

AGE	LENGTH (cm)			
	Andrusak & Parkinson (1984) Kootenay Lake	Scott & Crossman (1973) Okanagan Lake	Mean	Carlander (gen) (1969) Range
1+	22.6	6.5	13.0	2.8 - 27.9
2+	31.5	12.0	21.6	5.3 - 55.9
3+	45.6	29.0	29.2	10.2 - 71.1
4+	59.8	43.5	37.8	11.9 - 80.5
5+	70.1	51.5	48.6	14.2 -101.2
6+	74.3	59.0	60.5	15.7 - 90.9
7+	72.0	71.0	70.3	17.8 - 103.4
8+			65.3	19.6 - 95.3
9+			70.1	48.3 - 88.4

Young (1987) reported that rainbow trout growth rates were significantly reduced when exposed to dissolved oxygen concentrations below 5 mg/L. Several studies (Cordone and Kelly 1961; Crouse et al. 1981) have found that siltation can reduce the production of invertebrate fauna and the availability of instream cover for fry and adults. Raleigh et al. (1984) suggested that percent of fines in riffle areas should not exceed 10%.

Appropriate instream and overhead cover is also important for rainbow trout production, providing resting areas, refuge from predators, and overwintering habitat. Riparian vegetation is also an important component of stream cover, particularly for smaller streams as it can help stabilize channel erosion, maintain undercut banks, and provide shading that limits the warming of stream waters. Wesche et al. (1987) reported results of a study to determine the relative importance of different types of cover in small streams in Wyoming. Over-head bank cover, provided primarily by riparian vegetation, statistically explained the greatest amount of the variation in trout populations.

Juvenile rainbow trout show a preference for cobble and boulder substrate between 10 and 40 cm diameter and were most commonly found in substrate this size in the riffle sections of streams. The cobble/boulder substrate probably provides overwintering habitat and refuge from predators and overwinter habitat (Bustard and Narver 1975; Raleigh et al. 1984). A high level of fines in the gravel will fill the interstices and reduce escape habitat for fry. Studies reported by Raleigh et al. (1984) and Rose (1986) indicate that larger juvenile fish, 5 to 13 cm in length, are found in velocities between 10 and 12 cm/s with a maximum of 22 cm/s. Age 1+ juveniles make greater use of logs and upturned roots for overwintering habitat than overhanging vegetation and cobble (Bustard and Narver 1975). Depth ranges in stream dwelling juveniles was 0.3 to 1.2 m. In lakes juveniles were found between 3 and 6 metres depending on the time of year.

As rainbow trout grow they move into faster and deeper water. There is a trade-off in energy efficiencies in this behaviour. Everest and Chapman (1972) reported a positive correlation between water velocity and insect drift but there is a high energy cost to the fish in maintaining position in fast moving water. Larger fish were often observed in high velocity, mid-stream areas where food availability was highest. However, they remained close to the bottom where mid-channel water velocities were lowest.

Lake dwelling rainbow trout are found at depths related to temperature, dissolved oxygen, and food availability. Generally, adults will stay at depths below the 18°C isotherm and avoid areas where dissolved oxygen concentrations are below 3 mg/L if possible (Raleigh et al. 1984).

Raleigh et al. (1984) suggest that the optimal temperature and oxygen conditions for adult rainbow trout should be 7 mg/L of dissolved oxygen in water below 15°C and 9 mg/L in water above 15°C. The lower lethal limit of dissolved oxygen concentration is 3 mg/L;

areas with lower concentrations (e.g. at depth in certain circumstances) will be avoided if possible.

Adults have been observed in water temperatures from 0 to 28°C, however, temperatures over 22°C can be lethal depending on acclimation temperature and exposure time (Carlander 1969). The upper lethal limit of temperature for rainbow trout adults and subadults is 27°C (Lee and Rinne 1980). Adults show a preference for water temperatures between 7 and 18°C (Raleigh et al. 1984) and optimal growth occurs at 10-14°C (Carlander 1969).

Rainbow trout are not very tolerant of low pH. In natural waters the lower tolerance reported in Gunn and Keller (1980) was pH 5.5 - 6.0. Laboratory studies have reported tolerance for lower pH levels but other factors such as the synergistic effect of low pH and metal toxicity that may occur in the natural environment were not taken into account. Raleigh et al. (1984) suggest that the upper pH limit is 9.5.

3.3.4 Maturity, Adult Migration and Spawning

Generally, rainbow trout mature between ages 3+ and 5+. Males may mature as early as 1+ whereas females spawning for the first time can be as old as six years. Size at maturity is also variable depending on habitat and life history type. For example, rainbow trout from small streams can mature when they are 15 to 25 cm in length (Scott & Crossman 1973). The Gerrard stock of rainbow generally mature at an older age with ninety percent of the fish spawning for the first time at ages five and six and ranging in size from 43-89 cm (Andrusak and Parkinson 1984).

Iteroparity is common in interior rainbow trout populations. Scott and Crossman (1973) reported that survival after spawning is usually low and the number of repeat spawners is often less than 10% of the total spawning population. Carlander (1969) reported a range of 18 to 33% while Erman and Hawthorne (1976) found that repeat spawners (mostly 3+ fish) consistently made up 26% of fish migrating upstream to spawn. Poor food conditions may be the cause of low survival rates after the first spawning (Carlander 1969).

As mentioned above, migration to spawning areas of streams often begins before ice breakup with spawning occurring between March and August, depending on location and water temperature. There can be considerable variation in spawning period among populations, ranging from early winter to late spring. Scott and Crossman (1973) found that most populations in British Columbia spawn between mid-April and late June. Hartman and Galbraith (1970) observed Gerrard stock rainbow moving into the spawning area of the Lardeau River in April with spawning occurring in May. The movement of these fish into the spawning area coincided with the initial increase in water levels and with water temperatures of 5°C (Hartman 1969). Northcote and Hartman (1988) reported that spawning in the lower sections of tributary creeks to Kootenay Lake probably occurred in June with young-of-the-year first appearing in the stream in July. Populations upstream of falls spawned later than those downstream. Timing of spawning runs within one lake can differ with outlet spawning often beginning one month later than inlet spawning (Hartman et al. 1962; Tautz and Land 1976). Rainbow trout are also known to spawn in the fall but this is not common (Carlander 1969). Some hatchery reared and hybrid forms have been known to spawn in suitable gravel along lake shores (Penlington 1983; Raleigh et al. 1984). Rainbow trout are also known to spawn in intermittent tributary streams where fry emergence and movement downstream to more permanent trout habitat occurs prior to the stream channel drying up in mid-summer or early fall (Erman and Hawthorne 1976).

In the Peace River system rainbow trout tagged while on spawning grounds have been observed migrating up to 55 km downstream from the spawning tributary, into the Peace River (Renewable Resources 1979). Conversely rainbow trout in small streams have been reported to occupy small home territories throughout their lifetime and did not exhibit significant upstream or downstream movements (Cargill 1980; Ensign et al. 1990).

Females spawn with more than one male and dig more than one nest. Erman and Hawthorne (1976), reporting on a resident population of rainbow trout in the Sierra Nevada mountains, found that the males always entered spawning streams before the females, were on average a year younger than females, and usually outnumbered females 3:1.

The female deposits between 200 and 9000 eggs in each nest. Scott and Crossman (1973), reporting the egg numbers in British Columbia populations, found that females can produce as few as 200 and as many as 12,700 eggs. Fish size influences fecundity but not egg size. Carlander (1969) reported a range of 700 to 4000 eggs per kilogram of female fish with an average total number of eggs being 1500.

Raleigh et al. (1984) summarized information on spawning habitat used by rainbow trout and suggested that the optimal water velocity range is 30 to 90 cm/s, in water depths between 0.15 and 2.5 m. However, the main consideration with depth is that spawning areas have sufficient flow of water for incubation and for the fry upon emergence. Substrate size will be somewhat dependent on fish size. In general, rainbow trout spawn in substrate ranging from silt to 10 cm cobble. The large Gerrard strain of rainbow trout spawning in the Lardeau River use gravels 15 to 53 cm in size, even though smaller gravel was available but was not used (Hartman and Galbraith 1970). Most redd building and spawning of this stock occurred in water velocities between 50 and 90 cm/s with an upper limit of 150 cm/s. McPhail and Lindsey (1970) reported that rainbow trout in northwestern Canada usually spawn in gravel areas at the head of riffle areas just below pools. Hooper (1973) in Walburg et al. (1981) reported the spawning temperature for rainbow trout as ranging between 7.2 and 13.3°C, with 11°C optimal.

Rainbow trout maximum age and size also depends on geography, habitat, food resources and phenotype. Populations in streams and small lakes rarely exceed 3+ or 4+ and 50 cm, while Great Lakes populations may live for 6 to 8 years (Scott and Crossman 1973). In small, unproductive tributary streams adults rarely exceed 21 cm. The Kamloops variety rarely exceeds 4 kg; the largest, taken from Jewel Lake, B.C, weighed 23 kg. The

Gerrard strain generally ranges between 3 and 12 kg (Hartman 1969).

3.4 Mitigation and Compensation Strategies

Rainbow trout rely on the availability of clear, cool, tributary streams with gravel substrates for successful spawning and rearing. These tributary streams are probably the most sensitive component of rainbow trout habitat. Lakes and main rivers have the capacity to assimilate impacts that would destroy trout habitat in small streams. Those life stages that depend on tributary stream habitat for survival are therefore the ones most susceptible to environmental degradation.

Flow conditions, water quality, and available cover determine the capacity of streams to support successful hatching of eggs and development of fry. Low flow conditions are often cited as the most limiting factor in trout bearing streams. Refuge from low water temperatures, ice formation, and low flows during winter may be equally or more critical than the availability of summer rearing habitat during low flows (Bustard and Narver 1975; Raleigh et al. 1984). A general guideline for evaluating flow reductions or general stream suitability for trout production is the base or lowest flow of late summer or winter months. A base flow of greater than 55% of the average annual daily flow is considered excellent, 25 to 50% is considered fair and less than 25% is considered poor for maintaining good trout habitat (Raleigh et al. 1984).

Rainbow trout are extensively stocked throughout British Columbia. The majority of hatchery produced fish are put into lakes that either cannot naturally support rainbow trout or have insufficient natural production to satisfy sport fishing demand. Between 1988 and 1990 an average of 6.4 million rainbow trout were stocked into approximately 740 lakes and rivers in British Columbia (P. Slaney, Fish and Wildlife Branch, B.C. Environment, Victoria, pers comm. 1991).

Spawning channels may not be as successful as hatcheries for offsetting the loss of rainbow trout. In eastern British Columbia, a spawning channel at Whiteswan Lake, in the Kootenay River drainage, has yet to have egg survival much over one percent. The specific reasons for egg mortality are uncertain but there appears to be some critical period during incubation when water temperature or some other parameter causes high mortality. The by-products of decaying eggs further decreases the survival of the remaining viable eggs (G. Oliver, Fish and Wildlife Branch, B.C. Environment, Cranbrook, pers. comm. 1991). The specific design of the Whiteswan spawning channel has been linked to the poor egg survival. If the design were optimized, with useable substrate, good oxygen concentrations, proper temperatures, etc., the spawning channels would be expected to perform well (E. Parkinson, pers. comm. 1992).

More natural techniques for improving spawning and rearing habitat or compensating for lost instream habitat have been developed and successfully applied in small streams (Parkinson and Slaney 1975; Department of Fisheries and Oceans and British Columbia Ministry of Environment 1980; Hall and Baker 1982; Reeves and Roelofs 1982; Adams and Whyte 1990; and Marcus et al. 1990). These techniques include various forms of:

1) current deflectors, usually extending out from the stream bank and constructed of boulders, which enhance the natural meander pattern of a stream and increase pool depths and bank undercutting,

2) low-profile check dams that span the channel and are constructed of boulders, gabions or logs, which increase the depth of pools or runs,

3) boulder groupings and anchoring of large root wads or logs in mid-channel to create cover for rearing juveniles,

4) bank cover treatments including planting willow or other native species to stabilize stream banks, increase shading over the stream and provide cover, and

5) sediment removal from spawning areas.

As a rule of thumb, for the successful installation of instream habitat structures, the river or stream should have a wetted perimeter of 15 m or less (P. Slaney, pers. comm. 1991). Compensation techniques for larger riverine systems are just now being evaluated and include placement of boulder groupings and stream fertilization. For lakes, compensation could include aeration (to increase oxygen concentrations to mitigate winter kill), fertilization, or eradication of non-native species (E. Parkinson, pers. comm. 1992).

The effectiveness of habitat improvement techniques generally depends on accurately identifying the factors limiting the production of trout on a site-specific basis. For example, installing structures that improve spawning habitat will not be effective in increasing overall productivity of a stream if overwintering habitat is limiting production. It is also necessary to choose structures that match the hydrology and morphology of the stream channel to maximize the life of instream structures. In stable streams of Minnesota and Wisconsin, the lifespan of a stream improvement structure was 20 years, whereas in California freshets destroyed structures in only a few years (Parkinson and Slaney 1975). The fish species composition in the stream must also be considered when determining the appropriate habitat enhancement strategy. Trout will adjust their habitat utilization to minimize interspecific competition, therefore species-specific habitat utilization and limiting factors will vary depending on the other species present.

The lack of woody debris in stream channels has been identified as a potential limiting factor in the production of rainbow trout in streams in the Kootenay Region of British Columbia. Attempts to increase the channel area covered with woody debris will be accomplished through the installation of debris catchers. This technique has proven effective in the Nechako River (P. Slaney, pers. comm. 1991).

Managing sediment input to streams can be accomplished through revegetation and bank stabilization programs or by constructing sediment basins within the stream channel. For example, these techniques were effective in reducing the sand bedload in a Michigan trout stream. The basin reduced sandy sediment by 86%, from 56 mg/L to 8 mg/L, with a resultant increase in the number of 0+ and 1+ rainbow trout (Alexander and Hansen

1983). The increase was attributed to improved microhabitat in the form of cobble and other types of instream cover that were previously covered in sandy sediments. While sediment basins can improve fish habitat by initiating scouring to create deeper pools and reduce sediments in spawning gravels, they are not suitable for all streams. If the sediment basin traps a significant portion of the bedload it could upset the stream-sediment equilibrium and cause serious erosion downstream (Hansen et al. 1983). Streams with steep gradients and large bedloads may not be suitable for instream sediment traps.

Riparian vegetation is also important for controlling bank erosion. Characteristics of good trout habitat include buffer strips approximately 30 m wide of which 80% should be either well vegetated or have stable rocky stream banks to provide adequate erosion control and maintain undercut stream banks (Raleigh et al. 1984).

Logging and associated road building can be responsible for a number of impacts on rainbow trout habitat including increased sedimentation, degraded water quality, destabilized stream channels and reduced cover. Logging has resulted in the loss of stream side conifers and post logging clean-up has reduced or eliminated large organic debris (LOD) in stream channels. This condition can persist for several decades until a mature coniferous forest is reestablished (House and Boehne 1986). Anchoring artificial rootwads and other forms of LOD in the streambank or in mid-channel prompted rainbow trout to use parts of the stream channel not used in the absence of LOD. Salmonid biomass was observed to be significantly greater in enhanced sections compared with those sections devoid of LOD (House and Boehne 1986; Shirvell 1990). The addition of rootwads trapped gravel, stabilized spawning gravel, and created resting pools and cover (Marcus et al. 1990).

Impacts associated with mining include increased concentrations of heavy metals or increased acidity of stream or lake waters. Heavy metals can come out of solution, inhibit production of periphyton and benthic macroinvertebrates, and decrease spawning success (Marcus et al. 1990). Acidic conditions may delay spawning and reduce survival of eggs and fry. Rainbow trout seem to be less tolerant of acidic conditions than other salmonids. Gunn and Keller (1980) found that the life stage immediately after hatching was most susceptible to acidic conditions. Incubation boxes with limestone mixed into the gravel significantly increased survival of eggs and alevins. Gunn and Keller (1980) suggested that mixing limestone into the gravel of spawning beds could improve the survival of post-emergent rainbow trout. This could be effective if the acidic conditions occur during the period of incubation and emergence or if further steps are taken to buffer the water in the rearing habitat.

Livestock grazing can have a significant impact on the riparian habitat of streams. Stream banks can be damaged and stream side vegetation removed causing siltation and reduced cover for resident trout. Keller and Burham (1982) studied the effect of livestock grazing on trout habitat. When fencing was used to exclude livestock, rainbow trout were 1.5 times more abundant in the protected areas than in the grazed areas. Within the fenced areas, the stream channel tended to be narrower, the water deeper, the banks more stable, the aquatic plants more abundant, and pool habitat of higher quality.

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4.0 WESTSLOPE CUTTHROAT TROUT

(Oncorhynchus clarki lewisi)

4.1 Introduction

Cutthroat trout were originally classified as *Salmo clarki*. However, in June 1988 the American Fisheries Society changed the genus of native "*Salmo*" trout of the Pacific Ocean drainages to "*Oncorhynchus*" and cutthroat trout are now classified as *Oncorhynchus clarki*. the This change came about because Pacific coast *Salmo sp.* are more closely related to the Pacific salmon than they are to Atlantic and Eurasian *Salmo sp.* (Smith and Stearley 1989).

Cutthroat trout are a popular sport fish in British Columbia. The common name is derived from distinctive yellow or orange-red lines on the underside of the lower jaw. Individuals show "a bewildering array of colours and pigment patterns, different from watershed to watershed and between the anadromous and inland stocks" (Scott and Crossman 1973).

Cutthroat trout began separating into distinct evolutionary lines approximately one million years ago. As a result, the classification of subspecies has been challenging; Scott and Crossman (1973) identified two forms of *Salmo clarki* indigenous to British Columbia, the coastal cutthroat trout and Yellowstone cutthroat trout. More recently Behnke (1988) presented a classification of fourteen subspecies of *Oncorhynchus clarki* with two forms being indigenous to British Columbia. The more common in B.C. and over the entire cutthroat range is the coastal cutthroat, *Oncorhynchus clarki clarki*. The other form of cutthroat trout found in British Columbia was classified as the westslope cutthroat trout, *Oncorhynchus clarki lewisi* which Scott and Crossman (1973) and Carl et al. (1967) referred to as the Yellowstone cutthroat trout. This report focuses on the life history of *O. c. lewisi*. However, since there is a great deal of both variation and similarity among subspecies, information on other forms will be presented to augment that on *O. c. lewisi*.

The westslope cutthroat trout is a major subspecies of *O. clarki* and probably represents the first evolutionary divergence from the coastal cutthroat. Westslope cutthroat were initially found over a greater range than is the case today. Rainbow trout replaced populations of westslope cutthroat during the last glacial-postglacial period in the mid-Columbia basin below barrier falls on the Kootenay, Pend Oreille, and Spokane Rivers. Indigenous forms of westslope cutthroat and rainbow trout coexisted in only a few drainages in Oregon and Idaho (Behnke 1988).

Westslope cutthroat evolved in sympatry with other salmonids, particularly bull trout, *Salvelinus confluentus*, and mountain whitefish, *Prosopium williamsoni*, in areas west of the continental divide. In cases where westslope cutthroat exist below barrier falls, they have been found with the Kamloops strain of rainbow trout. East of the continental divide westslope cutthroat evolved with mountain whitefish and Arctic grayling, *Thymallus arcticus* (Liknes and Graham 1988).

The Yellowstone cutthroat subspecies, now classified as *Oncorhynchus clarki bouvieri*, is native to the Yellowstone River drainage in Montana and Wyoming and portions of the Snake River drainage in Wyoming, Idaho, Nevada, and Utah (Varley and Gresswell 1988). The Yellowstone cutthroat was perhaps the most widely transplanted of the cutthroat trout. Eggs from the Yellowstone Lake population have been widely distributed over the United States, most provinces of Canada, and overseas. For example, Carl et al. (1967) reported that Yellowstone cutthroat were introduced in lakes around the Mount Assiniboine Park area, throughout other parts of the Kootenay, and in coastal waters. Some introductions to British Columbia have established viable populations. However, Varley and Gresswell (1988) noted that the Yellowstone Lake population of *O. c. bouvieri* was perhaps least able to adapt to different environments and competed poorly with other fish populations. Hence, it was often not capable of establishing viable populations in new waters.

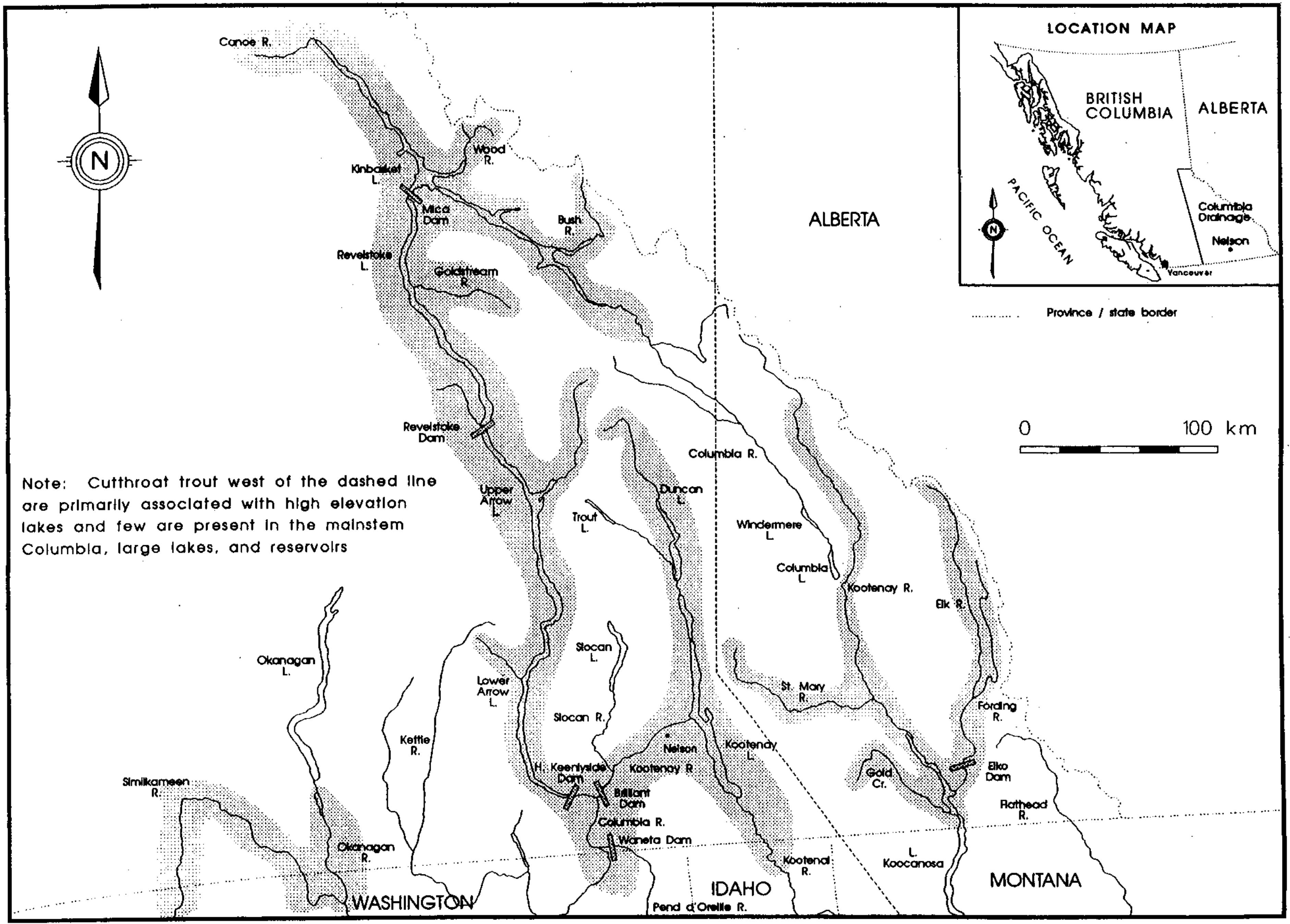
4.2 Distribution

The westslope cutthroat trout range extends from Idaho, through Montana, northwestern Wyoming, southwestern Saskatchewan, southern Alberta and southeastern British Columbia. In British Columbia, they are present in the Columbia and Fraser river systems (Scott and Crossman 1973; Carl et al. 1967). Specimens collected by C.J. Dymond in 1931 from tributaries in the upper Thompson and Fraser Rivers (near Mt. Griffin) and upper Columbia near Revelstoke were classified as *Salmo clarki alpestris*, the mountain cutthroat. Subsequent review of the original specimens suggests that these were an isolated form of *O. c. lewisi* (Trotter 1987). Figure 7 shows westslope cutthroat trout distribution in the Columbia River drainage.

4.3 Life History and Habitat Requirements

4.3.1 General

Cutthroat trout have proven to be very adaptable to their environment resulting in considerable variation in life histories, even within subspecies. Generally there are three life history types of the westslope cutthroat (Liknes and Graham 1988; Trotter 1987). These are adfluvial populations that spawn in tributary streams and migrate to lakes to grow to maturity, fluvial populations that move between the mainstem of rivers and headwater streams, and resident populations that remain in small headwater tributaries for their entire life. Lake dwelling cutthroat trout are generally found in clear, cold alpine lakes but are also found in larger oligotrophic lakes such as Kootenay Lake. The lake must have inlet or outlet streams with gravel substrate that can be used for spawning. Cutthroat trout are iteroparous and generally spawn in small streams with gravel substrate that are tributary to rivers and lakes. There is considerable variation in spawning time; Scott and Crossman (1973) reported spawning in the period February to May, Shepard et al (1984) in May and June and Northcote and Hartman (1988) in July and August. The latter two observations are from the Columbia drainage.



Note: Cutthroat trout west of the dashed line are primarily associated with high elevation lakes and few are present in the mainstem Columbia, large lakes, and reservoirs

Figure 7: Cutthroat Trout Distribution in the Columbia Drainage, British Columbia

Redds are constructed by the female. Emergent fry spend variable lengths of time in natal streams. Migratory populations may spend as little as a few months to as long as 4 years in their original streams (Liknes and Graham 1988). Once in rearing areas the river and tributary dwelling populations may make minor migrations to access appropriate winter habitat. Cutthroat trout in lakes generally grow faster than those in streams and the smaller the stream the slower the growth (Carlander 1969). Cutthroat trout life history is illustrated in Figure 8 .

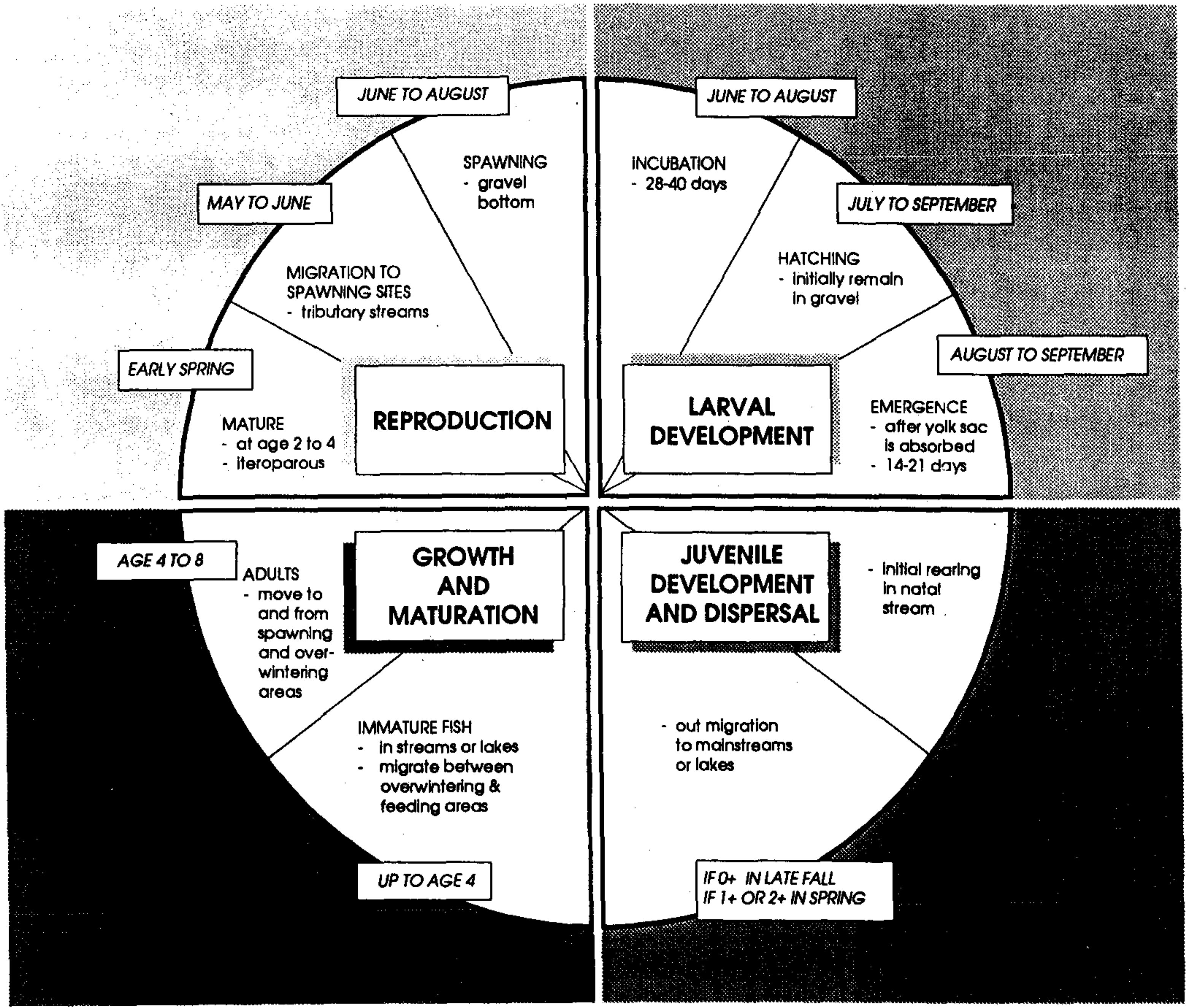
Generally, cutthroat trout are opportunistic feeders that consume various invertebrates; in most areas they are not known to be highly piscivorous. Liknes and Graham (1988) suggested that invertebrates are a preferred food item because cutthroat trout evolved with piscivorous bull trout and northern squawfish, and feeding on insects minimized competition with these species. Carlander's review (1969) identified snails, fish eggs, fry, sticklebacks, frogs, and earthworms as additional food items for various populations of cutthroat trout.

Westslope cutthroat migrations include spawning, smolting, movements to overwintering habitat, and movements to improved food availability. Movements of specific populations seem to depend on a number of factors including the amount of habitat in natal streams for overwintering, the flow regime of spawning and rearing streams, and the distance to and productivity of lake rearing habitat. Lake rearing populations will utilize inlet and outlet streams, (Raleigh and Chapman 1971) with emerging fry moving downstream or upstream to rearing areas in the lake in the fall of their first year or in late spring or early summer if outmigration occurs in the second or third year.

Cutthroat trout are found in a wide range of habitats, from lowland, coastal streams and lakes with gravel substrate to inland alpine lakes and small rivers, up to elevations of 2400 m (Scott and Crossman 1973). Hickman and Raleigh (1982) characterized optimal river habitat as:

> "clear cold water; a silt free rocky substrate in riffle run areas; an approximately 1:1 pool-riffle ratio with areas of slow, deep water; well vegetated stream banks; abundant instream cover; and relatively stable

FIGURE 8 - CUTTHROAT TROUT LIFE HISTORY



water flow, temperature regimes and stream banks".

Observed habitat use and selected biological characteristics of cutthroat trout are presented in Table 4 and discussed throughout the text.

4.3.2 Eggs and Incubation

Scott and Crossman (1973) reported that an incubation time of 6-7 weeks and a further 1-2 weeks before emergence from the gravel is typical for cutthroat trout. There is a wide range in the mortality of eggs during development, ranging from 6 to 74% (Carlander 1969). Kiefling (1978) found that egg survival was correlated to the percentage of fines in the substrate. For interior forms Scott and Crossman (1973) reported emergence occurring in August, which is consistent with findings by Northcote and Hartman (1988), while in the Skookumchuck River emergence takes place in mid-July (B. Westover, Fish and Wildlife Branch, B.C. Environment, Cranbrook, pers. comm. 1992). Scarnecchia and Bergersen (1986) recorded fry emerging from mid-August through September. Moore and Gregory (1988b) found that emergence could continue for up to 3 weeks after the first fry is observed. Griffith (1972) observed cutthroat trout in northern Idaho streams spawning in May and June with fry emerging from the gravel in the last week of July. Even though the time of spawning varies among populations and appears to be related to water temperature and level, the actual incubation and time to emergence seems to be relatively consistent among the studies reported here. Shepard et al. (1984) found that westslope cutthroat in the Flathead River required 310 accumulated temperature units (ATU, i.e. sum of mean daily temperatures above 0°C) to hatch and that yolk-sac larvae remain in the gravel until the sac is absorbed.

Carlander's (1969) synthesis suggests that 10°C appears to be the optimal water temperature for incubation. Emergence occurred 2 to 3 weeks after hatching or at approximately 110 to 150 temperature units. Dissolved oxygen concentrations reported in spawning streams have been in the order of 9 mg/L with intergravel dissolved oxygen concentrations of 6 - 8.2 mg/L.

Table 4. **Observed habitat use and selected biological characteristics by life stage for westslope cutthroat trout.** (for sources refer to text, NA - no data are available)

Eggs

Temperature tolerance range	6 - 12° C
Optimum incubation temperature	10° C
Recommended oxygen concentration	6 - 8.2 mg/L
Lower lethal oxygen concentration	3 mg/L
Range of incubation time	28 - 49 days
Incubation time at optimum temperature	30 days
Lower lethal pH	NA
Recommended current velocity	NA
Optimal depth	(in a Flathead River study) 17-20 cm
Substrate	<5% fines & 2-64 mm gravel

Juveniles

Temperature tolerance range	0 - 22° C
Optimum temperature for growth	9-13°C
Recommended oxygen concentration	9-11 mg/L
Lower lethal oxygen concentration	3 - 5 mg/L
Habitat type preference	gravel/cobble substrate
Depth preference	up to 40 cm
Preferred current velocity	7-12.5 cm/s
Turbidity tolerance	NA
Primary food category	dipterans, ephemeroptera
Secondary food taxa	trichoptera, plecoptera

Adults

Temperature tolerance range	(<20°C preferred) 0 - 22° C
Optimum temperature for growth	10-13° C
Recommended oxygen concentration	9 mg/L
Lower lethal oxygen concentration	3 mg/L
Habitat type preference	riffle - pool complexes
Depth preference	in streams = 50 cm
Preferred current velocity	10 - 14 cm/s; 36 - 44 cm/s in St. Mary River
Turbidity tolerance	NA
Primary food type	ephemeroptera, terrestrial insects
Secondary food type	*Daphnia* , fish (for larger cutthroat)
Form of reproduction	iteroparous
Nest construction	redds approx. 0.7 X 0.4 m
Spawning habitat type	small gravel tributary streams
Recommended spawning temperature	6 to 17°C
Observed spawning depth	6 to 40 cm
Observed spawning substrate	2 - 64 mm gravel
Estimated optimal spawning velocity	30-60 cm/s
Range of observed first age-at-maturity	2+ to 5+ yrs
Range of observed fecundity	average 1100 - 1700 eggs

Westslope cutthroat fry emerge from the gravel at approximately 20 mm TL and first form scales at 38-44 mm. The estimated survival rate for eggs to fry ranged from 30 to 34% (Shepard et al. 1984). Carlander (1969) reported that fry in small, cold streams do not grow sufficiently to develop scales in their first year and Shepard et al. (1984) found that approximately 65% of westslope cutthroat in the Flathead basin did not form scales in the first year.

According to studies reported by Reiser and Bjornn (1979) spawning gravels used by salmonids should contain less than 25% fines (less than 6.5 mm diameter) in order to ensure optimal survival to emergence of fry. Kiefling (1978) observed increased mortality rate of cutthroat eggs with increased sediment in the redds. Optimal spawning gravels should contain less than 5% fines.

4.3.3 Rearing, Food and Growth

After emergence westslope cutthroat trout have been observed to immediately take up positions in stream margin habitat where they remain for up to one month (Moore and Gregory 1988b).

Moore and Gregory (1988b) also found that interior cutthroat fry less than 30 mm long consumed primarily chironomid larvae. As fry grew the percentage of chironomids consumed decreased but still remained the dominant food. Other important food included ephemeropterans and ostracods.

Benson (1960) and Raleigh and Chapman (1971) reported on the movements of cutthroat fry in natal streams that were inlets and outlets to lake rearing areas. The majority usually migrated in summer or early fall. The triggering stimulus for fry migration was thought to be receding water levels. Fry from larger streams often overwinter in the stream and move into lake rearing areas as yearlings or two year old juveniles in late spring and early summer. Shepard et al. (1984) suggested that fry that migrate in the fall do so in search of winter habitat, possibly in response to low winter carrying capacity of upstream areas.

Moore and Gregory (1988b) studied habitat preferences in tributary streams of the Cascade Mountains and found that fry abundance was proportional to the area of lateral habitat, e.g. stream margins, backwaters, and isolated pools. Soon after emergence, 65% of fry were found in stream margins, 30% in backwaters and 5% in isolated pools. Fry typically moved into deeper water as they grew, hence the proportion of fry utilizing lateral habitats decreased as time from emergence increased (Griffith 1972; Moore and Gregory 1988b; Shepard et al. 1984). Fry preferred a substrate of cobble, rubble, pebbles, and gravel with approximately 50% of the substrate being between 1.0 and 16.0 cm in size. Fry used crevices in the substrate and overhanging boulders or wood as refuge. For the first six weeks after emergence fry remained in water less than 20 cm deep. Focal depth was generally correlated to fish size with the maximum depth being 35 cm by the first fall (Moore and Gregory 1988a). In a study of high altitude streams in Colorado, an increase in the percentage of gravel substrate and decrease in velocities corresponded to increased biomass and production of young of the year cutthroat trout (Scarnecchia and Bergersen 1986).

Moore and Gregory (1988b) also recorded velocity preferences, temperature, and dissolved oxygen in fry habitat. Fry less than 30 mm inhabited very shallow areas with water velocities too low to measure(<1 cm/s). Fry over 30 mm were found in water velocities less than 1 cm/s and fry 55 mm and greater utilized areas where water velocities were greater than 5 cm/s. Griffith (1972) reported finding westslope cutthroat fry in velocities of 7 to 10 cm/s. Age 1+ and 2+ fish were utilizing areas with average water velocities between 10 and 12.5 cm/s and a maximum of 22 cm/s. Water temperatures in the lateral habitats were generally within 1.5°C of the temperature in the main channel, which was normally about 13°C in the summer. Dissolved oxygen concentrations were found near saturation in the areas inhabited by fry (9.0-11.5 mg/L depending on elevation and temperature). The lowest observed dissolved oxygen level, measured in an isolated pool containing fry, was 6.1 mg/L.

Cutthroat living in association with other trout species generally alter their feeding behaviour to minimize competition with the other species. Westslope cutthroat trout over 110 mm in Flathead and Priest Lakes, which contain populations of planktivorous kokanee, fed primarily on terrestrial insects whereas smaller individuals mainly fed on common insects in the benthos which included dipterans and ephemeropterans (Shepard et al. 1984). Westslope cutthroat trout in Kootenay National Park fed primarily on corixidae, terrestrial insects, and trichoptera (Alger and Donald 1984).

Idyll (1942), studying coastal cutthroat in the Cowichan watershed in British Columbia, found that the river population fed primarily on insects with fish becoming important only to larger cutthroats (< 20 cm). The lake dwelling trout did not focus on fish as a food item until they reached 40 cm and the largest cutthroats (50 cm) fed almost exclusively on kokanee. The dominant insects consumed were chironomidae for the smaller fish and trichoptera and simuliidae for the larger cutthroat.

Growth rates tend to increase after fish emigrate from natal streams. Shepard et al. (1984) found that cutthroat trout in tributary streams grew an average of 40-60 mm per year but in the year after migration grew 89-119 mm. Trotter (1987) estimated that the lake form of the westslope cutthroat reached approximately 178-229 mm total length (TL) by the time they migrated to the lake after two years of rearing in tributary streams.

In creeks tributary to Kootenay Lake, westslope cutthroat populations below barriers were statistically longer than fish above for all age groups (Northcote and Hartman 1988). Table 5 summarizes mean total length at age for the westslope subspecies and for cutthroat trout in general. As fish increase in size they migrate to deeper water in pool sections of the stream. Griffith (1972) found a positive correlation ($P < 0.01$) between depth and age of the fish.

Table 5. Total length of cutthroat trout as a function of age.

	LENGTH (mm TL)		
	Shepard et al.(1984) Westslope	Scott & Crossman(1973) Yellowstone[1]	Carlander(1969) General
AGE			
1+	55	46	180
2+	100	129	236
3+	146	225	292
4+	194	312	320
5+	251	393	406
6+	301	444	440

[1] The subspecies Scott and Crossman (1973) referred to as Yellowstone cutthroat trout would now be called westslope cutthroat trout.

Shapley (1961) studied the movements of cutthroat trout in Kiakho Lake of the Moyie River drainage (near Cranbrook, British Columbia) where the majority of young spent one to two years in the outlet stream before migrating upstream to the lake in late spring. Northcote and Hartman (1988) assumed that the majority of trout migrating into Kootenay Lake had done so by the time they reached an age of 2+. Northcote (1969) noted that cutthroat trout populations existing above barriers in headwater inlet streams of Kootenay Lake exhibited a strong, non-migratory behaviour. Some populations of juvenile westslope cutthroat have been observed moving out of natal streams into larger streams to overwinter before they migrate to the lake rearing habitat in spring or early summer. For juvenile and adult trout living in a stream with inadequate winter habitat, emigration to winter habitat usually occurs in the fall. Movement to winter habitat, usually crevices in the substrate, occurs when water temperatures drop to 4-5°C (Bustard and Narver 1975; Liknes and Graham 1988). The tributary populations of westslope cutthroat will migrate back upstream in early summer and spend the summer and fall in the home stream.

Cover is an important component of cutthroat habitat for all life stages. During summer, cover is used primarily for predator avoidance and resting. Bustard and Narver (1975) researched habitat of juvenile coastal cutthroat and found a preference for channels with clean gravel and overhanging bank cover for winter habitat. These cutthroat trout also used rubble (10-30 cm in diameter) as over-winter cover. Hickman and Raleigh (1982) suggested that cover areas of 15% and more than 25% are adequate for juveniles and adults respectively. Westslope cutthroat in the upper Fording River have been observed using groundwater-fed ponds as overwintering habitat as well as large substrate in sections of the mainstem and tributary streams (Allan 1987). There is little information in the literature on preferred lacustrine habitat for lake populations of cutthroat trout. However, it appears that habitat used by cutthroat can vary depending on the presence of competing fish species such as bull trout, and the entire lake will be utilized if there are no competing species.

Hartman and Gill (1968) recorded the pH of streams containing cutthroat trout to range between 6.0 and 8.8. Kiefling (1978) reported the pH of cutthroat streams in the Snake River drainage in the range of 8.2 and 8.8 and cutthroat in Idaho ranged between 7.3 and 7.9 (Hickman and Raleigh 1982). Total dissolved solids (TDS) recorded in cutthroat streams range between 60 mg/L in coastal streams (Hartman and Gill 1973) to 130 and 260 mg/L in interior streams (Kiefling 1978). The Lahontan subspecies (*O. c. henshawi*) have adapted to extreme TDS levels of 10,000 mg/L in some lakes of the Great Basin area of Nevada (Gerstung 1988).

Adults and sub-adults of tributary populations may move only short distances (100-300 m) from spawning areas to area with suitable feeding or wintering habitat (Scarnecchia and Bergersen 1986). Miller (1957) reported that of 98 trout tagged, 67% of recaptures were made in the original pool while the other 38% had moved up to 2 km upstream leading him to suggest that the basic home territory of stream dwelling cutthroat trout may be quite small, perhaps only 20 m in length.

Griffith (1972) noted that adult westslope cutthroat in streams were most often found at the upstream ends of pools. Preferred water velocities ranged from 10 to 14 cm/s with a maximum of 22 cm/s, the average water depth was 0.5 m, the average distance from cover habitat was 0.79 m, and associated substrate sizes ranged from 5 - 30 cm (Griffith 1972; and Reiser and Bjornn 1979). Scarnecchia and Bergersen (1986) found a positive correlation between undercut banks and biomass of large cutthroat (over 155 mm TL) in small high altitude streams.

In Flathead Lake (Montana) adfluvial populations of westslope cutthroat trout were found near the surface in the fall, winter, and spring. In the summer, fewer fish were caught in surface gill nets and this was attributed to avoidance of high (>20°C) surface water temperatures (Shepard et al. 1984). Optimal water temperatures for fluvial cutthroat appears to be between 10 and 13°C. Lake rearing populations prefer the same range where the dissolved oxygen is greater than 3 mg/L (Hickman and Raleigh 1984).

4.3.4 Maturity, Adult Migration, and Spawning

Westslope cutthroat from the Flathead River mature between the ages of 3+ and 4+ (Kiefling 1978; Liknes and Graham 1988). In the interior of British Columbia males typically mature as early as 2+ and females as late as 5+ (Scott and Crossman 1973).

The size of westslope cutthroat at maturity varies considerably but is probably consistent with the different growth rates of various populations. Adults from lake-stream populations are usually greater than 350 mm TL, those from river-stream habitats vary between 250 and 350 mm TL, and the small tributary populations are usually less than 250 mm TL, with some mature fish as small as 150 mm TL (Shepard et al. 1984).

The timing of spawning migrations and spawning varies between systems and may be related to distance travelled, water levels, and temperature. Shepard et al. (1984) tracked migrating cutthroat in the upper Flathead River basin in Montana and found that some populations can move great distances to spawning areas. The longest migration recorded in the study was 212 km in 87 days i.e. an average 2.4 km/day. Many of these fish had moved out of Flathead Lake and into the lower mainstem of the Flathead River during the fall and winter. The migration began in March and April with spawning occurring in May and June. Westslope cutthroat in the Kootenai River system tend to enter creeks for spawning during declining flows (Marotz and Fraley 1986). Earlier spawning fish often move further upstream to spawn than do later arrivals (Cope 1957; Shepard et al. 1984). Cutthroat above waterfalls in tributary streams to Kootenay Lake were first observed spawning in mid-July even though maturing males were noted in April. Spent fish were observed mainly in late July through August (Northcote and Hartman 1988). In the Fording River, the majority of spawning occurred from mid-June to mid-July, when water levels began dropping and mean daily water temperatures ranged from 4.5 to 7.5°C. (Allan 1987).

On the spawning grounds the female to male sex ratio can range from 1:1 to 4:1 with an observed 3.4:1 ratio for studies in Montana and Idaho (Liknes and Graham 1988). The proportions of repeat spawners varies among populations. In some populations and in some years mortality can be as high as 50% (Scott and Crossman 1973; Kiefling 1978). Repeat spawning may occur every year in some areas while in others adults return every second or third year to spawn. Liknes and Graham (1988) reported that the proportion of repeat spawners can range from 0.7 to 24% in Montana.

The mean number of eggs per female from different populations ranged between 1100-1700. The full range was 226 - 4420 eggs for females between 202 and 434 mm. Repeat spawners tend to produce fewer eggs than first time spawners (Carlander 1969).

Carlander (1969) reported that males spend 12 - 35 (average 17) days while females spend 6 - 21 (average 7) days spawning. Some fish will immediately return to the lake or larger streams while others will spend the summer and fall in the stream and return to the lake or mainstem in late fall. Westslope cutthroat in the upper Flathead River were observed leaving tributary streams in the beginning of July, soon after spawning.

Shepard et al. (1984) reported that Flathead River cutthroat used gravels with a size range of 2 to 50 mm for spawning. Mean depths ranged from 17 to 20 cm and mean velocities between 30 and 36.7 cm/s. The smaller cutthroat forms that reside year round in tributaries built smaller redds and tended to utilize habitat at the low end of the ranges specified. Spawning gravel used by cutthroat in the Snake River tributaries ranged form 25 - 64 mm (Kiefling 1978). Reiser and Bjornn (1979) reported that cutthroat have been observed spawning in water between 6 and 40 cm deep. An upper range of water velocities for cutthroat spawning appears to be 91 cm/s. Other studies reported in Hickman and Raleigh (1982) indicate that cutthroat spawn in velocities between 11 and 90 cm/s and estimated that an optimal range would be between 30 and 60 cm/s. Scott and Crossman (1973) reported that spawning takes place when the water temperature is near 10°C. Reiser and Bjornn (1979) presented a range of 6.1 to 17.2°C as recommended temperatures for cutthroat spawning. Moore and Gregory (1988b) observed that spawning cutthroat trout in tributary streams in the Cascade Mountains preferentially sought out suitable gravels in or near lateral habitats. This would place emerging fry in or close to preferred rearing habitat. In some drainages, spawning occurs in only the small headwater tributaries. This behaviour may prevent the egg, larvae, and fry mortality that could occur in larger tributaries that have more frequent occurrences of high runoff and streambed scouring (Liknes and Graham 1988).

Westslope cutthroat usually live 7+ years. Lake dwelling individuals can attain a size of 450-500 mm TL and 900 to 1400 g while river dwelling forms are usually less than 400 mm TL (Shepard et al. 1984).

4.4 Mitigation and Compensation Strategies

Over exploitation, introgressive hybridization with other species (e.g rainbow trout), competition with introduced salmonids, and habitat degradation or loss are perhaps the greatest threats to westslope cutthroat trout populations (Liknes and Graham 1988).

A review of the status of westslope cutthroat in Montana's Glacier National Park identifies introductions of native and non-native salmonids as having a significant impact on these indigenous populations (Marnell 1988). The greatest threat was the hybridization with stocked populations of Yellowstone cutthroat (*O.c. bouvieri*) and rainbow trout. Since 1972 fish stocking has been discontinued as a management tool. While introgression continues to be a threat, there are still indigenous populations of fluvial and lacustrine westslope cutthroat trout that have not been impacted by stocking.

The life stages most threatened by habitat degradation are spawning, incubation, and initial rearing. The westslope cutthroat populations that spend their entire life in headwater streams are therefore very susceptible to environmental degradation in these environments as all phases of their life cycle are exposed to impact. As mainstem and lacustrine populations also use headwater streams for spawning, incubation and initial rearing, they are equally sensitive to long-term impacts on spawning tributaries. However, these populations may be able to survive short-term impacts to tributary streams since subadult populations in lake and river rearing areas may escape impact and survive to maturity.

Hydroelectric projects and other impoundments may block migrations to spawning grounds for those populations that live in lake or mainstem areas. Water diversions resulting in channelization or low flows, sediment input, and near-stream or instream works will impact spawning, rearing, and overwintering habitat for stream dwelling populations. The formation of reservoirs can inundate spawning and rearing habitat in the lower sections of tributary streams.

The traditional techniques used to compensate for cutthroat trout losses include hatcheries and rearing ponds. Wyoming has been using hatcheries to sustain cutthroat trout and planting eyed eggs (held in hatching baskets) into tributary streams to increase fry production (Kiefling 1978). Egg mortality was between 2 and 7% in hatching baskets and ultimately aided an increase of and greater consistency in spawning population (Kiefling 1978). Additional methods of compensating for losses in cutthroat habitat include the manipulation of existing habitat and the creation of new habitat. The effectiveness of habitat improvement generally depends on accurately determining the limiting conditions in the stream in question and is therefore site specific. The literature suggests that the availability of rearing habitat for newly emergent fry is often a limiting factor for cutthroat populations, particularly for those that move to lakes and larger creeks and rivers after the initial rearing stage.

Most of the instream habitat improvement techniques that have been developed and successfully applied have been used for small streams (Department of Fisheries and Oceans and B.C. Ministry of Environment 1980; Adams and Whyte 1990; Marcus et al. 1990). These include various forms of:

1) current deflectors, usually extending out from the stream bank and constructed of boulders, which enhance the natural meander pattern of a stream and increase pool depths and bank undercutting,

2) low-profile check dams that span the channel and are constructed of boulders, gabions or logs which increase the depths of pools or runs,

3) boulder groupings and anchoring of large root wads or logs in mid-channel to create cover for rearing juveniles,

4) bank cover treatments including planting willow or other native species to stabilize stream banks, increase shading over the stream, and to provide cover, and

5) sediment removal from spawning areas.

The conventional rule of thumb is that for successful habitat enhancement or modification of rivers or streams, the wetted perimeter should be 15 m or less (P. Slaney, Fish and Wildlife Branch, B.C. Environment, Victoria, pers. comm. 1991). In British Columbia, the techniques for larger systems are just now being evaluated and include the placement of boulder groups and strategies for stream fertilization.

Cutthroat trout one year and older were often found in pocket water behind large boulders that had been placed in the channelized section of Line Creek, tributary to the Fording River in southeastern British Columbia (Allan 1987). The pocket waters formed downstream of these boulders created suitable depth, substrate, and velocities for cutthroat spawning. However, there was no direct evidence that these areas were used for spawning.

Moore and Gregory (1988a) studied the effect of manipulating stream margin habitat on density of 0+ cutthroat in Oregon's Cascade Mountains. The area of lateral or edge habitat was increased by the placement of cobble and small boulders in short rows perpendicular to the bank while backwater areas were increased through placement of cobble and small boulders in semicircular rows along the bank. All treated stream segments had significantly higher densities of fry than control segments or those areas with reduced lateral habitat.

Reducing or restricting sediment input to spawning streams can be important in enhancing or maintaining cutthroat populations. Sediment buildup can reduce pool volume, restrict access to interstitial spaces which reduces overwintering fry habitat, and decrease the area available to macroinvertebrates, a primary food source for cutthroat trout (Reiser and Bjornn 1979).

In some cases the loss of cutthroat habitat can be compensated by the removal of barriers which prevent access to suitable upstream spawning or rearing habitat. Populations that live their life in small tributary streams have a strong tendency to remain in a small segment of the stream and are more likely to move upstream than downstream. Shepard et al. (1984) suggested that by moving upstream to spawn during peak spring flows, cutthroat trout can pass partial barriers, move further upstream, and use smaller tributaries than other species that are found in the same system. As a result of this behaviour, providing access to upstream habitat may prove more effective than creating or manipulating downstream habitat.

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5.0 BROOK TROUT

(*Salvelinus fontinalis*)

5.1 Introduction

The brook trout (*Salvelinus fontinalis*) is actually a char, and is considered the most generalized, in terms of life history and habitat requirements, of the char species. Populations are found in small headwater streams, coastal rivers where they may be anadromous, and lacustrine environments ranging from ponds to large lakes (Behnke 1980). Despite the wide variation in habitat utilization, and associated variations in colour and growth rates, brook trout are generally recognized as a single, well-defined species (McPhail and Lindsey 1970; Scott and Crossman 1973; Behnke 1980). They are not indigenous to British Columbia but have been introduced throughout the province.

Fishing for brook trout has been a favourite pastime throughout its natural range since the mid-1800's. The largest (authenticated) brook trout caught was 6.6 kg from the Nipigon River, Ontario in 1915 (Scott and Crossman 1973). Over-exploitation through sport, subsistence, and commercial fishing resulted in the need for development of artificial propagation techniques in the early 1900's. Hatchery-reared brook trout have been extensively distributed throughout British Columbia. In 1985, anglers in the Okanagan region ranked brook trout as the third most popular catch after rainbow trout and kokanee (Stone 1988). An average of 1,250,000 fry per year were stocked into approximately 130 streams and lakes between 1988 and 1990 (H. Andrusak, Fish and Wildlife Branch, B.C. Environment, Victoria, pers comm. 1991). Brook trout are a popular winter fishery in the interior regions of British Columbia. Brook trout are often stocked into lakes which are mesotrophic to eutrophic in the northern interior of B.C. However, because they are not native to British Columbia, the current Fisheries Branch policy is to restrict stocking to closed systems or to areas where they have already become established. These restrictions have been established to protect native species such as cutthroat trout (*Oncorhynchus clarki*) from being displaced by brook trout and to limit the possibility of brook trout spawning with bull trout (*Salvelinus confluentus*) and producing a sterile hybrid (H. Andrusak, pers. comm. 1991).

5.2 Distribution

Brook trout are endemic to North America but under natural conditions occur only in lakes and streams of the northeastern portion of the continent. They have been introduced to many parts of the world and their range in North America has been greatly extended through stocking programs. In eastern British Columbia, for example, lakes and streams of the Columbia drainage including Elk, Moyie, St. Mary, Salmo and Lardeau rivers have been stocked. Table 6 lists some Columbia drainage lakes and streams where brook trout have been stocked or captured after movement from stocked areas. In the Peace River area, brook trout are regularly stocked into approximately ten small closed lake systems (D. Ableson, Fish and Wildlife Branch, B.C. Environment, Prince George, pers. comm. 1991). Figures 9 and 10 show brook trout distribution in the Columbia and Peace drainages respectively.

Table 6. Some recorded occurrences of brook trout in the Columbia drainage of British Columbia.

Facchin and King (1983)	UBC Zoology Dept. Fish Museum
Closed Lake	Elk River
Elk River	Erie Lake (near Salmo)
Koocanusa Reservoir	Goat River
Moyie River	Kootenay Lake
Norbury Creek	Lardeau River
Rosebud Lake	Leviathan Lake
Slocan River	Palmer Bar Creek
St. Mary River	Rosebud Lake
Toby Creek	Surveyors Lake (near Field)
Salmo River	
W[illegible] Creek	
Wapiti Lake	
Wood River	
Woodbury Creek	

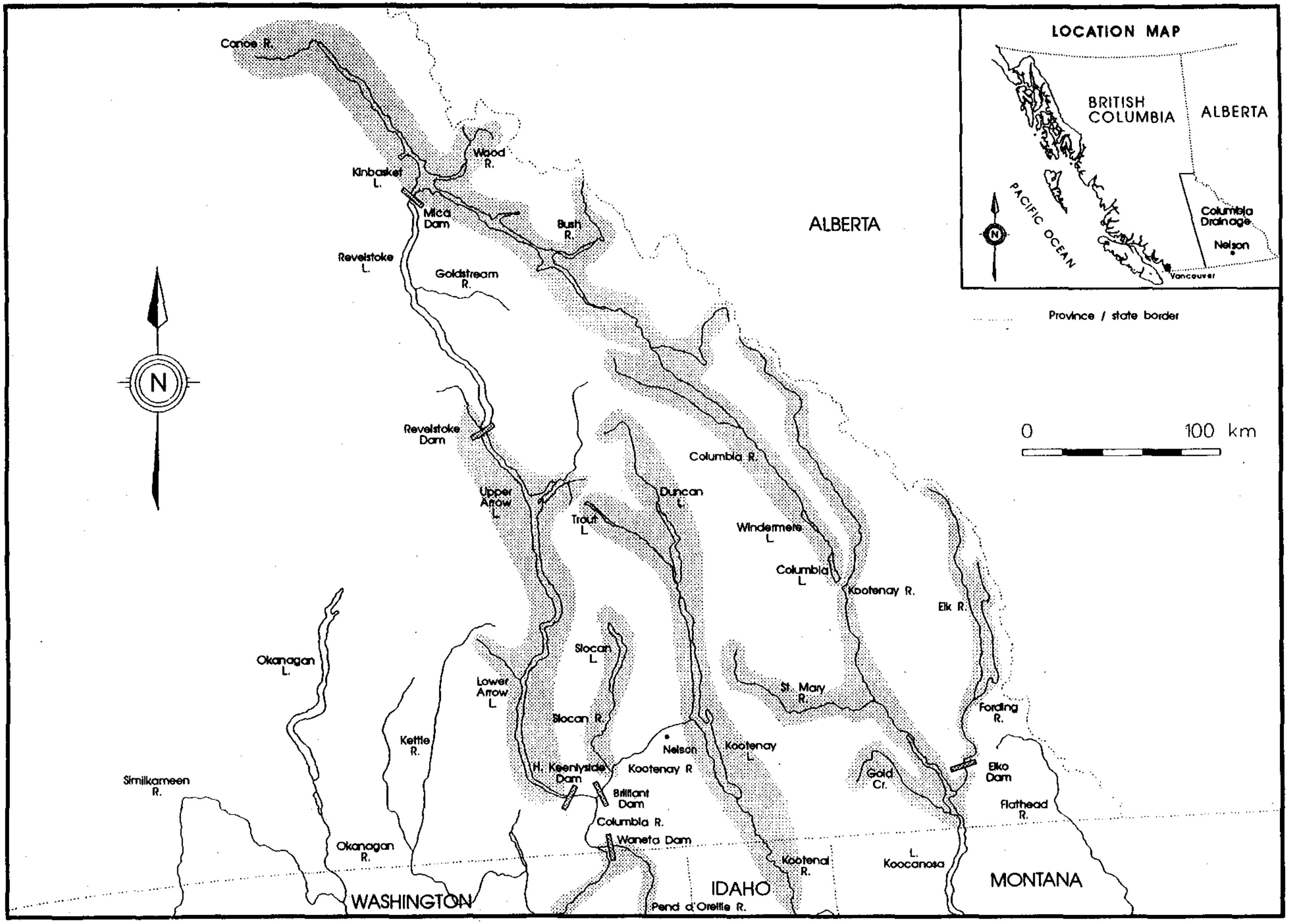


Figure 9: Brook Trout Distribution in the Columbia Drainage, British Columbia

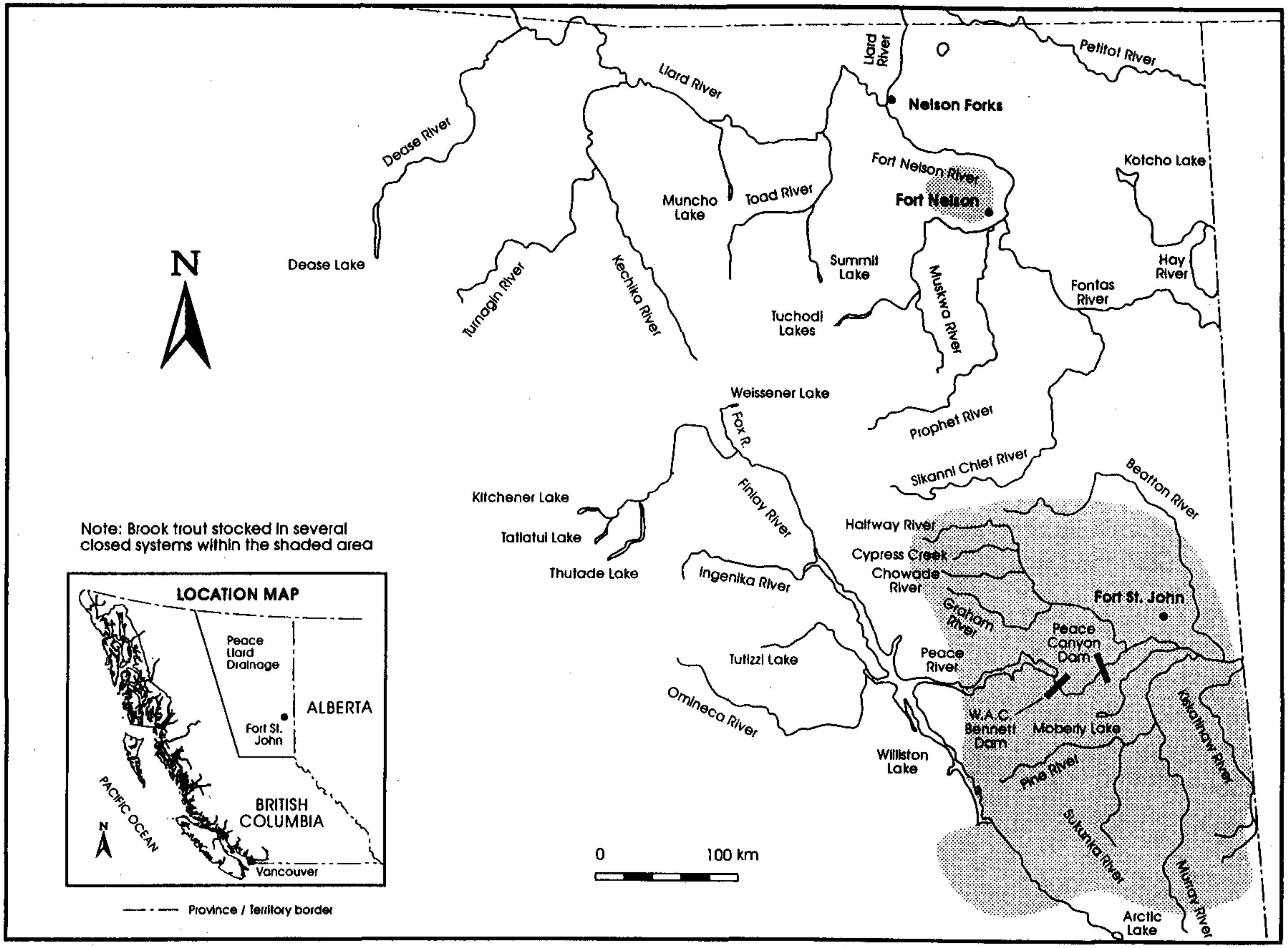


Figure 10: Brook Trout Distribution in the Peace and Liard Drainages, British Columbia

Brook trout are often displaced by the introduction of brown trout (*Salmo trutta*) and rainbow trout(*Oncorhynchus mykiss*) (Raleigh 1982; Rose 1986). However, brook trout have been known to displace cutthroat trout and Arctic grayling (*Thymallus arcticus*) in headwater tributaries of western streams. Meisner (1990) discusses the impact of global warming on the distribution of brook trout over the next century and has postulated that increases in the temperature of ground water may significantly limit brook trout in the southern extent of its range.

5.3 Life History and Habitat Requirements

5.3.1 General

Brook trout are normally found in clear cold streams and lakes. Spawning occurs in late summer or autumn in headwater streams on gravel substrate or over shallow gravel bars in lakes. Areas of moderate current or groundwater upwelling are preferred. There is some evidence of homing to spawning areas (Carlander 1969). Females clear debris and silt from the nesting area, deposit their eggs, and then cover the eggs with gravel. Emergence from the gravel usually occurs in early spring. The rate of growth varies considerably depending on local conditions such as temperature, habitat productivity, population density and competition with other species.

Within North America there are two general forms of brook trout that are recognized; a smaller (20 - 25 cm) short-lived (3 - 4 yrs) form that is generally found south of the Great Lakes, inhabiting cold stream and lake habitats, and second, a larger (4 - 6 kg) and longer lived (8 - 10 yrs.) form usually found associated with large lakes, rivers, the sea or estuaries in the northern portion of the native range. Anadromous forms are found along the east coast and in some areas of Hudson Bay.

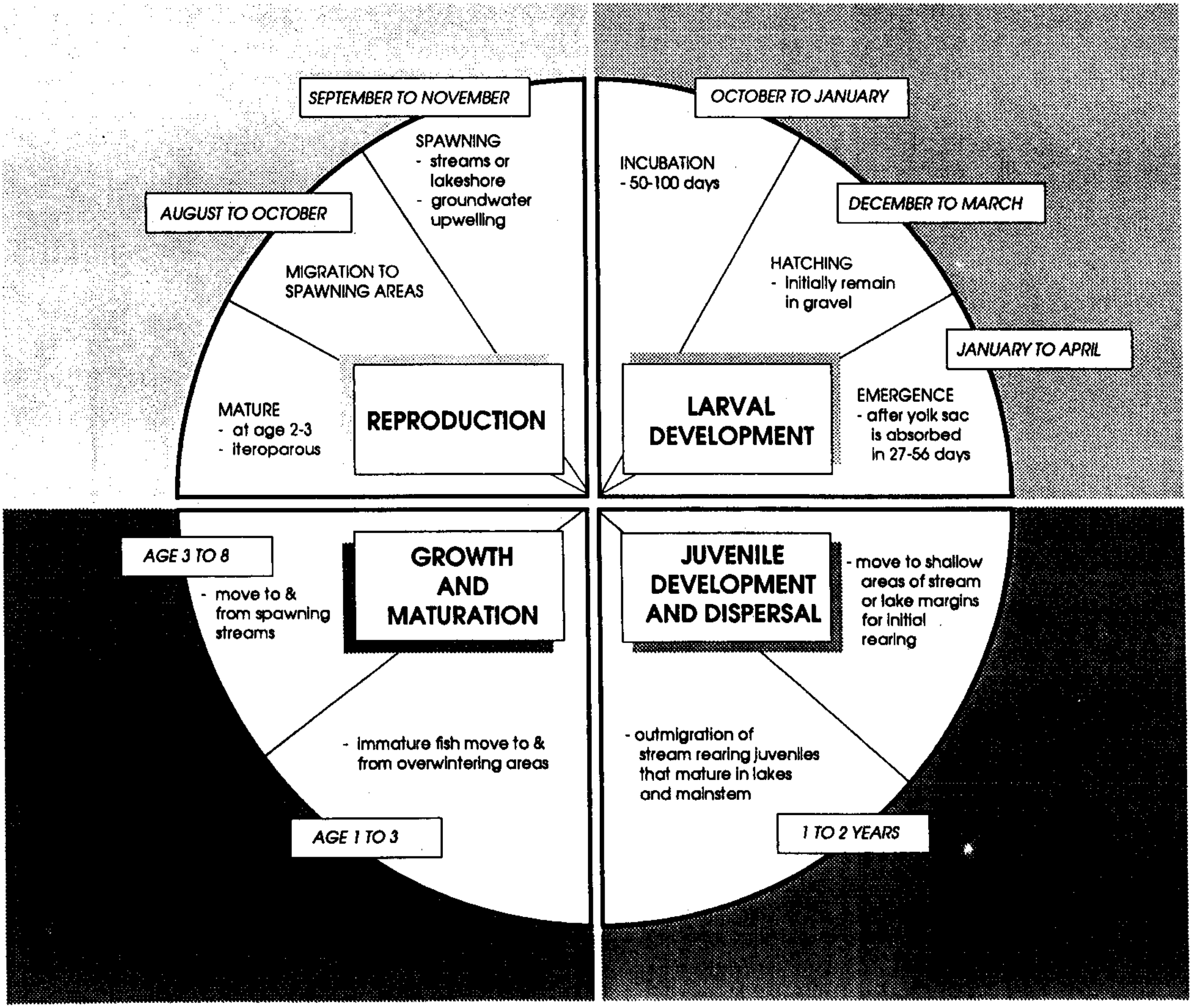
Brook trout have evolved three life history strategies (Power 1980). The first is associated with warmer, highly exploited creeks and streams where the fish are usually short lived and remain in the same stream section for their entire lives. The second is associated with unproductive northern or high elevation southern streams, where the fish are longer lived. Males mature at 2+ or 3+ and females a year later. Some fish spawn more than once and the spawning population is spread over several year classes. Sex ratios are generally skewed in favour of females in the older age groups. The third strategy is common in southern and central areas of the range and includes a migratory phase which separates spawning and nursery areas from feeding areas. The migration may be from stream to river, stream to lake or stream/river to estuary and sea. Mature individuals are usually larger as a result of better growth and lower mortality. Males sometimes mature before migrating but in most cases all fish mature after migration. Males mature before females and spawning occurs annually once they become mature. Brook trout life history is illustrated in Figure 11.

During the fish's life, diet changes with season, habitat, and increasing size. Brook trout are opportunistic carnivores that feed on a wide variety of organisms. Insects and aquatic invertebrates are the most common food items but in some areas plankton may also be important (Carlander 1969). Scott and Crossman (1973), in summarizing work by Ricker (1932) in Ontario state that:

> "the list of organisms [eaten] is astonishing and suggests that brook trout will eat any living creature its mouth can accommodate: worms, leeches, crustaceans (cladocerans, amphipods, decapods), aquatic insects (over 80 genera eaten but mayfly, caddisfly, midge, and blackfly larvae common), terrestrial insects (over 30 families, ants sometimes in abundance), spiders, mollusks (including clams and snails), a number of fish species, including young brook trout and brook trout eggs, minnows, sticklebacks, and cottids, frogs, salamanders, and a snake (in a 7 inch trout) ."

As brook trout increase in size they move from shallow stream margins to deeper water with undercut banks and other forms of cover. Stream resident fish are most commonly found in pool habitats with low water velocities (Cunjak and Green 1984). The standing crop of older brook trout may be limited in small streams by the availability of suitable cover such as pools with undercut banks and brush cover (Elwood and Waters 1969).

FIGURE 11 - BROOK TROUT LIFE HISTORY



Observed habitat use and selected biological characteristics of brook trout are presented in Table 7 and discussed throughout the text.

5.3.2 Eggs and Incubation

As mentioned above, eggs are laid in gravel substrate in streams or gravel bars in lakes. Water velocity through redds is an important factor in maintaining the viability of eggs and fry. This is accomplished either through adequate water velocity in the stream itself or through groundwater upwelling through the spawning substrate. For spawning sites that depend on stream flow for oxygen exchange, substrate size is important. The optimum substrate size for brook trout embryos ranges between 3.4 to 50.5 mm in diameter (Raleigh 1982). Burns (1970) found that brook trout survival decreased as the percent of material less than 2.5 mm in diameter increased. Reiser and Bjornn (1979) suggested a preferred flow through substrate during the incubation of anadromous salmonid eggs should be greater than 0.01 cm/s to provide adequate oxygen exchange and removal of metabolic wastes. Hausle and Coble (1976) demonstrated that as the amount of sand in spawning gravel increased from zero to 25%, alevins had increasing difficulty in emerging; above 20% sand there was an overall reduction in percentage of alevins emerging.

Egg incubation time is dependent on temperature and dissolved oxygen levels. Where oxygen levels are close to saturation, eggs will hatch in approximately 100 days at 5°C, 75 days at 6°C, and 50 days at 10°C (Scott and Crossman 1973). Carlander (1969) reported that eggs will develop normally in temperatures as high as 13°C while Scott and Crossman (1973) reported that the upper lethal limit for long term exposure of brook trout eggs is approximately 11.7°C. On the other hand, Power (1980) reported that the upper lethal temperature for a seven day exposure of developing eggs was 20.2°C and for alevins, 24.5°C. The highest percentage of normal hatching eggs occurred at 6°C and abnormalities in hatching larvae were highest at 15°C.

Table 7. **Observed habitat use and selected biological characteristics by life stage for brook trout** (for sources refer to text, NA-data not available)

Eggs

Temperature tolerance range	(long term exposure) 0 - 12°C
Optimum incubation temperature	6°C
Recommended oxygen concentration	>8.8 mg/L
Lower lethal oxygen concentration	(causes reduced size and vigour) 6.5 - 8 mg/L
Range of incubation time	50 - 100 days
Incubation time at optimum temperature	75 days
Lower lethal pH	6.5
Recommended current velocity	flow through gravel > 0.01 cm/s
Optimal depth	NA
Substrate	(preferred spawning substrate) 3 to 80 mm

Juveniles

Temperature tolerance range	0 - 24°C
Optimum temperature for growth	12 - 15°C
Recommended oxygen concentration	> 7 mg/L
Lower lethal oxygen concentration	3 mg/L
Habitat type preference	stream margins
Observed depth preference in one study	0.42 m
Observed preferred current velocity in one study	8.7 cm/s
Substrate	cobble and gravel
Cover	cobble
Optimum turbidity levels	(maximum tolerance 130 JTU) 0 - 30 JTU's
Primary food category	macroinvertebrates
Secondary food taxa	zooplankton

Adults

Temperature tolerance range	0 - 25°C
Optimum temperature for growth	13 - 16°C
Recommended oxygen concentration	> 7 mg/L if water temp. <15°C and > 9 mg/l if >15°C
Lower lethal oxygen concentration	< 3 mg/L
Habitat type preference	lakes and low gradient sections of streams
Depth preference	< 70 cm
Preferred current velocity	8.4 - 11 cm/s
Substrate	cobble, gravel
Cover	rock and undercut banks
Optimum turbidity levels	0 - 30 JTU's
Primary food type	aquatic and terrestrial insects
Secondary food type	zooplankton and fish
Form of reproduction	iteroparous
Nest construction	yes
Spawning habitat type	tributary steams, groundwater upwelling in lakes
Preferred spawning temperature	9 °C
Preferred spawning depth	> 9 cm
Preferred spawning substrate	gravel 3 - 80 mm
Observed spawning current velocity	(3 to 42 cm/s)
Range of first age-at-maturity	typically 2 to 3 yrs
Range of fecundity	3330 - 3890 eggs/kg or 100 - 5000 eggs

Brook trout eggs appear to require over 8.8 mg/L of dissolved oxygen for optimal development. Hausle and Coble (1976) found that egg development in oxygen concentrations of 6.5 to 8.8 mg/L resulted in reduced size and vigour of the fry.

Once the eggs hatch, the larvae remain in the gravel until the yolk sac is absorbed. Fifty percent of alevins reach the swim-up stage in 56 days at 7.1°C and in 19-27 days if the temperature is between 9.8 and 19.5°C (McCormick et al. 1972). Survival of brook trout eggs to the fry stage has been documented as being between two and eight percent (Latta 1969).

Brook trout have a wide tolerance for pH and appear to be more tolerant of low pH conditions than other salmonids. Menendez (1976) studied the affect of pH on mature brook trout and their eggs. The survival of eggs to hatching was significantly reduced in pH below 6.5 as was the survival of alevins maintained in a reduced pH environment for 30 days after hatching. Survival of eggs and alevins from parents not exposed to pH levels below 6.5 was also reduced pH relative to the survival of controls kept at pH 7.04).

5.3.3 Rearing, Food and Growth

Upon emergence, typically between January and April, brook trout disperse into shallows along the edges of streams, in suitable eddies or even mid-stream in slower currents, establishing territories over gravel/cobble substrate (Power 1980). Lake spawning populations also move to the shallows after emergence. As the fish grow, they expand their territories and take up positions in deeper water. Fish that move to lakes usually do so in their second or third summer when they reach a length of 80 - 150 mm (Saunders and Power 1970). The greatest downstream movement usually coincides with declining flows, a time when population densities are highest and recently emerged fry are trying to establish territories. Winkle et al. (1990) observed young of the year using beaver ponds for rearing. In most cases the fry had emerged from gravels upstream of the pond and subsequently drifted downstream to the pond. Griffith (1972) also observed brook trout using beaver ponds in streams with sympatric populations of cutthroat trout. Scales first form when fry reach a length of 40 mm, usually by the end of the first growing season (Power 1980).

Growth and mortality of brook trout in the first eight weeks is strongly dependent on temperature. McCormick et al. (1972) found that optimal growth rates for alevin and fry occurred between 12 and 15°C. Mortality rates increased significantly in temperatures above 15°C and upper lethal temperatures (7 day TL50) were between 20 and 24°C depending on age and acclimatization temperatures. Weitkamp and Katz (1980) reported that brook trout fry are negatively affected by total gas pressures of 112% or higher.

Latta (1969) found a significant correlation between young-of-the-year brook trout and ground water flow levels and reported large number of brook trout fry in years of high flow. The report speculated that in headwater areas where groundwater made a significant contribution to total stream flow, increased groundwater flow resulted in increased edge habitat utilization by fry immediately after emergence and provided a cooler, more stable temperature regime.

Water velocity preferences for brook trout fry were reported by Griffith (1972) to be 8.7 cm/s in association with a mean stream depth of 0.42 m. The maximum velocity observed was 16.9 cm/s. Raleigh (1982) suggested that habitat requirements necessary for optimal survival of fry are silt free substrates 100 - 400 mm in diameter which make up 10% or more of the total stream habitat. As is the case with other life stages, fry are tolerant of low pH; they have been observed in bog streams with a mean pH of 4.75 that often dropped to 4.0 - 4.2 (Dunson and Martin 1973).

Generally, young and medium sized fish consume smaller prey items such as ostracods, copepods and cladocera. Individuals over 10 to 15 cm are usually piscivorous, and larger fish have been known to consume small mammals such as field mice (Scott and Crossman 1973; Johnson 1981). Lake populations tend to feed on plankton and other fish while stream and river populations prey on aquatic and terrestrial insects, crustaceans (e.g. crayfish), and mollusks (Power 1980). Johnson (1981), studying stream dwelling brook trout observed that larger fish, over 15 cm, primarily consumed fish, trichopterans, and terrestrial insects. Smaller brook trout fed heavily on trichopterans and decapods. Waters (1982) reported that brook trout abundance in streams was closely correlated to the main invertebrate food, *Gammarus sp*. When invertebrate production was reduced due to siltation, brook trout annual production declined.

In southern areas, brook trout grow rapidly and can reach 75 mm in their first year. Growth is somewhat slower in northern areas. Carlander (1969) reports that in Wisconsin, some populations of brook trout young-of-the-year will continue to grow through the winter. However, in most populations 1+ and older fish show little evidence of growth over the winter and usually most of the season's growth is complete by August or September. In streams with low productivity, slower growing brook trout populations exhibit high mortality of two and three year old fish over winter (Whitworth and Strange 1983).

Allan (1981) reported a correlation between densities of brook trout in small streams in Colorado and mean depth, the amount of rock and undercut bank cover, and the presence of deep turbulent water. Adult brook trout use stream sections with pools and overhanging streambank cover. These habitats have been cited as limiting factors to trout carrying capacity, particularly in the winter months (Hunt 1974).

As mentioned above, brook trout inhabiting small streams appear to remain in fairly small home territories. Whitworth and Strange (1983) reported that the majority of brook trout in small Appalachian streams moved upstream an average of 13 metres over the course of a year. Many fish were recaptured in the same area of initial capture and the maximum recorded movement was 300 metres. Moore et al. (1985) reported similar movement patterns but also found that a small number of marked fish moved considerable distances, usually downstream, and into different tributary streams. In Wisconsin, brook trout in downstream sections of a small headwater stream were observed moving upstream into the tributaries to spawn in the fall and adults moved downstream to deeper pools for the winter. Generally, lake populations are found inshore in water less than 7.5 m deep

(Lackey 1970).

Brook trout seek out water temperatures below 20°C; high summer water temperatures are often cited as a factor limiting distribution. If water temperatures exceed 20°C, brook trout will move to deeper water or into tributaries in search of cooler waters. The preferred temperature range is 14 - 19°C and maximum growth and food consumption occurs at 13°C (Schofield et al. 1989). Raleigh (1982) reported that brook trout appear to tolerate pH levels between 4.0 and 9.5 with the optimal range being 6.5 - 8.0.

Cunjak and Green (1984) suggested that brook trout have a preference for lentic habitats and found that brook trout were able to establish territorial dominance over rainbow trout in slow stream flows. Further evidence of the preference of brook trout for slower stream conditions was presented by Chisholm and Hubert (1986). Their study showed that stream gradient is correlated to the standing stock of brook trout. Brook trout were found in a Wyoming stream in all gradients ranging from 0.4 to 9.2% but were approximately three times more abundant in low gradient than in high gradient reaches.

Beaver ponds in small streams in the central Rocky Mountains have been recognized as providing habitat beneficial to the production of brook trout. In small mountain streams with low water temperatures, the pool habitat created by beavers can stabilize water flows, allow water temperatures to increase to more optimal levels and provide additional forage items and overwintering habitat (Winkle et al. 1990). The standing stock (kg/ha) of brook trout in beaver ponds was negatively correlated to surface area, mean depth, and pool volume but positively correlated to the morphoedaphic index (total dissolved solids/mean depth; Winkle et al. 1990).

The temperature preference for maturing brook trout is 10 - 19°C, with the optimal temperature for growth being 16°C (Power 1980). The upper lethal temperature is approximately 25°C depending on the temperature to which the fish are acclimatized. The overall temperature range in which brook trout are known to exist is 0 to 20°C (MacCrimmon and Campbell 1969). In small, thermally stratified ponds, brook trout show a preference for the metalimnetic zones where temperatures range from 10 to 15°C.

Raleigh (1982) reported that brook trout normally require high concentrations of dissolved oxygen, needing levels close to saturation in water temperatures over 15°C. Optimum levels of oxygen suggested by Raleigh (1982) are over 7 mg/L for temperatures below 15°C and over 9 mg/L in temperatures above 15°C. However, lake dwelling brook trout are found at depths where the temperature is near optimum and the dissolved oxygen is greater than 3 mg/L.

Preferred velocities for brook trout in Idaho streams were studied by Griffith (1972). Focal point velocities for adults ranged between 8.4 and 11 cm/s with a maximum of 25.8 cm/s. However, Cunjak and Green (1984) reported that dominant brook trout could be found in focal point velocities up to 34 cm/s. The larger fish tended to hold in slower waters near overhead bank cover at the sides and tails of pools. On average, fish 1+ and older were found within 0.59 m of cover and in water depths less than 0.7 m deep.

Menendez (1976) reported that adult trout in laboratory conditions did not survive five month exposures to pH levels of 4.5. However, in natural environments, the brook trout sensitivity to pH may be dependent on the effects of acidification on water chemistry. Acidified lakes often have elevated levels of aluminum and reduced concentrations of calcium. Mount et al. (1988a & b) found adverse effects of acidification (pH 4.4-5.2) to be related to the concentrations of aluminum and calcium ions in the water. Elevated aluminum (over 300 µg/L) and low levels of calcium resulted in a 25% reduction in survival, reduced growth rates, and a 25% reduction in fecundity.

Raleigh (1982) considered 0 - 30 JTU's as optimum turbidity values for brook trout growth while a range of 0 - 130 JTU's can be tolerated. Brook trout occur in waters with a wide range of alkalinity and specific conductance. The small size of headwater populations has been attributed to low productivity as measured by total alkalinities below 10 mg/L and TDS values less than 20 mg/L.

Brook trout are generally short-lived. Scott and Crossman (1973) state that individuals from most wild populations seldom live five and never more than eight years. Power (1980) reported that fish over three years old are rare in some brook trout populations in Ontario and Wisconsin. It appears that slower growing populations live longer. The oldest recorded brook trout, at least 15 years old, came from a high altitude lake in California (Carlander 1969). Donald et al. (1980) observed considerable variation in maximum age and weight of brook trout populations sampled from high mountain lakes in Alberta; the weight of age 5+ fish from these lakes varied from 65 to 1751 grams. Growth was positively correlated to increasing water temperature, amphipod abundance, and specific conductance, and was negatively correlated to increasing elevation. In some lakes the maximum age appeared to be six while in others the fish lived for up to 10 years. The lakes with the bigger fish were not the lakes with the longer lived fish.

5.3.4 Maturity, Adult Migration, and Spawning

Carlander (1969) reported that male brook trout can mature as fingerlings at 94 mm and females at one year at 104 mm. However, most fish mature at age two and three, the males usually maturing a year before the females. For example, in a southwestern Ontario study male brook trout matured at 1+ and females at 2+ (Witzel and MacCrimmon 1983).

Spawning occurs between late summer and late fall. Variations are chiefly related to different temperature regimes and photoperiods. Northern populations and those at high elevations in the south spawn in late August or September; some populations in Maine and California spawn as late as December (Carlander 1969). Larger fish tend to spawn earlier than smaller fish. Witzel and MacCrimmon (1983) observed that the spawning period for brook trout in southeastern Ontario lasted three to five weeks. Males usually move into spawning areas before the females. Brook trout are iteroparous but in some of the short lived populations individuals will only have one opportunity to spawn. In longer lived populations fish may not spawn every year after first spawning because of inadequate diet or the effect of parasites (Power 1980).

Fish that mature in larger rivers or lakes begin moving into spawning areas when water temperatures are between 3 and 13°C. In one Quebec study, the spawning migration of stream spawning brook trout occurred in late July (O'Connor and Power 1976). During the spawning period, water temperatures should optimally be at or below 9°C and should not exceed 12°C. Egg production in females is optimal at temperatures near 10°C. Spawning often will not occur above 16° C. Males fail to produce viable sperm above 19°C (Power 1980).

In streams, brook trout are found spawning on gravel banks at the downstream ends of pools in water velocities ranging between 1 and 92 cm/s (Power 1980). The optimal velocities for spawning habitat suggested by Raleigh (1982) is between 25 and 60 cm/s. However, Witzel and MacCrimmon (1983) reported velocity over redds ranging 3.0 - 42.0 cm/s with a mean of 17.6 cm/s. The Oregon Game Commission recommend water velocities of 1 to 23 cm/s and a minimum depth of 9 cm for brook trout spawning (Smith 1973). The preferred substrate for spawning is between 3 to 80 mm in diameter (Raleigh 1982) with Witzel and MacCrimmon (1983) reporting average spawning gravel of 5.7 mm grain size.

As mentioned above, lake and stream spawning brook trout populations demonstrate a preference for areas with groundwater upwelling. In systems where groundwater input is available brook trout have shown preferences for sites with aquifer discharges over areas that consist of optimal substrates. In some cases spawners have chosen areas of upwelling with sandy, heavily silted substrates (Webster and Eiriksdottir 1976; Witzel and MacCrimmon 1983). Spawners in small spring fed ponds used areas where the seepage velocities ranged from 11.5 to 45.0 cm/h (Carline 1980).

The eggs are slightly adhesive and the female covers them with gravel after spawning. Eggs range in size from 3.5 - 5.0 mm. Fecundity ranges from 14.4 cm (fork length) females producing 100 eggs to 56.5 cm fish producing up to 5000 eggs (Scott and Crossman 1973). Carlander (1969) reports that on average females at age two produce 3329 eggs/kg and at age three produce 3887 eggs/kg.

Experimental studies determined that spawning female brook trout avoided potential redd sites where the upwelling water had a pH of less than 5.0 (Johnson and Webster 1977). Spawning fish ceased normal breeding behaviour when subjected to a pH of 4.1 to 4.3.

5.4 Mitigation and Compensation Strategies

Brook trout are sensitive to environmental change, especially during early life history stages. Eggs in the gravel are susceptible to winter floods and resultant scouring of spawning areas. The period of highest mortality is the first months after emergence from the gravel when food availability, temperature, habitat availability and presence of other species (including predator species) are critical factors. Higher flows at this time result in better survival through improved productivity and cooler water temperatures. The next critical period for brook trout survival is over the first winter. Larger fry exhibit higher overwinter survival rates. Therefore, not only is the availability of suitable winter habitat important, but the summer and fall productivity of the stream must be sufficient to allow fry to reach a size that maximizes overwinter survival.

A general guideline for evaluating flow reductions or general stream suitability for trout production is the base flow of late summer or winter months. A base flow that is greater than 55% of the average annual daily flow is considered excellent, 25 to 50% is considered fair and less than 25% is considered poor for maintaining good trout habitat (Raleigh 1982). Kraft (1972) recorded a 62% reduction in the number of age 1+ and older brook trout in stream sections classified as runs when normal stream flow was reduced by 90% for a three month period. This flow reduction had no consistent effect on underyearlings. The decreased flow reduced water surface area, depth, and velocity. Kraft (1972) also suggested that increased siltation and temperature because of decreased water velocities may have had a greater impact on the shallower run sections than the deeper pools.

Many techniques for improving or compensating for lost instream habitat have been developed and successfully applied in small streams (Parkinson and Slaney 1975; Dept. of Fisheries and Oceans and B.C. Ministry of Environment 1980; Hall and Baker 1982; Reeves and Roelofs 1982; Adams and Whyte 1990; and Marcus et al. 1990). These include various forms of:

1) current deflectors, usually extending out from the stream bank and constructed of boulders or rock-filled gabions, which enhance the natural meander pattern of the stream and increase pool depths and bank undercutting,

2) low-profile check dams that span the channel and are constructed of boulders, gabions or logs. These structures increase the depth of pools or runs,

3) boulder groupings and anchoring of large root wads or logs in mid-channel to create cover for rearing juveniles,

4) bank cover treatments including riprap or gabion placement, planting of willow or other native species to stabilize stream banks, increase shading over the stream, and provide cover,

5) sediment removal from spawning areas or introduction of suitable spawning substrate, and

6) water control structures to maintain flows over critical low flow periods.

Generally, rivers and streams should have a wetted perimeter of 15 m or less for successful installation of instream habitat structures. Compensation techniques for larger systems are just now being evaluated and include placement of boulder groupings. (P. Slaney, Fish and Wildlife Branch, B.C. Environment, Victoria, pers. comm. 1991).

There has been considerable research on the response of brook trout to instream habitat management, primarily in the eastern United States and Canada, the native range. The studies, summarized by Hall and Baker (1982), primarily evaluated the effect of creating bank cover, and installing revetments and deflectors. Saunders and Smith (1962) modified approximately 400 m of a small tributary stream by installing 13 weirs, 12 wing deflectors and creating instream cover out of debris in shallow areas. The following year the standing crop of fry was above average and the standing crop of 1 year fish was approximately double the average for the previous 13 years. There was also an increase in the survival rate from fry to age 1 year along with a marked increase in the number of age 2 year fish. However, fish in the study section showed no change in growth rates relative to those in control sections. Hale (1969) performed similar stream habitat improvements in more than 3 km of stream and obtained similar increases in brook trout production at a cost considerably less than producing an equivalent number in a hatchery. Hunt (1969 & 1974) reported similar results when studying the effects of stream channel modification in a small creek in Wisconsin. The modifications focused on increasing pool area and streambank cover. Brook trout in the modified section showed a marked increase in over winter survival of the age 1 year and older fish. Annual production of fry remained the same. Hunt (1974) concluded that overhanging cover and pool area were critical habitat requirements for brook trout and determined carrying capacity, particularly during the winter period.

Loss of riparian habitat associated with activities such as logging, grazing, and other industrial developments can also degrade fish habitat. Riparian vegetation is important for controlling bank erosion and subsequent siltation of spawning habitat. To protect trout habitat, buffer strips approximately 30 m wide should be maintained, of which 80% should be either well vegetated or have stable, rocky stream banks which will provide adequate erosion control and maintain undercut stream banks (Raleigh 1982).

Forestry practices were noted by Power (1980) as one of the main causes for decline in brook trout populations in the south Appalachian Mountains. The increase in water temperature from the loss of riparian vegetation is usually the logging impact most affecting brook trout.

Acid rain and mining can contribute to the acidification of trout habitat. Of the salmonids, brook trout are probably the most tolerant of acidic conditions (Gunn and Keller 1981). Brook trout fry usually emerge after peak spring run-off, thus avoiding the period when the greatest decrease in pH is observed in acidified areas. However, the acidification of lakes in eastern Canada and northeastern United States has reduced many brook trout populations. Attempts at rehabilitation have included the construction of spawning boxes and neutralizing the lakes through the addition of $CaCO_3$. Liming of the lakes has changed the pH from 4.5 to over 7.0. The condition and growth of brook trout in lakes treated with lime were similar to lakes with neutral pH as long as the water quality was maintained (Schofield et al. 1989). Lakes with short retention times reacidified in a few months and trout productivity again decreased (Gloss et al. 1989; Schofield et al. 1989).

In light of the current B.C. Environment policy of restricting brook trout introduction to closed lake systems, possible enhancement techniques, which are primarily aimed at inducing the fish to spawn, alleviating any spawn bound conditions and enhancing the quality of fish and the angling experience include the following:

1) gravel placement near shore at areas of upwelling or subject to wave action; although brook trout will shore spawn, there is little, if any, egg-to-fry survival,

2) construction of an upwelling facility or artificial spawning channel to encourage the fish to spawn,

3) winter aeration systems in lakes where winterkill is a serious problem (D. Jesson, Fish and Wildlife Branch, B.C. Environment, Prince George, pers. comm. 1992).

Fishery improvement opportunities include the stocking of brook trout into suitable lakes. Ideally stocking would be into closed lake systems that also contain minnow populations (chub, redside shiner), providing food items. Although brook trout provide good winter fisheries in contrast to the summer fishery that rainbow trout often provide, the introduction of brook trout into some closed systems also stocked with rainbow trout (e.g. Vivian Lake, near Prince George) have produced both a summer and winter fishing experience. In some closed lakes where brook trout are stocked in the northern interior, spawning does take place in fall over gravel near shore. However, no natural production appears to occur but the spawning activity relieves spawn bound conditions thereby ensuring healthier fish (D. Jesson, pers. comm. 1992).

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6.0 BULL TROUT

(Salvelinus confluentus)

6.1 Introduction

The bull trout, *Salvelinus confluentus*, is actually a char and until recently was not formally recognized as distinct from Dolly Varden char, *Salvelinus malma* (Cavender 1978). Indeed, Dolly Varden themselves were only formally separated from Arctic char, *Salvelinus alpinus*, forty years ago (DeLacy and Morton 1943; McPhail 1961).

Bull trout are large relative to other char and trout; the largest on record was captured in Pend Oreille Lake, Idaho and weighed 14.5 kg. Several individuals exceeding 12 kg have been captured in Kootenay Lake (Scott and Crossman 1973).

The differences in morphometric and meristic characteristics between bull trout and Dolly Varden are consistent throughout their range and are used to distinguish the two species (Haas 1988; Cavender 1978). In comparison to Dolly Varden, bull trout have a larger, broader, and flatter head, and a more ventrally flattened body (Cavender 1978). Branchiostegal number, anal fin rays, and the maxillary length to standard length ratio can also be used to make positive identification (Haas 1988). The species have not been separated based on electrophoresis, possibly due to the low level of variation present within the genus (Allendorf and Utter 1979).

In British Columbia, the ranges of Dolly Varden and bull trout overlap, suggesting that the habitat requirements of the two species are similar and that there is overlap in resource use. However, Dolly Varden are anadromous over much of their range whereas the existence of anadromous bull trout is uncertain. There is no apparent interbreeding as hybrids have not been collected. However, the distribution of the two species is parapatric, suggesting competitive exclusion (Haas 1988). One obvious difference between the species is the lower tolerance level of bull trout for saltwater as indicated by its absence on major offshore islands such as Vancouver Island and the Queen Charlotte Island (Haas 1988).

6.2 Distribution

Bull trout are native to North America and are found in areas between 41° and 60° north latitude (Cavender 1978). North of 49° the bull trout is found in major drainages on both sides of the continental divide. However, even with differences in life history traits and morphometry, confusion between bull trout and Dolly Varden is common and much of the available information on distribution is suspect (Haas 1988). For example, most of the studies supposedly made on Dolly Varden in the interior of British Columbia were in fact made on bull trout.

Bull trout recolonized British Columbia from the Pacific, Missouri, and Bering refugia after the last ice age which ended about 10,000 years ago (Haas 1988). They are distributed throughout the province and are most abundant in the interior, being found in the Fraser, Columbia, Kootenay, Peace, Liard, Stikine, Bear, Nass, Skeena, Klinaklini, and Homathko drainages (Haas 1988). They are not found in the Okanagan watershed, or, as mentioned, Vancouver Island, Queen Charlotte Islands and possibly other large offshore islands. They occur in only certain parts of most watersheds; for example, bull trout are found in 71% of streams surveyed in the Flathead basin, but in only 50% of the reaches within these streams (Shepard et al. 1984). Figures 12 and 13 show bull trout distribution in the Columbia, and Peace and Liard river drainages respectively.

6.3 Life History and Habitat Requirements

6.3.1 General

Bull trout are iteroparous fish that inhabit well-oxygenated water, living in small streams with boulder and cobble substrate during their first one to four years of life, and then

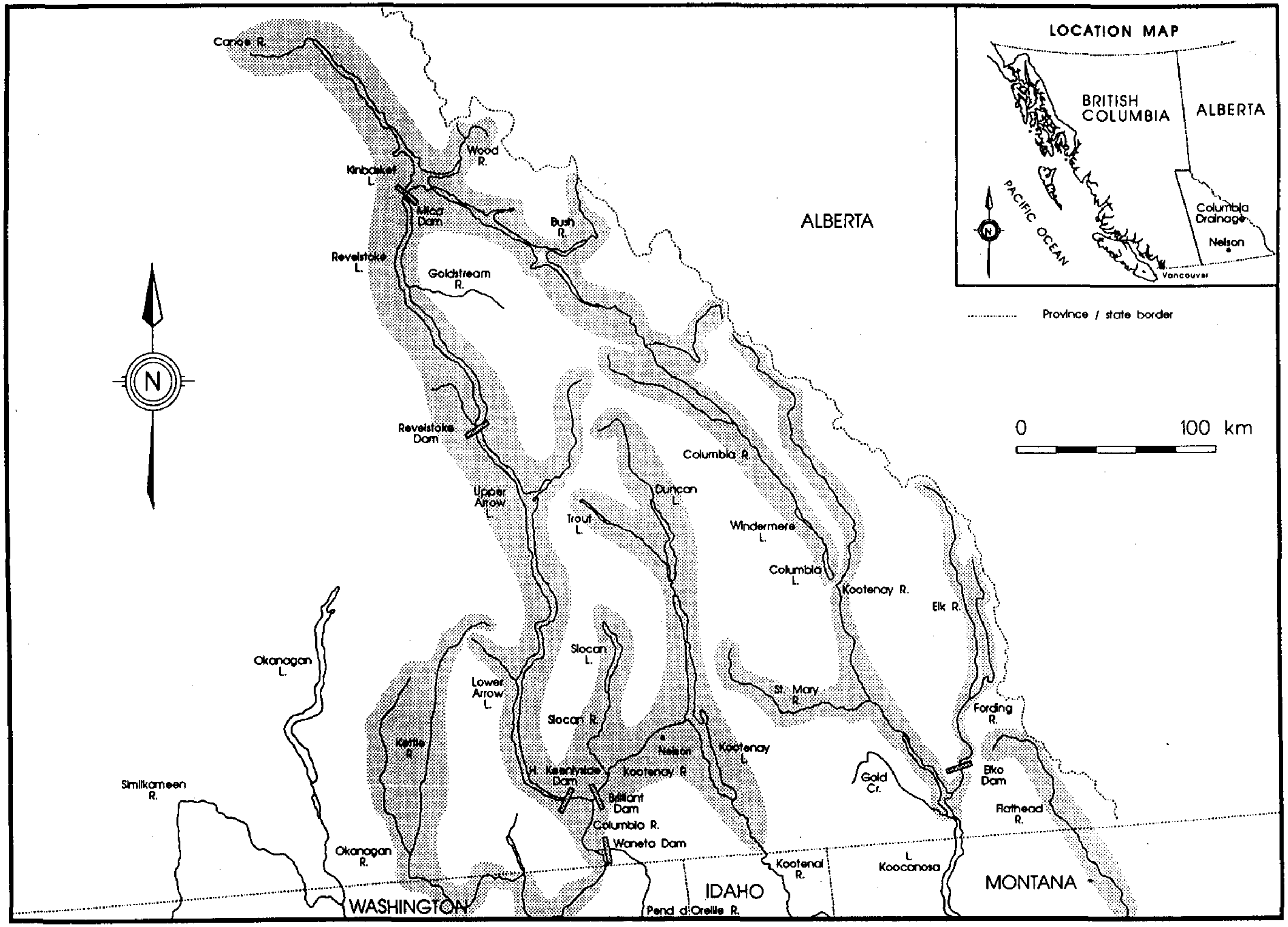

Figure 12: Bull Trout Distribution in the Columbia Drainage, British Columbia

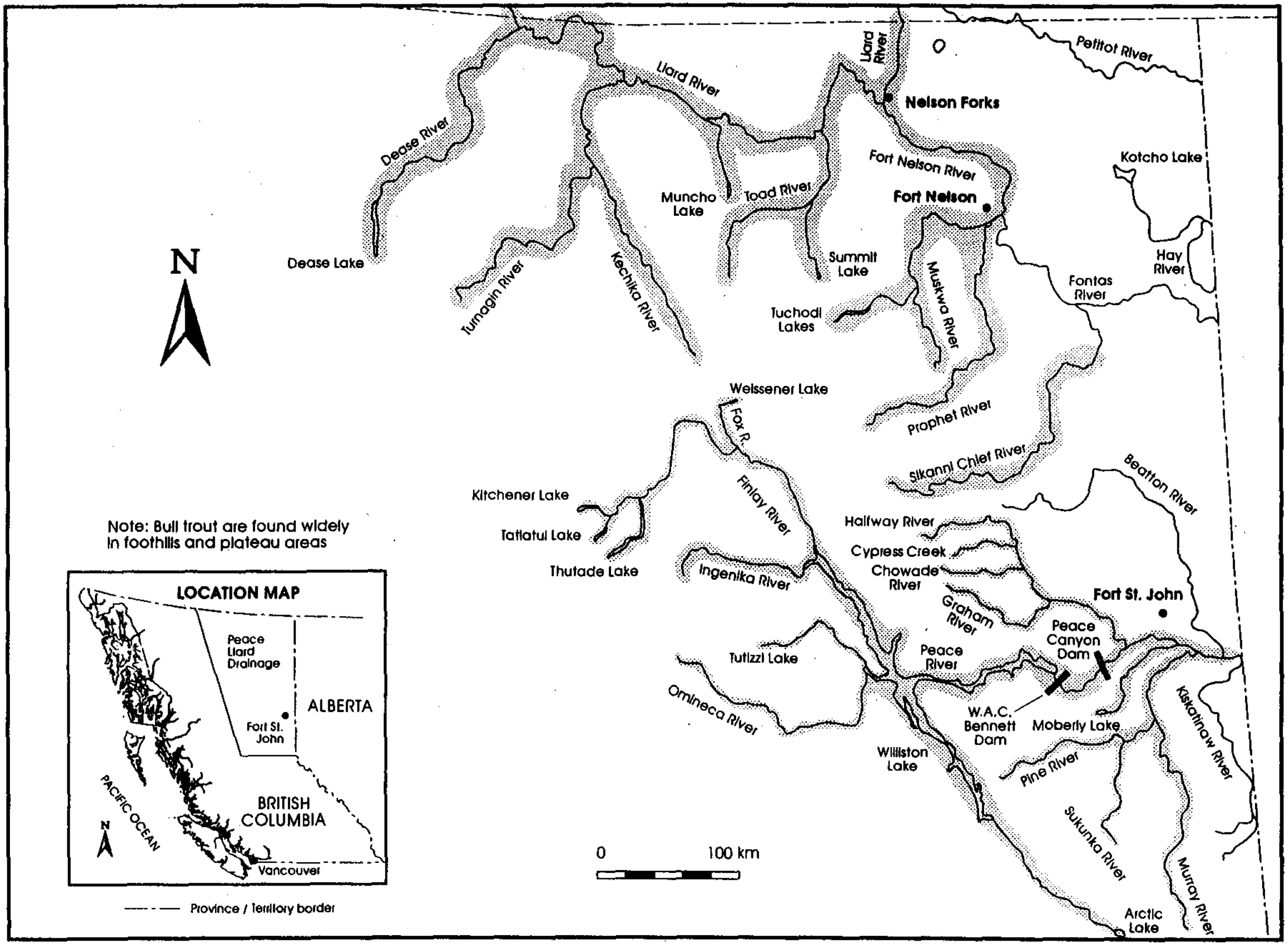

Figure 13: Bull Trout Distribution in the Peace and Liard Drainages, British Columbia

moving to river or lake habitats to reach maturity. Juveniles commonly feed on aquatic insects and may migrate upstream to rear in areas less accessible to adults, or into lakes. Adults are opportunistic piscovores, reaching maturity from three to five years of age. They spawn in gravel and cobble pockets in streams during late summer and early fall. In general, eggs hatch before the end of January (Weaver and White 1984) with emergence occurring in late spring. Bull trout life history is illustrated in Figure 14. Observed habitat use and selected biological characteristics of bull trout are presented in Table 8 and discussed throughout the report.

6.3.2 Eggs and Incubation

Eggs hatch in 34 days at 12°C, in 74 at 6°C, and in 125 at 2°C . Time to hatch is related to temperature by the equation:

$$ln\ \text{days} = 5.086 - 0.131 \text{ x temperature } (^\circ\text{C});$$

which demonstrates the inverse relationship between development time and temperature (McPhail and Murray 1979). Embryonic development of bull trout is less retarded by low temperatures than that of other salmonids and, as mentioned above, eggs generally hatch before the end of January. Bull trout emerge from the gravel during May in Arrow Lake tributaries and at 6°C, emergence takes 126 $(ln_e = 5.59-0.126T)$ days (McPhail and Murray 1979). Yolk absorption requires 65 to 90 days (Shepard et al. 1984). In Line Creek, a Fording River tributary, bull trout emerge in middle to late May (Allan 1980).

Bull trout eggs incubate most successfully at temperatures of 2 to 4°C and egg mortality increases with increasing temperature (McPhail and Murray 1979). Although no work on the oxygen requirements of bull trout eggs has been conducted, the recommended oxygen concentration for incubating eggs and alevins is 9.5 mg/L (Davis 1975). Forty to fifty percent of eggs survive in the wild (Allan 1980) and laboratory studies have demonstrated the importance of substrate size to survival.

FIGURE 14 - BULL TROUT LIFE HISTORY

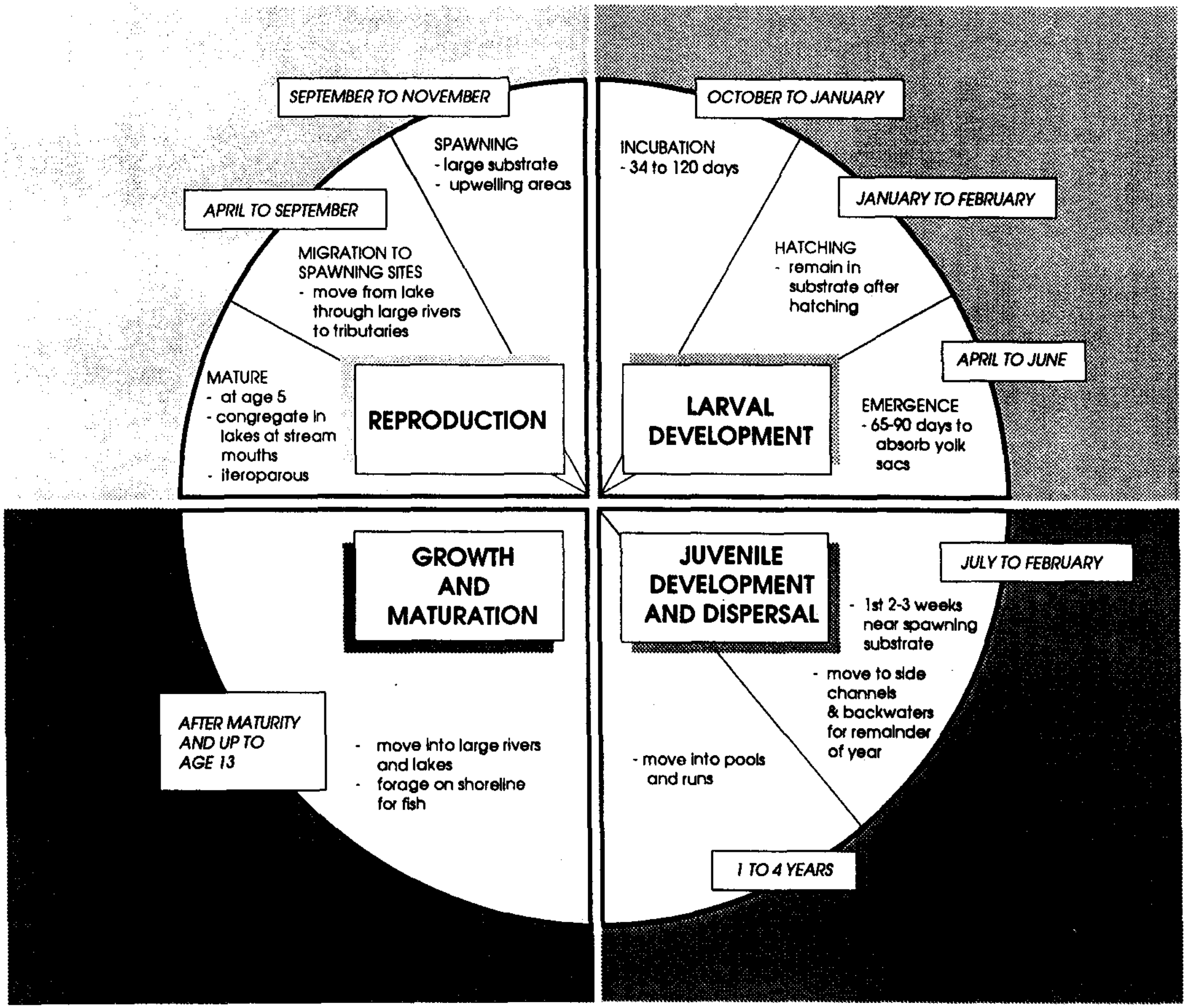

Table 8. **Observed habitat use and selected biological characteristics by life stage for bull trout** (for sources refer to text, NA- data are not available)

Eggs

Temperature tolerance range	0 to 8°C
Optimum incubation temperature	2 to 4°C
Recommended oxygen concentration	9.5 mg/L
Lower lethal oxygen concentration	NA
Range of incubation time	34 to 125 days
Incubation at optimum temperature days	95 to 125 days
Lower lethal pH	NA
Recommended current velocity	below level causing gravel scour

Juveniles

Temperature tolerance range	0 to 18°C
Optimum temperature for growth	<12°C
Recommended oxygen concentration	7.75 mg/L
Lower lethal oxygen concentration	NA
Habitat type preference	pools
Depth preference	to 1.0 m
Preferred current velocity	< 0.5 m/s
Substrate	cobble and boulder
Cover	cobble and fine debris
Turbidity tolerance	NA
Primary food category	benthic insects
Secondary food taxa	drift

Adults

Temperature tolerance range	0 to 12.8°C
Optimum temperature for growth	NA °C
Recommended oxygen concentration	7.75
Lower lethal oxygen concentration	NA
Habitat type preference	lake or large river
Observed depth preference	varies, up to at least 18 m
Preferred current velocity	none
Substrate	NA (primarily in lakes)
Cover	depth
Turbidity tolerance	NA
Primary food type	fish
Secondary food type	benthic insects
Form of reproduction	iteroparous
Nest construction	yes
Spawning habitat type	small streams
Preferred spawning temperature	< 9°C
Preferred spawning depth	0.15 to 0.84 m
Preferred spawning substrate	cobble/gravel
Preferred spawning current velocity	0.25 to 0.65 m/s
Range of first age-at-maturity	(precocious males age 3) age 5
Range of fecundity	660 to 6,750 eggs/female or 920 eggs/kg @ 600 mm FL

As summarized below, survival increases from 0% with more than 50% fines (<6.35 mm) to about 40% with no fines (Shepard et al. 1984):

Survival rates of bull trout embryos in various substrate mixtures in laboratory channels (unpublished data, Montana State Cooperative Fisheries Research Unit, Bozeman, Montana in Shepard et al. 1984)

Percent Gravel Mixture		Surviving Embryos
<6.35 mm	>2.0 mm	(%)
50	29	0
40	23	1
30	18	21
20	12	38
10	6	48
*	0	38

*anomalous data point

6.3.3 Rearing, Food and Growth

Bull trout fry do not attain neutral buoyancy until three weeks after yolk absorption, in contrast to other salmonids, which are neutrally buoyant soon after absorption (McPhail and Murray 1979). The late attainment of neutral buoyancy may be an adaptation to the high water velocities in which bull trout spawn. Fry are too weak to hold their positions against the current when they first emerge, and by holding near the substrate they avoid being swept downstream.

After hatching, bull trout fry rear in low velocity backwaters and side-channels and avoid riffles and runs (McPhail and Murray 1979). They hold in substrate interstices or within 0.03 m of the substrate and are associated with cover in cobble and boulders or submerged fine debris where water velocity averages 0.09 m/s (Shepard et al. 1984; Allan 1987). Juveniles also use large woody debris as cover, particularly in areas where depths are less than 0.5 m (Allan 1987).

Prior to emergence, fry are photophobic but after emerging they become photopositive. Initial mortality is high. Newly emerged fry average 25 mm in fork length in June and grow 40 mm during their first summer (McPhail and Murray 1979; Jeppson 1960). Fry begin to feed within one day of emergence, but because of their negative buoyancy, feeding is awkward and feeding failure is a cause of early mortality. Bull trout fry are more aggressive under conditions of low fry density and high water velocity than under conditions of high fry density and low water velocity. Subyearling bull trout migrate from streams to lakes in the spring whereas yearlings and superyearlings migrate in the autumn (McPhail and Murray 1979).

Bull trout sampled from the Jordan and Illecillewaet Rivers (tributaries to the Columbia River above Upper Arrow Lake in British Columbia) ranged in age from less than one to three years (Mason 1985). In the Flathead drainage in Montana, juveniles migrate from tributaries to major rivers and lakes at age 3 or 4 (Block 1955). Bull trout migrate to Pend Oreille Lake from tributary streams at age 2 (Mason 1985).

McPhail and Murray (1979) studied the migration of bull trout from Mackenzie Creek to the Arrow Lakes and found that even thought most of the annual creek production migrated as fry, 75% of lake-caught adults showed two or three summers of stream growth. They concluded that fish with two or three summers stream growth have a higher probability of survival upon entering the lake than do fry.

Juvenile bull trout feed primarily on aquatic insects and occasionally other fish (Scott and Crossman 1973). Ephemeropterans, plecopterans, trichopterans, and coleopterans are the preferred foods of bull trout in the Muskeg River system of western Alberta (Boag 1987). In the Flathead basin of Montana, juvenile bull trout (<100 mm) commonly feed on ephemeroptera (heptagenid and baetid) and diptera (chironomid) (Shepard et al. 1984).

Bull trout rearing in streams are 100 to 150 mm by age 2 to 3, and grow faster once they enter lakes (McPhail and Murray 1979). In MacKenzie Creek, a tributary of the Arrow Lakes, mature bull trout ranged in size from 390 to 610 mm in fork length in 1978

(McPhail and Murray 1979). Table 9 summarizes the length of bull trout at specific ages in three systems.

Table 9. Size at age of bull trout.

Age	Mean Length (mm)		
(years)	Libby Reservoir[1]	Arrow Lake[2]	Line Creek[3]
0	-	33.6	49.0
1	-	81.6	108.2
2	275	119.3	164.8
3	380	156.0	-
4	410	-	271.0
5	440	450.0	319.8
6	454	534.3	421.0
7	765	573.9	-
8	-	577.5	557.2
9	-	614.3	
10	-	646.0	695.0
11	-	664.3	
12	-	708.7	
13	-	782.0	

Source: [1] Chisholm et al. 1989
[2] Mason 1985
[3] Allan 1987

Yearling and older juveniles rear in pools with water velocities less than 0.25 m/s and up to 1 m deep, and in runs where water velocities are less than 0.5 m/s and depths average 0.25 m (McPhail and Murray 1979). In some small streams yearling and older juveniles avoid riffles and side channels, perhaps because cover there is unsuitable or because feeding opportunities are greater elsewhere.

In the Jordan River, juvenile bull trout are most abundant in areas with low water velocity, depths of 0.3 m, and a gravel and cobble substrate (Mason 1985). However, in the Flathead basin in Montana, they have been found in pools, riffles, runs, and pocket water where they hold 0.08 m off the substrate in water velocities of 0 to 0.12 m/s, water depths of 0.45 m, and associate with large submerged debris (Shepard et al. 1984). It should be noted that Swales and Levings (1989) found that off channel ponds are not used by Dolly Varden, even when accessible.

In the Flathead basin, bull trout are not found in streams where maximum monthly water temperatures exceed 18°C and are most abundant where water temperatures are 12°C or less (Shepard et al. 1984). This preference for cooler water manifests in the frequent association of bull trout with cold perennial springs (Oliver 1979 in Shepard et al. 1984; Allan 1980).

Adfluvial bull trout fry migrated from MacKenzie Creek to Upper Arrow Lake during the spring freshet while juveniles migrated in the spring and summer (McPhail and Murray 1979). In the Wigwam River, juvenile bull trout migrate during the summer and fall (Oliver 1979 in Shepard et al. 1984). In tributaries to the Flathead River, bull trout migrate during the summer months (Shepard et al. 1984). Some of these fish mature in the mainstem of the Flathead River, but most migrate to the lake.

Bull trout adults live in open water during the summer and near shore during the fall in the Libby Reservoir (Chisholm et al. 1989). In Flathead Lake, bull trout tend to use the littoral zone (Block 1955), but Dolly Varden in coastal British Columbia lakes use offshore and benthic habitats when in competition with cutthroat trout (Andrusak and Northcote 1971). Bull trout occupy the lower portion of the thermocline at depths of 12.2 to 18.3 m in Priest Lake, Idaho, presumably to take advantage of water temperatures of 7.2 to 12.8°C and move to the surface when surface water temperatures drop to 12.8°C or lower (Bjornn 1961).

Adult bull trout are generally opportunistic piscivores. In Libby Reservoir, fish account for over 99% of the biomass consumed by bull trout (Chisholm et al. 1989). The species consumed were, in order of importance, kokanee, largescale suckers, rainbow trout, cutthroat trout, and peamouth chub. In the Arrow Lakes, kokanee are a significant food. In one study, over 450 stomach samples from bull trout (> 2 kg) indicated a diet of 99%

kokanee (R. Lindsay, Fish and Wildlife Branch, B.C. Environment, Nelson, pers. comm. 1991). Studies by Withler (1948) in lakes in the Skeena watershed showed that bull trout, some of which were mistakenly identified as Dolly Varden, ate mostly fish. Bull trout also enter streams to feed on kokanee eggs, for example; bull trout were captured in Tonkawatla Creek, an Arrow Lake tributary, during fence trapping from June 10 to October 2 during 1981, but did not spawn there (Mason 1985).

As mentioned above adult bull trout are found in both lakes and rivers. Where lakes are available they are used as the primary rearing area (e.g. in the Upper Arrow Lake). But wholly fluvial stocks exist in the Elk River, and although some fish there do use the reservoir at Elko for overwintering, the river is the primary rearing area (Allan 1987). Both fluvial and adfluvial (lake dwelling) stocks migrate upstream to use small streams for spawning.

6.3.4 Maturity, Adult Migration, and Spawning

Bull trout in Upper Arrow Lake reach sexual maturity at age 5 years (McPhail and Murray 1979; Mason 1985); from 1979 to 1983, mature bull trout ranged from 450 to 782 mm in fork length (Mason 1985). In Flathead Lake, bull trout reach maturity at age 5 years, however, precocious males may mature by age 3 years (Block 1955; Shepard et al. 1984).

The timing of spawning migration and spawning depends on a variety of factors including water temperature, stream and stock of fish. Heimer (1965) observed migration during the fall with immature bull trout also participating. Migration to McDonald Creek, a tributary of Upper Arrow Lake, starts in July with the peak occurring in August (Lindsay 1977). The average stream residence time in MacKenzie Creek is 46.5 days (McPhail and Murray 1979). Bull trout migrated into Jordan River from September to November in 1979 (Mason 1985). In Meadow Creek, a tributary of Kootenay Lake, the main spawning period was September 15 to October 11 (Leggett 1969). In Line Creek, a tributary of the Fording River, bull trout migrate upstream to spawn during August and early September

(Allan 1987).

In tributaries to Pend Oreille Lake, adult bull trout migrate into larger tributaries during freshet, although they do not spawn until the fall (Jeppson 1960). Prior to spawning, bull trout hold in deep pools in tributaries and at the base of Cabinet Gorge Dam and do not enter small tributaries until the fall. In Flathead Lake, Montana, bull trout travel along the shoreline except during the spring when they congregate at the mouths of major tributaries to the lake (Block 1955). At this time the lake acts as a staging ground for spawning migrations (Shepard et al. 1984). The spawning migrations may be as long as 160 km in the Flathead River (Block 1955). Upstream migration may begin as early as April and the combined upstream and return migration may take seven months (Shepard et al. 1984). Bull trout enter tributaries of Flathead Lake to spawn from May through July when temperatures are below 12°C (Fraley and Shepard 1989). Spawning appears to be cued to temperatures below 9°C (Shepard et al. 1984).

In Arrow Lake tributaries (e. g. MacKenzie Creek) spawning begins in mid-September and continues until late October (McPhail and Murray 1979) which is similar to that in other streams in the Kootenays (Leggett 1969) and in Idaho (Heimer 1965). In the Flathead River and tributaries, bull trout begin spawning in mid August, reach peak spawning during September, and complete spawning by early November (Block 1955).

Females select a redd site and construct a series of nests by arching their bodies and beating the substrate with their caudal fins. One or more males attend the female during nest construction. Nests are built over several days and are built upstream of one another. Redds are 1.0 m long and 0.5 m wide; nest depth is 0.10 to 0.16 m (McPhail and Murray 1979). Bull trout fecundity ranges from 660 to 6,750 with eggs 5 to 6 mm in diameter (McPhail and Murray 1979). Mason (1985) found relative fecundity of 920 eggs/kg at 600 mm fork length.

Adults survive after spawning and migrate downstream from spawning streams to rivers or lakes. Outmigration of bull trout from MacKenzie Creek ends in late October

(McPhail and Murray, 1979). Bull trout in Line Creek move downstream in late September and early October, after spawning. This downstream migration is more rapid than the upstream migration (McPhail and Murray 1979; Shepard et al. 1984).

In Arrow Lake tributary streams, bull trout spawn in low gradient areas (<1%) with water velocities (1 cm above the substrate) between 0.25 to 0.64 m/s, and with loose gravel substrate (diameter 25 mm) containing less than 10% fines (i.e. 1.0 mm or less) (McPhail and Murray 1979). Subsurface oxygen is always close to saturation. [Data from a supplemental spawning area for bull trout in Northern Idaho indicated that intragravel dissolved oxygen was a better predictor of nest site selection than gravel porosity (Heimer 1965)]. Proximity to cover such as overhanging terrestrial vegetation, pools, and cutbanks is characteristic of spawning sites. In Line Creek, bull trout spawn in areas where overhead cover is nearby and where water velocity is 0.28 m/s and water depth is 0.21 m (Allan 1987). Redd size is approximately 0.76 m^2 and ranges from 0.34 to 1.36 m^2. In Meadow Creek spawning substrates with gravel and cobble 3.8 to 12.7 cm in diameter are selected (Leggett 1969). In tributaries to Flathead Lake areas with low gradient, loosely compacted gravel, ground water influence, and cover are selected (Fraley and Shepard 1989). In general, chars spawn in areas influenced by groundwater which may be beneficial since groundwater reduces the risk of redds freezing and subsequent egg mortality (Shepard et al. 1984). Table 10 presents characteristics of bull trout spawning habitat.

As adult bull trout grow, they become too large to enter small creeks and may shift spawning streams. (McPhail and Murray 1979). Such lack of fidelity to the home stream has been observed in Kootenay streams (Fleck 1977).

Maximum age of bull trout varies between lakes. One cause may be differences in sports-fishing harvest. In Priest Lakes in Idaho, bull trout live to age 10 years (Bjornn 1961) whereas in Upper Arrow Lake they may reach ages of 13 years (Mason 1985). The maximum recorded age is 20 years (Carlander 1953 in Scott and Crossman 1973).

Table 10. Characteristics of bull trout spawning habitat in river drainages of Montana, Idaho, and British Columbia.

Drainage	Mean water depth over redd (m)	Mean velocity over redd (m/sec)	Mean disturbed area (m)	Streambed composition (%) Cobble and larger	Large gravel	Small gravel	Sand	Depth of egg deposition(m)	Source
				(>50 mm)	(16-50 mm)	(2-16 mm)	(<2 mm)		
Flathead R., Montana	0.28 (0.15-0.35)	0.29 (0.24-0.61)	2.3	18	30	39	13	0.1-0.2	
Flathead R., Montana	0.3	-	3.72	Predominantly medium-course gravels			0.2		Block 1955
				(>60 mm)	(35-59 mm)	(2-16 mm)	(<2 mm)		
Clearwater R., Alberta									
Sawmill Springs	0.24	0.52	0.69	5	12	72	10	0.03-0.18	Allan 1980
Timber Creek	0.58	0.44	0.62	4	14	70	9		
				(75 mm)	(26-75 mm)	(1.5-25 mm)	(<1.5 mm)		
MacKenzie Creek (Upper Arrow Lakes, British Columbia)	-	0.57-0.64	0.5	0	31	61	8	0.10-0.16	McPhail & Murray 1979
					(>50 mm)		(10-50 mm)	(<10 mm)	
Wigwam R. & Ram Creek (Kootenay River, British Columbia)	0.34	0.43	1.47	20		50	30	0.17-0.25	Oliver 1979 in Shepard et al. 1984
				(>50 mm)	(25-60 mm)	(2-25 mm)	(<2 mm)		
Pend Oreille Lake (Clark Fork River, Idaho)	-	-	-	0	5	85	10	0.08-0.15	Heimer 1965
				(>50 mm)	(10-50 mm)		(<10 mm)		
Meadow Creek (Kootenay Lake, British Columbia)	0.73-0.84	0.04-0.61		29	59		12	0.1	Leggett 1969
Line Creek (British Columbia)	0.21	0.28	0.76	-	-		-	-	Allan 1987

6.4 Mitigation and Compensation Strategies

Bull trout are sensitive to habitat disruption and may serve as an indicator of environmental disturbance (Fraley and Shepard 1989). Throughout their range, they face impacts from industries including hydroelectric and other impoundments, forestry, mining, oil and gas development and agriculture and grazing. (Shepard et al. 1984). The spawning adult, incubating egg, fry and juvenile stages are considered most vulnerable. For example, grazing and logging on land adjacent to spawning and rearing stream can introduce sediment and debris, damaging riparian habitat and scouring the substrate, which in turn kills eggs and reduces habitat quality. Spawning often occurs in small streams during low water when the capacity to dilute sediment and other deleterious substances is limited.

McPhail and Murray (1979) believe that fry survival limits production in MacKenzie Creek, and have identified the low velocity side channel and margin areas as the limiting habitat; they prescribed an increase in the number and extent of side channels as a measure to enhance the population. Artificial propagation, including artificial channels for rearing fry and hatchery propagation, was also recommended as a means of enhancing bull trout populations. Hatchery propagation has been used to offset losses to the Upper Arrow Lakes fishery.

Hydroelectric developments impact bull trout by blocking access to spawning areas and by flooding spawning and rearing habitat. The construction of the Revelstoke Dam in the late 1970's and early 1980's blocked a large population of Upper Arrow Lake bull trout from their spawning and juvenile rearing areas. Enhancement measures have regained some of the production losses. However, at the present time, it is unlikely that natural production of fry is sufficient to meet the potential for production in Upper Arrow Lake. Similarly, bull trout in Flathead Lake may be limited by the quantity and quality of rearing and spawning habitat (Fraley and Shepard 1989).

When access to spawning streams is blocked, bull trout may move to other streams to spawn, as was observed in the Columbia River. About 40 bull trout blocked by the

Revelstoke Dam diversion tunnel and tagged at the base of the dam were later observed spawning in the Jordan River (Mason, 1985). However, those age classes corresponding to the first two years that the Columbia River was blocked by the Revelstoke Dam were not found in the lake, suggesting that the majority of bull trout blocked by the dam did not successfully reproduce (Fleming et al. 1990). Bull trout naturally switch to larger spawning streams as they age, and perhaps the Jordan River did not meet the habitat requirements of larger fish from the Columbia River stock.

Losses in habitat caused by the Revelstoke Dam have been offset by the colonization of adjacent, barren tributary streams through the outplanting of fry reared in the Hill Creek Hatchery (unpublished data, British Columbia Fisheries Branch, Nelson, B.C.). The success of this program is limited by the availability of sufficient brood stock. The Jordan River and Columbia River close to the Revelstoke Dam are presently the main source of eggs for Arrow Lake bull trout production (R. Lindsay, pers. comm. 1990). Bull trout have been outplanted to the middle reaches of the Jordan River since 1982 where there are approximately 28 km of otherwise inaccessible habitat (Teleki 1979). This enhancement strategy is the most effective way of harnessing the production of this stream, since there are four barriers to migration in the Jordan River and construction of a fishway would be expensive (R. Lindsay, pers. comm. 1992). No quantitative assessment of the success of these outplants has been performed. However, the lack of recruitment to the lake until 1987 suggests that outplanting failed during the first three years (Fleming et al. 1990).

Another mitigative strategy is the removal of dams or natural blockages to adult migration. A 10 m high dam on the Illecillewaet River blocked all upstream migration in the early 1900's. The dam was removed in the early 1980's, and presently bull trout migrate up approximately 20 km of river to tributaries where they spawn. Where barrier removal is not feasible, fishway construction can provide access to spawning areas upstream. On lower Arrow Lake the Inonoaklin fishway has been proposed to provide additional habitat for, among other species, bull trout.

In certain cases, bull trout production may actually be enhanced by hydroelectric projects. The production of forage food fishes in reservoirs provides food for bull trout and, in theory, can increase their abundance. Bull trout abundance appears to be increasing in Upper Arrow Lakes and Revelstoke Reservoir (Fleming et al. 1990). However, their preference for habitats deeper than those of trout, when in sympatry, (Andrusak and Northcote 1971) may preclude them from effectively using shallow reservoirs.

Logging adjacent to streams can introduce organic debris that can block migration, damage banks, scour the stream bed, introduce toxic leachates, and reduce gravel porosity (Bryant 1983). Removal of logging debris is a common mitigation strategy for logging impacts, however, it can negatively impact Dolly Varden (Dolloff 1986; Elliot 1986) and presumably has similar effects on bull trout. Removal of limbs, needles, and fragmented logs by hand resulted in a 60 to 80% reduction in macrobenthos density and invertebrate drift in Alaska streams and a subsequent 10 fold reduction in Dolly Varden density.

Logging may also reduce flows and increase temperature during the summer period, reducing the extent of juvenile habitat and delaying adult spawning. Increased sedimentation from logging may lower bull trout egg-to-fry survival and reduce pool volume, which in turn may reduce juvenile habitat during both summer and winter as well as decrease holding areas for adult bull trout.

Several other industries impact bull trout habitat. Coal mining may increase habitat alienation and stream sedimentation, introduce nutrients and heavy metals, and increase fishing pressure (Shepard et al. 1984). Oil and gas extraction will increase sedimentation, fishing pressure, and possibly disrupt groundwater aquifers during drilling. Although no mitigation of these impacts has been attempted solely for bull trout, methods of mitigation for impacts on other salmonids have been attempted and accepted as effective (Marcus et al. 1990).

Sediment inputs can be mitigated through settling basins, interception ditches to divert stream water away from the workings, and physical removal including hydraulic cleaning (Marcus et al. 1990). When banks have been eroded and cover is removed, there are many mitigative methods including log overhangs, tree revetments, bank revegetation, riprap, erosion control matting, streambank fencing, grazing control, buffer strips, and the addition of large organic debris (Marcus et al. 1990). Where stream channels have been damaged by scour, complexing of the channel can be accomplished with the installation of a current deflector and small dams, and further scouring can be prevented through the installation of trash racks.

In some cases the application of enhancement measures for other salmonids has no positive effect on bull trout. In Line Creek boulder placement increased rainbow trout density but had no effect on bull trout density (J. Allan, Pisces Environmental Resources Consulting Services Ltd., Red Deer Alberta, pers. comm. 1991). The preference of bull trout juveniles for cobble and gravel substrate may explain the failure of this mitigation measure.

Introduction of other species may impact bull trout. In sympatry, trout and char show marked differences in vertical distribution and in diet whereas in allopatry these characteristics are more similar, suggesting that the species shift habitats in response to competition. For example, in sympatry with cutthroat trout, Dolly Varden, and presumably bull trout, are found throughout the water column, whereas cutthroat trout use shallow areas (Andrusak and Northcote, 1971). In streams, rainbow trout and bull trout segregate - rainbow trout occupy areas of higher water velocity such as runs, particularly during the summer (McPhail and Murray 1979). The more rapid growth of bull trout in sympatry with rainbow trout in an Arrow Lake tributary suggests that bull trout are superior competitors in that habitat (McPhail and Murray 1979), nonetheless introductions of rainbow trout could reduce food availability and bull trout growth.

Harvest has the potential to impact bull trout, since they typically do not reproduce until age 5 years or older. Sports fishing regulations applied usually include the closure of river and streams during the spawning period, and restrictive catch limits. However, duration of the bull trout spawning migration puts them at risk of mortality from poaching.

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7.0 LAKE TROUT

(Salvelinus namaycush)

7.1 Introduction

The lake trout, *Salvelinus namaycush*, is considered to be a principal recreational and commercial species in Canadian freshwaters. Although commercial fishery effort has declined over the last 20 years (Healy 1978), this has, to a certain extent, been compensated by an expansion of sports fisheries for the species (Martin and Fry 1973; Yaremchuk 1986). In northern Canada, particularly the Northwest Territories, there is a recurring interest in expanding the sport fishing lodge industry and establishing commercial fisheries that target lake trout (Yaremchuk 1986). In northwestern British Columbia, there were domestic lake trout fisheries in Atlin and Tagish Lakes, where harvest was estimated to average 0.5 tonne per year (Pearse Bowden Economic Consultants Ltd. 1971). Indian foodfish permittees also harvest lake trout, but statistics for these catches are unavailable.

The generic name of lake trout is still a matter of controversy. Some taxonomists designate the lake trout into a separate subgenus, *Cristivomer*, to emphasize particular differences in morphology from other *Salvelinus* species (Behnke 1980). However, for the most part, lake trout is classified in the subgenus *Salvelinus* to emphasize its relationship with other char (McPhail and Lindsey 1970). Fertile hybrids have been created by crossing lake trout and brook trout (*S. fontinalis*), and are called "splake". The splake is a popular sport fish in some areas because of its rapid growth, often to a maximum size of 7 to 8 kg, and capability to form self-sustaining populations (Berst et al. 1980). These hybrids are not common in British Columbia but have been stocked in some lakes in the Kootenay and Yoho National Parks in southeastern British Columbia (Carl et al. 1967).

7.2 Distribution

Lake trout occur naturally throughout North America, and are particularly abundant in the more northern latitudes. In Canada, the species is found in all provinces except Prince Edward Island and Newfoundland. In the United States, lake trout are found in the New England states, New York, Pennsylvania, Michigan, Wisconsin, and Minnesota, and the western states of Montana, Idaho, and Alaska (Carlander 1969; Scott and Crossman 1973).

In British Columbia, lake trout are found in the Skeena, upper Stikine, Taku, Chilkat, upper Fraser, Yukon, Laird, and Peace river systems (Carl et al. 1967). They are absent from the Columbia River system and Vancouver Island. Figure 15 shows the distribution of lake trout in the Peace and Liard River drainages.

7.3 Life History and Habitat Requirements

7.3.1 General

Generally, the lake trout life cycle takes place entirely within lakes. However, there is some evidence of river spawning populations (Loftus 1958). Lake trout are iteroparous but may not spawn each year. Spawning occurs in late summer or fall, often in October, in relatively shallow areas of lakes. Eggs are deposited on large rubble substrate and incubate for 4 to 5 months over the winter and early spring.

Fry emerge and usually remain at inshore nursery areas adjacent to the spawning beds to feed on insects and crustaceans for a period that can range from several weeks to several months. As the juveniles grow the diet changes, and the fish move into deeper offshore waters. Lake trout are the top aquatic predator in most lakes in which they are found (Martin and Olver 1980). They are primarily piscivorous where possible but also consume plants, annelids, crustaceans, insects, arachnids, mollusks, and mammals (Scott and Crossman 1973; Martin and Olver 1980). Lake trout are highly mobile as sub-adults and

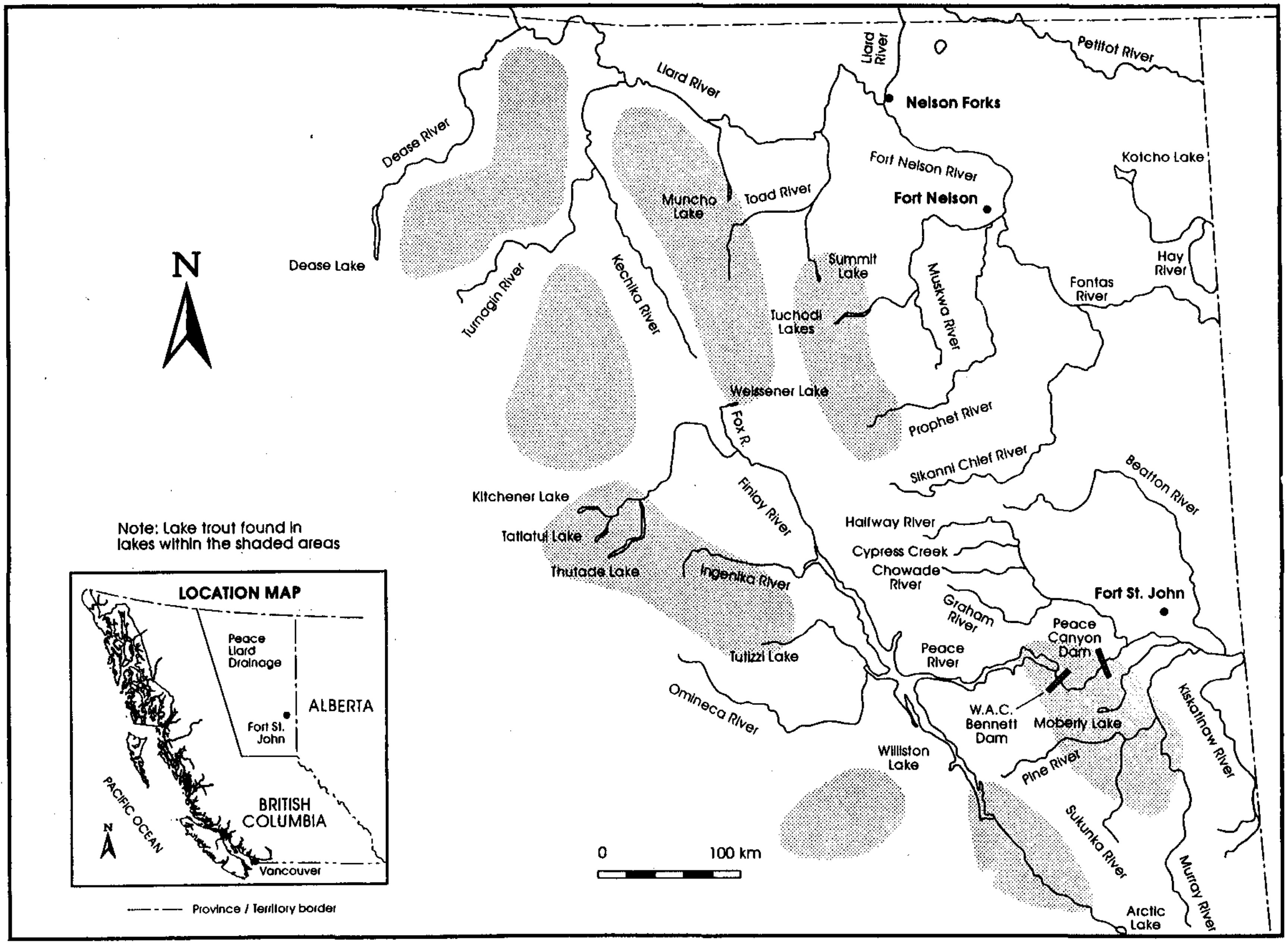

Figure 15: Lake Trout Distribution in the Peace and Liard Drainages, British Columbia

adults and mature in offshore waters, returning inshore to spawn. On average, age-of-maturity first occurs at age 11 years and never before age 5. Lake trout life history is illustrated in Figure 16.

Lake trout are usually thought of as a solitary species that forms loose aggregations in response to preferred environmental conditions. Their movement patterns and distribution are dependent on many factors including season, age of the fish, feeding, spawning, and physical and chemical conditions such as temperature, light and oxygen. Lakes that contain this species are typically at higher altitudes, deeper, clearer, colder, better oxygenated, slightly more acidic, and lower in total alkalinity buffering capacity, total dissolved solids and morphoedaphic index values than those lakes that do not contain lake trout (Martin and Olver 1980). Johnson et al. (1977) compared 2500 Ontario lakes and found that lake trout were found most frequently in lakes that possessed (1) a mean depth greater than 6 m; (2) total dissolved solids less than 50 mg/L; and (3) average hypolimnetic oxygen concentrations of greater than 6 mg/L and metric morphoedaphic values (i.e. mean depth/total dissolved solids) greater than 6. Observed habitat use and selected biological characteristics of lake trout are presented in Table 11 and discussed throughout the text.

7.3.2 Eggs and Incubation

The length of egg incubation will differ among lakes and in individual lakes from year to year. Incubation takes approximately 120 days in lakes of the southern part of the species range; longer times are likely required for northern populations. Incubation is considerably shorter in river spawning stocks, even when temperature in river spawning beds is lower than that of lake spawning areas (Martin and Olver 1980).

Water temperature is the primary factor that will affect the development and survival of eggs and larvae of lake trout. Reported incubation time ranges from 49 days (Emody 1934) to more than 175 days (Martin and Olver 1980) depending upon the ambient temperature of the water in the spawning beds and the genetic origin of the stock. Emody (1934) reports that hatching time for eggs increases with decreasing temperature, requiring

FIGURE 16 - LAKE TROUT LIFE HISTORY

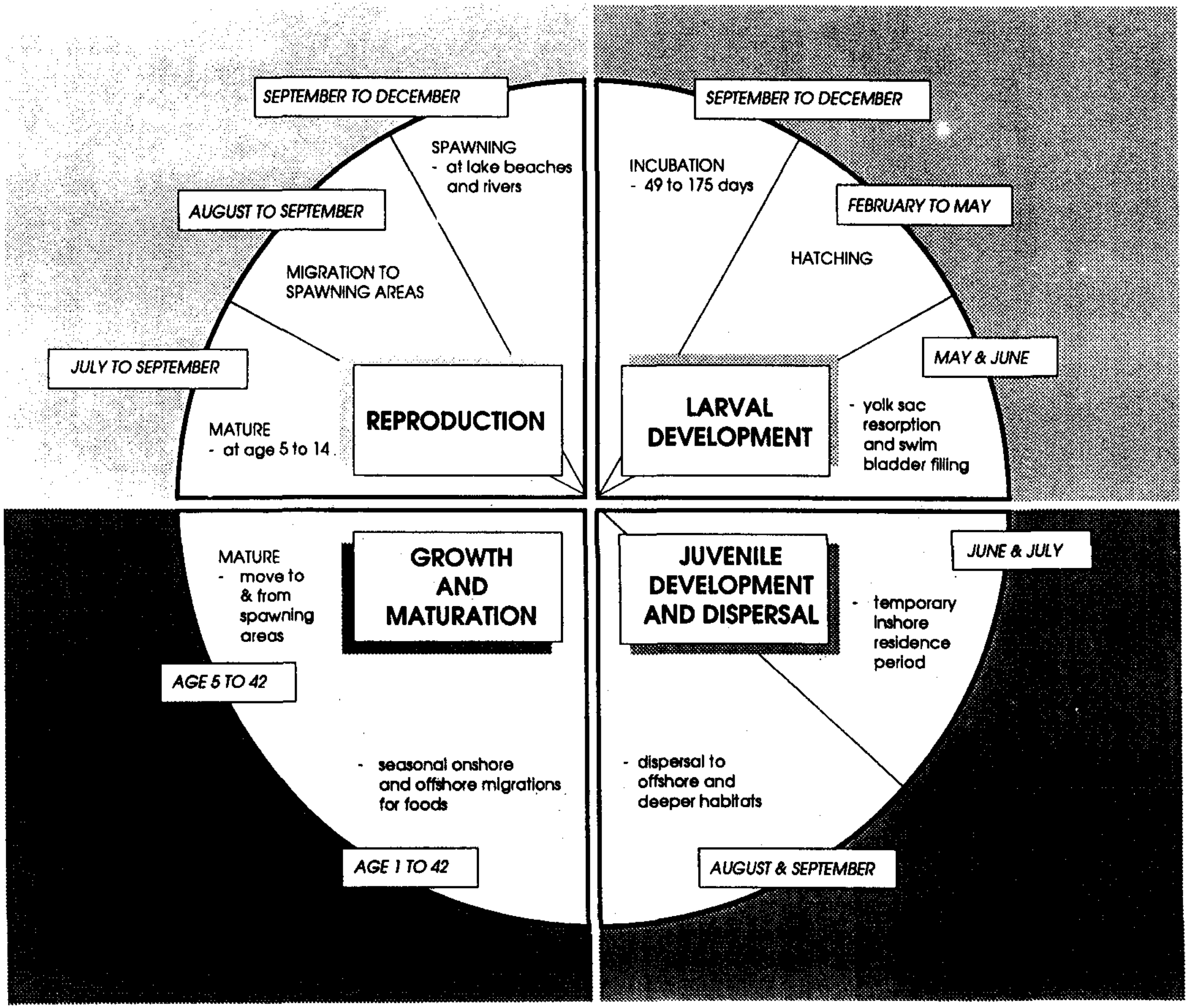

Table 11. Observed habitat use and selected biological characteristics by life stage for lake trout. (for sources refer to text, NA - data are not available).

Eggs	
Temperature tolerance range	0.3° C to 10° C
Optimum incubation temperature	5.0° C
Recommended oxygen concentration	(for larvae if water 7 - 10° C) > 6 mg/L
Lower lethal oxygen concentration	2.5 mg/L
Range of incubation times	49 to 175 days
Incubation time at optimum temperature	100 to 117 days
Lower lethal pH	NA
Recommended current velocity	none
Juveniles	
Temperature tolerance range	-0.8°C to 23.5°C
Typical temperature range	6.0°C to 13°C
Recommended oxygen concentration	9.75 mg/L
Lower lethal oxygen concentration	3.0 mg/L
Habitat type preference	shallow inshore area of large lakes
Depth preference	variable, up to more than 100 m
Preferred current velocity	none
Substrate	cobble/rubble
Cover	boulder/woody debris
Recommended maximum turbidity	<10 mg/L
Primary food category	benthic or planktonic invertebrates
Secondary food taxa	fish
Adults	
Temperature tolerance range	0.0°C to 23.8°C
Optimum temperature for growth	15°C
Recommended oxygen concentration	7.75 mg/L
Minimum acceptable oxygen concentration	4.0 mg/L
Habitat type preference	pelagic zone of large lakes
Depth preference	variable
Preferred current velocity	none
Substrate	none
Cover	none
Recommended maximum turbidity	<10 mg/L
Primary food type	fish
Secondary food type	invertebrates
Form of reproduction	iteroparous
Nest construction	no
Spawning habitat type	shallow inshore areas of large lakes, occasionally rivers
Preferred spawning temperature	10.0°C
Observed typical spawning depth	5 to 10 m
Preferred spawning substrate	rubble (2 cm to 30 cm diameter)
Preferred spawning current velocity	none
Range of first age-at-maturity	males - age 5 to age 13 females- age 6 to age 14
Range of fecundity	1,000 to 15,000 eggs/female

49 days at 10°C, 100 to 117 days at 5°C and 141 to 156 days at 2°C. Garside (1959) found hatching time for lake trout was 50 days at 10°C, 67 to 85 days at 7.5°C, 108 to 117 days at 5°C and 141 to 156 days at 2.5°C. Oxygen concentration, exposure to waves, substrate composition, and abundance of predators will have secondary effects on egg survival.

Dissolved oxygen concentration also affects the development of larvae. Garside (1959) studied the effect of low dissolved oxygen concentration on the development of lake trout embryos and found that low levels of oxygen concentration (2.6, 3.7, 4.5 mg/L) caused retardation in the development rates resulting in delayed hatching, longer hatching periods, and increased proportion of larvae with abnormalities (reduction of vitelline circulation and abnormalities of the head and trunk). Hatching time for a given temperature was shorter at 10 mg/L oxygen than at 2.6 mg/L, with 3.7 mg/L and 4.5 mg/L giving intermediate hatching times. Carlson and Siefert (1974) report that dissolved oxygen concentrations of greater than 6 mg/L are required for normal development and for survival in temperatures between 7°C and 10°C.

Lake trout eggs are usually deposited in areas free of mud, silt, sand, and detritus (Martin 1957). Substrate composition is important as the size must be appropriate both to secure the neutrally buoyant eggs and to allow adequate water circulation around the eggs. Eggs usually filter through the interstices in the substrate within hours or days after spawning which provides some degree of protection from egg predators. Thus, preferred spawning substrate consists of rounded or angular cobbles exceeding 2 cm in diameter (Marcus et al. 1984; Thibodeau and Kelso 1990).

Ice contact and seasonal movements of spawning bed substrate also may affect egg survival. In areas of coarse cobble-gravels, where sediment accumulation rates are high, egg deposition may occur within the range of depth of subsequent ice contact. The natural pattern of sediment transport along a shoreline can also destroy eggs. Sly and Schneider (1984) observed that where spawning preceded seasonal movements of the substrate, there was no egg survival.

7.3.3 Rearing, Food and Growth

Information on the movement patterns and distribution of lake trout immediately after hatching is limited by the difficulty of capturing small fry. It is believed that in some cases fry leave the spawning ground and move directly into deep water after emergence (Royce 1951) while in others they remain near the spawning beds until the yolk sac has been absorbed (Eschmeyer 1955). Shortly after the yolk sac has been absorbed, fry migrate to the surface and fill their swim bladders after which it is not known how long they remain near the spawning areas (Balon 1980). In stream spawning populations, Patterson (1968) noted that the emergent lake trout fry move directly towards their nursery lake. In lake spawning populations, fry were captured in the vicinity of a shallow water reef in Lake Superior for up to three weeks (Peck 1981). Horrall (1981) suggested that this period is likely important for olfactory imprinting before dispersal into hypolimnetic waters. After this initial inshore residence period, Eschmeyer (1956) reported that fry were found in depths less than 37 m in Lake Superior. However, they have also been found in depths greater than 100 m in Lake Tahoe (Martin and Olver 1980). Thus, the inshore residence period and depth distribution of fry likely varies among lakes and is dependent on local environmental conditions.

Newly emergent fry have been found to prefer water temperatures of approximately 12.0°C (McCauley and Tait 1970; Peterson et al. 1979).

The food consumed by lake trout is highly dependent upon lake productivity, the size and age of the fish and the type of food available. During their first few years lake trout feed on benthic and planktonic food. In some lakes where forage fish are not abundant, lake trout will continue to consume these food items for their entire life. Where fish are available invertebrate food sources become less important and small forage fishes are consumed more frequently as lake trout grow. Carlander (1969) reported that lake trout as small as 38 mm can consume fish. With increasing size, larger fish such as kokanee (*Oncorhychus nerka*), burbot (*Lota lota*) and lake whitefish (*Coregonus clupeaformis*) are consumed, rather than greater numbers of small fish (McPhail and Lindsey 1970; Martin and Olver 1980).

Seasonal changes in diet have been documented and are likely caused by the availability of different food items throughout the year. With increasing surface water temperatures, juvenile lake trout move into deeper waters, shallow water invertebrate species disappear from the diet, and deeper water benthic prey items and fish become more prevalent. In the fall, when the surface water temperatures decline, lake trout again use the surface waters and shallow water invertebrate species are again found with greater frequency in the diet (Martin and Olver 1980).

Food supply is a primary factor controlling growth rates of different populations of lake trout (Martin and Olver 1980). Martin (1955) compared the growth curves of 11 populations and suggested that lake trout populations that feed on fish grow faster than populations that feed exclusively on plankton. Introduction of forage fish species or invertebrate prey items where food was limiting has resulted in improved growth of lake trout (Hacker 1962; Budd and Fry 1960).

Lake trout growth rate varies both between age classes and among stocks. Healy (1978) showed that the growth rate between populations can vary by a factor of two while the variation in average weight of fish from different populations is even more extreme. Differences in size and growth can be ascribed to genetic and environmental variables (Martin and Olver 1980). However, Healy (1978) cautioned that other factors adding to the above variations are the sampling practices used to determine growth rate; the effect of gear selectivity and variations in ageing techniques may lead to incorrectly estimating growth rate (the difficulties in ageing lake trout are discussed further in Section 3.4).

Growth rate varies among age classes (Eschmeyer 1956) and in some cases growth is faster in smaller fish than in larger fish, while in other stocks, the reverse is true. Growth rate may also be affected by the onset of sexual maturity, although there is no difference in growth rate between the sexes (Martin and Olver 1980). Longer lived stocks have a smaller length at age and reach a smaller maximum size. Growth rate is also affected by stock density and exploitation (Kennedy 1954; Healy 1978).

A compilation of the range of average length at age for various lake trout populations is given below (adapted from Martin and Olver 1980):

Age (years)	Length (cm)	Age (years)	Length (cm)	Age (years)	Length (cm)
1	9 - 18	11	41 - 87	21	56 - 64
2	13 - 33	12	39 - 90	22	58 - 68
3	18 - 42	13	49 - 91	23	62 - 25
4	22 - 49	14	55 - 95	24	56 - 70
5	26 - 54	15	50-100	25	57 - 70
6	33 - 63	16	54 - 90		
7	29 - 71	17	54 - 99		
8	28 - 79	18	55 - 92		
9	27 - 77	19	55 - 63		
10	33 - 84	20	52 - 63		

Temperature is likely a secondary factor determining the growth rate of lake trout (Rawson 1961; Kennedy 1954; Eschmeyer 1956) as lake trout in more northern latitudes grow more slowly than in southern regions. Different growth rates observed in different basins of the same lake have been attributed to temperature differences (Cuerrier and Schultz 1957; Kennedy 1954; Rawson 1961). Eschmeyer (1956) found that growth of the juvenile lake trout is greater at higher temperatures than those optimal for adults.

Temperature is also considered to be the primary factor controlling the quality of the habitat for juveniles (Martin and Olver 1980). The temperature range for juveniles is typically between 6 and 13°C (Martin and Olver 1980); they have been found in temperatures ranging from -0.8°C in Arctic Canada (Boulva and Simard 1968) to 18°C in Ontario (Martin 1952). The upper lethal temperature has been experimentally determined to be 23.5°C (Gibson and Fry 1954).

Oxygen concentrations do not appear to limit the movements of lake trout, but oxygen concentrations of below 3 mg/L have been proven to be lethal (Patterson 1968). An oxygen concentration of 4 mg/L is thought to be the minimum acceptable level of oxygen for lake trout (Martin and Olver 1976; Davis 1975). Dissolved oxygen concentrations of

9.75 mg/L or greater are required to provide optimum conditions for salmonids, including juvenile lake trout (Davis 1975).

No specific data are available to indicate the tolerance of juveniles to suspended solids. The Canadian Council of Resource and Environment Ministers (1987) recommend that concentrations of less than 10 mg/L are required to provide adequate conditions for aquatic life.

The feeding rate of mature lake trout decreases in the fall prior to the spawning season, tends to remain low during the winter, and increases in spring and summer (Frantz and Cordone 1970).

Lake trout are a mobile species and depending on the size of the lake, may make extensive migrations. Generally, the home range of adult lake trout is relatively small, however, migrations of as great as 300 km have been observed in a period of less than one month (Eschmeyer et al. 1952). Smaller lake trout tend to be less migratory than larger individuals (Eschmeyer et al. 1952). There is also evidence that some stocks of lake trout do not migrate and tend to remain in their natal habitat or part of the lake for their entire life (Keleher 1963).

Temperature is a critical factor determining adult distribution. In thermally stratified lakes, lake trout tend to concentrate in the cooler hypolimnetic waters, but in unstratified, vertical distribution is essentially random. Thus, changes in vertical distribution occur on a seasonal, rather than on a diel basis (Martin and Olver 1980). Lake trout prefer water of 10°C to 12°C (Eschmeyer 1964), but are abundant in lakes that range between 6°C and 13°C (Martin and Olver 1980). Below 7°C, productivity is low because of physiological constraints. Productivity increases for temperatures up to 15°C and above 15°C productivity drops until the upper lethal temperature of 23.8°C (Gibson and Fry 1954) is reached.

Dissolved oxygen is not believed to limit the movements of adult lake trout but evidence exists that 4 mg/L is the minimum acceptable dissolved oxygen concentration (Martin and

Olver 1980), and Davis (1975) recommends that concentrations of 7.75 mg/L or greater are required to provide optimum condition for salmonids, including adult lake trout.

7.3.4 Maturity, Adult Migration and Spawning

Ageing lake trout is difficult (Scott and Crossman 1973; Healy 1978). The number of discernable circuli on fish scales is a function of fish length, and little correlation exists in older fish between age estimated from otoliths and from circuli. These observations suggest that growth stops in lake trout when sexual maturity is reached, and erosion of scale edges and circuli crowding obliterates individual annuli (Healy 1978). This will result in underestimating the true age of the fish which in turn leads to overestimates of growth and mortality rates.

Maturity of lake trout typically varies from age 5 to 13 (Healy 1978; Martin and Olver 1980), and may not occur until age 19 (Bond 1975). In most populations , males mature one year earlier than females. The onset of sexual maturity is related to size, as larger members of the population mature earlier than smaller members (Kennedy 1954; Rawson 1961). Rate of growth may also be a factor regulating maturation as slow growing lake trout from northern populations mature later than those from southern regions (Healy 1978). However, different light regimes and other environmental conditions may also be significant in affecting the timing of maturation (Royce 1951; Martin and Olver 1980).

The maximum recorded weight for lake trout is 46.3 kg and it is not uncommon for 20 kg lake trout to be found (Kennedy 1954; Rawson 1961; Scott and Crossman 1973). In northern populations where growth is relatively slow, lake trout typically reach 0.5 kg at age 10 and 2.0 kg at age 20. Stunted populations have also been observed in a subalpine lake where the mean weight at age 10 was 0.12 kg and at age 20 was 0.28 kg (Donald and Alger 1986).

There is considerable information on lake trout reproduction. Understanding reproduction is complicated by the fact that there are often many localized populations within a lake, preserved through behavioral characteristics such as differences in the location, depth and timing of spawning (Eschmeyer 1955).

As mentioned above, lake trout generally spawn in late summer and fall. However, there is variation both between years and among stocks. In general, northern populations spawn earlier than those in southern regions (Martin and Olver 1980). Earlier spawning may also occur in smaller, shallower lakes where the temperature regime is more rapidly affected by ambient air temperature. Berst et al. (1980) presented evidence for the inheritance of spawning time and Griest (1977) observed that stocks of different origins planted within the same lake spawned at different times depending on the source of the parent stock. The size and age composition of spawners varies considerably among lakes. Lake trout do not actively feed during the spawning period.

Intermittent spawning, where females do not ripen every year, is not uncommon in lake trout, particularly those stocks found in northern latitudes (Johnson 1973; Sprules 1952; Cuerrier and Schultz 1957). The reasons for interrupted sexual development are not fully understood, but there appears to be a clinal relationship between latitude and frequency of spawning. It is possible that a photoperiod regime may be a factor (Hoover and Hubbard 1937; Hazzard and Eddy 1951; Royce 1951; Henderson 1963). The unproductive nature of northern lakes may also play a role in lake trout fertility (Scott 1962; Martin 1970; Johnson 1973).

During the prespawning period, lake trout swim randomly back and forth across the spawning beds and at this time some spawning bed cleaning activities have been observed (Royce 1951). Spawning occurs at night; individuals may be found on the spawning shoals during daylight hours (Royce 1951; DeRoche and Bond 1957; DeRoche 1969), but most spawning occurs during darkness. Beginning in late afternoon fish move on to the spawning shoals, males typically preceding females. Spawning occurs between dusk and midnight and as dawn approaches the fish move off the grounds. Males usually outnumber females on the spawning ground. Sex ratios of lake spawners of 2:1 and 3:1 are common (Loftus 1958; Griest 1977) while river spawning populations tend to have equal numbers of males and females (Loftus 1958). Younger and smaller fish spawn earlier and the average length of spawners tends to increase over the spawning season (Martin and Olver

1980).

Fecundity of lake trout generally increases with body size. However, Hurler et al. (1983) noted that after a certain size has been achieved the fecundity declines, suggesting that there is some intermediate body size that is optimum for egg production. Average fecundity can range from 1,000 to 15,000, depending on the size of the female and the genetic predisposition of the stock. Once extruded from the female, eggs immediately filter down through the interstices of the rocks.

Variability in the time of spawning may occur between years, largely in response to different environmental conditions. Light was found to play a role in determining the time of spawning and the duration of the spawning period (Royce 1951), as both factors appeared to be related to the accumulated number of hours of sunlight after the fish moved on to the spawning shoals. Temperature also affects the time of initiation and duration of spawning. Spawning usually occurs in temperate lakes when lake temperature drops to about 10°C (Scott and Crossman 1973), and in many cases coincides with the initiation of lake turnover.

Lake trout have been documented to spawn on material ranging from bedrock to silts, however, the spawning substrate is usually broken rubble or angular rock interspersed with large boulders (Martin and Olver 1980; Thibodeau and Kelso 1990). Marcus et al. (1984) suggest that clear patches of cobble that are devoid of silt, 2 cm to 30 cm in diameter, and located at a depth of 0.5 to 50 m are the most suitable spawning substrate. Alternative substrates that provide protection from egg predation are assumed to be more suitable than those that do not. In rivers, the substrate used for depositing eggs is similar to that used by lake spawners, however, more rounded river cobbles are found amongst the large boulders (Loftus 1958).

Lake trout have been reported to spawn in depths from 15 cm to over 100 m, but for the most part spawning occurs between the depths of 5 and 10 m (Martin and Olver 1980; Thibodeau and Kelso 1990). Shoal depth typically increases with lake size. In smaller lakes, the spawning shoals are usually in less than 6 m of water, whereas in large lakes, spawning occurs at greater depths, presumably because the longer fetches allow greater wave action, deeper cleaning action and greater oxygenation. Dumont et al. (1982) found that eggs were deposited in very shallow water on lake shoals at water depths between 0.2 and 1.0 m in areas with thick rubble substrate. Maximum egg density was found in depths less than 60 cm. They suggest that, in some cases, the substrate particle size is more important than depth of water.

Longevity is a particularly noteworthy aspect of lake trout. The maximum age recorded to date is 42+ years (Fumiss 1974), with age classes above 20 years common in most populations (Miller and Kennedy 1948; Martin 1952; Kennedy 1954; Rawson 1961; Martin and Olver 1980). Hurler et al. (1983) found that up to 26 age classes occurred within a single Yukon lake where the maximum age recorded was 31+ years.

7.4 Mitigation and Compensation Strategies

Lake trout spend most of their life in the lake environment and are, therefore, most vulnerable to resource or urban developments that impact lakes. There is a large body of literature that documents the decline of lake trout in the Great Lakes and acidified lakes of eastern Canada. The literature indicates that impacts to spawning and incubation habitat have the most significant effects on lake trout populations.

Quality of spawning beds may be degraded by impoundment, for example. Erosion and silt deposition in the inshore areas of reservoirs is a serious mortality factor for developing eggs and larvae of various fish species, including lake trout (Fudge and Bodaly 1984). Siltation of spawning beds may have become more common in recent years due to the increased numbers of hydroelectric, agricultural, forestry and construction operations.

Impoundment for irrigation, flood control or hydroelectric development can have significant effects on lake trout populations. During the fall and winter incubating lake trout eggs are vulnerable to impacts from reservoir drawdown and fluctuating water levels. Martin (1955; 1957) studied the effects of drawdown on lake trout reproduction and found that fluctuating water levels can leave spawning beds dewatered, desiccate or freeze eggs, preclude access to the preferred sites, force fish to select sites with sub-optimal temperature regimes, increase sediment loads, alter substrate characteristics, and affect depth of spawning. It was suggested that stable water levels are best but where untenable, water level should be lowered before spawning to prevent ova from being deposited in areas that will be isolated. In certain Ontario reservoirs, water levels decline in the fall and spring as a result of electrical generation. Investigations on some of these reservoirs (Martin 1955) indicate that each presented a unique problem because spawning occurred at different depths. In some cases, eggs were exposed and spawning beds dewatered. In other cases, where the preferred spawning areas were dewatered before the spawning period, the fish may spawn in undesirable areas where conditions for egg deposition and embryo development is not optimal. For example, in Bark Lake, Ontario, water levels fluctuate by up to 10 m and egg losses have been documented (Wilton 1969). In British Columbia, two proposed hydroelectric developments would have raised water levels by 7 and 21 m respectively, submerging existing spawning grounds to depths not used by lake trout (Withler 1956). Exposure to wave action is important as it may affect the depth at which fish deposit their eggs and the degree to which eggs are disturbed. Fungal growth may result in egg loss on the spawning beds (Martin 1957; Martin and Olver 1980).

A change in thermal regimes may accompany impoundment or diversion and can affect the timing of spawning and influence year class strength by interfering with spawning activities or by affecting embryos and larvae (Machniak 1975).

Raising water levels in impoundments will not have as serious an effect as drawdown because lake trout increase their vertical spawning distribution in response to raised water level (Rawson 1961). Runnström (1951) provided evidence that raising water levels actually improved conditions for spawning arctic char (*Salvelinus alpinus*) by increasing the total area of the spawning grounds, permitting spawners to disperse over a wider area and preventing overcrowding of a limited spawning area.

Artificial spawning beds can be used to compensate for impacts from drawdown or increased water levels which can not be mitigated (Machniak 1975). Martin (1955) created three artificial spawning grounds in Algonquin Park, Ontario, using waste rock from a feldspar mine. Hacker (1962) was also successful in constructing productive spawning beds at Green Lake in Wisconsin, noting that angularity of the substrate was important for protection against egg predators. Swanson (1982) used artificial turf as a substrate to incubate lake trout eggs that were stripped from adults collected from Lake Superior. He estimated that the 50,000 eggs incubated on the 30 cm by 90 cm turf sandwiches had the potential to produce 25 spawning pairs. DeRoche (1969) pointed out that although artificial spawning beds have their merit, more research is required to evaluate habitat preferences on a site by site basis because construction of such spawning areas requires a considerable amount of time and money. Machniak (1975) points out that artificial spawning beds can compensate for degraded or destroyed spawning beds. However, these are not always appropriate, particularly where lake trout exhibit strong homing tendencies. Recent literature reviews on the spawning requirements of lake trout suggest that further study of artificial spawning areas is required.

Despite the success of some stocking programs, most attempts to rehabilitate lake trout populations have failed. The apparent reasons for failure are: (1) eutrophication and associated sedimentation and suffocation of eggs (Martin 1957; Martin and Olver 1980); (2) introduction of toxic substances (Stauffer 1979; Willford 1980); (3) predation (Scott and Crossman 1973; Martin and Olver 1980); (4) insufficient numbers of spawners or inappropriate stocking methods (Loftus 1976); and (5) genetically influenced stock or strain-specific differences associated with egg development, behaviour, or reproduction that affect the survival in the wild (Loftus 1976). The failure of hatchery-reared lake trout to survive to reproduce is a critical concern to managers involved in the rehabilitation and preservation of lake trout populations. For example, stocking programs have been used extensively in attempts to rehabilitate declining stocks in the Great Lakes. These programs have been unsuccessful.

Incomplete knowledge of population structure may be a significant factor with respect to poor lake trout rehabilitation (Loftus 1976). Lake trout populations are sparse and have low productivity. Because of the late age of first reproduction, there may be a lag in the response of a population to compensation measures and hence a significant period of time would be required to observe population responses. Rehabilitation strategies must take this into account. Because both genetic and environmental factors affect propagation, the ability to differentiate between stocks and understand stock-specific responses to various environmental conditions are required in order to successfully manage enhancement and mitigation programs. Healy (1978) indicates that because of low population growth rates, diverse age structure and relatively late age-at-first reproduction, successful management requires adequate stocking rates coupled with reduced exploitation to ensure survival to reproductive age. However, beyond stocking programs and management of exploitation by man, spawning site improvement and food supplementation with forage fish and mysids appear to be effective methods for successfully compensating for impacts to lake trout populations.

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8.0 ARCTIC GRAYLING

(Thymallus arcticus)

8.1 Introduction

The Arctic grayling (*Thymallus arcticus*) is a member of the family Salmonidae, which also includes the coreogonids, (whitefishes and ciscoes), and salmonids (trout, salmon and char). The term *Thymallus* is derived from the apparent thyme-like aroma in the flesh of these fish. The large, vividly coloured dorsal fin, especially in the males, is a striking feature of grayling. (Scott and Crossman 1973).

The genus *Thymallus* is considered to have been the first to branch off the mainline evolution of the salmonids. Grayling retain many 'primitive' salmonid characteristics, and behaviours including nonanadromy, small egg size, absence of nest building and lack of kype in breeding males (Smith and Stearley 1989). There are two species in the genus: the Arctic grayling (*T. arcticus*) and the European grayling (*T. thymallus*). The two are similar in life history and biology, with naturally occurring hybrids existing where the distributions overlap (Shubin and Zakharov 1984).

Arctic grayling are popular sport fish in northern Canada and Alaska because of their widespread distribution, preference for cold, clear streams and rivers, good fighting ability, tendency to attack nearly anything on the water surface, and beauty. Catch statistics from 1985 show over 500,000 caught in Canada, surpassing Atlantic salmon (Stone 1988). In one study (Butcher 1981), grayling constituted 21% of the sport fish sampled in northeastern British Columbia. Sinclair and Sweitzer (1973) noted that grayling were the most common fish in the Yukon, and accounted for 54% of the total sport fish catch for that territory. Large sport fisheries exist in the Northwest Territories on Great Slave and Great Bear lakes, and grayling fishing provides a large input into the economies of these areas (Scott and Crossman 1973; Carl et al. 1977; Falk and Gillman 1974; Falk et al. 1975). Despite this, or perhaps because of their ubiquity, flesh quality, or presence of

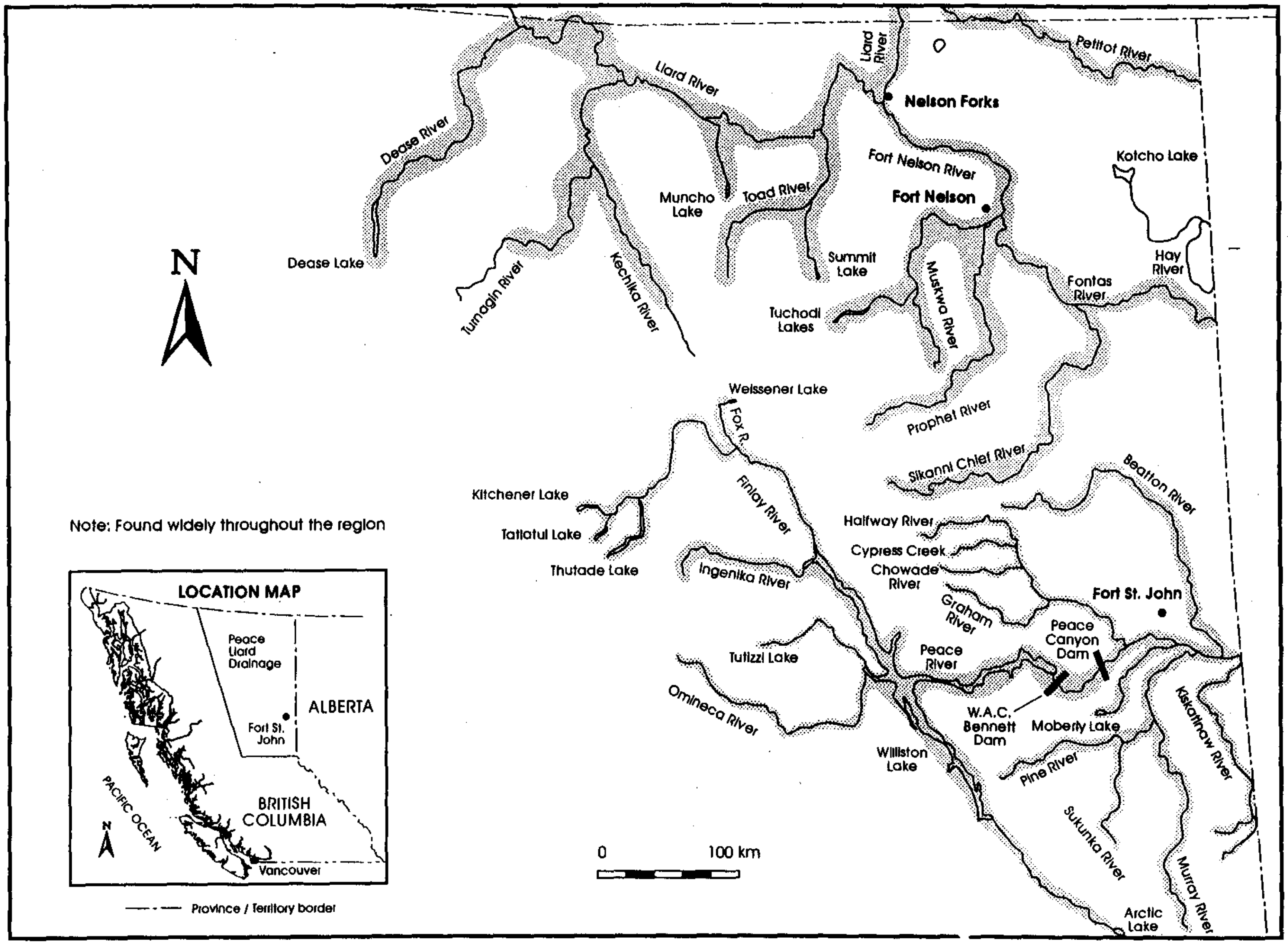

Figure 17: Arctic Grayling Distribution in the Peace and Liard Drainages, British Columbia

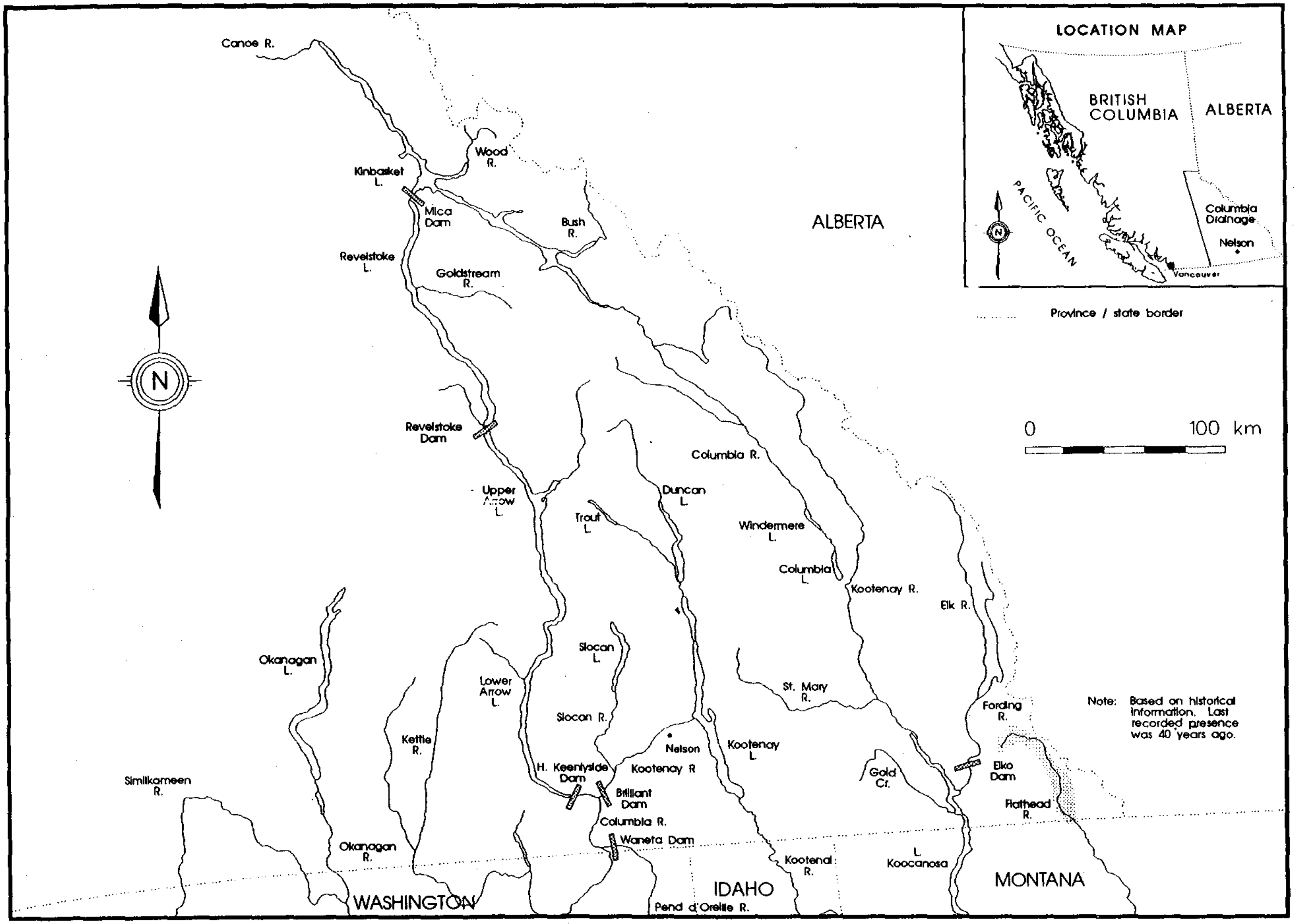

Figure 18: Arctic Grayling Distribution in the Columbia Drainage, British Columbia

into smaller headwater tributaries for spawning and rearing (Scott and Crossman 1973; Carl et al. 1977). Spawning occurs in spring shortly after ice breakup. Eggs hatch within a month or so, and the emerging fry begin feeding on zooplankton and later larval insects as they disperse and grow. Juveniles and adults feed primarily on aquatic and terrestrial insects. Arctic grayling life history is illustrated in Figure 19.

The Arctic grayling riverine habitat is characteristically cold, clear water with abundant pools and riffles. Grayling primarily utilize the pools, both as a food source and resting area. They are often found just downstream of the riffle areas but seldom in the riffles except during spawning or migration. The stream bottom is usually small boulder and gravel with little silt or sand. Observed habitat use and selected biological characteristics of Arctic grayling are presented in Table 12 and discussed throughout the text.

8.3.2 Eggs and Incubation

Egg incubation and embryo development ranges from 8 to 32 days and is dependent primarily on water temperature. For example Krueger (1981) reported only eight days for incubation at a temperature of 15.5°C (124 degree-days) whereas Kratt and Smith (1977) found that 32 days were required at a mean temperature of 5.8°C (186 degree-days). Newly-hatched alevins spend a further three to five days under the substrate, possibly until complete absorption of the yolk sac. Similar data were reported for European grayling fry (Scott 1985).

The absorption of the yolk sac may also facilitate increased swimming ability and speed, as suggested by Bams (1967 in Kratt and Smith 1977) for sockeye fry. Data compiled by Dane (1978) showed that small grayling (less than 2.0 cm) were considerably better swimmers than were comparably sized suckers, char, pike or whitefish.

Kratt and Smith (1977) postulated that the post-hatching substrate stage served to develop the physical attributes required for position maintenance. The fry reside in semi-deep pools and side channels with a water depth of 30 to 50 cm and velocities less than 0.8

FIGURE 19 - ARCTIC GRAYLING LIFE HISTORY

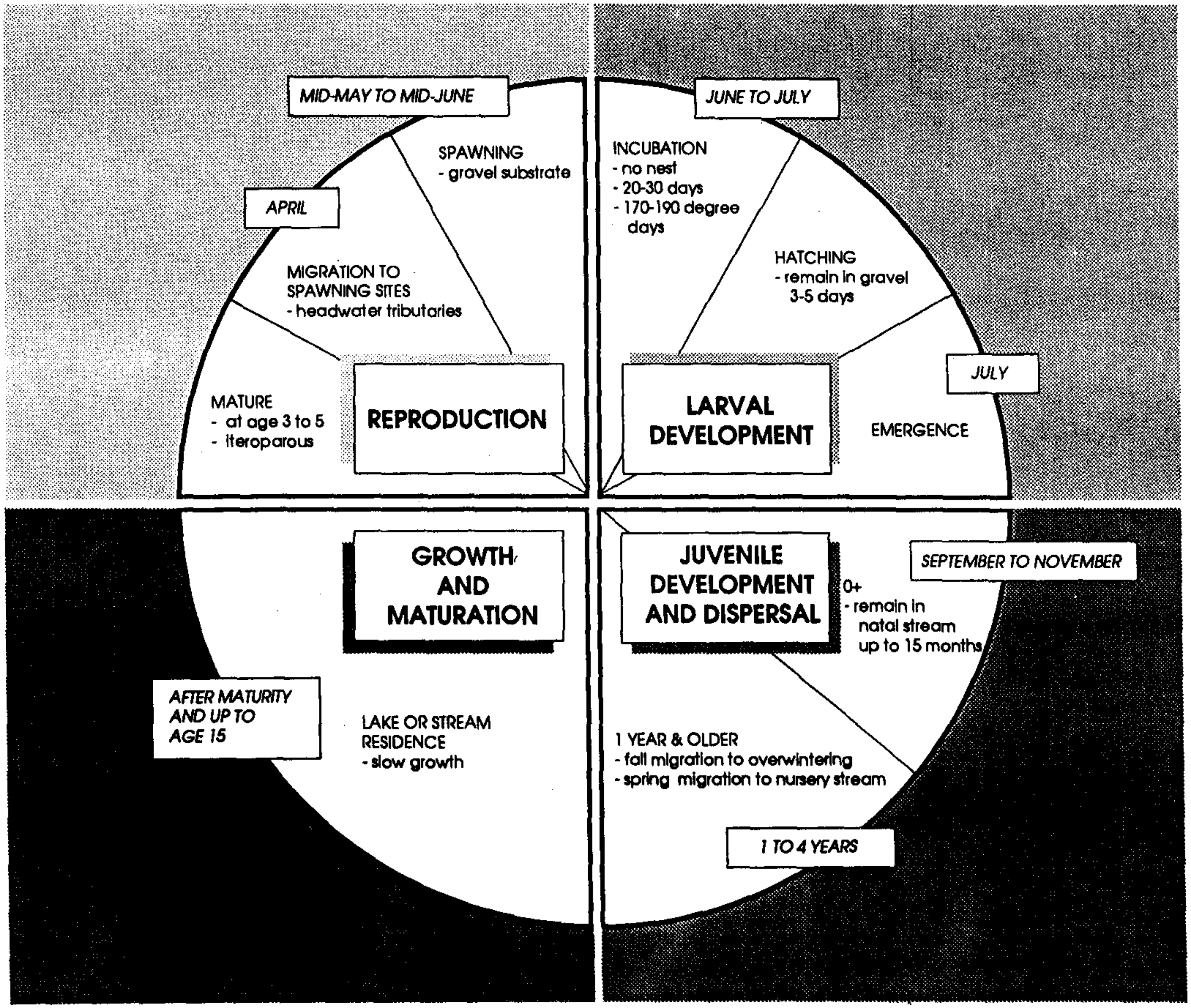

Table 12. **Observed habitat use and selected biological characteristics by life stage for Arctic grayling.** (for sources refer to text, NA - data are not available).

Eggs	
Temperature tolerance range	2 - 16°C
Optimum incubation temperature	6 - 10°C
Recommended oxygen concentration	NA
Lower lethal oxygen concentration	NA
Range of incubation time	8 - 32 days
Incubation time at optimum temperature	20 - 24 days
Lower lethal pH	NA
Recommended current velocity	<0.3 m/s
Substrate	gravel/boulder (<20% sand)
Cover	1-3 cm within gravel
Juveniles	
Temperature tolerance range	2 - 24.5°C
Optimum temperature for growth	10 - 12°C
Recommended oxygen concentration	NA
Lower lethal oxygen concentration	1.4 mg/L
Habitat type preference	stream
Depth preference	< 50 cm
Preferred current velocity	<0.5 m/s
Substrate	gravel,cobble, sand
Cover	boulders
Turbidity tolerance	< 50 mg/L
Primary food category	insect larvae
Secondary food taxa	variable
Adults	
Temperature tolerance range	1 - 20°C
Optimum temperature for growth	10°C
Recommended oxygen concentration	NA
Lower lethal oxygen concentration	2.0 mg/L
Habitat type preference	river/lake
Depth preference	< 10 m
Preferred current velocity	0.2-0.8 m/s
Substrate	gravel, rocks, boulders
Cover	boulders
Turbidity tolerance	effects noted after short term exposure to > 100 mg/l
Primary food type	insects
Secondary food type	variable
Form of reproduction	iteroparous
Nest construction	(broadcast spawners but rudimentary redds) 0.7 X 0.4 m
Spawning habitat type	small gravelly tributary streams
Preferred spawning temperature	7-10° C
Preferred spawning depth	variable
Preferred spawning substrate	gravel, (< 20% sand)
Preferred spawning current velocity	0.3-1.5 m/s
Range of observed first age-at-maturity	3 - 9 yrs
Range of observed fecundity	(range 3,000 to 15,000) average 4000 - 7000 eggs/female

m/s, i.e. away from strong currents. (Townsend 1976; Stuart and Chislett 1979; Ennis et al. 1984; Hubert et al. 1985; Kaya 1989). Initially, the fry school together but within three weeks begin to exhibit some antagonistic behaviour and by 6 weeks appear to have established a hierarchy of small territories (Kratt and Smith 1979).

8.3.3 Rearing, Food and Growth

As mentioned above, emergent grayling principally feed on zooplankton, switching to larval insects (caddis flies, mayflies, midges, etc.) as they increase in size (McLeay et al. 1984). The food preference of the juvenile and adult stages is extremely broad, primarily aquatic insects and terrestrial insects including bees, wasps, grasshoppers, ants and beetles, in addition to those mentioned previously. Additional items include small fish, fish eggs, crustaceans, and lemmings (Scott and Crossman 1973). Stuart and Chislett (1979) reported that 80% of the stomach contents of young of the year fry were benthic organisms, primarily chironomid larvae. For juveniles (2+ to 5+), they noted that in the summer, surface foods made up 67% of the food, but 100% of the food found in overwintering fish were from the bottom of the streambed and primarily chironomid larvae, with stonefly larvae also significant.

Kupchinskaya et al. (1983) reported that Arctic grayling within the Ust'-Ilim Reservoir consumed some 65 different food items, with chironomid larvae and amphipods (*Gmelinoides* sp.) predominating. The spectrum of food choices was broadest in the summer months and most limited during the winter. Feeding activity was greatest in the afternoon to evening. They noted little difference between juvenile and adult diets or between sexes. A similar spectrum of food items was given by Ryzhova and Tugarina (1979).

The early phase of the life cycle is characterized by an extremely rapid growth rate, up to 118 mm in the first year of life (Kratt and Smith 1979; Liknes and Gould 1987; Kindschi and Barrows 1990), but average growth rates appear to be on the order of 60-80 mm per year (Craig and Poulin 1975). As a rule, there is a decrease in growth rates from southern to northern latitudes. Lateral scales are not present on the fry when they emerge from the gravel and are not found until the young fish reach about 30-35 mm. Stuart and Chislett (1979) found scale formation was complete at 45-50 mm. The first circuli begin to form on the anterior scales before the completion of scale formation. Growth is usually slower in juveniles than yearlings, on the order of 35-45 mm per year (Hubert et al. 1985; Craig and Poulin 1975). The growth rate of adults is further reduced from that of juveniles. Individuals reach 300 mm or more by their fifth year. Lake populations may grow faster and larger than river or stream dwelling populations (Machniak et al. 1980; Hubert et al. 1985) and may possibly reach maturity at an earlier age as a consequence.

Arctic grayling fry show a tolerance to low dissolved oxygen levels and are able to survive levels as low as 1.4 mg/L in winter temperatures (Feldmeth and Eriksen 1977 in Hubert et al. 1985). This is undoubtedly important for fry survival in the streams, where summer flows and dissolved oxygen may be low (Stuart and Chislett 1979). Craig and Poulin (1975) noted that many young of the year were displaced downstream due to low flows. The preferred stream substrates are boulder and cobble or sand and the presence of adequate cover for concealment is also important.

Juveniles often overwinter in the same large rivers and lakes as the adults. In many cases they migrate to the spawning ground areas in the spring, but do so 2-4 weeks after the spawners have left. They remain in these nursery streams, within the larger pools and side channels, until the onset of winter conditions force them to migrate back to the overwintering grounds. The various age groups (fry and juveniles) within the nursery stream establish territories, with the larger fish getting the optimal locations in terms of food supply and, possibly, hydrodynamics (Craig and Poulin 1975; Kratt and Smith 1979; Stuart and Chislett 1979). As with the migration to summer resources, temperature appears to be the driving force for the timing of grayling overwintering migrations (Machniak et al. 1980), with the fish moving downstream to the larger, deeper mainstream waters as freeze-up begins and/or dewatering occurs.

There is little information regarding diel movements in Arctic grayling. Feeding is visually oriented and activity is, therefore, much higher during daylight hours than at night. Hughes and Dill (1990) noted that grayling in a northern Alaskan stream often maintained their feeding positions 24 hrs a day, and rarely seemed to become satiated.

Liknes and Gould (1987) found the majority of adult fish at water velocities of 0.21 m/s, in a mean water depth of 28.4 cm. Similar studies report ranges of 0.26 to 0.8 m/s (Hubert et al. 1985). Dane (1978, citing data from Bell 1973) place the top cruising speed (that which can be maintained for up to one hour) of average-sized adult grayling at 0.8 m/s. Sustained swimming speed (that which can be maintained for 10 minutes) and burst speed (that which can be maintained for 60 seconds) were found to be 0.8-2.1 m/s and 2.1 - 4.3 m/s respectively. These are considerably lower than the comparable figures for other salmonids such as sockeye, coho or steelhead (Dane 1978). Adults require deep pools or lakes for overwintering. However, little is known regarding water quality requirements during winter.

8.3.4 Maturity, Adult Migration, and Spawning

Grayling typically reach sexual maturity between 4-6 yrs in northern British Columbia and slightly earlier in the south (Scott and Crossman 1973; Hubert et al. 1985; Liknes and Gould 1987). Maturation in the northern regions of the Yukon and Northwest Territories may be delayed until the seventh to ninth year. As a general rule, maturity occurs after reaching 270-300 mm in length (Liknes and Gould 1987). Grayling spawn several times during their lifetime, but not necessarily every year.

In northern British Columbia, the spawning season generally runs from mid-May, when ice breakup occurs, to mid-June. It may be earlier in southern distributions and later further north in the Yukon and Northwest Territories drainages (Scott and Crossman 1973; Craig and Poulin 1975). Water temperature plays a critical role in the timing of the spawning, as well as the associated migration to the spawning grounds. Spawning generally occurs over a range of 7-10°C (Scott and Crossman 1973; Craig and Poulin

1975; Beauchamp 1990).

Pre-spawning males arrive at the spawning grounds before the females and begin to exhibit territoriality and antagonistic behaviour. As grayling are iteroparous spawners the size range within a spawning population may be considerable. The largest and most aggressive males establish rectangular territories, with the long axis parallel to the stream flow. The average size of the territories partially depends on stream size, but seems to be consistent over a number of reports: 2-3 m wide and 3-4 m long or approximately 12-14 m^2 (Bishop 1971; Kratt and Smith 1980; Beauchamp 1990). The total number of territories is dependent upon the spawning ground area and the number of dominant males. Overall spawning success may be limited by overly antagonistic (Beauchamp 1990). Males which are unsuccessful in establishing territories congregate in deeper pool regions, referred to as refuge areas. The presence of large boulders and/or debris within these refuge areas will decrease the number of attacks by males holding adjacent territories (Kratt and Smith 1980; Beauchamp 1990). Females also group within these refuge areas on the periphery of the spawning territories, but actively cruise throughout the grounds. Little antagonistic or courtship behaviour occurs within this refuge area, even when fairly densely populated (Beauchamp 1990). The majority of spawning occurs during the midday and late afternoon periods, possibly when the water temperature is at its peak. Very little spawning occurs at night, and the fish may migrate downstream during the night, returning to the spawning grounds in the morning (Beauchamp 1990).

Courtship begins as the female approaches the male. Following several lateral displays, the male will drape his dorsal fin over the female, perhaps to position her properly over the stream bottom. While no redd or nest is dug, mating is accompanied by vigorous vibrating which can disturb the bottom sediment slightly and bury the eggs under 1-3 cm of gravel. Furthermore, the caudal peduncle of the female and/or male may often be buried 1-2 cm into the substrate during spawning, resulting in even more disturbance (Beauchamp 1990). The eggs are small, generally less than 3.0 mm, demersal, and sticky for a short time. Usually 50 - 60% of the spawning adults spawn to completion (Kratt and Smith 1980; Beauchamp 1990), and both males and females appear to spawn with several partners during any one season. Female fecundity ranges from 3,000 to 15,000, although the average is probably closer to 4,000-7,000 (Scott and Crossman 1973). The fertilized eggs are shallowly deposited in the substrate, with a minimum of surface gravel to protect them (Kratt, 1981).

The preferred substrate is gravel although a percentage of sandy bottom (e.g. <15-20%) is also found in many spawning grounds (Scott and Crossman 1973; Stuart and Chislett 1979; Kratt and Smith 1980; Machniak et al. 1980; Gardiner 1984; Beauchamp 1990). Eggs are most abundant in the transition areas of riffles and pools, with little silt or sand (Scott and Crossman 1973; Beauchamp 1990). Current velocities at spawning sites range from 0.3 to 1.5 m/s (Krueger 1981), although lower velocities may be favoured (Beauchamp 1990). Depth does not appear to be of considerable importance (Machniak et al. 1980), although Beauchamp (1990) noted that spawners moved downstream as water depth decreased below a critical depth. The grayling also seem to prefer stream gradients of 0.3% or less (Liknes and Gould 1987; Beauchamp 1990).

The spawning period lasts approximately 2 to 3 weeks and there is no parental care of the eggs or young. After spawning the adults may remain in the area for a considerable time or migrate back to the larger mainstream waters or overwintering sites.

The maximum age for grayling appears to be 12 to 15 years, although there have been reports of fish 20 years and older, particularly from Alaska (Scott and Crossman 1973).

8.4. Mitigation and Compensation Strategies

The Arctic grayling's preferred habitat in cold, clear arctic and subarctic headwater tributaries, along with its spawning and overwintering migrations, creates potential interaction between the fish and hydroelectric, pipeline and highway construction projects in northern British Columbia and other areas. Despite these potential interactions there is a lack of specific information on mitigation and/or compensation measures for Arctic grayling (A. von Finster, Department of Fisheries and Oceans, Whitehorse, Yukon Territory, pers. comm., 1991).

As grayling are generally riverine in northern British Columbia and prefer shallow headwater or outlet streams for spawning, river impoundment and reservoir formation is particularly harmful, because of the shift to a more lacustrine environment and inundation of spawning grounds. If dam sites are in mountainous areas, the remaining potential spawning grounds are generally too small or at such a steep gradient as to be useless to grayling (Kupchinskaya et al. 1983). Wither (1959), in a pre-construction report on the W. A. C. Bennett Dam project in northern British Columbia, suggested that the reservoir would have a large negative impact on the grayling population, due to loss of riverine habitat and submergence of spawning grounds. Approximately 15 years after construction, Barrett and Halsey (1985) reported grayling were still present in the reservoir, but expressed concern that the majority of fish were 4+ and 5+. The lack of younger and older individuals indicated possible deficiencies in recruitment of younger grayling and overfishing of older grayling. Kupchinskaya et al. (1983) noted that the grayling population was significantly reduced in the Ust'-Ilim Reservoir and attributed the decline to loss of habitat and alterations in the food composition. Weagle and Cameron (1974) noted a complete absence of grayling from the Snare Falls Reservoir in the North West Territories. Proposed grayling mitigation procedures for the construction of the second phase included increasing spawning habitat by the clearing and disposal of flooded vegetation and maintenance of minimum water flows from the spillways. Of additional concern at hydroelectric dams is the passage of fish through penstocks and turbines. While there is no specific information on Arctic grayling, European grayling were relatively tolerant of the compression and decompression experienced when passing through efficiently operating turbines (Lambert 1976).

Butcher (1981) outlined three areas of fish habitat sensitivity to instream construction: spawning and rearing areas, overwintering areas, and migration routes. The greatest impact on grayling from instream construction activities (excluding hydroelectric development) affect spawning and nursery streams. For example, the lack of nest building, shallow depth of the eggs and the relatively small water flow in some streams make the grayling extremely susceptible to negative impacts such as changes in water velocity, increases in temperature, and increases in siltation that often occur during the construction of a pipeline. Siltation is probably the most detrimental effect of construction, mostly to eggs which become covered in silt and often die from suffocation. Juvenile grayling are also affected in nursery streams as they have no alternative residence areas within small tributaries and may be displaced downstream to mainstream waters where the risk of predation is much greater. Grayling overwintering areas tend to be large rivers/lakes, where the fish can avoid detrimental effects by movement and siltation can be minimized by dilution (Butcher 1981). Many pipeline construction projects mitigate environmental impacts on fish by moving stream crossings to upstream or headwater areas, but this measure may negatively affect grayling (Butcher 1981). Of further concern, especially during pipeline construction, is the pollution of the waters with crude oil and/or benzene compounds. Moles et al. (1979) noted that while Arctic grayling had higher tolerances to both these contaminants than did other salmonids (i.e. chinook, coho, and sockeye), their limits were substantially lower than those observed for species that often share the same general habitat such as Arctic char, slimy sculpins, and sticklebacks.

Carson and Milke (1976) recounted several instances of stream diversion, siltation, and alterations in water flow during the construction of a fuel gas line in Alaska. Even with federal intervention, the contractors violated many of the mitigative proposals and restrictions. No compensatory actions or resolutions were disclosed. Similarly, Huck and Champion (1976) noted that, even when construction occurred (also in Alaska) during the time windows established by previous surveys, environmental damage to grayling spawning grounds was substantial, especially from construction camp and associated activities such as water utilization, solid and liquid waste entering the streams, sludge washouts, gravel removal for roads and work site construction.

Townsend (1976) suggested that straw bale dams within streams would lessen downstream siltation loads. Butcher (1981) suggested that by restricting construction to specific windows in late July to September, the majority of impact on spawning, incubation,

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9.0 WALLEYE

(Stizostedion vitreum)

9.1 Introduction

The walleye (*Stizostedion vitreum*) is a member of the family Percidae and is commonly referred to as yellow walleye, wall-eye, pickerel, yellow pickerel, and yellow pike (Scott and Crossman 1973). The walleye is a valuable economic species in Canada's inland waters, providing a commercial and sport fishery in Ontario and the prairie provinces, and a sport fishery in Quebec (Scott and Crossman 1973). In British Columbia, walleye are a significant sport fish in the Peace region (38% of total fish caught), and are caught in the Columbia mainstem and tributaries.

9.2 Distribution

The natural distribution of walleye is limited to freshwater lakes and rivers of North America with rare occurrences in brackish waters (Scott and Crossman 1973). They range from near the Arctic coast in the MacKenzie River, south-eastward through Quebec to the St. Lawrence River, and south to the Gulf Coast in Alabama. The natural distribution is generally restricted to east of the foothills of the Western Cordillera and west of the Appalachian Mountains although there is a residual stock, apparently native, along the Atlantic coast from Pennsylvania to North Carolina.

Walleye have been widely introduced outside their natural range, particularly in western reservoirs in the United States and Canada and along the Atlantic sea-board. The only introduction outside North America was to the United Kingdom (Scott and Crossman 1973).

Walleye are present in the Peace and Liard River drainages of northeastern British Columbia. Maxhamish Lakes and the Klua Lakes in the Liard drainage contain large natural populations (E. N. Down, Fish and Wildlife Branch, B.C. Environment, pers. comm. 1991). Individuals five years and older are found in the Peace River drainage upstream to Lynx Creek (R. Pattendon, RL&L Consultants Ltd., pers. comm. 1991) and are found in several tributaries of the Peace including the Pine, Beatton, Blueberry, and Kiskatinaw Rivers. Adults move into the upper drainage, west of the British Columbia/Alberta border, in the spring, feed for the summer months and then move downstream into Alberta in the fall to overwinter (R. Pattendon, pers. comm. 1991). There is limited evidence that walleye presently spawn in the mainstem of the Peace River. Juveniles have been collected in the Kiskatinaw River and in the upper watershed of the Beatton system. Juveniles from the Beatton River were apparently transferred into Charlie Lake (near Fort St. John) in the early 1950's. Spawners were observed at the mouth of the Beatton River and upstream in the spring of 1991 (E. N. Down, pers. comm. 1991).

Walleye in the Columbia River originated from populations stocked in the upper Clark Fork River in Idaho (Brege 1981) and in Lake Roosevelt. Spawning is believed to occur in Lake Roosevelt after which the walleye migrate north up the Columbia River into Canada as far as Keenleyside Dam at the lower end of the Lower Arrow Lake during the spring, feed in this area during summer and return to Lake Roosevelt during the fall. (L Hildebrand, RL&L Consultants Ltd. pers. comm. 1991). Figures 20 and 21 show walleye distribution in the Peace and Liard, and Columbia river drainages respectively.

9.3 Life History and Habitat Requirements

9.3.1 General

Walleye spawn in shallow shoals of lakes, streams and rivers shortly after ice break up. Some northern populations may not spawn every year because of unfavourable temperature conditions (Hokanson 1977; Colby et al. 1979). Spawning may occur as early as January or February in southern populations, and as late as June in northern

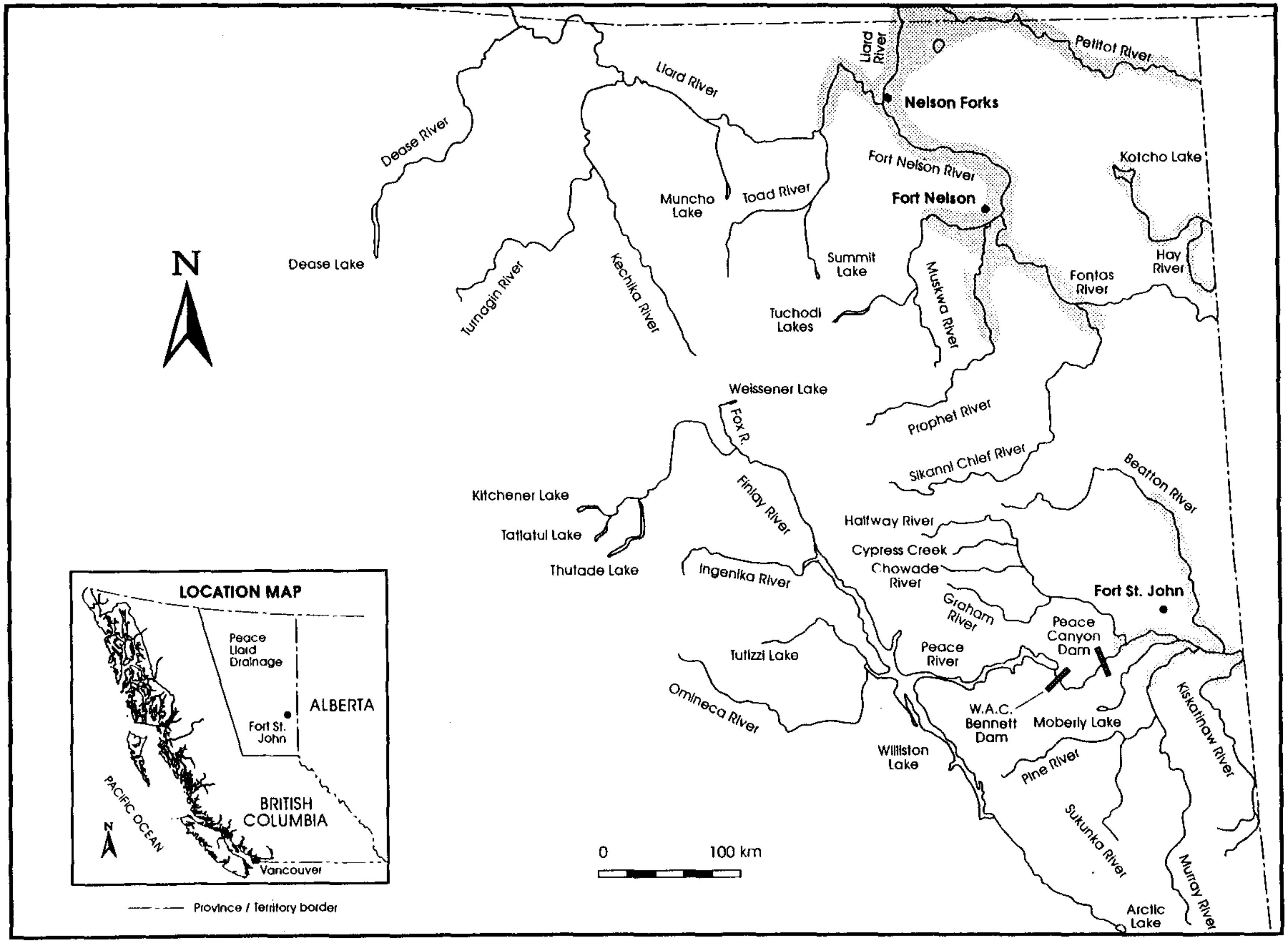

Figure 20: Walleye Distribution in the Peace and Liard Drainages, British Columbia

Table 13. **Observed habitat use and selected biological characteristics by life stage for walleye.** (for sources refer to text, NA- data are not available)

Eggs

Temperature tolerance range	<6 to 19°C
Optimum incubation temperature	9-15°C
Recommended oxygen concentration	>5 mg/L
Effect of lower oxygen concentration	<3 mg/L causes hatch delay, smaller fry
Range of incubation time	4-33 days
Observed incubation time	12-18 days
Lower lethal pH	5.5
Recommended current velocity	0.73 - 0.91 m/s
Substrate	highest survival in gravel/rubble substrate
Cover	interstices of gravel

Juveniles

Temperature tolerance range	15-34°C
Optimum temperature for growth	22-28°C
Recommended oxygen concentration	≥5.0 mg/L
Lower lethal oxygen concentration	< 3.0 mg/L retards development
Habitat type preference	rivers, lakes
Depth preference	variable, dependant on water clarity
Preferred current velocity	dependent on size, typically slow current
Substrate	NA
Cover	turbid regions, dark waters, logs, banks
Observed turbidity range	> 1 m and < 5 m Secchi depth
Primary food category	zooplankton, aquatic insects, selection varies with juvenile and prey size

Adults

Temperature tolerance range	0 to between 29 and 35°C
Optimum temperature for growth	20-24°C
Recommended oxygen concentration	> 3.0 mg/L
Lower lethal oxygen concentration	< 1.0 mg/L over an extended period
Habitat type preference	rivers, lakes
Depth preference	variable, dependant on water clarity, 1 to 15 m
Preferred current velocity	slight currents
Turbidity tolerance	> 1 m and < 5 m Secchi depth provides nominal feeding
Substrate	gravel-cobble, avoid submergent vegetation
Cover	turbid regions, dark water, logs, banks
Primary food type	fish
Secondary food type	aquatic insects
Form of reproduction	iteroparous
Nest construction	no, broadcast spawners
Spawning habitat type	inlet streams, rocky lake bars
Observed spawning temperature	5 - 12°C
Preferred spawning depth	several cm to several m
Preferred spawning substrate	gravel, rubble
Preferred spawning current velocity	0.73 - 1.5 m/s
Range of observed first age-at-maturity	2 - 6 years
Range of observed fecundity	50,000 to 600,000 eggs/female
Optimum range of dissolved solids	40 - 80 mg/L

after which the larvae begin to feed on zooplankton (Colby et al. 1979; Li and Ayles 1981a; Mathias and Li 1982). The mouth, jaws, and teeth are strongly developed by the time feeding begins. During this period, larvae require habitat of high zooplankton production or many will die of starvation (Li and Mathias 1982). Larval walleye are known to feed first upon copepods, cladocera, and other plankton within the size range of 200 - 1200 µm (Hokanson and Lien 1986; Krise and Meade 1986), although there have been reports of both rotifers and copepod nauplii in stomachs of walleye larvae (generally less than 200 µm). Mathias and Li (1982) believe that rotifers and nauplii are too small for walleye larvae to see and catch and are probably taken in with respiratory currents.

Walleye embryos adapt to the increasing water temperature during the spring and early summer months. Busch et al. (1975) observed a high positive correlation between walleye year-class strength and the rate and regularity of water temperature rise on the spawning grounds during the spawning and incubation period. The walleye embryo has a tolerance range from less than 6.0°C up to 19.2°C (Smith and Koenst 1975 in McMahon et al. 1984; Hokanson 1977). Temperatures of 6 - 12°C are considered optimum for fertilization and 9 - 15°C optimum for incubation (Smith and Koenst 1975 in Colby et al. 1979; Koenst and Smith, 1976). If eggs hatch below the required temperature, feeding may be delayed and larvae may die as a result (Serns 1982). Hubbs (1971) suggested that there may be racial differences in maximum developmental temperature tolerances. For example, eggs from Lake Meridith, Texas developed at 20°C whereas eggs from the Thames River, Ontario developed poorly at 16.5°C.

Embryos require well oxygenated water and dissolved oxygen levels $\geq$ 5 mg/L are necessary for high survival and growth (Oseid and Smith 1971). Oxygen concentrations below 3 mg/L may result in delayed hatching and significantly smaller fry (Siefert and Spoor 1974). Under natural conditions, extremely low oxygen levels may be encountered when eggs are deposited on substrate such as mud and detritus which, because of oxidation, have reduced oxygen levels causing increased mortality (Priegel 1970 in Colby et al. 1979).

Johnson (1961) studied the survival of eggs on several bottom types in Lake Winnibigoshish, Minnesota and found the lowest survival rates on the soft mud and detritus substrate, intermediate rates on fine sand , and highest survival on a gravel-rubble. Eggs on clean firm gravel-rubble substrate were subject to less entanglement in debris and presumably less scouring from waves than on the other bottom types. Corbett and Powles (1986) also found that the highest embryo survival was associated with clean gravel-rubble substrate.

Stream flow and wind-generated currents in spawning areas must be sufficient for adequate circulation of oxygenated water around embryos (Priegel 1970 in McMahon et al. 1984). Flow velocities over spawning areas are optimal at 0.73 to 0.91 m/s (McMahon et al. 1984); higher than optimal velocities can dislodge the non - adhesive eggs from the substrate, while low velocities can cause inadequate circulation around the eggs. Water velocity must also be sufficient after hatching to transport fry downstream to regions of lakes or rivers with high plankton production if not available locally. For example, walleye larvae in Wolf River, Wisconsin will starve to death within 3 to 5 days after hatching unless they reach a lake environment where plankton production is high (Priegel 1970 in Hokanson 1977). However, regions of high water velocity or wave action may result in egg mortality when water movement either strands eggs on shore or moves eggs onto regions of poor substrate such as mud or detritus (Colby et al. 1979).

9.3.3 Rearing, Food and Growth

By 10 - 15 days after hatching the young have dispersed from the spawning grounds into the upper levels of open water. In Oneida Lake, newly hatched fry drift passively as currents moving over the spawning grounds carry them into the limnetic zone (Houde and Forney 1970). Larval walleye, less than 9.5 mm in length, have a sustained swimming ability (current velocity that 50% of the larvae can sustain for one hour) of less than 3.0 cm/sec (Houde 1969) and would be subject to transport by currents of greater velocity. In Oneida Lake, larvae are typically found congregated in bays where water velocity is generally less that 3.0 cm/sec and are absent from the open lake where currents commonly range from 4 to 10 cm/sec approximately 1 m below the surface (Houde 1969; Houde and Forney 1970).

Fry may regulate their distribution by coordinated vertical migrations and active swimming to orient in currents (Olson et al. 1978 in Kendall 1978; Colby et al. 1979). Fry remain offshore for the remainder of their first year (Priegel 1970 in Colby et al. 1979) or move near shore once they reach at least 25 mm in length (Ryder 1977; Forney 1976).

Juvenile walleye select prey based on size rather than by species (Mathias and Li 1982). As walleye grow from larval to juvenile stages, their prey capture ability becomes stronger, allowing a shift from smaller, slower prey to larger, faster organisms (Parson 1971; Colby et al. 1979; Mathias and Li 1982; Li and Ayles 1981b). Mathias and Li (1982) observed juvenile walleye shift from zooplankton to larger, faster prey starting with *Chaoborus* sp. then mayflies, and later *Gammarus lacustris* and fish. Colby et al. (1979) found that walleye fry switched from copepods (*Epischura*) and cladocerans (*Daphnia* and *Leptodora*) to larger insects (predominantly mayfly nymphs) and fish as they grew. Under conditions when invertebrates are abundant the transition from invertebrates to fish may be postponed (Li and Ayles 1981b).

In some cases piscivorous behaviour of walleye begins with cohort-cannibalism (feeding upon like or smaller size siblings) from six to seven days after hatching until the end of the larval stage at about 16 days to 18 days when larvae are about 19 mm (Li and Mathias, 1982). However, Mathias and Li (1982) found that cannibalism continues among juveniles of a length of 34 mm (1-2 months). When the sizes of walleye in a pond differ sufficiently (cohorts 60% of own size) and alternative prey are unavailable or absent, cannibalism is probable (Li and Ayles 1981b; Swanson and Ward 1985; McIntyre et al. 1987). Cuff (1980) observed larvae consuming cohorts of the same size. Li and Ayles (1981b) did not observe cohort cannibalism, perhaps because of the abundance of invertebrates which allowed all the walleye fingerlings to grow at a rate which made even the smallest fish too large to serve as prey for the larger ones. The frequency of cannibalism ranges from 0.14% to 2.2% in natural lake populations (Eschmeyer 1950 in Colby et al. 1979; Rawson

1957; Chevalier 1973) to a high of 7% in experimental ponds (Mathias and Li, 1982).

Smith and Moyle (1945) reported that fish are not of any dietary importance to walleye until they reach an average length of 60 to 80 mm; Smith and Pycha (1960) observed a similar switch from zooplankton to fish (perch) at 50 mm. According to Walker and Applegate (1976), walleye longer than 62 mm included minnows in their diet and walleye longer than 106 mm fed primarily on minnows. Li and Ayles (1981b) observed that walleye did not consume fish until they were over 110 mm in length.

The absolute growth rates of walleye can vary markedly from one body of water to another, even among water bodies in close proximity (Colby et al. 1979). In general, the growth rate of walleye is greatest in the more southern regions of their range, where temperatures are higher and the growing season is longer, and slower in the more northern regions (Colby et al. 1979; Maule and Horton 1985). For example, the average size of one year old fry is 152 mm in Lac la Ronge, Saskatchewan, but they reach an average of 460 mm in the Belton Reservoir in Texas (Colby et al. 1979). Variability in water temperature and food availability likely play a key role in the different growth rates.

Growth rates of young-of-the-year walleye gradually increase during the spring and early summer months, are nearly constant during early and mid - summer, and begin to decrease by late summer or early autumn (Grinstead 1971; Wolfert 1969; Brege 1981; Li and Ayles 1981a). In experimental ponds in Manitoba, young-of-the-year walleye grew between 5 and 6 mm/week in the spring (May - June) and late summer (August - September) compared with 9 mm/week in mid-summer (June - August (Li and Ayles 1981b). Growth rates between July and September in several other lakes and reservoirs (Lake Gogebic, Michigan; Canton Reservoir, Oklahoma; Lake Erie; John Day Reservoir, Columbia River) ranged between 11 and 16 mm/week (Eschmeyer 1950 in Colby et al. 1979; Grinstead 1971; Wolfert 1969; Brege 1981). Little or no growth occurs during late fall and winter, a period when availability of food and temperatures are generally low (Kelso and Ward 1972).

The bioenergetic model for walleye growth developed by Kitchell et al. (1977) indicates that the thermal optimum and maximum for weight specific consumption are 22°C and 27°C respectively. This is consistent with observations made by Smith and Koenst (1975 in: Colby et al. 1979), Hokanson and Koenst (1986) and Huh (1976 in Colby et al. 1979) that the temperature range for optimum growth of juveniles 84 - 86.5 mm in length is 22 to 28°C. Many northern lakes do not usually reach the thermal optimum (Rawson 1957; Swenson 1977) and lakes which stratify in the summer months, as in many southern lakes, may exceed the thermal maximum (MacLean and Magnuson 1977), both of which result in a reduction in growth rates (Maule and Horton 1985).

The quality and quantity of food are important factors limiting walleye growth (Kerr and Ryder 1977; Kitchell et al. 1977; Fox 1989; Fox et al. 1989). Schupp (1978) found that walleye which consume mostly young-of-the-year yellow perch have substantially greater growth rates than walleye that consume mostly invertebrates and small minnows. Fox (1989) noted that juvenile walleye growth was regulated by the density and type of prey available. Colby et al. (1979) and Fox and Flowers (1990) found an inverse relationship between walleye density and growth thus indicating the populations they studied were food limited. This may not always be the case since Li and Ayles (1981a) found that growth of walleye in ponds studied was not dependent on population density.

Walleye of all ages move locally during the summer, autumn and winter months. In late summer, adults and young-of-the-year walleye move into deep water (Rawson 1957; Forney 1966; Johnson 1969 in Colby et al. 1979; Grinstead 1971) possibly a negative reaction to rising water temperatures (Johnson 1969 in Colby et al. 1979) or a positive response to movement of prey species such as ciscoe and whitefish to deeper water (Rawson 1957). In the case of fry, Ryder (1977) suggests that such movement could be an avoidance of high daytime intensities as fry becoming progressively photonegative. In most waters, walleye exhibit a diurnal vertical migration associated with changing light intensities; fish move into shallow water at night to feed when light levels are low (Swenson and Smith, 1973; Mathias and Li, 1982).

Cool spring temperatures may delay plankton production with a resultant decline in fry growth rates and survival. Poor growth during the first season of life may result in increased predation and a reduction in year class strength (Colby et al. 1979). Limited growth of walleye may occur above 30°C in the presence of abundant forage, but the upper lethal temperature for walleye is 34.1°C (Hokanson and Koenst 1986).

Juveniles are typically found in areas with slight currents (Ryder 1977) except during the winter when they tend to avoid currents (Colby et al. 1979). Jones et al. (1974) found that the critical velocity (maximum velocity in cm/sec that can be maintained for 10 min) for walleye increased with fish length ($V = 13.07\ L^{0.51}$ where V is the critical velocity and L is the fork length in centimeters). Thus, the critical velocity for juveniles with a fork length of 10 cm is 42 cm/sec.

Optimum oxygen concentrations for fry are $\geq$5 mg/L (Siefert and Spoor 1974). Oxygen levels less that 3 mg/L retard fry development (Oseid and Smith 1971) and Siefert and Spoor (1974) observed that larvae raised at 2.4 mg/L and 1.9 mg/L were weak swimmers.

Light is probably the primary factor affecting the diurnal distribution of walleye. Fry are photopositive prior to reaching lengths of about 25 to 30 mm and are found in the pelagic zone of lakes (Scherer 1971; Ryder 1977). Juveniles larger than approximately 25 mm are generally photonegative and although often found in shallow inshore regions will seek shelter or dim light during the day (Scherer 1971) by moving under cover (boulders, logs, brush, or submerged vegetation), into turbid regions, or into deeper water to avoid high daytime light intensities (Ryder 1977). This behaviour is maintained through maturity.

The diel feeding pattern of walleye is largely dependent on water clarity and associated light levels. In clear lakes or rivers, walleye find shelter under rocks or vegetation or migrate to deeper waters during the daytime and feed only from dusk to dawn when light levels are low (Swenson and Smith 1973). In turbid lakes (Secchi depth of <2 m), where light levels are low throughout the day, the nocturnal feeding pattern breaks down and walleye may feed during the day (Colby et al. 1979). Mathias and Li (1982) found that feeding activity of juvenile walleye (1-2 months old) peaked in the late evening and during mid-morning in turbid ponds. Although walleye prefer turbid lakes and rivers and peak feeding activity occurs at light levels of 300 lux or less (1 to 2 m Secchi disk depths), cessation of feeding occurs when light levels fall below 5 lux (Ryder 1977).

Adult walleye can be highly piscivorous but opportunistic in their selection of forage fishes, including yellow perch and ciscoe (Ryder and Kerr 1978; Colby et al. 1979; Poe et al. 1986) as well as invertebrates. Walleye predation can be the major source of post larval yellow perch mortality and has a large impact on yellow perch abundance and recruitment (Swenson and Smith 1976; Forney 1980; Nielsen 1980; Lyons and Magnuson 1987). When yellow perch are unavailable or rare, other species such as lake emerald shiners, trout-perch, nine-spine sticklebacks, suckers, cyprinids, white perch, alewives, rainbow smelt, lake herring, northern pike and centrarchids become more important prey (Ryder and Kerr 1978; Colby et al. 1979). However, in Charlie Lake insects continue to be the primary prey of walleye into adulthood even though yellow perch are present. This results in rapid early growth with a plateau at age 3 to 4 (E.N. Down, pers. comm. 1992).

Adults may tolerate temperatures between 0 and 30°C, however, the optimum temperature for growth is between 20 to 24°C and temperatures above 24°C are avoided (Huh et al. 1976; Fitz and Holbrook 1978). The upper lethal temperature for adults may range from 29 to 35°C (Hokanson 1977; Wrenn and Forsythe 1978). Because of these temperature requirements, walleye are usually found above the thermocline in thermally stratified lakes, although the hypolimnion may be penetrated for feeding forays or for shelter in extremely clear lakes (Colby et al. 1979). The movement of walleye to deep still pools (up to 3.4 m) in rivers or streams during the summer may be to avoid high temperatures (up to 30°C) near the surface (Paragamian 1989).

In the laboratory, adults may tolerate dissolved oxygen concentrations as low as 2 mg/L; oxygen levels at 1.0 - 1.5 mg/L cause walleye to rise to the surface and at 0.6 mg/L a loss of coordination and equilibrium occurs. Extended periods of dissolved oxygen concentrations of less than 1 mg/L are lethal (Scherer 1971). Walleye generally achieve their greatest numbers at dissolved oxygen concentrations greater than 3 mg/L (Dendy 1948 in Colby et al. 1979).

Adults are negatively phototrophic (Ryder 1977) and are normally found in moderately shallow waters where sufficient shelter (submerged logs, boulders or overhanging brush), turbidity or colour occurs to block high daytime light intensities or they may move to deeper pools. Although usually found in 1 to 15 m of water in lakes (Colby et al., 1979) they may swim to depths as great as 27 m (Regier et al. 1969 in Colby et al. 1979). Walleye may migrate daily into shallow water for feeding as light intensity declines and return to depth at sunrise (Ryder 1977). A clean, hard substrate is preferable as walleye may spend the daylight hours resting in contact with the bottom; deep organic substrate are usually avoided (Colby et al. 1979). In rivers or streams, walleye prefer regions comprised of deep intermittent pools with gravel-cobble and boulder substrate (Paragamian 1989). Adults, like juveniles, are found in areas with slight currents (Ryder 1977; Paramagian 1989). In the Cedar River, Iowa, stream velocity was important to walleye because it governed the use of various substrate, cover and pool depths, and as velocity changed with season so did habitat use (Paramagian 1989). During the autumn and summer months when most active, walleye were found in shallow regions with slight currents, but used submerged boulders or logs as current breaks. During the winter months, when less active, they avoided regions with turbulence or currents and moved to deeper pools and occupied a wider depth range (Colby et al. 1979; Paramagian 1989). The critical velocity for adult walleye, as for juveniles, is positively related to fish length (Jones et al. 1974).

Although walleye are tolerant of a wide range in turbidity, they reach their highest numbers in moderately turbid conditions (Ryder and Kerr 1978; Kitchell et al. 1977). Peak feeding occurs at water transparencies of approximately 1 to 2 m Secchi disk depths, with decreased activity at <1 or >5 m Secchi disk depths (Ryder 1977).

9.3.4 Maturity, Adult Migration, and Spawning

Male walleye mature at two to four years of age while females mature at three to six years of age (Scott and Crossman 1973; Machniak and Bond 1979). Growth rates of females are generally greater than those of males (Colby et al. 1979). The age of maturity is dependent on the growth rate. Rapidly growing fish reach maturity earlier in Oneida Lake, New York (Forney 1965) than do walleye which grow in colder waters (Colby et al. 1979). Early maturity is also characteristic of heavily-exploited walleye stocks as in Saginary Bay, Lake Huron (Hile 1954 in Colby et al. 1979), the western basin of Lake Erie (Wolfert 1969) and in Dexter Lake, Ontario (Moening 1975 in Colby et al. 1979).

As mentioned above walleye commonly spawn after ice breakup in the rapids of streams, shallow offshore reefs, or along shorelines of lakes, although some populations are also known to spawn in marshes (Priegel 1970 in Colby et al. 1979; Machniak 1975). Spawning adults select shallow water of a few centimeters to several metres depth (Chevalier 1977; Colby et al. 1979) and generally use clean, hard substrata, especially coarse gravel or small boulders if available, while they rarely use submergent vegetation (Colby et al. 1979; Paramagian 1989). Spawning may occur over other bottom substrate in streams and lakes if sufficient exchange or movement of water permits an adequate supply of oxygen to the developing embryo (Colby et al. 1979). Substrate of low oxygen and/or poor water circulation (i.e. sand, silt and detritus) are associated with low embryo survival (Johnson 1961; Priegel 1970 in McMahon et al. 1984).

Bodaly (1980) found that stream discharge did not appear to affect walleye upstream spawning migrations, unless increases in flow were also associated with decreases in stream temperatures. Walleye may not return to the exact location of spawning each year, but are known to use streams or shoals within close proximity (Rawson 1957; Forney 1963; Johnson and Johnson 1971 in Colby et al. 1979; Olson et al. 1978; Bodaly 1980). Bodaly (1980) observed low rates of homing to spawning streams (natal) averaging 20%, but rates of return of fish to the general vicinity of spawning streams were much higher, averaging 62%.

Males precede females to the spawning grounds by several days and remain for a number of days after the females leave (Eschmeyer 1950 in Colby et al. 1979; Johnson and Johnson 1971 in Colby et al. 1979; Machniak and Bond 1979; Bodaly 1980). The sex ratio of walleye during spawning runs and on the spawning ground usually favours males probably because males mature earlier. Individual observations vary between 51 to 99% males, depending on the time of peak spawning (Colby et al. 1979; Bodaly 1980).

Spawning occurs at night, in groups ranging from one larger female with one or two smaller males to two females with up to six males (Colby et al. 1979). Individual females deposit most of their eggs in one night of spawning. No nest is built and eggs and milt are released into the water column just above the substrate. The number of eggs produced may vary considerably; average egg production ranges from 29,700 to 82,700 per kg of fish with as many as 600,000 eggs produced per female (Machniak 1975). There appears to be a curvilinear relationship between the number of eggs produced and the total length of the walleye (Wolfert 1969); the relation between weight and the number of eggs produced is almost linear (Wolfert 1969; Johnson 1971 in Colby et al. 1979). Thus, it is not surprising that fecundity of walleye increases with age (Colby et al. 1979). There is also a positive relationship between the fecundity of walleye and the availability of food (Colby and Nepszy 1981; Baccante and Reid 1988). The percentage viability of walleye eggs at spawning may vary widely ranging between 3.4 - 100% (Baker and Scholl 1969 in Colby et al. 1979; Johnson 1961).

After spawning, adults disperse into deeper water (Bodaly 1980). While some populations of walleye remain close (less than 16 km) to the spawning grounds (Colby et al. 1979), movements of 75 km or more are not uncommon in larger lakes and rivers (Rawson 1957; Machniak and Bond 1979; Bodaly 1980; Paragamian 1989). As mentioned above walleye typically migrate up the Columbia and Peace drainages for summer feeding, (where some individuals also spawn) and overwinter downstream.

In the Cedar River, walleye spawn in riffles with a water velocity between 1.4 to 1.5 m/sec. Spring lake levels can be important in determining spawning success since clean gravel or rubble beaches created by wave action are typically flooded in spring and provide the preferred spawning habitat (Chevalier 1977). In spite of a diversity of spawning habitat, the absence of suitable spawning areas for walleye seems a significant factor preventing the fish from establishing themselves in certain eutrophic lakes (Moyle 1954 in Colby et al. 1979; Schupp 1978).

Walleye spawn at water temperatures between approximately 5 and 11°C. Any reversal of stream temperature below the 5°C threshold after the start of the spawning run may reduce the rate of, or stop upstream movement of spawners (Bodaly 1980) Such a delay in spawning may result in resorption of ova (Schumann 1964 in Hokanson 1977). Females may require cool winter water temperatures (10°C) for maturation of the gonads (Hokanson 1977); for example, walleye that have been planted in El Capitan Reservoir, San Diego County, California where winter water temperatures rarely drop below 10°C, have rapid growth rates, but do not reproduce (Miller 1967 in Colby et al. 1979). However, a cooling period may be necessary for high walleye egg viability but the requirements vary greatly between races, since some walleye populations can produce eggs in lakes where temperatures rarely drop below 10°C (Colby et al. 1979). Poor growth conditions (i.e. suboptimum temperatures and/or lack of food) during the summer months can reduce the rate of the resorptive processes and delay the period of oocyte growth causing females to miss the following spawning period (Forney 1965).

Walleye prefer waters with a pH between 6 and 9 (Scherer 1971). Below a pH of 5.5, McMahon (1984) reported recruitment failure while Anthony and Jorgensen (1977) noted that walleye cease to spawn in Duchesney Creek, Lake Nipissing, Ontario, when the pH drops below 4, but return to the creek when the pH rises to 7. The optimum range of dissolved solids lies between 40 and 80 mg/L (Regier et al. 1969 in Colby et al. 1979), but walleye may tolerate up to 15,000 mg/L (Rawson 1946).

The average life-expectancy of walleye varies with latitude. Colby et al. (1979), found that walleye live approximately 5 to 7 years near the extreme southern limits and about 12 to 15 years near the extreme northern limits of the range. Females generally live longer than males and may reach a maximum age of 10 - 12 years in the south and up to 20 years in the north (Carlander and Whitney 1961; Smith and Pycha 1961; Scott and Crossman 1973).

9.4 Mitigation and Compensation Strategies

The walleye life stages typically most threatened by development are spawning, incubation and initial rearing. Several measures may be taken to mitigate the effects of human disturbance on walleye during these periods of their life or to compensate for habitat loss or population declines. Factors limiting production of walleye vary between populations, but it is evident that there is substantial mortality from egg to early juvenile stages. During egg development, survival rates are as low as 0.5 to 36% (Johnson 1961; Forney 1976). Mortality of walleye larvae is also high. Li and Mathias (1982) found that 75% of larvae survived from egg to depletion of the yolk sac, but only 25% survived through the switch from endogenous to exogenous feeding by larvae. The quantity and quality of spawning habitat in lakes and river may determine egg to larvae survival (Chevalier 1977), while predation on eggs, larval and juvenile stages and competition for food resources also limit walleye production.

Hydroelectric developments can negatively affect walleye production:

(1) by blocking upstream migration of spawners;

(2) through entrapment and mortality in penstocks and passage through turbines;

(3) by altering water temperature and flow regimes;

(4) by increasing sedimentation as a result of erosion or decreased water flow, and

(5) through loss of spawning and rearing habitat either because of flooding (reservoirs) or reduced water flow downstream of dams.

Construction of dams may prevent the movement of walleye upstream to spawning habitat. For example, potential movement of walleye upstream in the Peace River is restricted by the Peace Canyon Dam. Fishways have been used in only a few cases as a means of moving walleye past obstacles (Colby et al. 1979). On the Des Moines River, a modified Denil fishway provided walleye access to regions upstream of dams 4.6 m or less in height (Harrison and Speaker 1950 in Colby et al. 1979).

Controlling reservoir water levels can mitigate the impacts of dams, particularly during the spawning season. Low or falling water levels during spawning and incubation reduce spawning success by limiting the quantity of optimal spawning habitat and by dewatering the embryos or fry. In the United States, these impacts are mitigated by maintaining fairly stable or slightly rising levels during the spawning and incubation period (Machniak 1975). In Kansas reservoirs where water levels are raised in the spring to improve spawning and nursery conditions, followed by a mid-summer drawdown for revegetation, there has been improvement in the walleye forage base and water quality (Groen and Schroeder 1978). Erickson (1972 in Colby et al. 1979) found that impoundments which have gradual water level fluctuations have productive walleye populations.

Controlling the rate of water discharge from reservoirs can reduce the impacts of impoundments on downstream walleye populations. Insufficient downstream flow may result in limited spawning habitat, lower oxygen concentrations in spawning gravels due to low water velocity over spawning substrate, post-spawning mortality because of higher water temperatures and low oxygen levels, and inadequate flow rates of water for transport of fry (Machniak 1975). Bidgood (1968 in Machniak 1975) concluded that lowered water levels in the Athabasca River from regulation by the W. A. C. Bennett Dam on the Peace River led to poorer post-spawning survival of walleye. However, increasing discharge must be done prudently as high discharge rates from reservoirs may also increase post-spawning mortality since larvae less than 16 mm in length can maintain their position only in currents of less than 5 cm/s (Machniak 1975).

Water withdrawal from reservoirs may remove pelagic stages of walleye that are present near the water surface, particularly if water is withdrawn from the surface (Machniak 1975; Colby et al. 1979). Walburg (1971) estimated a 42% loss of sauger and walleye fingerlings from Lewis and Clark Lakes through water releases to the Missouri River at 3 m depth during a single month in early summer. These losses can be mitigated by withdrawing water at depth; for example in Lake Francis water was drawn from 40 m and few fish were lost from the reservoir (Benson 1973 in Colby et al. 1979).

Loss and siltation of spawning habitat from reservoir flooding can result in poor spawning success of walleye. Coarse substrate in a reservoir bottom may become exposed over time through wave washing, but Erickson (1972 in Colby et al. 1979) found it may require five years for sufficient substrate buildup to occur.

Shoreline development and agricultural and sewage runoff have had negative effects on the production of walleye (Colby et al. 1979; Machniak 1975; Colby et al. 1987). Spawning failure of populations has been attributed to increased production of littoral vegetation, including periphyton, which is thought to have reduced oxygen levels in spawning gravel following the input of sewage and nutrients from agricultural runoff (Colby et al. 1987). These impacts may be mitigated with artificial spawning beds constructed of gravel and cobble substrate and placed at up to several metres depth in areas with water velocities of 0.73 to 0.91 m/s. Riffle regions in streams or rivers and along lake shores where wave action due to winds and currents keeps the water in motion are appropriate locations (Machniak 1975). Such artificial beds provide optimal oxygen concentration for developing eggs and prevent sedimentation into the substrate.

The most frequently used method to increase walleye populations in North America is stocking. Walleye stocking is a large scale enhancement technique, and in some hatcheries up to 80 million walleye eggs are incubated (Alberta Fish and Wildlife 1985; Giles and Foster 1987). The development of mobile hatchers provides a cost effective means to rear larvae locally, as well as reduce mortality from handling and transporting (Giles and Foster 1987). Fry are either transplanted directly from one lake or river to another, or larvae or fry that have been reared in hatcheries or ponds are introduced. Hatchery and pond rearing programs are prevalent in the United States, Ontario, Manitoba, Saskatchewan and Alberta. In British Columbia, as mentioned above, fry were successfully introduced into Charlie Lake in the 1950s. Adults from Charlie Lake were introduced into the most northerly of the Cameron Lakes (which drain into Moberly Lake), and Swan Lake. To date, Cameron Lake has not produced a viable fishery while Swan Lake has a marginal fishery. However, as was the case in Charlie Lake, these fisheries may take 30 years to establish (E.N. Down, pers. comm. 1995). As mentioned above, walleye in the upper Columbia River result from stocking programs in the upper Clark Fork River, Idaho and Lake Roosevelt. These programs are effective because they improve survival during early life history, when mortality from predation and starvation is high. As mentioned above, egg to larvae survival in the wild is from 0.5 to 30%. However, survival in artificial hatcheries may exceed 65% (Giles and Foster 1987). Walleye larvae are reared in natural or artificial ponds until they reach the size required for transplant to other systems (e.g. 50 mm in eastern Ontario; Fox and Flowers 1990). High mortality of larvae has been attributed to starvation, since larvae require a high density of small zooplankton (>200 and <450 μm) at first feeding, and to cohort-cannibalism (Colby et al. 1979; Li and Mathias 1982; Krise and Meade 1986; Loadman et al. 1989).

Stocking of fingerlings has been successful in 48% of plants into water bodies not previously supporting walleye stocks. Maintenance stocking has had a success rate of 32%, but supplemental stocking has had a success rate of only 5.2% (Laarman 1978). Stocking success appears to depend on availability of prey and density-dependent mortality resulting from cannibalism or predation rather than on the number and size of walleye that were stocked (Laarman 1978). Warm, complex lakes >1000 ha seem best for stocking (E.N. Down, pers. comm. 1992). Juveniles greater than 50 mm survive stocking better than smaller larvae that have not yet begun feeding (Li and Ayles 1981; Campbell and Rowes 1980; Fox and Flowers 1990).

Artificial spawning grounds are successful in the Lonetree Reservoir, Colorado, where spawning adults utilize two newly constructed spawning beds to the same degree as natural spawning beds (Weber and Imler 1975 in Colby et al. 1979). The beds are constructed of rock and gravel (< 203 mm in diameter) and cover an area of 463.6 m^2. Although these artificial beds increase the spawning area of the lake by only 17%, there has been a two to ten fold increase in the number of young-of-the-year walleye. In North Cameron Lake, artificial spawning habitat was created in 1988 by placing approximately 500 m^3 of gravel and cobble of 100 to 300 mm diameter on the ice during the late winter over areas where lake depth was between three to four metres (E.N. Down, pers. comm. 1991). It is presently unknown if the provision of spawning habitat has resulted in natural recruitment to the introduced walleye population.

Fertilization of lakes may increase juvenile walleye production. For example, the addition of organic fertilizers, such as soybean meal or manure to ponds, has resulted in increased growth and survival of juveniles (Fox et al. 1989; Smith and Moyle 1945). In a comparison of ponds where fertilizer was held constant (36 $g/m^{-3}/week^{-1}$) to those where fertilizer was reduced (32 to 0 $g/m^{-3}/week^{-1}$), Fox et al. (1989) observed that walleye length increased by 32%, survival increased by 83%, and biomass harvest increased by 294%. The greater walleye production in the constant fertilization ponds was a result of higher chironomid density during the last half of the experiment by which time juvenile walleye had reached 22 mm in length and aquatic insects comprised 49 - 86% of their diet. Smith and Moyle (1945) found that the average production of 31 unfertilized ponds in Minnesota was 8.4 kg/ha (751 fingerlings/ha) whereas in 24 ponds fertilized with manure, production was 46.7 kg/ha (6,876 fingerlings/ha). The increase in walleye production was the result of the increase in zooplankton standing crop in the spring.

Introduction of forage fish is another method to increase production of walleye in small lakes. Introduction of minnows to ponds increased the growth rate and survival of juveniles (Smith and Moyle 1945; Colby et al. 1979). Minnesota ponds stocked with sucker fry produced six times the yield of control ponds, while those stocked with bluntnose and fathead minnows produced 12 times the yield of the control ponds (Smith and Moyle 1945). It is essential that forage fry used for stocking be smaller than the existing walleye fry. If too large, forage fry may be inedible or compete with walleye for food (Colby et al. 1979). The cost of transporting forage fish may, however, limit this method for increasing walleye production to small lakes.

Improvement of rearing habitat through the addition of cover has not been a widely applied method for walleye habitat improvement. Krueger (1969 in Colby et al. 1979) observed that walleye congregated under oak log cribs (2.4 x 2.4 x 1.5 m), but did not report how this influenced the survival of walleye.

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10.0 MOUNTAIN WHITEFISH

(Prosopium williamsoni)

10.1 Introduction

The mountain whitefish, *Prosopium williamsoni* (Girard) is one of six species of the genus found in North America (Norden 1961). *Prosopium* (Milner), is one of three genera of the subfamily Coregoninae, family Salmonidae. Members of Coregoninae differ from other salmonids by the presence of a well osified hypethmoid bone and the lack of teeth on the maxillae at any life history stage (Norden 1961). Externally, *Prosopium* are distinguished from other whitefish by the presence of a single internarial flap and parr marks on juveniles. The mountain whitefish is closely related to the more widely ranging round whitefish, *P. cylindraceum.* McPhail and Lindsey (1970) believe the two species evolved in geographic isolation, but their range now overlaps (e.g. in Dease Lake and the Liard River). There is no evidence of interbreeding, and the mechanisms that allow coexistence of these species are not yet documented.

Mountain whitefish have the potential for becoming an important sport fish in British Columbia. In areas with declining stocks of more popular species, the wide distribution and abundance attract significant fishery interests. Some investigators have suggested that although the mountain whitefish possess qualities that make it a desirable sport fish, it also competes for food with, and at times consumes the eggs of, other salmonid sport fish species (McHugh 1940; Sigler 1951).

10.2 Distribution

Mountain whitefish are found only in western North America and are abundant in most rivers, cold water lakes and reservoirs from the west slope of the Rocky Mountains to the Pacific Ocean and from northern British Columbia to Utah (Jordan and Evermann 1905;

Scott and Crossman 1973). They occur in all major coastal drainage systems of British Columbia including the Fraser, Bella Coola, Nass, Skeena, Taku and Stikine (Carl et al. 1967; Scott and Crossman 1973). Mountain whitefish are found in the MacKenzie River headwaters, in the Upper Liard, and in the Peace downstream as far as the Peace River town site (McPhail and Lindsey 1970). The Liard River system marks the northern limit for the species (Dailey 1971). They are also abundant in the Columbia system (Sigler 1951; Godfrey 1955; Lindsey 1957; Ash et al. 1981). Figures 23 and 24 show mountain whitefish distribution in the Columbia drainage, and Peace and Liard drainages respectively.

10.3 Life History and Habitat Requirements

10.3.1 General

Mountain whitefish are usually associated with flowing waters and are abundant in large rivers, streams, and shallow portions of lakes. In British Columbia spawning occurs from October through February. No nest is constructed and the eggs are deposited on gravel, usually in tributary streams and sometimes on gravel shoals along the shoreline of lakes. Eggs incubate over the winter and hatch in early spring (e.g. March), at which time the emergent fry move to the margins of streams and backwaters downstream of spawning areas for several weeks. If necessary, rearing mountain whitefish migrate to favourable habitat during the early summer and remain there through the mid summer low flow period. Sexual maturity is reached from age 2 to 4 at which time the mature adults may make extensive migrations to spawning habitats. Mountain whitefish life history is illustrated in Figure 25.

Mountain whitefish predominantly feed on aquatic insect larvae and the pupae of chironomidae and other aquatic diptera. Trichoptera, ephemeroptera, plecoptera, acari, hemiptera, and coleoptera are other common taxa found in the diet (McHugh 1939; Sigler 1951; Laasko 1951; Carl et al. 1967; Pontius and Parker 1973; Overton et al. 1978).

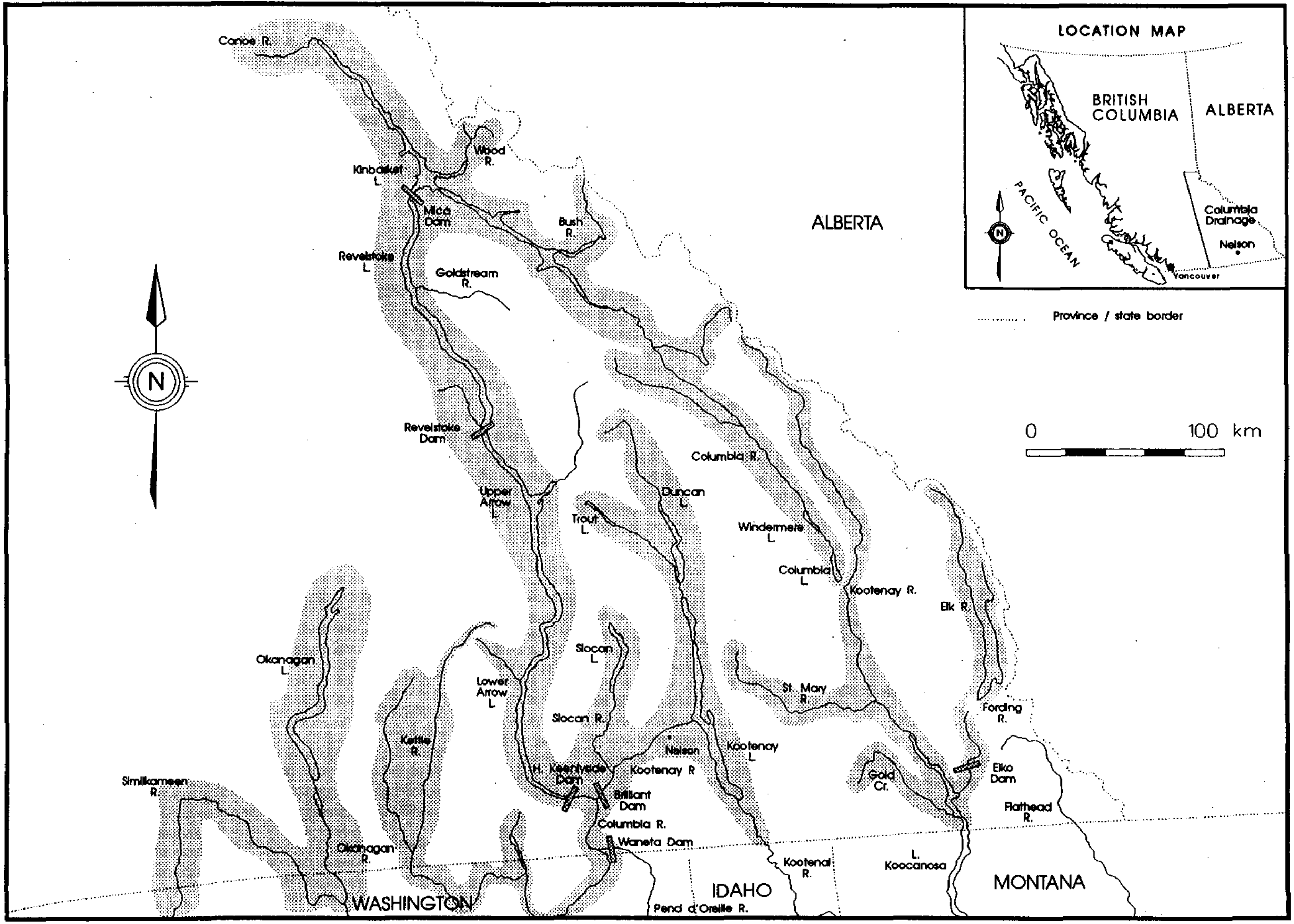


Figure 23: Mountain Whitefish Distribution in the Columbia Drainage, British Columbia

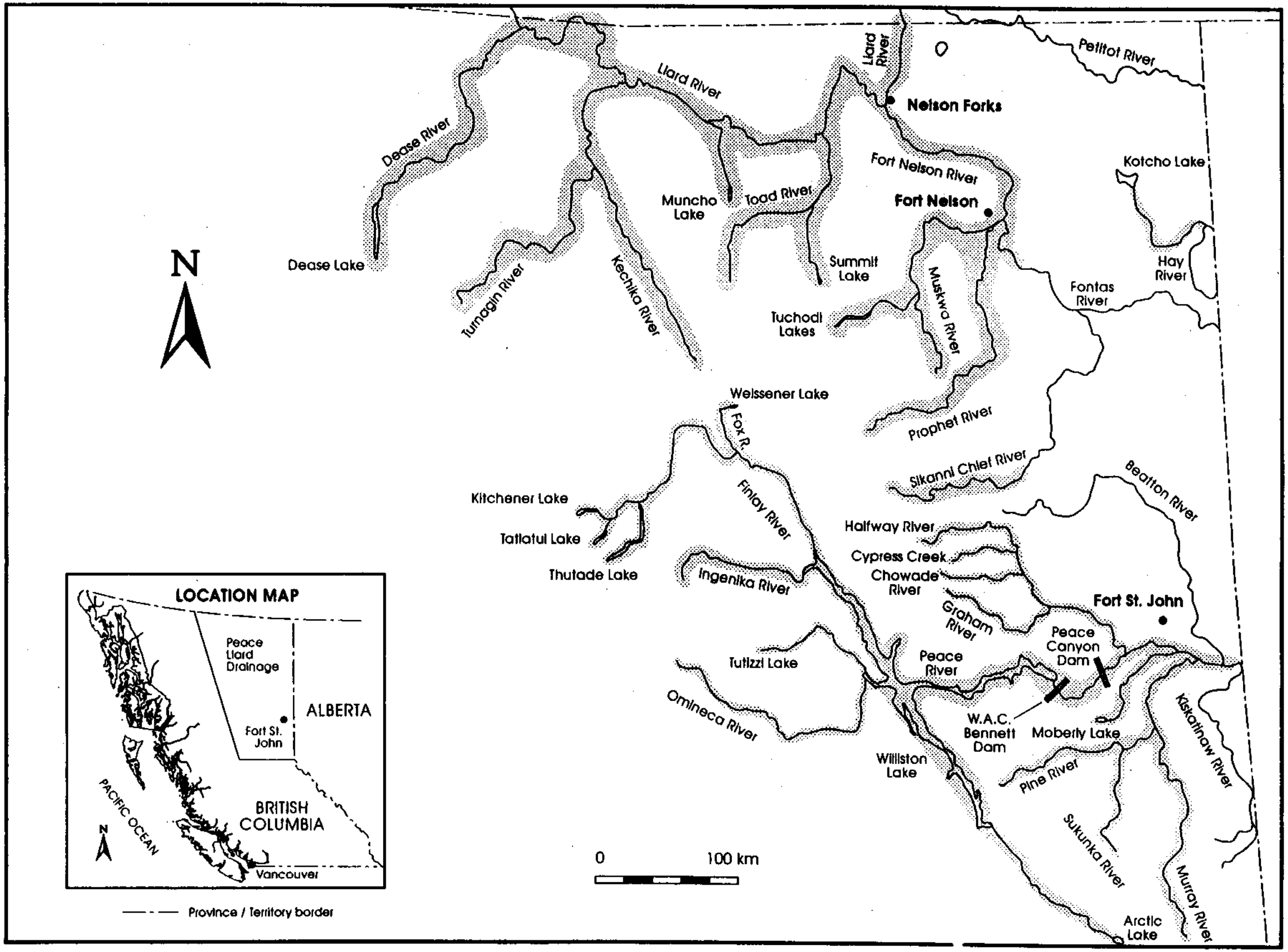
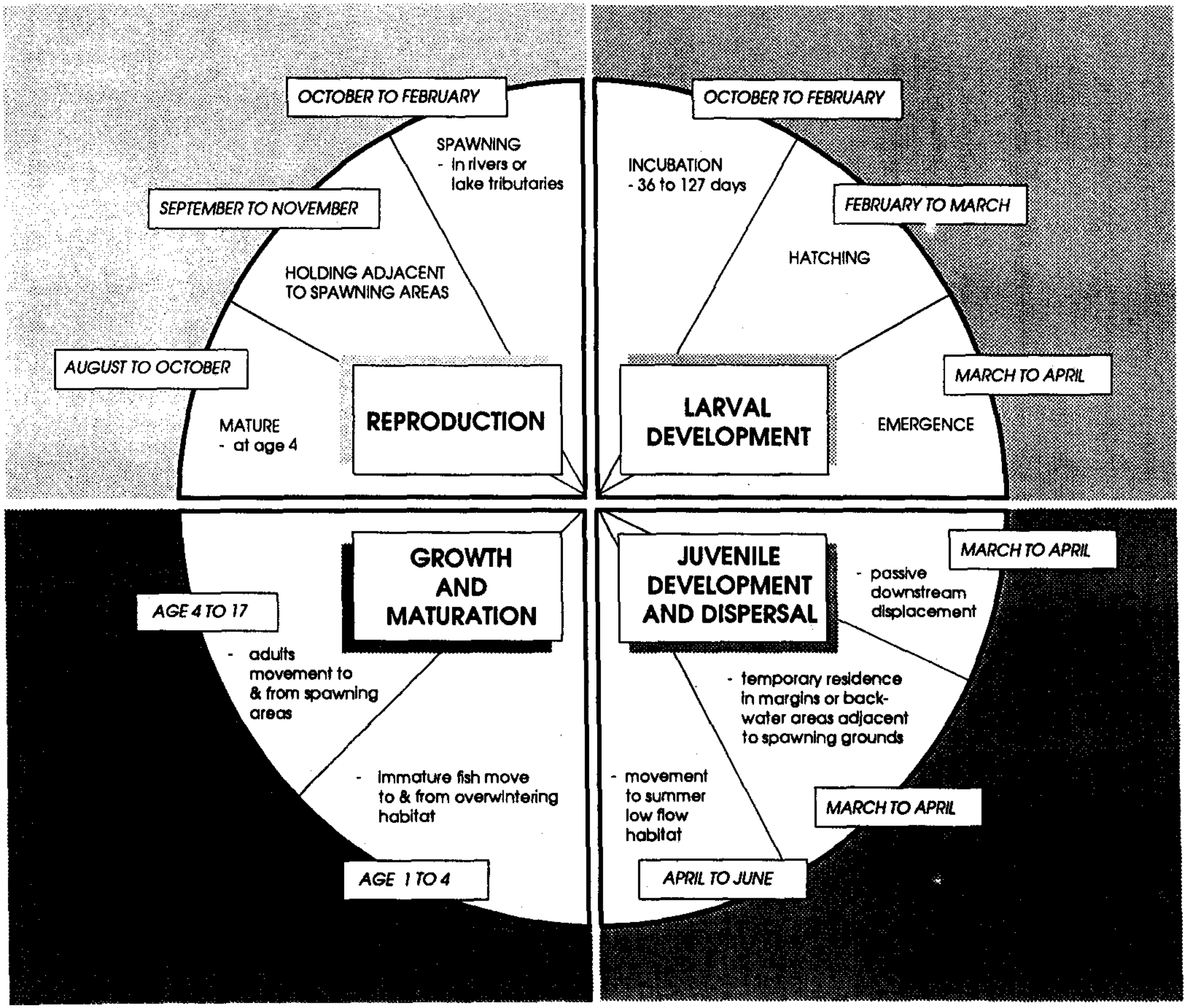


Figure 24: Mountain Whitefish Distribution in the Peace and Liard Drainages, British Columbia

FIGURE 25 - MOUNTAIN WHITEFISH LIFE HISTORY



Food habits are related to age and size (Overton et al. 1978; Pontius and Parker 1973). Similar diets were observed for age 1 and 2 fish but differed from age 3, 4 and 5 fish. This suggests that these certain age classes may compete for food. Larger fish exhibit more diverse diets and are capable of handling a greater size range of prey items than are smaller fish (Pontius and Parker 1973). Riverine or stream dwelling populations have also been found to consume a greater variety of food organisms than do lake dwellers (Carlander 1969).

Observed habitat use and selected biological characteristics by life stage for mountain whitefish are presented in Table 14 and discussed throughout the text.

10.3.2 Eggs and Incubation

Rajagopal (1979) provided experimental data to suggest that mountain whitefish eggs are adapted to a narrow temperature range during incubation and that 6°C is the upper optimum temperature for successful development. For temperatures greater than 9°C, the development process was disrupted and deformities such as abnormalities in the formation of the lower jaw, coloboma or fissure of the eye, and monomicrophthalmia were observed in the hatched larvae. At 10°C, the mortality ranged from 34 to 95%. All eggs incubated at temperatures above 12°C died within two weeks.

Incubation time and temperature for several mountain whitefish stocks are presented below; these data show that the time required to hatch eggs is dependent on incubation temperature, and to a certain extent may be stock dependent.

Source	Incubation Temperature (°C)	Incubation Time (d)	Accumulated Thermal Units (°C·d)
Rajagopal (1979)	6.0	74	444
Thompson and Davies (1976)	7.5	61	457
Brown (1952)	3.2	127	406
Brown (1952)	11.1	38	421
Stalnaker and Gresswell (1974)	7.2	45 to 75	321 to 540

Table 14. **Observed habitat use and selected biological characteristics by life stage for mountain whitefish.** (for sources refer to text, NA-data are not available).

Eggs	
Temperature tolerance range	0°C - 12°C
Upper limit of optimum incubation temperature	6°C
Minimum oxygen concentration required for normal development	8.0 mg/L
Range of incubation time	36 -127 days
Incubation time at optimum temperature	74 days
Lower lethal pH	NA
Recommended current velocity	in areas where the velocity will not displace spawning bed materials
Juveniles	
Temperature tolerance range	0.0°C to 20.6°C
Optimum temperature for growth	9.0°C to 12.0°C
Recommended oxygen concentration	>5.63 mg/L
Lower lethal oxygen concentration	3.98 mg/L
Habitat type preference	lakes, rivers, tributaries
Depth preference	< 3.0 m
Preferred current velocity	slow to moderate
Substrate	sand/gravel
Cover	cutbanks/woody debris/aquatic vegetation
Turbidity tolerance	<10 mg/L
Primary food category	benthic invertebrates
Secondary food taxa	zooplankton
Adults	
Temperature tolerance range	0.0°C to 20.6°C
Optimum temperature for growth	9.0°C to 12.0°C
Recommended oxygen concentration	7.75 mg/L
Short term minimum oxygen concentration	4.25 mg/L
Habitat type preference	rivers and streams
Depth preference	<3.0 m
Preferred current velocity	moderate to fast
Substrate	gravel/cobble
Cover	cutbanks/woody debris/aquatic vegetation
Turbidity tolerance	<10 mg/L
Primary food type	benthic invertebrates
Secondary food type	zooplankton
Form of reproduction	iteroparous, broadcast
Nest construction	no
Spawning habitat type	riffle sections of streams
Preferred spawning temperature	> 6.0°C
Preferred spawning depth	0.10 m to 1.0 m
Preferred spawning substrate	gravel/cobble
Preferred spawning current velocity	0.89 to 1.02 m/s
Range of first age-at-maturity	age 2 to age 4
Range of fecundity	averages 5,000 to 7,700 eggs/female

These data indicate that the number of degree days required to hatch eggs ranges from at least 321 to 540. This flexibility of incubation temperature and period suggests that eggs exhibit adaptive mechanisms which enable shorter incubation time and allow hatching to occur when conditions for survival may be best (Rajagopal 1979).

There is limited information on the effect of oxygen concentration on the survival and development of corregonid eggs and larvae. Fluechter (1980) indicated that concentrations of 8 mg/L are required for normal development from the fertilized to eyed whitefish eggs. Minimum oxygen requirements increase as the embryos develop. This is similar to pacific salmon; as embryonic development proceeds the concentration of oxygen required increases from 0.72 mg/L to 7.1 mg/L (Alderdice et al. 1958).

Turbidity and siltation can affect the development and survival rate of mountain whitefish eggs and larvae. Eggs lack mechanisms to strip the solids adhering to their surfaces that cause suffocation. Silt reduces the amount of oxygen available to the embryo and retards the rate that metabolic wastes are removed. Survival of lake whitefish (*Coregonus clupeaformis*) eggs is adversely affected by the settling of suspended particles (i.e. siltation) over spawning beds (Christie 1963; Hartman 1973).

10.3.3 Rearing, Food and Growth

Newly emergent mountain whitefish exhibit poor swimming ability (Thompson and Davies 1976) which result in passive downstream movements until a suitable holding area is encountered (Davies and Thompson 1976).

Pettit and Wallace (1975) found that young-of-the-year mountain whitefish in the North Fork Clearwater River, Idaho spent their first growing season in the upper reaches using side pools near spawning areas. With decreasing water temperatures in the fall fry moved downstream where they remained for the next two growing seasons prior to reaching sexual maturity. As water temperatures and day length increased in the late spring and early summer, mature adults moved upstream to the vicinity of spawning grounds and held there until November for spawning. After spawning, the fish moved back downstream to hold in deep pools over the winter. Homing to these spawning sites was demonstrated in a portion of the population.

Juveniles are strongly phototactic (Liebelt 1970), which may relate to their selection of shallow backwater areas and stream margins with instream or overhanging cover during downstream movements in spring. Movements slow in late spring and cease during summer, when fish tend to concentrate in more favourable habitats during low summer flows (Pettit and Wallace 1975). Schooling becomes apparent in early fall when the juveniles reach a size of 65 mm - 80 mm (Nelson 1962; Davies and Thompson 1976) and is thought to be associated with the movements of young of the year and age 1 fish in late fall to overwintering habitats. This migration coincides with adult migrations to spawning habitats.

During summer, Godfrey (1955) caught the greatest number of mountain whitefish in depths of 0 to 3 m in the Babine and Lakelse Lakes of the Skeena River system. Catches declined sharply at depths greater than 3 m and no fish were captured below 25 metres. Echo (1954) found that as summer water temperatures increased in the shallow inshore waters of Lower Thompson Lake, Montana, greater numbers of mountain whitefish were captured at increasing depths, presumably in response to temperature. These studies suggest that lake dwelling populations will remain inshore to feed on abundant benthic organisms with some inshore-offshore migrations occurring in response to changing water temperature.

Overton et al. (1978) found that chironomidae were the most abundant food item in the diet of mountain whitefish in the Teton River. Chironomids occurred in all fish in all age classes, however, the proportion of the diet composed of chironomids decreased with increasing age of the fish. Immature aquatic insects, mollusks, and crustaceans were the most important food items of mountain whitefish in the lakes and rivers of the Skeena, Peace and Liard river systems (Godfrey 1955; Machniak and Bond 1979; E.V.S. Consultants 1982) but juvenile fish and fish eggs have also been observed to be minor food items (Munro and Clemens 1937; Pontius and Parker 1973). In Okanagan Lake, the diet also includes zooplankton species, particularly cladocerans (McHugh 1939). Similar results have been obtained for food studies on mountain whitefish in other systems in Wyoming (Baxter and Simon 1970), British Columbia (Carl et al. 1967), and Idaho (Carlander 1969; Pontius and Parker 1973).

Even though mountain whitefish have a subterminal mouth, which is a morphological adaptation to bottom feeding. feeding on planktonic and drifting organisms has also been observed (McHugh 1939; Hagen 1956; Thompson and Davies 1976). It is impossible to determine from stomach contents whether food organisms are taken from the bottom or from the drift since all aquatic organisms that are found (alive) in drift are associated with the bottom at some point in their life cycle. The occurrence of sand and gravel in the stomachs of mountain whitefish tends to support the assumption of benthic feeding (Pontius and Parker 1973). However, Thompson and Davies (1976) observed that mountain whitefish rarely picked food items off the bottom but rather fed on drifting organisms near the bottom.

There is considerable variation in the growth rate of mountain whitefish throughout its range. McPhail and Lindsey (1970) report the largest specimen of mountain whitefish recorded to date (captured in the Lardeau River, British Columbia) was 572 mm in length and more than two kilograms in weight. McHugh (1941) observed no differences in the growth rates of males and females in Okanagan Lake. It was observed that growth was related to environmental factors; populations were smaller at any given age the greater the elevation of their habitat and slow growing populations tended to live longer than, but still reach a similar maximum size as, faster growing populations. Godfrey (1955) suggested that food abundance was the main factor that limited the growth and abundance of mountain whitefish in the Skeena River system.

Northcote (1957) compiled the variations in average lengths for mountain whitefish in British Columbia, Alberta, Utah, and California populations:

Age	Range of Average Length (mm)
1	66 - 135
2	107 - 224
3	163 - 297
4	196 - 328
5	221 - 330
6	325 - 391
7	325 - 417
8	351 - 417
9	376 - 442

Stalnaker and Gresswell (1974) and Rajagopal (1979) found 9°C to 12°C was optimal for the growth of juvenile mountain whitefish. However, juveniles have been collected in temperatures of 12.2°C to 20.6°C (Ihnat and Bulkley 1984).

No species specific data are available regarding dissolved oxygen requirements, turbidity tolerances, and velocity or depth preferences of juveniles. Davis (1975) provides guidelines for minimum dissolved oxygen concentrations for mixed populations that include salmonid species as 3.98 mg/L for short durations with the optimum concentration above 5.63 mg/L. The Canadian Council of Resource and Environment Ministers (CCREM) (1987) suggested that suspended sediment concentration that will not provide substantial risk to aquatic organisms is <10 mg/L. Juvenile mountain whitefish have been reported to use habitats that encompass a wide range of water velocities and depths, ranging from inshore areas of lakes to fast flowing tributary streams.

The seasonal movements and migrations of mountain whitefish are system specific and have apparently evolved to maximize utilization of habitat while reducing the potential for predation and intraspecific competition for food and space. Although some adult mountain whitefish are non-migratory, the majority of adults exhibit complex movement patterns related to spring feeding, summer feeding, prespawning, and overwintering. (Thompson and Davies 1976; Pettit and Wallace 1975; Davies and Thompson 1976). Fish may move entirely within a single river or stream (Thompson and Davies 1976; Pettit and Wallace 1975; Davies and Thompson 1976) or between large rivers and tributary streams (Brown 1952), or between lakes and inlet or outlet streams (McHugh 1939).

Godfrey (1955) suggested that within the Skeena River lake system of northern British Columbia the main predators of mountain whitefish are lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*).

Knowledge of the thermal requirements of adult mountain whitefish is limited. They have been found in summer water temperatures from approximately 11°C to 20°C (Carlander 1969). Water temperature preferences vary with season as illustrated by Ihnat and Bulkley (1984) where laboratory work indicated that the temperature preference was 17.7°C prior to spawning, 11.9°C after spawning, 9.9°C during winter, and 16.3°C during spring. These data indicate that the temperatures preferred by prespawning fish are too high for embryo survival. Most reported spawning temperatures are below 6°C (Brown 1952; Breder and Rosen 1966; Thompson and Davies 1976). Preferences for higher temperatures in spring could be due to anticipation of greater food intake associated with rising spring temperatures after a longer period of reduced feeding during winter. Changing photoperiod might also contribute to seasonal differences in temperature preferences.

There are no published experimental data nor circumstantial field observations to determine lower incipient lethal oxygen concentrations for adult mountain whitefish. Davis (1975), in a review of the oxygen requirements for aquatic life, recommends three levels of protection for mixed freshwater fish populations. For populations that include salmonids, 7.75 mg/L are suggested to provide a high degree of safety for fish stocks in prime areas. It was also suggested that 4.25 mg/L will provide suitable conditions for exposures that are not prolonged more than a few hours. Thus, for mountain whitefish

7.75 mg/L are required for long term oxygen conditions, whereas short term concentrations of approximately 4.25 mg/L will not have significant effects on individuals of the population.

Similarly, no data exist regarding adult tolerance to suspended sediments. The CCREM (1987) guideline of <10 mg/l is considered adequate.

10.3.4 Maturity, Adult Migration and Spawning

Brown (1952) found that whitefish in Montana matured predominantly at age 3 but in some cases at age 2. In Utah, mountain whitefish were found to be sexually mature at age 3 and age 4 (Sigler and Miller 1963). Thompson and Davies (1976) found that the earliest age-at-maturity was age 2 in the Sheep River, Alberta, with most fish maturing at age 4.

Mountain whitefish are known to make spawning migrations ranging from less than 1 km to over 80 km. Brown (1952) observed migrations from rivers into tributary streams from large rivers and using the lower 100 m of the tributary stream for spawning. Similarly, McAfee (1966) found that some populations migrated less than 10 km from lakes into tributary streams to spawn. In the Sheep River some mountain whitefish made migrations of greater than 60 km to their spawning ground (Thompson 1974). Pettit and Wallace (1975) noted movements of up to 88 km between spawning areas and overwintering areas of the North Fork Clearwater River, Idaho. Other accounts indicate that some mountain whitefish do spawn in lakes and likely undergo limited migrations along the lake shore from overwintering habitats (McAfee 1966).

Mountain whitefish generally spawn in late fall or early winter, but the exact time of spawning varies over their range. Carl et al. (1967) found spawning in mid-November in the Okanagan Valley whereas McPhail and Lindsey (1970) noted that there are two or more races that spawn at different locations and times (ranging from October to February) in Kootenay Lake. In Montana, Brown (1952) found differences in spawning period among populations in different streams but also observed that water temperatures at spawning were consistent at approximately 4°C. Spawning in northern parts of the species range has received much less attention than in southern areas. However, northern populations probably spawn earlier than southern fish since later spawning in the north would be limited to areas where there was sufficient flow under the ice.

Males undergo greater morphological changes prior to spawning than do females. As early as two months prior to the spawning period, males develop pronounced snouts and prominent tubercles. During the height of the spawning season erected pearl tubercles develop on three or four rows of the scales on both sides of the body below the lateral line. Females generally develop smaller tubercles than do males (McAfee 1966; Thompson and Davies 1976) and in some populations do not develop any (Vladykov 1970). Coloration of the mature adults varies among systems. In some populations a lateral stripe consisting of a dark lateral band with a lighter dorsal surface and a very light ventral surface also develops on maturing mountain whitefish (Stalnaker and Gresswell 1974). In others, neither sex becomes highly coloured during the spawning season (Scott and Crossman 1973).

Mountain whitefish are nocturnal spawners but are present on the spawning grounds throughout the day and night. Spawning activities begin at dusk when the fish initiate courtship behaviour (Brown 1952; McPhail and Lindsey 1970; Stalnaker and Gresswell 1974; Thompson and Davies 1976). No nest is prepared, and the fish assemble into groups of two to five near the margin in about 30 cm of water in areas of moderate to high current velocity. Eggs are deposited as the fish hold their position against the current approximately 5 cm from the bottom.

Fecundity is correlated to length and weight, with egg numbers and size varying among stocks (Dailey 1971). Brown (1952) found that the number of eggs can be highly variable ranging from 1,426 for a 259 mm female to 24,143 for a 495 mm female. Hagen (1970) estimated the average fecundity to be 7,757, however, in most cases it is thought that 5000 eggs is more realistic (Scott and Crossman 1973). Brown (1952) reported that the relative fecundity of Montana mountain whitefish ranged from 9,682 to 11,754 per kilogram of female. Sigler and Miller (1963) reported that relative fecundity ranges from 15,180 to 20,680 per kilogram of female. Egg diameters varied from 3.1 mm to 4.2 mm (Brown 1952) and 1.94 mm to 2.12 mm (Sigler 1951). These differences in egg size may account for the variability in egg numbers.

The findings of investigators regarding the choice of substrate, water depth and current velocity for spawning differ. McAfee (1966) states that mountain whitefish usually deposit their eggs in the gravel of riffles. Brown (1952) indicated that mountain whitefish appear to show little preference for spawning substrate size, as eggs were observed at different stages of development on various bottom types ranging from fine gravels to coarse rubble. The depth that eggs were observed ranged from 0.1 m to 1.0 m. Because mountain whitefish do not prepare nests and there is no disturbance to substrate materials, spawning sites are usually found by locating the deposited eggs.

Thompson and Davies (1976) investigated the reproductive biology of mountain whitefish in the Sheep River, Alberta. They found that spawning substrate was composed of small to very large rock and rubble ranging from 5 to 50 cm in diameter. No spawning substrate was found to be less than 5 cm in diameter. Water depths at the spawning sites ranged from 0.30 m to 0.63 m and current velocity ranged between 0.89 m/s to 1.02 m/s (Thompson and Davies 1976). Most spawning occurred in shallow parts of riffles but additional observations in this study indicated that a subpopulation was spawning in slower and deeper water in pool type rather than riffle type habitat. This demonstrated the adaptability of the species in utilizing available spawning habitats.

Lake or reservoir rearing mountain whitefish generally live longer than stream dwelling individuals. Maximum observed ages of lake populations, for example, range between 14 and 17 years (McHugh 1941 and Hagen 1970) whereas ages of 10 or less years have been reported in most river systems (Pettit and Wallace 1975; Thompson and Davies 1976).

10.4 Mitigation and Compensation Strategies

Mountain whitefish are abundant in lakes, river, and streams and therefore exposed to a wide range of natural resource and urban development impacts. Although the species appears to be adaptable to a wide range of habitat conditions, juveniles and adults exhibit complex migration patterns for spring and summer feeding and for accessing spawning and overwintering areas. These migrations can be affected by resource or urban developments (Thompson and Davies 1976; Pettit and Wallace 1975; Davies and Thompson 1976).

Reservoir impoundment for hydroelectric development, flood control and irrigation projects may affect flow and temperature regimes and interrupt mountain whitefish seasonal movement and migration patterns. Run of the river hydroelectric facilities and diversions may also affect movement patterns and downstream river productivity. Dam construction for hydroelectric power generation, irrigation or water storage has been shown to have both positive and negative impacts on mountain whitefish populations. There is some evidence that after impoundment mountain whitefish may begin spawning in shallow areas of lakes rather than in tributary streams (Hagen 1970). Thus, the mountain whitefish appear to be flexible in altering their habitat preferences to coincide with the types of habitats that are available. However, the success of this flexibility is dependent on the operation of the reservoir, particularly during the winter months when eggs are incubating. Nelson (1962) suggested that mountain whitefish were not adversely affected by hydroelectric development on the Kananaskis River system in Alberta, as the species became the most abundant sport fish species in the Kananaskis and Barrier Reservoirs. Availability of alternate spawning habitats was hypothesized to be the reason for the recovery of the population. However, in those reservoirs where no alternative habitat exists that will satisfy requirements for spawning and rearing, populations will be reduced. As mentioned above, mountain whitefish make extensive migrations to access spawning and overwintering habitats (Thompson and Davies 1976), and constructing dams on rivers may create barriers that adversely affect the population by restricting access to spawning and overwintering habitats. Mountain whitefish abundance declined as a result of the construction of the Revelstoke Dam (Fleming et al. 1990), which inundated 148 km of the mainstem Columbia River and the lower reaches of over 30 tributary streams. The decline in population abundance was attributed to loss of river spawning and rearing habitats and a physical barrier to fish passage (Fleming et al. 1990). Habitat limitations must then be assessed and mitigative measures initiated.

Alteration of temperature regimes may result from impoundment or diversion. This has implications for incubation time, stimuli for maturation, and initiation of seasonal movements. Release of water withdrawn from reservoirs at depth can result in cooler waters downstream in the spring and summer and warmer waters in fall and winter than were present prior to impoundment as well as affect the seasonal range of downstream water temperatures. Studies of benthic invertebrates below reservoirs indicate that a smaller range of fluctuation in stream temperature can result in a decrease in the number of resident species by providing competitive advantages to one or a few species (Ward 1974). Presumably the same physiological and developmental relationships exist for fish, therefore, some fish species may be excluded from the downstream area. Thus, impoundments can reduce habitat quality by altering temperature regime and the production and diversity of fish food organisms. Water quality may be affected by impounding or diverting water. Dams can trap nutrients causing reduced nutrient availability downstream, and can reduce food sources for mountain whitefish populations.

Habitat may be affected by forestry related activities if streambanks are logged or disturbed. Logging can also result in the introduction of excessive amounts of organic debris in streams. Although large organic debris can have positive effects on stream habitat by trapping gravels, stabilizing channels, providing cover and resting pools, it can also clog spawning gravels with fine particulate organic materials (Everest and Talhelm 1982).

Road construction activity can reduce stream habitat quality by altering flow regimes, removing streambank cover, blocking migration corridors and increasing sediments inputs. Removal of riparian vegetation may elevate water temperatures, reduce the drop of riparian insects into the stream and decrease the stability of streambanks. This usually results in increased sediment loads, and the creation of wide, shallow and unstable channels. As pools fill with sediments and become shallower, they become less suitable for rearing and production of fish food organisms, especially during low flow periods in the summer and winter. Food production may also decline as a result of altered flow regime and excessive sediment inputs.

Urban development may lead to stream habitat loss through channelization, and degradation of water quality by the introduction of toxic substances and suspended sediments. Industrial and urban development may also cause leaching or direct discharge of toxic chemicals to the river or stream during periods when sensitive stages of mountain whitefish are present. Where toxic organic compounds such as dioxins and furans are present, these may also accumulate in the fatty tissues of mountain whitefish.

Currently, mountain whitefish populations are not actively enhanced in British Columbia and effects of development are mitigated through enforcement of habitat regulations (D. Ableson, Fish and Wildlife Branch, B.C. Environment, Prince George, pers. comm. 1991). Past mitigative efforts in habitats used by mountain whitefish were directed toward other salmonid species such as rainbow trout (*Oncorhynchus mykiss*) or bull trout (*Salvelinus confluentus*), and as a result there is no documentation of efforts to mitigate the species.

Physical disruption of stream and river habitats can be mitigated with instream structures or the development of off channel rearing or spawning areas in relic fluvial channels. Sediment inputs can be mitigated with settling ponds, stabilizing eroding banks through revegetation, revetments, buffer strips, and addition of large organic debris (Marcus et al. 1990). Channel characteristics and hydraulics that affect habitat quality in streams and rivers can be modified to suit specific requirements (i.e. depth, velocity, substrate size) and to improve food production capabilities. There is no available information regarding the use or effectiveness of techniques for enhancing mountain whitefish. However, because habitat requirements and diet of the mountain whitefish tend to overlap those of trout, mitigative actions effective in improving trout habitat (Hall and Baker 1982) will likely be effective in enhancing mountain whitefish habitat.

Mountain whitefish are usually found inhabiting areas with other sport fish species and may compete for food and space with those species. Donald (1987), in a review of stocking programs carried out in over 1,400 Canadian mountain park lakes over the last eighty years, found that the presence of mountain whitefish affected stocking success. It was found that rainbow, cutthroat, and brook trout introductions into lakes where mountain whitefish were abundant were not as successful in lakes where the latter were not abundant. Thus, plans to mitigate or compensate for effects on mountain whitefish populations must consider species interactions and the relative value of each species as a sport fish.

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12.0 BURBOT

(Lota lota)

12.1 Introduction

Burbot (*Lota lota*) belong to the Family Gadidae and have been separated into two subspecies *Lota lota lacustris* and *Lota lota lota* (Pivnicka 1970) based on differences in the morphometrics of the caudal peduncle and meristic values. *Lota lota lacustris*, also referred to as *Lota lota maculosa*, occurs in southern Canada, the United States, and western Europe while *Lota lota lota*, also referred to as *Lota lota leptura* or *kamensis*, occurs from the Volga River system through Siberia and Alaska to the Mackenzie River system in Canada. Studies by Lindsey (1956), Lawler (1963) and McPhail and Lindsey (1970) have provided evidence that there is only clinal variation of the caudal peduncle morphometrics and meristic values, and that the recognition of subspecies may be unwarranted. Ling, eelpout, loche, and maria are some other common names used in Canada (MacCrimmon and Devitt 1954; Scott and Crossman 1973).

Historically, the burbot has been regarded as a competitor of commercially important fish such as whitefish and pike (Kirillov 1988) and a nuisance because it eats fish caught in gillnets and trapnets (Hewson 1955; Bailey 1972; Hanson and Qadri 1980). Burbot in Canada have limited commercial value and are generally not a target sport fish. For example, anglers in Kootenay Lake generally take fewer than 10,000 burbot annually (Andrusak 1981). In the Omineca sub-region in central B.C., adult burbot are caught year round in shallow lake areas by anglers using set lines; most of this activity occurs at night (D. Cadden, Fish and Wildlife Branch, B.C. Environment, Prince George, pers. comm. 1992).

12.2 Distribution

Burbot are found mainly in the freshwaters of continental Eurasia and North America, southward to about 40°N, although there are a few populations in Europe and the Yukon that migrate as juveniles to brackish water and return to freshwater to spawn each year (Percy 1975 in Thornburgh 1986; Johnson 1981). Burbot are absent from the Kamchatka Peninsula of eastern USSR, Scotland, Ireland, and the east coast of Norway, but present in southern England and on Kodiak Island, Alaska (Scott and Crossman 1973). In Canada, this species occurs in New Brunswick, Labrador, Quebec, throughout Ontario, Manitoba, Saskatchewan, Alberta, British Columbia, and the continental portion of the Northwest and Yukon Territories, exclusive of the northernmost tips (Scott and Crossman 1973).

In British Columbia, burbot are found in most lakes and rivers except those along the coast. In the Kootenay region, they are caught in the Kootenay and Columbia rivers and in lakes associated with these drainages (R. Lindsay, Fish and Wildlife Branch, B.C. Environment, Nelson, pers. comm. 1991; R. Carveth, Fish Museum, Department of Zoology, University of British Columbia). In the Peace River drainage, they are present in the mainstem upstream to and including Williston Lake, in the Moberly River upstream to Moberly Lake, and in the Pine River (Renewable Resources Consulting Ltd. 1979). Figures 29 and 30 show burbot distribution in the Columbia drainage and Peace and Liard drainages respectively.

12.3 Life History and Habitat Requirements

12.3.1 General

Burbot spawn at night during winter, generally over gravel substrate located in shoals or along shorelines of cool lakes or rivers. Spawning may occur in either open or ice covered waters (Clemens 1951b; Sorokin 1971; Breeser et al. 1988). Through its range, burbot

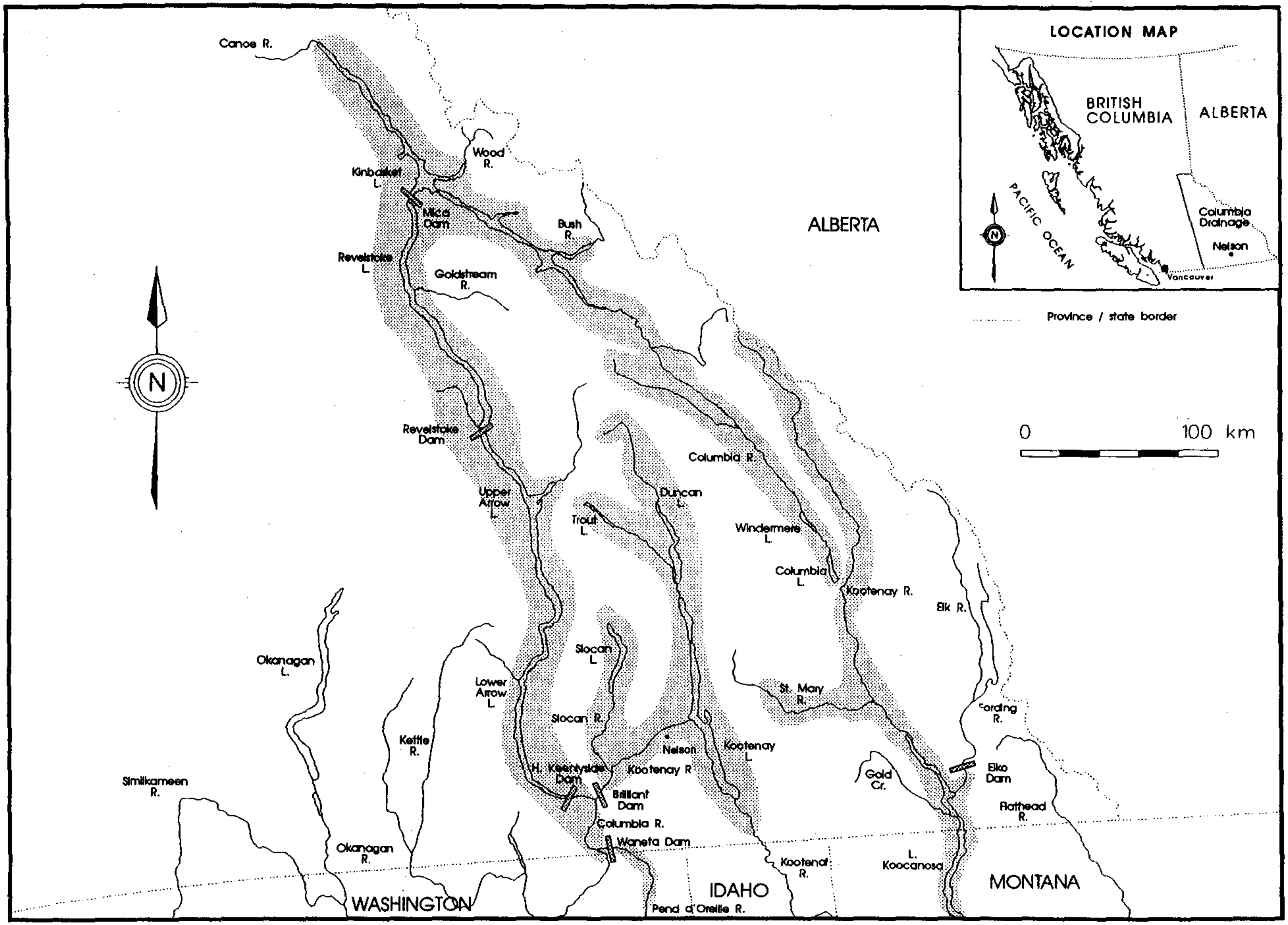


Figure 29: Burbot Distribution in the Columbia Drainage, British Columbia

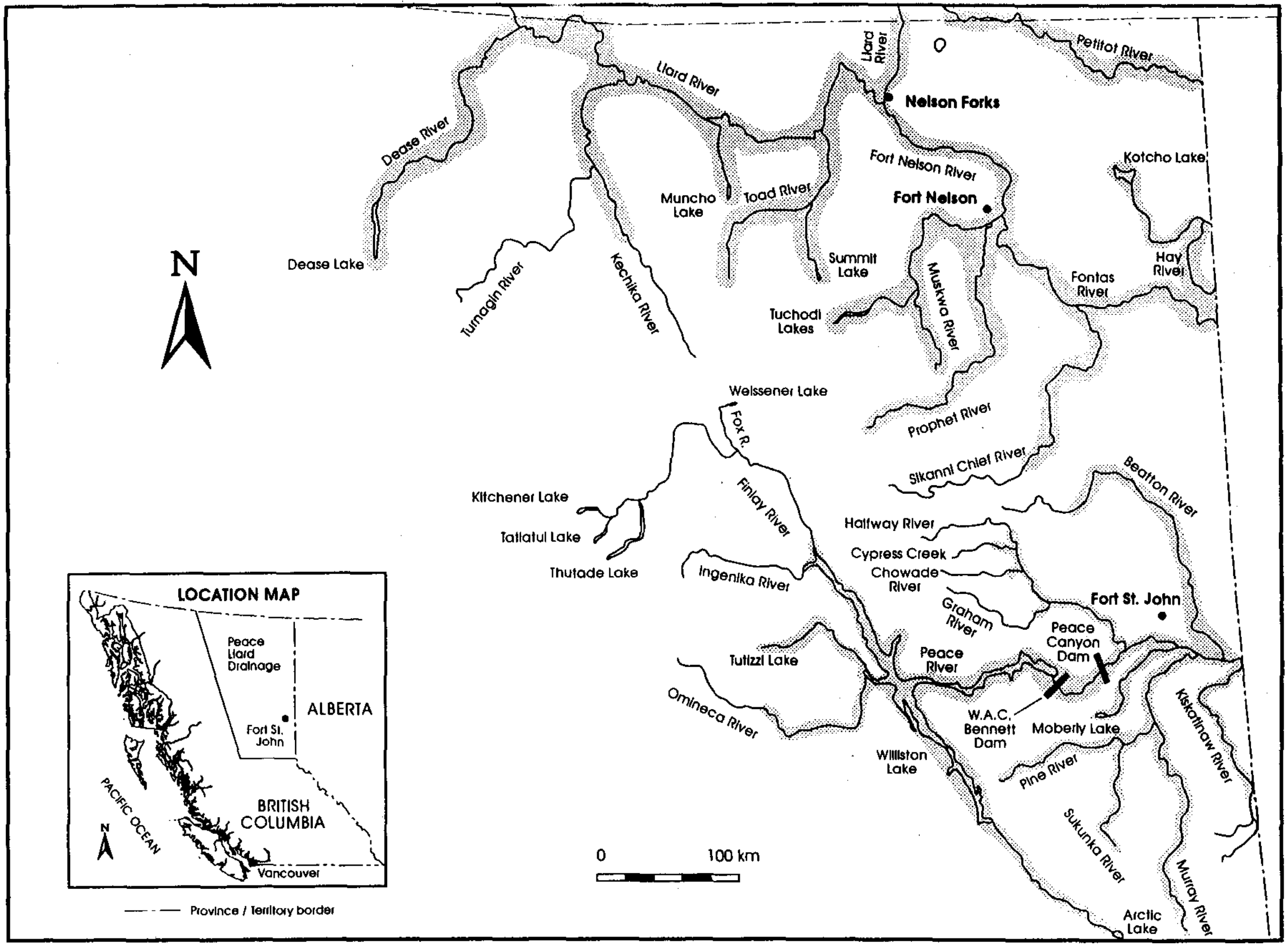


Figure 30: Burbot Distribution in the Peace and Liard Drainages, British Columbia

may spawn between November and May, mainly from January to April in Canada (Scott and Crossman 1973). In the Kootenay region, spawning occurs in February (Carl et al. 1967).

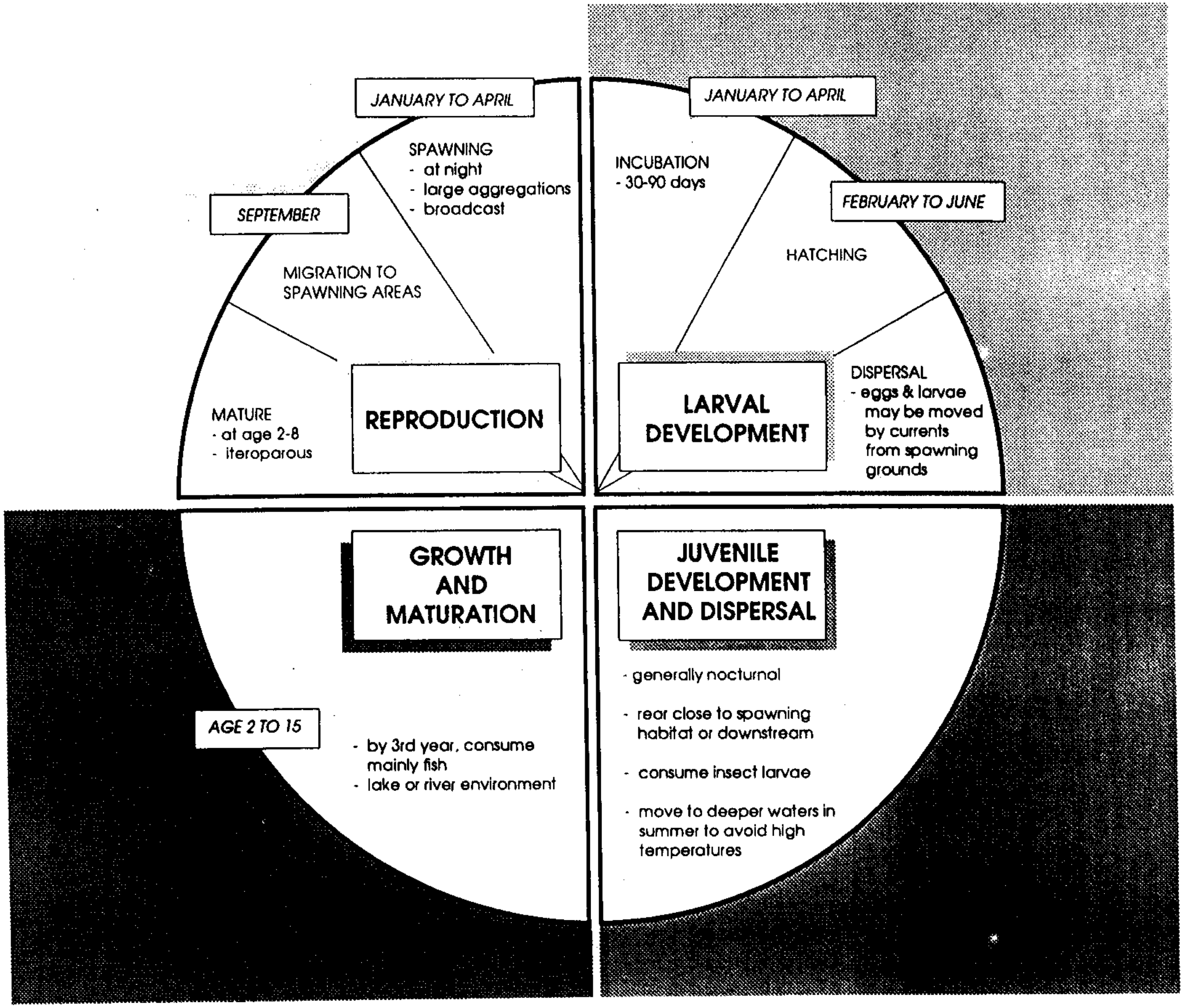
Although eggs are semi-buoyant when first laid, they become demersal within a few days, sinking to the substrate and settling in interstices if the substrate is comprised of gravel or cobble (Fabricius 1954). Eggs incubate for three weeks to three months, depending on water temperature (Mansfield et al. 1983). In Lake Erie, for example, eggs may hatch from early summer until the last week of June (Clemens 1951b). Larvae are buoyant and may disperse some distance from the spawning grounds with water currents (Mansfield et al. 1983). In Alaskan rivers, juveniles rear near the hatching area in tributaries and sloughs (Alaskan Dept. Fish & Game 1983b in Thornburgh 1986).

Juveniles are usually found over rocky or gravel bottoms or rocky shorelines. They reach maturity between two and eight years of age with females generally reaching maturity a year later than males. In the fall, sexually mature adults migrate to the spawning grounds. Although burbot are iteroparous, they may not spawn on consecutive years. During most of their life history, burbot are rather sedentary and there are periods during which they do not move for days (Thornburgh 1986; E. Burgerson, pers. comm. 1991). There are, however, definite movements toward spawning areas. Burbot life history is illustrated in Figure 31.

The diet varies with size and age and is comprised primarily of aquatic insects and fish. However, rodents, mysids and fish eggs have also been found in burbot stomachs (Clemens 1951a; Kirillov 1988).

Burbot are generally sedentary and found in deep pools of rivers and in the hypolimnion of lakes, but may also live in small streams, elevated lakes, and low ponds (McPhail and Lindsey 1970), and have been reported in the brackish waters of the Yukon Territory's coast and in the MacKenzie River delta (Percy 1975 in Thornburgh 1986; Kendel et al. 1975 in Thornburgh 1986). Within rivers, burbot are rare in clearer slough and tributary

FIGURE 31 - BURBOT LIFE HISTORY



mouth regions and absent from shallow main channel sandbar and side channel habitats, except during high river stages. Water temperature is important in determining the distribution of burbot within lakes and rivers and during the summer months when surface temperatures approach the upper tolerance limit for burbot (23.3°C).

Although some studies have documented habitat requirements of burbot (i.e. temperature, oxygen, velocity, turbidity, substrate) it is evident that more studies are required to obtain a more detailed assessment of the habitat requirements at particular life stages. Observed habitat use and selected biological characteristics of burbot are presented in Table 16 and discussed throughout the text.

12.3.2 Eggs and Incubation

The optimal temperature for development of burbot eggs ranges between 4 and 7°C, with a rapid decrease in survival when temperatures are below 4°C (Jager et al. 1981). The incubation period is temperature dependant. For example, at 6.1°C Bjorn (1940) found that burbot eggs hatch in 30 days, while at 4°C in Lake Erie incubation is prolonged from 60 to 90 days (Clemens 1951b).

The eggs of burbot are non-adhesive, and because of their large oil droplet have a slight positive buoyancy. Eggs float at a flow rate of 4 cm/s, and may be carried away from the spawning grounds when water velocity reaches 8 cm/s (Sorokin, 1971). Mortality from egg to larval stage is considerable (i.e. >99.8%) in the Kichera River, USSR because of the movement of eggs downstream from spawning gravels to heavily silted regions (Sorokin 1971). Optimal substrate for egg development is sand, gravel or cobble material with little accumulation of silt, detritus, or organic debris allowing flow of water and oxygen. Lake Baikal burbot spawn in areas with a weak current of approximately 3 cm/s, which turns the eggs and cleanses them of silt (Sorokin 1971).

Data regarding dissolved oxygen requirements during incubation are sparse. Sorokin (1971) reported that burbot eggs develop only when oxygen content in the water is fairly

Table 16. **Observed habitat use and selected biological characteristics by life stage for burbot.** (for sources refer to text, NA- data are not available).

Eggs

Temperature tolerance range	1 - 7°C
Optimum incubation temperature	4 - 7°C
Recommended oxygen concentration	6.5 mg/L (interstitial)
Lower lethal oxygen concentration	NA
Range of incubation time	30-90 days
Incubation time at optimum temperatures	NA
Lower lethal pH	NA
Recommended current velocity	< 8 cm/s
Substrate	interstices of sand, gravel, and cobble free of silt and debris

Juveniles

Temperature tolerance range	8 - 23.3°C
Optimum temperature for growth	15.6 - 18.3°C
Recommended oxygen concentration	>7.25 mg/L
Lower lethal oxygen concentration	NA
Habitat type preference	rivers, lakes, tributaries
Depth preference	dependent on temperature
Preferred current velocity	NA
Substrate	gravel, rock, cobble
Cover	rocks, cobble, vegetation, logs
Turbidity tolerance	NA
Primary food category	aquatic insects
secondary food category	fish

Adults

Temperature tolerance range	0.6 - 23.3°C
Optimum temperature for growth	15.6 - 18.3°C
Recommended oxygen concentration	>7.25 mg/L
Lower lethal oxygen concentration	NA
Habitat type preference	rivers, lakes
Depth preference	dependent on temperature
Preferred current velocity	< 30 cm/s
Substrate	gravel, rock, cobble
Cover	darker waters at depth
Turbidity tolerance	(feeding may be hampered at this level) 1000 NTU
Primary food type	fish
Secondary food type	aquatic insects
Form of reproduction	iteroparous
Nest construction	no
Spawning habitat type	shoals, shores in lakes and rivers
Preferred spawning temperature	0.6 - 1.7 °C
Preferred spawning depth	0.3 - 3 m
Preferred spawning substrate	sand, gravel, cobble
Preferred spawning current velocity	< 122 cm/s
Range of observed first age-at-maturity	2 to 8 years
Range of observed fecundity	45,000 to 1,000,000 eggs

high (specific values are not given) and that spawning grounds usually have an undercurrent of fresh water ensuring a supply of oxygen. Gravel or rocky substrate is the preferred substrate for incubation since soft silty bottoms provide insufficient circulation of oxygen around the eggs (Sorokin, 1971). Hewson (1955) reported oxygen concentrations of 8 mg/L in spawning grounds in Lake Winnipeg, Manitoba. According to the guidelines of the Canadian Council of Resource and Environment Ministers (1987) for freshwater fish, oxygen concentration in waters overlying spawning regions should be maintained at 9.5 mg/L and in interstitial water of the gravel should be at least 6.5 mg/L.

Although spawning occurs in freshwater, eggs may tolerate salinity levels between three to six ppt (parts per thousand) (Jager et al. 1981). Fertilization, embryonic development, and hatching were observed in salinities up to 12 ppt, but the mortality rate increases at later embryonic stages. At 14 ppt salinity no larvae hatch.

Larvae may be found throughout the water column since they are more buoyant than eggs and have little fin development; they are thus susceptible to movement by water currents following hatching (Mansfield et al. 1983). Abiotic factors such as water velocity may also reduce burbot survival by moving eggs to soft, silty substrate where they do not develop, or to regions where water temperatures are too low. Jager et al. (1981) found that larvae require at least 8°C to initiate feeding and avoid starvation, and survived in water temperatures to 20°C. Mansfield et al. (1983), found that in Lake Michigan, burbot larvae were collected most often in temperatures from 6 to 12°C.

12.3.3 Rearing, Food, and Growth

Hewson (1955) found that younger fish depend primarily on smaller bottom organisms such as insect larvae, whereas young-of-the-year burbot consumed mostly amphipods as well as minnows, isopods, oligochaetes, dipterans, odonatans, and gastropods (Hanson and Qadri 1980).

In the Yukon and Tanana rivers, juveniles feed mainly on insect larvae, especially plecoptera, ephemeroptera, and diptera and on slimy sculpins (Chen 1969 in Thornburgh 1986). By the third to fourth year, they consume mainly fish, but may also consume both crayfish and aquatic insects (Clemens 1951a; Hewson 1955; Lawler 1963; Chen 1969 in Thornburgh 1986). In Fraser Lake, in the Nechako River drainage, burbot caught in the recreational fishery had been feeding heavily on juvenile rainbow trout. Burbot have also been observed during the spring where the Stellako River enters Fraser Lake, presumably targeting the migrating sockeye juveniles and smolts (D. Cadden, pers. comm. 1992).

As mentioned above, juveniles are typically found in the littoral regions of lakes and in shallow regions of streams and rivers where they forage for benthic invertebrates (Hartmann 1977) over gravel, rock or cobble bottoms or rocky shorelines in close association with the bottom (Lawler 1963; Thornburgh 1986; A. Townsend, Habitat Protection Division, Alaska Fish and Game, Fairbanks, pers. comm. 1991). They may also use weed cover in sandy areas if rocky habitat is limited (Scott and Crossman 1973; Hanson and Qadri 1980) and the cover of submerged logs, rocks, vegetation and other debris or undercut banks (Hanson and Qadri 1980). They typically move from the shallow regions to deep pools in rivers and the hypolimnion of lakes during the summer months when temperatures approach the upper tolerance limit of 23.3°C (Hartmann 1977; Thornburgh 1986), however young-of-the-year and yearlings are occasionally found along shallow rocky shores (Lawler 1963).

The optimum temperature range for both juvenile and adult stages of burbot lies between 15.6 and 18.3°C and the upper temperature tolerance is 23.3°C (Scott and Crossman 1973). In St. George Creek, approximately 30 km southwest of Prince George, juvenile burbot up to 20 cm are found in great abundance in the shallow pool areas throughout the year. During low flow periods (e.g. late July through August) these pools become warm and (presumably) low in dissolved oxygen, resulting in high mortality. Although there is access downstream to a lake until the lowest flow periods, the juvenile burbot do not migrate out of the system to refuge (D. Cadden, pers. comm. 1992).

Juvenile burbot inhabit brackish waters with salinity to six ppt along the coast of the Yukon, in the MacKenzie River delta and in the Gulf of Bothnia (Johnson 1981; Percy 1975 and Kendel et al. 1975 in Thornburgh 1986). They move to the sea during their first year where they spend up to six months before returning to freshwater during the winter.

Information on the specific requirements of juveniles in terms of water velocity, turbidity or oxygen concentrations is not available. If the guidelines of Davis (1975) are used, then oxygen concentrations should be maintained at or above 7.25 mg/L for both juveniles and adults to maintain more or less ideal conditions with little depression of oxygen from full saturation.

Growth rate varies substantially between populations. For example, burbot reach an average length of 147 mm in their first year in Heming Lake, Manitoba, 191 mm in Lake Koocanusa and 210 mm in Lake Erie (Table 17). There does not appear to be a consistent difference in the growth rates of males and females.

Table 17. The relationship between age and total length (mm) of burbot in three lakes.

Age	Lake Koocanusa[1]	Heming Lake[2]	Lake Erie[3]
1	191	147	210
2	251	246	323
3	311	279	377
4	371	323	424
5	431	366	492
6	491	399	540
7	551	429	558
8	611	465	579
9	671	-	591
10	731	-	616
11	791	-	-

1. Chisholm et al. 1989
2. Lawler 1963
3. Clemens 1951a

While Kirillov (1988) found that female burbot grow faster than males at least until age 4 in Vilyuysk Reservoir, Holcik and Nagy (1987) observed neither a difference in growth rate nor in length-weight relationships between males and females in the River Turiec, Czechoslovakia.

During most of the year, burbot have a nocturnal activity pattern but in November to January they are more active during daylight periods (Solem 1973). The change from nocturnal to diurnal activity is associated with the reduction in light intensity during these months (Solem 1973; Kroneld 1975). During periods of activity, burbot move into shallow regions to forage (Morrow 1980), except during the summer months when surface temperatures approach the upper limit of 23.3°C (Scott and Crossman 1973).

Adult burbot feed primarily during prespawning and postspawning periods; for example, in the Vilyuysk Reservoir, the peak feeding period of burbot is between September to December, prior to spawning and March to June, following spawning (Kirillov 1988). MacCrimmon and Devitt (1954) also noted a reduction in feeding during the spawning period. Burbot have a diel pattern of feeding, foraging during periods of low light between dusk and dawn and remaining sedentary during daylight hours (McPhail and Lindsey 1970; Solem 1973; Thornburgh 1986; E. Burgerson, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, pers. comm. 1991). They consume a wide variety of fish throughout their range including tugun, whitefish, dace (Kirillov 1988), yellow perch, ninespine sticklebacks, trout-perch, suckers (Lawler 1963; Chisholm et al. 1989), freshwater herring, emerald shiner, pumpkinseed, rock bass (MacCrimmon and Devitt 1954), cisco, sauger, walleye (Hewson 1955), johnny darter, sculpins, common shiner, and creek chub (Bonde and Maloney 1960).

Diet also varies with food availability. For example, Kirillov (1988) found that burbot switched from fish to invertebrates such as chironomids and caddis fly larvae as invertebrate biomass increased in the Vilyuysk Reservoir, USSR and returned to fish when invertebrate biomass declined. Lawler (1963) observed that burbot in Heming Lake, Manitoba feed almost exclusively on sticklebacks in the winter months, because of the availability of sticklebacks and lack of other prey items. Ninespine sticklebacks in these northern lakes are more active relative to other fish species during the winter months when water temperatures are colder and consequently are more available as prey. In Lake Koocanusa, the diet of burbot also varies seasonally. Largescale suckers are the most important fish prey during the fall and winter whereas during the spring, when burbot move to shallower sandy regions, they feed primarily on yellow perch (Chisholm et al. 1989). In Alaskan rivers, adults are found along the river bottom during the summer and consume mainly bottomfish (Chen 1969 in Thornburgh 1986).

Adults, like juveniles, congregate in regions with gravel, rock or cobble substrate. Adults have been observed as deep as 213 m in lakes and tend to congregate in deep holes in rivers except during the spawning period (Rawson 1951 in McPhail and Lindsey 1970; Morrow 1980). In the Susitna River, Alaska, adult burbot inhabit deep eddies in the main river during the summer and winter (Alaskan Dept. Fish and Game 1983a in Thornburgh 1986).

Adults, like juveniles, have an upper temperature tolerance limit of 23.3°C and avoid shallow regions in summer. Waters with temperatures between 15.6° and 18.3°C provide optimum habitat (Scott and Crossman 1973). The temperature tolerance of burbot is one of the major factors determining their depth distribution. For example, in the Vilyuysk Reservoir, high summer temperatures by the end of June force burbot to move from the littoral zone to within the hypolimnion in the limnetic zone where food is less abundant (Kirillov 1988). Temperatures in the surface are generally around 25°C while hypolimnetic temperatures (>35 m deep) may be 10 to 12.5°C cooler. Burbot return to littoral regions in the fall when temperatures decline. Lawler (1963) also found that during the warmer summer months larger burbot are usually restricted to the hypolimnion of the lake and only occasionally are taken in nets in shallower regions. In late fall, when the water temperature declines large burbot sometimes move inshore to shallower regions.

Adults are found most often in low velocity regions along lake bottoms or at depth or in deep pools in rivers. In the Susitna River, they inhabit lower-velocity backwater areas with velocities ranging from 0 to 30 cm/s (Alaskan Dept. Fish and Game 1983a in Thornburgh 1986). Dryden and Stein (1975), however, found that the maximum velocity barrier for burbot is 20 cm/s, but did not indicate the size of burbot to which this pertained. Burbot may, however, tolerate high water velocities characteristic of glacial rivers during the summer. Breeser et al. (1988) found that burbot are able to tolerate high summer peak flows in glacial Tanana River, Alaska and it was evident that adults prefer the main channel of the Tanana River to clear regions in tributaries. Favourable holding and feeding areas for burbot in Poplar Creek are in deep-fast riffles, and back-eddies where prey items concentrate (O'Neil 1979).

Little is known about the turbidity levels that are harmful to burbot (Thornburgh 1986). Burbot have been observed in some Alaskan rivers when turbidity has reached up to 1000 nephelometric turbidity units (NTU) during the summer months when flows are highest in glacial rivers (A. Townsend, pers. comm. 1991). However, burbot appear to feed only at much lower turbidity levels (100 to 200 NTU). Chen (1969 in Thornburgh 1986) reported that burbot in the Tanana and Yukon rivers are more abundant in the silty, main rivers than in the smaller, clear tributaries. However, such turbid regions are poor for spawning since burbot eggs are unable to develop on soft, silty bottoms (Volodin 1966 in Sorokin 1971).

Predation by other fish species (e.g. smelt, perch, and lake trout) affects the survival rate of eggs and juvenile life stages (Johnson 1975; Hallberg 1979 in Thornburgh 1986), as does competition for invertebrate prey at the juvenile stage (Clemens 1951a).

12.3.4 Maturity, Adult Migration, and Spawning

Age of maturity ranges from two to eight (Clemens 1951b; Hewson 1955; Kirillov 1988). Generally, burbot mature from ages two to four in the southern part of their range, but not until they reach age six or seven in Alaska (Chen 1969 in Thornburgh 1986). In Lake

Simcoe, most burbot mature during their third year with the remainder maturing by their fourth (MacCrimmon and Devitt 1954). In the Vilyuysk basin, female burbot reach sexual maturity in their seventh and eighth year, while males probably mature one year earlier (Kirillov 1988). The time of maturity seems to be associated more with size than with age (Hewson 1955). In Lake Erie, for example, burbot may mature in their third, fourth, and fifth years but are at least 300 mm (Clemens 1951b).

Breeser et al. (1988) found that lengthy (up to 125 km) upstream movements of adult burbot from November through March in the Tanana River, Alaska, may have been associated with spawning. Sorokin (1971) observed that, in the USSR, burbot begin to migrate into small rivers and tributaries of Lake Baikal in September when water temperatures fall to the range 10 - 12°C. This is initially a feeding migration to the lower reaches of the rivers and slightly later, the burbot move farther upstream for spawning. Many populations of burbot rear and feed in lakes and return to tributary rivers to spawn. Others rear and spawn within the same habitat type, i.e. river or lakes (Sorokin 1971; Bond and Berry 1980), while fewer populations rear in brackish water and return to freshwater lakes and rivers to spawn (Scott and Crossman 1973; Johnson 1981).

Sorokin (1971) found that the mean rate of migration to spawning locations was 1.5 - 2 km per day. Distance travelled may be considerable with some fish migrating up to 400 km. In the Susitna River, Alaska, burbot have been observed to migrate up to 98 km during the winter for spawning as early as mid-September to mid-January (Alaskan Dept. Fish and Game 1983a in Thornburgh 1986). Burbot migrate from Lake Athabasca to spawn in the Athabasca River mainstem or its tributaries (Machniak and Bond 1979). Generally, the spawning migration is one of individual movements, rather than as a group (Morrow 1980). After spawning there is generally a downstream migration of fish into the lower reaches of rivers (Sorokin 1971; Alaskan Dept. Fish and Game 1983a in Thornburgh 1986), although post-spawning burbot have also been observed to move upstream of spawning regions, apparently for feeding (MacCrimmon 1959).

Spawners aggregate in writhing groups of 10 to 12 individuals and broadcast both eggs and milt together into the water column, generally over clean sand, gravel or large cobblestones with little accumulation of silt, detritus or organic debris (Sorokin 1971; Morrow 1980). As mentioned above, the eggs are initially buoyant and then sink, settling in interstices of substrate comprised of gravel or cobble. No nest is built and no care is given to the young (Scott and Crossman 1973).

Males typically precede females to the spawning grounds by three to four days (Scott and Crossman 1973; Morrow 1980) although in the Susitna River females arrive first (Alaskan Dept. Fish and Game 1983a in Thornburgh 1986). Males spawn intermittently over a period of seven to ten days while females spawn generally within a day (Sorokin 1971).

Burbot are iteroparous ,i.e. repeat spawners. Some adults do not spawn every year (Chen 1969 in Thornburgh 1986; Alaskan Dept. Fish and Game 1983a in Thornburgh 1986). The reason for the intermittent spawning is apparently unknown. However, Pulliainen and Korhonen (1990) found that such 'rest years' are not because of insufficient nutrients for gonad development.

Fecundity is proportional to the size of the female and may vary between 45,000 to just over a million eggs (MacCrimmon and Devitt 1954; Lawler 1963; Chen 1969 in Thornburgh 1986; Sorokin 1971; Morrow 1980).

Burbot spawn in both rivers and lakes, usually under ice in shallow water from 0.3 to 3 m deep, but sometimes 18 to 20 m deep (Clemens 1951b; McPhail and Lindsey 1970; Scott and Crossman 1973). In glacial Alaskan rivers, Breeser et al. (1988) observed that most spawning takes place in the main channels between December and March, when water velocity is low and the river is generally clear. Burbot in the Susitna River spawn at the tributary mouths in regions characterized by upwelling and with low to medium (0 to 122 cm/s) water column velocities (Alaskan Dept. Fish and Game 1983a in Thornburgh 1986).

Scott and Crossman (1973) report that spawning generally occurs during a period when temperatures range between 0.6 and 1.7°C (Scott and Crossman 1973). In Lake Winnipeg, spawning coincided with the beginning of the period of minimum water temperatures, 1°C at the bottom and 0°C at surface under the ice (Hewson 1955).

As mentioned above, Sorokin (1971) noted that burbot spawn around the mouths of streams and channels where water exchange is slow and adequate to supply oxygen to the eggs, but oxygen concentrations were not reported. In Lake Winnipeg burbot spawn in regions where dissolved oxygen at the lake bottom is 8 mg/L. According to the Canadian Water Quality Guidelines (Canadian Council of Resource and Environment Ministers 1987) oxygen concentrations should be maintained at 9.5 mg/L in spawning habitats so that interstitial oxygen concentrations are maintained at or greater than 6.5 mg/L.

12.4 Mitigation and Compensation Strategies

A number of human-related disturbances influence size and production of burbot populations. These including overfishing and decreases in available spawning and rearing habitat resulting from flooding or dewatering (Thornburgh 1986). In the Vilyuysk Reservoir, USSR, for example, an increase in the burbot catch was recommended because of its popularity as a commercial fishery and because burbot consume other valuable commercial species. However, the commercial overfishing reduced the maximum age of maturity from 13 to 9 years (Kirillov 1988). Overfishing also caused a decline in the abundance of older burbot in Heming Lake, Manitoba (Lawler 1963).

Alteration of water levels with the construction of hydro-electric dams and for irrigation needs have also resulted in the decline of burbot populations. Flooding of the Kootenai River by Lake Koocanusa following the construction of the Libby Dam may have led to the decline of burbot populations (D. Skaar, Montana Fish and Wildlife, Libby, Montana, pers. comm. 1991). High water levels during winter reduce the extent of shallow regions for spawning. As well, sedimentation of spawning areas through erosion of shorelines following flooding leads to poor egg survival because of insufficient flow of oxygen around eggs. Drawdown of Lake Koocanusa may influence rearing habitat for juveniles during the spring and summer, since densities of benthic invertebrates are negatively affected by these low water levels (Chisholm et al. 1989; D. Skaar, pers. comm. 1991). In Bull Lake, Montana, the removal of water for irrigation has resulted in an approximate 50% decline in spawning and nursery habitat for burbot (E. Burgerson, pers. comm. 1991; D. Skates, Wyoming Fish and Wildlife Service, Lander, Wyoming, pers. comm. 1991). The shallow regions remaining in the lake during the spawning season contain soft, silty materials, unsuitable for spawning (E. Burgerson, pers. comm. 1991). As yet, no measures have been taken in Lake Koocanusa or Bull Lake to mitigate or compensate for the loss of burbot habitat; however, there are several potential techniques to do so. Controlling water levels within reservoirs can mitigate the impacts of dams, particularly during the spawning season. Low or falling water levels during spawning and incubation reduce spawning success and egg to fry survival by limiting the quantity of optimal spawning habitat and by dewatering the embryos or fry. Water drawdown will also reduce production of aquatic insects in shallow regions thereby reducing the food supply for juvenile burbot. A recommendation has been made to limit the drawdown of Bull Lake during winter and spring months when burbot are spawning and rearing (E. Burgerson, per. comm. 1991). However, the interests of the burbot fishery conflict with those of farmers requiring irrigation downstream of Bull Lake and this mitigation option is unpopular.

Flooding of a reservoir lowers spawning success by reducing the spawning area and covering the remaining areas with silt eroded from the shorelines. Coarse substrate in a reservoir bottom may become exposed over time through wave washing, but Erickson (1972 in Machniak 1975) found it may require five years for substrate to buildup sufficiently for spawning. The construction of artificial spawning beds could mitigate the loss of spawning habitat as a result of flooding, but this technique has yet to be used for burbot. Artificial spawning beds constructed of gravel and cobble substrate and placed at up to three meters depth in areas with water velocities of less than 122 cm/s would provide burbot with optimal spawning habitat.

Controlling the rate of discharge of water from reservoirs is another way to reduce impacts of impoundments on burbot. Insufficient flow below dams may result in limited spawning habitat, lower oxygen concentrations in spawning gravels because of low water velocity over spawning substrates, and post-spawning mortality because of elevated water temperatures and low oxygen levels. However, discharge rates must be regulated prudently since high rates from reservoirs may also increase egg and larvae mortality if currents within the reservoir move these early life stages to areas with suboptimal substrate, temperature or both. Water withdrawal from reservoirs may also remove egg, larval and juvenile stages of burbot. Mortality due to turbine entrainment is not known.

Artificial propagation of burbot has not received much attention. Both Bjorn (1940) and MacCrimmon (1959) described hatchery techniques used to rear burbot eggs, but did not report their success. Montana attempted hatchery rearing in the 1960's, but burbot larvae were apparently difficult to feed and survival was extremely low (G. Pearse, Sport Fish Division Alaska Fish and Game, Fairbanks, Alaska, pers. comm. 1991). There are presently no hatchery operations rearing burbot (D. Skates pers. comm. 1991; G. Pearse, pers. comm. 1991).

The only measure taken currently to increase burbot production is to ban or limit fishing (D. Skates, pers. comm. 1991; G. Pearse, pers. comm. 1991). Lake fertilization may be a viable alternative to increase burbot productivity, however, to date there have been no studies to evaluate the effects of lake fertilization on burbot populations. Populations of burbot in Alaskan rivers and lakes are maintained by monitoring abundance and limiting sport and subsistence fishing accordingly (G. Pearse, pers. comm. 1991). In addition, reports from anglers indicate that overfishing, possibly a result of liberal catch limits, have depressed burbot stocks and reduced the size of burbot in some of the large lakes in the Omineca sub-region. A reduction of the catch quotas may be necessary to address this problem (D. Cadden, pers. comm. 1992).

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13.0 NORTHERN PIKE

(*Esox lucius*)

13.1 Introduction

The northern pike, *Esox lucius*, occupies the shallower vegetated areas of lakes, marshes, and backwater sloughs, and to a much lesser extent, rivers. Of the family Esocidae only *E. lucius* colonize northern environments and British Columbia (Scott and Crossman 1973; Crossman 1978).

The highly specialized esocid fishes fall into a single family, and a genus with five species. Within the Esocidae, there are two closely related groups, the pikes and pickerels, which are readily distinguishable, with obvious morphological, biochemical, and genetic differences (Crossman 1978). The incomplete reproductive isolation between pike and pickerel enables both artificial and wild production of hybrids.

Over at least the northern extent of the northern pike range, a mutant form occurs irregularly. Features that distinguish the "silver pike" from ordinary northern pike are that it is always silvery blue or silvery green and lacks the yellow and white spotting characteristic of the species (Lawler 1960; Crossman 1978), and is hardier (Lawler 1964).

Despite the popularity of northern pike as a sport fish in other parts of North America it is not highly sought in British Columbia. For example, anglers in the Peace River region rate northern pike as the least desirable of the sport fish present in the drainage (Renewable Resources Consulting Services Ltd. 1979). However, there are a few very popular pike fisheries, particularly in winter (E.N. Down, Fish and Wildlife Branch, B.C. Environment, Fort St. John, pers. comm. 1992).

Management planning for northern pike in British Columbia is affected by several factors, two of which are discussed here. First, as adults, northern pike are typically voracious piscivorous predators and may prey upon more desirable sport fish species such as rainbow trout (*Oncorhynchus mykiss*), arctic grayling (*Thymallus arcticus*), or whitefish (*Prosopium* sp. and *Coregonus* sp.) (Renewable Resources Consulting Services Ltd. 1979). Secondly, they host the cestode parasite, *Triaenophorus crassus*, which causes unsightly cysts in the flesh of trout, grayling and whitefish. For these reasons, regional fisheries managers are opposed to the introduction of northern pike into drainages where they are not presently found. (D. Ableson, Fish and Wildlife Branch, B.C. Environment, Prince George, pers. comm., 1991).

13.2 Distribution

Northern pike have the broadest geographic and environmental range of the Esocidae. The species is circumpolar, with the Eurasian and North American populations considered to be a single species despite their geographic isolation (Crossman 1978). These groups have been divided into two subspecies on the basis of morphological differences (eg. body proportions, asymptotic size, etc.) and circumstantial distinctions such as the use of brackish water environment (Crossman 1978). Differences in meristic characters exist among North American populations but appear to be correlated to latitude. The populations found in Canada are thought to be the result of Pleistocene isolation in separate refuges (McPhail and Lindsey 1970).

In the United States, the species occurs from Alaska south to Texas and Nebraska east of the Rocky Mountains and west of the Appalachian Mountains. In Canada, northern pike occur from Labrador south of Ungava Bay, are absent from the Maritime Provinces, and are found throughout Quebec, Ontario, Manitoba, Saskatchewan, and Alberta. In British Columbia, they have been collected from the Yukon, Peace, Laird, and Hay River drainages (Lindsey 1957; R. Carveth, University of British Columbia Museum of Ichthyology, pers. comm. 1991) as well as the headwaters of the Alsek River (Pine Lake), and the Taku River (Taysen Lake). Northern pike in the Peace River drainage are generally absent upstream of Peace Canyon Dam. (McPhail and Lindsey 1970) There have been occasional reports of northern pike in the upper portion of the Parsnip River drainage; these may be from transplanted stock.

Figure 32 shows northern pike distribution in the Peace and Liard river drainages.

13.3 Life History and Habitat Requirements

13.3.1 General

Northern pike are spring spawners with the migration to spawning areas beginning immediately after the ice melts in April to early May. Spawning generally takes place during daylight hours on vegetated floodplains of rivers, marshes, and bays of large lakes. No nest is built, and the adhesive eggs are broadcast onto submerged vegetation. Eggs usually hatch approximately two weeks after fertilization, and the post-hatch larvae remain attached to the vegetation for an additional six to ten days, surviving on yolk sac reserves. When these reserves are depleted, larvae become free swimming, remaining in the vicinity of the spawning grounds for two or three weeks feeding on zooplankton and aquatic invertebrates. During this period growth is very rapid.

Although there are some reports of extensive migrations of juveniles, northern pike generally remain sedentary where there is adequate food and cover for the remainder of their early life. Young-of-the-year eat macroinvertebrates, while older fish are typically voracious predators feeding on fish and invertebrates. As their demand for food increases with increasing body size, northern pike have been observed to move slowly along the shoreline (less than 400 m per day), occasionally moving offshore in search of prey. Mature northern pike make annual spring migrations to spawning grounds and after spawning return to shoreline habitats occupied prior to spawning migrations. Northern pike life history is illustrated in Figure 33.

An extensive review of the limnological characteristics of lakes containing northern pike evealed that they are most often found in lakes with mean depths of 2 to 6 m, littoral areas ess than 6.0 m deep) which are 60% to 80% of the total surface area of the lake, secchi disc transparencies of 2 to 4 m, and total dissolved solids of 50 mg/L to 125 mg/L (Johnson et al 1977).

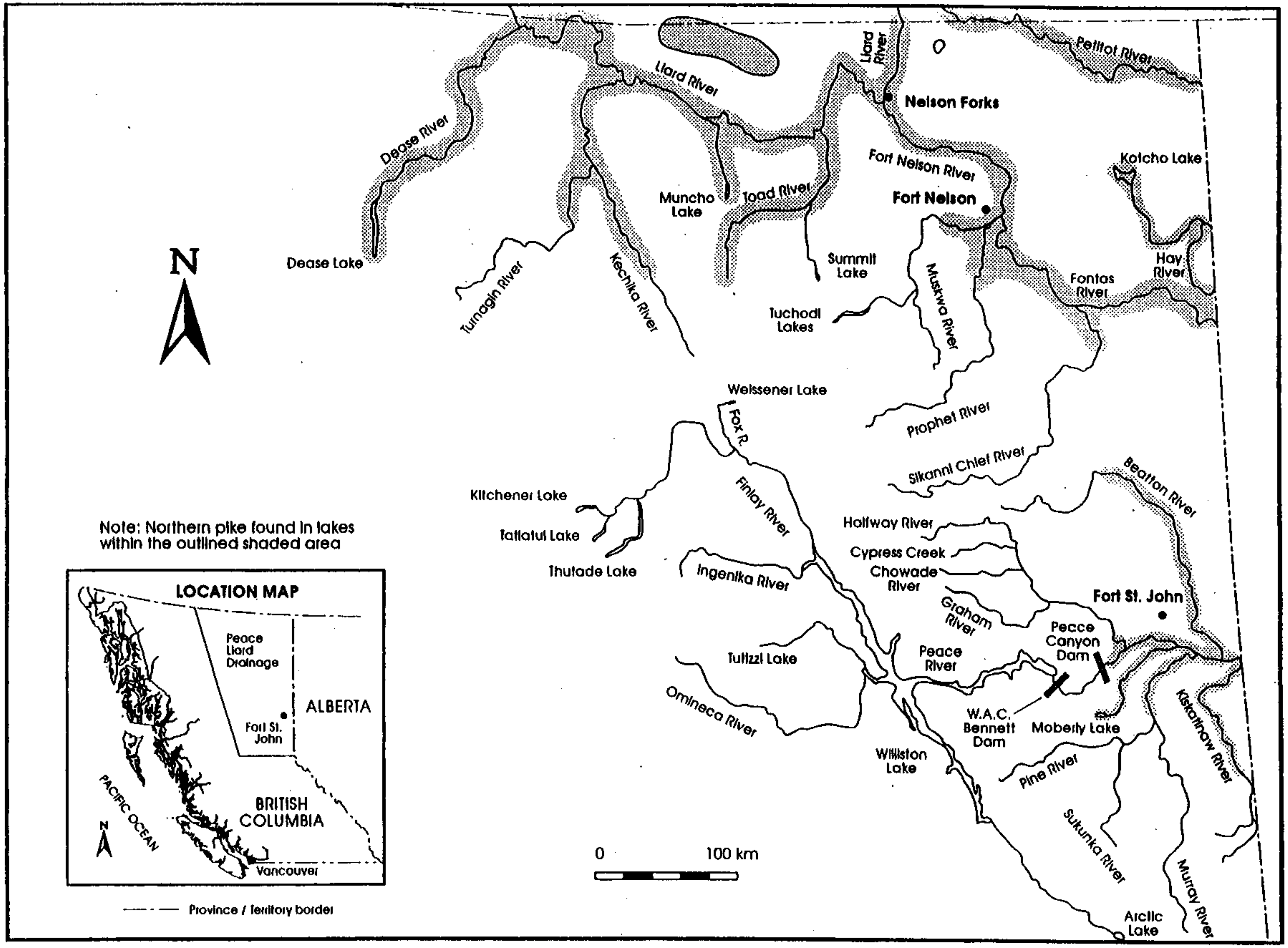

Figure 32: Northern Pike Distribution in the Peace and Liard Drainages, British Columbia

Observed habitat use and selected biological characteristics of northern pike are presented in Table 18 and discussed throughout the text.

13.3.2 Eggs and Incubation

Of the physical and chemical factors that might influence northern pike production, water temperature and dissolved oxygen appear most significant. Temperature affects the rate of egg development and survival to hatch. Swift (1965) found that no eggs hatched at incubation temperatures above 20.0°C. However, Hokanson et al. (1973) found that embryos hatch over a range of 3.0°C to 24.2°C, with a high proportion of deformities occurring at the extremes of this range. Greater than 80% hatched normally between 6.4°C to 17.7°C, with 6.4°C providing a maximum 86% normal hatch. Eggs usually hatch in 12 to 14 days, depending on incubation temperature (Swift 1965), and most investigators consider that 210 to 270 degree days above 0°C are required to bring embryos to the hatch point. This incubation can be accelerated to four to five days when the temperature is between 17.8°C and 20.0°C (Scott and Crossman 1973).

Significant mortality of northern pike embryos may be caused by rapid changes in water temperature (Swift 1965). Hassler (1970) investigated the effects of sudden temperature changes and siltation on the survival of northern pike embryos and found that egg mortality approached 75% when temperatures dropped from 10.0°C to 7.5°C, and increased to 100% when the temperature was maintained for a prolonged period at 5°C. Embryos appeared to tolerate diurnal fluctuations of 4°C. Silt deposition (on eggs) of 1.0 mm per day during the first five days of incubation caused 97% mortality. After five days, silt deposition did not significantly affect survival. When silt deposition was accompanied by temperature drops greater than 4°C, mortality was 100%. Temperature and siltation, along with changing water levels during the spawning and incubation period in spring, are hypothesized to regulate northern pike year class strength (Johnson 1957).

FIGURE 33 - NORTHERN PIKE LIFE HISTORY

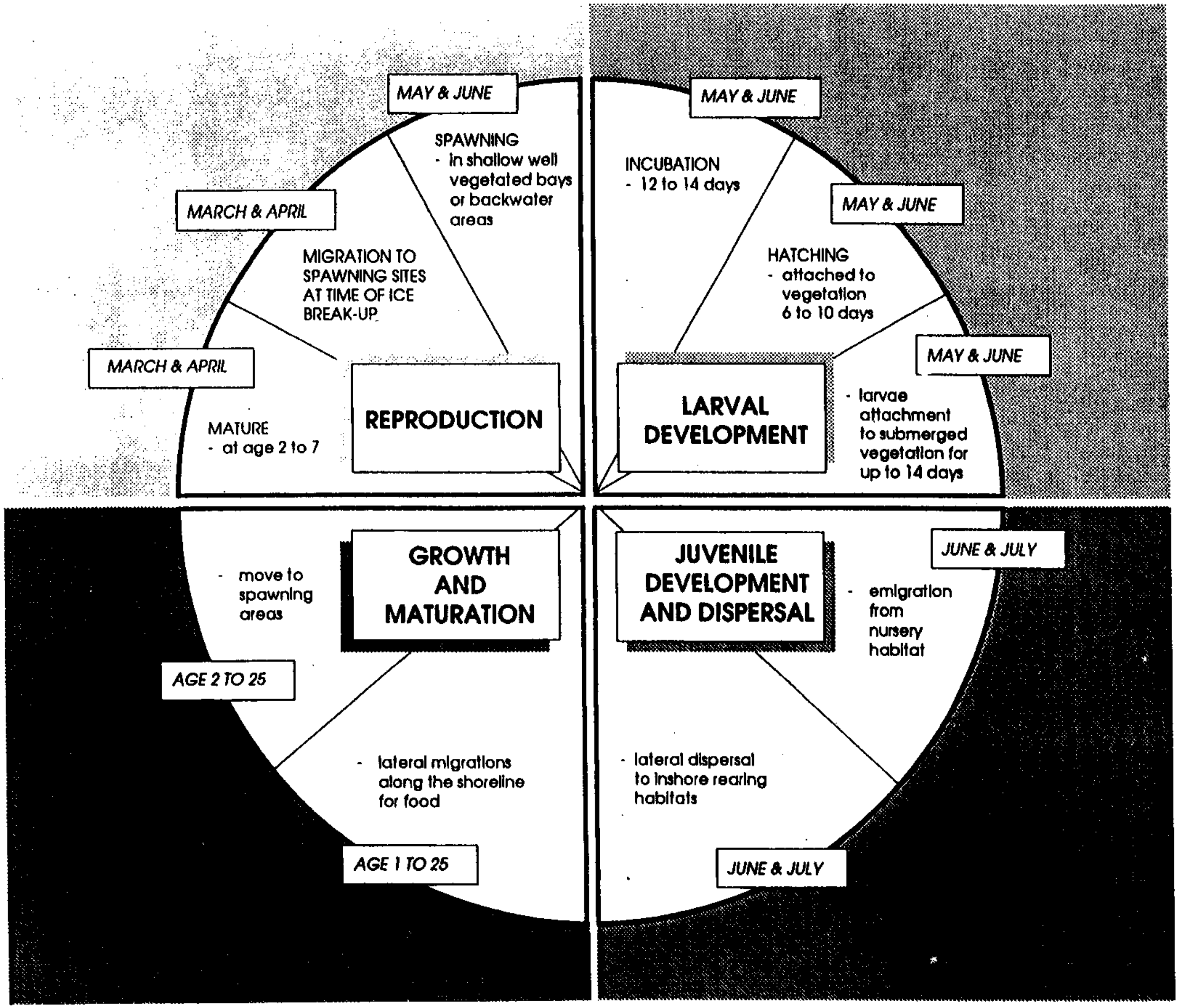

Table 18. Observed habitat use and selected biological characteristics by life stage for northern pike (for sources refer to text, NA- data are not available)

Eggs

Temperature tolerance range	(high % deformities at extremes) 3.0°C to 24.2°C
Optimum incubation temperature	6.4°C
Recommended oxygen concentration	> 3.0 mg/L
Lower lethal oxygen concentration	1.8 mg/L
Range of incubation time	4 to 14 days
Incubation time at optimum temperature	12 to 14 days
Substrate	aquatic vegetation
Lower lethal pH	NA
Recommended current velocity	none

Juveniles

Temperature tolerance range	5.8°C to 33.0°C
Optimum temperature for growth	26.0°C
Recommended oxygen concentration	> 3.0 mg/L
Lower lethal oxygen concentration	0.1 mg/L at low temperature
Habitat type preference	marshes and sloughs
Depth preference	< 2.0 m
Preferred current velocity	none
Substrate	mud and silt (coincident with vegetation)
Cover	aquatic vegetation
Lower lethal pH	approximately 5.0
Observed typical turbidity	50 - 125 mg/L
Primary food category	fish
Secondary food taxa	invertebrates

Adults

Temperature tolerance range	0°C to 29.4°C
Optimum temperature for growth	19.0°C to 21.0°C
Recommended oxygen concentration	> 5.63 mg/L
Lower lethal oxygen concentration	0.04 mg/L
Habitat type preference	shallow portions of lakes, rivers, and backwater sloughs
Depth preference	shallow
Preferred current velocity	none
Substrate	mud and silt (coincident with vegetation)
Cover	aquatic vegetation
Observed typical turbidity	50 - 125 mg/L
Primary food type	fish
Secondary food type	invertebrates, reptiles and mammals
Form of reproduction	iteroparous
Nest construction	infrequently
Spawning habitat type	marshes and sloughs, sometimes rivers and large bays
Preferred spawning temperature	7.2°C to 11.7°C
Preferred spawning depth	< 25 cm
Preferred spawning substrate	Dense, submerged vegetation
Preferred spawning current velocity	none
Range of first age-at-maturity	males - age 2 to 6 females - age 3 to 7
Average fecundity	32,000 eggs/female

Chemical parameters also affect the growth and survival of eggs and larvae. For example, oxygen conditions have a significant influence on the survival, rate of development, and number of deformities in eggs and larvae. Gulidov (1969) found that the lower threshold dissolved oxygen concentration for eggs and larvae was 1.8 mg/L while the upper was approximately 40 mg/L. He found that under conditions of low oxygen (3.4 mg/L) the rate of development was accelerated over conditions where oxygen concentration was at or above air saturation levels. Siefert et al. (1973) investigated the effect of intermediate oxygen concentrations on the survival and development of embryos and larvae. They showed that northern pike can survive through hatching at oxygen saturations as low as 33% (approximately 3 mg/L at 6°C) provided that the other environmental conditions are favourable, but survival is not ensured once feeding is initiated.

Franklin and Smith (1963) observed that elevated iron concentrations could cause mortality of northern pike embryos and larvae. Smith and Oseid (1970) found exposure of eggs to hydrogen sulfide produces more deformities than exposure to lower oxygen concentrations. Adelman and Smith (1970) stated that the maximum possible safe level of hydrogen sulfide is between 0.018 and 0.040 mg/L for eggs and 0.004 to 0.006 mg/L for fry.

Immediately after hatching the larvae attach themselves to submerged vegetation with an adhesive organ (Frost and Kipling 1967) and the larvae hang vertically on the vegetation for approximately ten days until the yolk sac is absorbed and the swim bladder is filled.

Emergent fry begin feeding within 10 days of hatching and are 10 to 12 mm long (Franklin and Smith 1963). Food availability is critical to survival during this initial post-hatch period (Hassler 1970). The initial diet of zooplankton broadens as the fish grow and the young fish are increasingly able to handle larger, more mobile prey items (Lawler 1965).

13.3.3 Rearing, Food and Growth

After becoming free swimming, northern pike remain in the shallow spawning areas for several weeks and begin feeding in small, aggressively defended territories (Frost and Kipling

1967). During this period fry are sensitive to bright illumination and remain hidden in vegetated shoreline areas (Holland and Huston 1984).

Emigration of juveniles from the nursery habitat may occur during a short period or over a more prolonged period. Forney (1968) found that in three successive years 82%, 99%, and 37% of the fry left a marsh within 20 days after emigration started. Franklin and Smith (1963) found that fry usually attain a threshold size of 20 mm before emigrating to other parts of the lake. Light intensity can be a significant factor regulating juvenile movements, and be inhibited on overcast days (Franklin and Smith 1963; Forney 1968).

Young-of-the-year northern pike grow rapidly, eating large quantities of macroinvertebrates such as amphipods, isopods, and insect larvae, and gradually shift to a diet composed mainly of small fishes (Hunt and Carbine 1951; Holland and Huston 1984; Diana 1979). By the time the juveniles reach 50 to 60 mm, typically one or two months after hatching, they begin to consume increasing amounts of small fish, if available (Hunt and Carbine 1951; Franklin and Smith 1963; Fago 1977). Throughout the rest of their life northern pike are typically voracious predators, primarily feeding on fish and secondarily feeding on leeches, aquatic insects, crayfish, waterfowl, and even small mammals where and when available (Diana 1979; Inskip 1982). However, several small lakes in the Peace system are monoculture for pike and analysis of stomach contents shows that adults feed primarily on zooplankton. In addition, pike show cannibalistic behaviour (E.N. Down, pers. comm. 1992).

Northern pike are visual predators that are primarily active during the day (Diana 1980). Their ambush style of feeding requires cover which is usually in the form of aquatic vegetation, tree stumps or fallen logs (Inskip 1982). Cannibalism among juvenile and adult northern pike has been widely observed and appears to be more frequent in waters with few fish species and in communities with low species diversity. Hunt and Carbine (1951) found cannibalistic northern pike fry as small as 21 mm. Alt (1968) found that the diet during the early summer and early fall in several Alaskan lakes consisted primarily of northern pike. Jessup et al. (1973) noted a high incidence of cannibalism during spawning migrations in a Northwest Territory stream.

The growth rate of northern pike is highly variable among and within populations. Southern populations tend to grow faster than those in the north and attain greater maximum length, despite individual fish from northern populations being heavier and living an average of five years longer than southern individuals. (Miller and Kennedy 1948).

Doyon et al. (1988) examined the relationship between condition (the relative weight of fish of the similar total body length), latitude, temperature, and sex of 38 populations of northern pike from Europe, Asia, and North America. Their analysis indicated that:

1) females were generally 9% heavier than males of the same length,
2) body weight of fish of equal length increased approximately 5% for each 10° increase in north latitude,
3) body weight of similar sized fish increased 4% for each 10°C decrease in mean annual air temperature, and
4) European and Asia populations attained 13% greater weights for a given length than did North American populations.

Their results suggest that body condition is highest at high latitude and low temperature. This variation is most likely linked to the physiological need for energy storage where summer growing seasons are short.

Temporal variability in growth has been observed to be associated with changes in food availability (Kempinger and Carline 1978). There are also sexual differences in growth rate; it has been found that females grow faster than males (Frost and Kipling 1967; Bregazzi and Kennedy 1980).

Daily and seasonal movements of northern pike vary between individual fish and among populations from different lakes. Cook and Bergerson (1988) used ultrasonic telemetry to determine habitat use and seasonal migration patterns. Typical daily and longer term movements entailed zigzag patterns parallel to the shoreline; movements directly across the open water were rare (Diana et al. 1977; Ross and Winter 1981; Cook and Bergerson 1988).

Northern pike do not generally occupy distinct home ranges, rather they prefer vegetated shallow areas (less than 4 m) within 100 m of shore (Cook and Bergerson 1988). Although capable of swimming long distances during the day, they generally move only short distances. Cook and Bergerson (1988) reported that during summer northern pike in Eleven Mile Reservoir, Colorado moved on average 400 m between consecutive mornings. During winter the fish continued to move, but the distances travelled were much shorter than those observed in summer. Thus, movement and activity patterns are believed to be primarily dependent on the effect of water temperature on metabolism.

Macrophyte distribution, weather conditions, fish sex and time of the year also affect habitat selection (Holland and Huston 1984; Cook and Bergerson 1988). Northern pike are most active at dawn and dusk during summer and exhibit diurnal peaks in activity during winter. In addition, they are more active in early spring prior to the spawning period and less active in mid fall (Diana et al. 1979).

There is limited information regarding the habitat requirements of juveniles. Temperature and the presence of submerged vegetation appear to be the primary factors determining the quality of juvenile habitat (Hokanson et al. 1973). Growth and survival rates of juveniles depend on temperature, with poor survival of fry at temperatures below 5.8°C (Inskip 1982). The physiological optimum temperature for growth for juveniles is approximately 26°C while the upper incipient lethal water temperature was found experimentally to be 33°C (Scott 1964). The optimum temperature decreases with increasing age of the fish (Hokanson et al. 1973; Casselman 1978) and the fish move from protected bays and backwater sloughs with submerged vegetation into deeper, cooler areas of lakes. Submerged vegetation is important for juveniles as it provides refuge from predation and cannibalism.

Dissolved oxygen concentration is considered the most important habitat variable affecting overwintering survival of northern pike, including juveniles (Inskip 1982). Shallow heavily vegetated lakes and rivers with low discharges frequently develop low oxygen concentrations during winter. Although juveniles can tolerate concentrations as low as 0.1 mg/L for at least several days at low temperature, prolonged exposure will result in winter kill. Tolerance to this condition also appears to be inversely related to the size of fish (Inskip 1982). Adelman and Smith (1970) determined the effects of varied oxygen concentration on growth rate, food consumption and food conversion efficiency on juvenile northern pike. They found that growth rate is reduced by any decrease in oxygen concentration, but growth rate is not significantly inhibited by concentrations of greater than 3 to 4 mg/L.

There are no data to indicate the tolerance of juveniles to suspended solids. However, Johnson et al. (1977) found that lakes containing northern pike had concentrations of suspended solids of between 50 mg/L and 125 mg/L.

Self sustaining populations of northern pike can persist at pH levels as low as 5.0 (Harvey 1980). Below this level, substantial fry mortality has been documented, with pH 4.2 resulting in 96.5% mortality, compared to only 25.6% at pH 5.2, and 17% at pH 6.8. At the other extreme, fingerling northern pike can survival pH as high as 9.5, but it is not clear if successful reproduction can occur under these alkaline conditions (McCarraher 1962).

Consumption rates vary seasonally, with maximum daily intakes occurring in spring and early summer (Diana 1979). High rations are consumed throughout the period of maximum body growth (Diana 1979) and after spawning has occurred. Periods of high consumption are believed to counteract depleted body reserves resulting from the period before spawning when the fish are producing gonadal tissue and generally not feeding. Female rations are usually greater than male rations for fish of equivalent sizes during both summer and winter, given that large amounts of energy are required for egg production and recovery after spawning (Diana 1979). Growth continues throughout the winter even though metabolic rate and food resources are low.

The growth rate of adults is low below temperatures of 4°C, although some populations achieve as much as 35% of their annual growth in winter, when water temperatures are about 1.0°C (Diana 1979). Adults withstand temperatures near 0°C as they move into spawning areas after ice break up and this does not appear to be stressful to them as long as the cooling is gradual (Casselman 1978). The optimum temperature for adult growth is between 19.0°C and 21.0°C. As temperature increases above the optimum, growth rate decreases rapidly and ceases at temperatures of 27.5°C or greater. The upper incipient lethal temperature for adult northern pike is 29.4°C (Casselman 1978).

As was the case for juveniles the amount of submerged vegetation is an important component in the habitat suitability for adults. Rooted macropyhtes supplement planktonic production, and presumably increase production of invertebrate organisms that are consumed by northern pike. Vegetation also provides cover for the ambush type predation typical of adults. Complete vegetative cover, however, is considered to be suboptimal as pike are usually associated with the vegetation-open water interface. Furthermore, decomposing vegetation can affect water quality by depleting dissolved oxygen during winter. Optimal habitat should therefore contain extensive submerged aquatic macrophyte interspersed with open water (Inskip 1982).

Adult northern pike are extremely tolerant of low oxygen concentrations and in shallow lakes can survive in minimum oxygen concentrations of 0.3 mg/L for extended periods of time (2% air saturation) (Cooper and Washburn 1949; Casselman 1978). The incipient minimum lethal oxygen concentration is dependent on temperature, but northern pike have been captured alive in oxygen concentrations of 0.04 mg/L (0.3% air saturation). Adults are able to detect low oxygen conditions in winter and will avoid those areas if possible (Casselman 1978).

Davis (1975) provided guidelines for dissolved oxygen concentrations of mixed populations that included salmonid species. A minimum oxygen concentration of 3.98 mg/L was suggested for short durations with the optimum concentration being above 5.63 mg/L. A rough guideline for suspended sediment concentration used by Canadian Council of Resource and Environment Ministers (CCREM) (1987) that will not provide substantial risk to aquatic organisms is <10 mg/L.

13.3.4 Maturity, Adult Migration, and Spawning

The age at which northern pike become sexually mature depends on their growth rate. Male northern pike are typically 34 to 42 cm and females 40 to 48 cm when they first become sexually mature (Frost and Kipling 1967; Priegel and Krohn 1975). Due to variable growth rates throughout their range, the age-at-maturity varies among different populations. In southern Canada, males mature at age 2 or 3 and females mature at age 3 or 4 (Scott and Crossman 1973). Miller and Kennedy (1948) found that males matured at age 5 or 6 and females at 6 or 7 in Great Bear Lake in the Northwest Territories, and this is typical for northern populations (Crossman 1978). In extreme cases, maturity can occur after the first year of life in warm productive reservoirs in Kansas (Schryer et al. 1971), Missouri (Vasey 1974) and Texas (Crabtree 1969).

Generally, northern pike spawn in spring. However, some northern populations spawn in early summer. At Kotcho Lake in northeastern British Columbia, McPhail and Lindsey (1970) reported that ripe males were captured in early June. However, as some males continue to spermiate ("run") after spawning is complete, evidence of ripeness in males is not by itself proof of current spawning (E.N. Down, pers. comm. 1992).

Spawning migrations usually are initiated when there is sufficient clearance between inshore ice and the bottom to provide access to spawning grounds (Carbine 1942; Clark 1950: Franklin and Smith 1963; Machniak 1975). Frost and Kipling (1967) showed that northern pike repeatedly returned to the same site each year to spawn, however, Franklin and Smith (1963) found no homing tendency for particular spawning grounds. Thus, in some populations homing to particular spawning grounds occurs and in others it does not (Machniak 1975). The spawning migration period lasts approximately 10 to 24 days with the greatest movement of fish occurring during darkness (Johnson 1957; Carbine 1942; Franklin and Smith 1963).

The ratio of males and females on the spawning grounds has been reported to range from one male per female to three per female (Clark 1950; Franklin and Smith 1963; Diana 1979).

This ratio varies between the early and later parts of the run where males and females, respectively, may predominate. During the spawning periods groups of spawning fish move slowly along the shoreline with females and males exuding gametes simultaneously. The spawning act occurs frequently during the day and individual fish will carry out this behaviour for up to three days.

Northern pike spawn during daylight hours (Clark 1950; Franklin and Smith 1963; Fabricius and Gustafson 1958; Scott and Crossman 1973). The duration of the spawning period may range from a few days to a month or more (Machniak 1975), but the exact period of spawning is difficult to ascertain because the adults tend to remain in the vicinity of spawning locations for a varying length of time after the eggs have been deposited. Franklin and Smith (1963) found that some adults remain in the vicinity of the spawning grounds for a period of 71 to 108 days, although they do not exhibit parental care of eggs or larvae.

The eggs are deposited onto flooded grasslands or aquatic vegetation where available in the inshore areas of lakes. The preferred spawning substrate for the northern pike is a dense mat of short vegetation (Fabricius and Gustafson 1958) in a shallow wind sheltered area. The type of vegetation does not appear to be critical (Forney 1968) although grasses and sedges appear to be preferred (McCarraher and Thomas 1972) and submerged species are generally preferred over floating varieties. The type of bottom over which spawning occurs varies widely, but a soft, silt-filled rubble with decaying vegetation is common (Machniak 1975). Observations indicate that this bottom type is not favourable for egg survival but rather is coincident with the type of habitats with vegetation suitable for spawning substrate. The close association of larval pike with vegetative cover provides survival advantage (Frost and Kipling 1967) by keeping larvae removed from the oxygen poor and hydrogen sulfide rich sediments typical of pike spawning grounds and for providing cover from potential predators. Inskip (1982) stated that eggs falling to the bottom are unlikely to survive because of anoxic conditions in the organic rich sediments.

There is a wide range of reported fecundities for northern pike. Egg numbers increase with the size of the female and the relative fecundity has been estimated to be 19,800 eggs per kg of female, with approximately 32,000 eggs per female being the average (Scott and Crossman 1973). Fecundities as high as 595,000 have been reported. Egg diameter ranges from 2.3 mm to 3.4 mm (Carbine 1942; Scott and Crossman 1973; Machniak 1975).

Most northern pike tend to spawn in water less than 0.25 m (Brynildson 1958), but spawning has been observed in depths ranging from 5 to 700 cm (Machniak 1975). Flowing water is not a requirement for spawning sites. Observed spawning temperatures range from 1.0°C to 20°C (Machniak 1975), but Scott and Crossman (1973) cite 7.2°C to 11.7°C as the range of preferred temperatures. The pH of spawning waters has been observed to be between 6.8 and 8.2 (Brynildson 1958).

In general, northern populations attain maturity later and live longer than southern populations (Miller and Kennedy 1948). Individuals 25 years old have been recorded and ten year old pike are common in northern Canada and Alaska (Miller and Kennedy 1948; Alt 1968). In southern extremes of the range the population is generally composed of age four fish and younger (Schryer et al. 1971).

13.4 Mitigation and Compensation Strategies

Many factors influence the production of northern pike, but the availability of suitable spawning habitat and high mortality of egg to juvenile stages appear to be the most critical. Survival of young in spawning marshes is generally low, with mortality of greater than 80% of the juveniles between egg deposition and fry emigration (Carbine 1942; Franklin and Smith 1963; Forney 1968; Holland and Huston 1984). Thus, mitigation and enhancement efforts should protect northern pike spawning and nursery marsh areas. Compensatory actions should consider the creation of artificial spawning and rearing marshes.

Creation of impoundments as a result of hydroelectric, water control or irrigation projects has considerably improved the spawning habitats of northern pike by the inundation of vegetated lands (Machniak 1975). However, once northern pike are established in the reservoir, water level fluctuations affect production. The year class strength has been correlated to spring water levels (Johnson 1957; Franklin and Smith 1963; Hassler 1970; Machniak 1975; Inskip 1982). Reducing water levels and stream flows will affect the amount of spawning habitat, usually because of the loss of suitable substrate. Decreased water levels will likely reduce the frequency and quantity of vegetation flooded and deposit silt on the shoreline. However, no studies are available that document this impact. Reduced stream flows may also impede access to the spawning areas and retard the rate that juveniles return to the reservoir or river.

Without institution of proper mitigation and enhancement programs, population abundance will decline as a result of any development that affects spawning and nursery habitats of northern pike. Such programs could include the construction of impoundments for spawning (McCarraher 1957), flooding low lying areas adjacent to lakes in order to create spawning habitat (Fago 1977), establishing suitable water supplies (Franklin and Smith 1963), seeding newly expose shorelines, and protecting existing vegetated areas (e.g. exclusion of cattle from the riparian area) (Nelson 1978). Fall and winter trapping of northern pike from shallow lakes and sloughs at risk of winter kill from oxygen depletion has been used to ensure survival of local populations. The fish, mainly young of the year, are captured in large numbers and planted in lakes with underutilized suitable habitat (Maloney and Schupp 1977).

Production of northern pike in hatcheries and pond culture has been used extensively to supplement declining stocks in Canada and the United States (Graff 1978) and is a potential method to compensate for population declines due to habitat loss. Small ponds may be a more cost effective method of produce fingerlings for stocking programs; McCarraher (1957) and Howard and Thomas (1970) describe techniques that utilize small drainable ponds to produce juveniles for stocking. These techniques should be inexpensive and result in rearing costs, stocking rate, and survival that make the enhancement efforts more economical. Furthermore, stocked fish should survive in sufficient numbers for anglers to have a reasonable chance of catching them, grow large enough to be attractive catches, and be self propagating so that a management plan can be developed to protect the stock (Flickinger and Clark 1978).

Since the 1950s transplant from the Peace River to Charlie Lake, there have been no efforts to enhance northern pike populations in British Columbia. (E.N. Down, pers. comm. 1992). Given sufficient brood stock, introduction may be a viable method for mitigating or compensating for the effects of resource development on the species, but the needs of the sport fishery and the potential impacts on other sport fish already present must first be considered. As mentioned in the introduction, concern over the potential introduction of the cestode parasite *Triaenophorus crassus* for which the northern pike is the final (or primary) host, has led the British Columbia Ministry of Environment and Canada's Department of Fisheries and Oceans to reject any proposals to introduce northern pike into systems in British Columbia where they do not occur naturally. However, one unauthorized stocking to Summit Lake, in the Fraser River drainage near Prince George, has occurred (D. Ableson, pers. comm. 1991). This parasite attains sexual maturity in the gut of northern pike, and produces eggs that are consumed by copepods (*Cyclops* sp.) where they develop into procercoid larvae. When an infected copepod is eaten by a fish, the larvae burrows into the gut wall, encysts in the musculature and develops into a plerocercoid larvae. When the infected fish is in turn consumed by the primary host (e.g. northern pike) the adult form develops and the life cycle continues.

In British Columbia habitat and sport fishery managers endeavour to preserve existing stocks. The importance of maintaining beds of emergent vegetation in the management of spawning northern pike has been demonstrated by Threinen et al. (1966). Holland and Huston (1984) showed that submerged vegetation (as opposed to floating vegetation) is also critical to young northern pike in backwater nursery areas. Critical nursery habitat can also be improved by increasing the open-water vegetation edge with channels through the beds (Holland and Huston 1984).

Protection and restoration of backwater spawning and rearing areas are habitat management options for preserving populations of northern pike, which have the unique capability of utilizing these habitats whereas many species cannot. Where suitable habitat does not exist, it may be possible to create artificial habitats for spawning and rearing. Favourable characteristics of artificial northern pike spawning and nursery habitats include that they can be completely drained into the lake, closeness to a water supply, and predominant sedge or grass vegetation (Fago 1977). An inlet should be constructed to regulate water levels and screen any predator species that may seek access to the pond. Holland and Huston (1984) suggest that methods used to mitigate a rapid loss of backwaters, or to revitalize backwater habitats, must protect the integrity of submerged vegetation near spawning beds and protect nursery areas. Although juveniles are closely associated with vegetation through much of the year, movement out of backwater areas occurs later in the summer when oxygen levels approach lower thresholds for survival. This suggests that habitat improvement can be achieved by maintaining flow through these areas.

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14.0 WHITE STURGEON

(Acipenser transmontanus)

14.1 Introduction

The white sturgeon, *Acipenser transmontanus*, (Richardson 1836) is a member of the family Acipenseridae, anadromous and freshwater fishes of the northern hemisphere known from the Upper Cretaceous era. They are Canada's largest freshwater fish, and an important sport and commercial fish. The largest specimen caught in the Fraser River weighed 816 kg; the largest in the Columbia system was from the Snake River and weighed 680 kg (Anderson 1987). The white sturgeon was listed as an endangered species in Idaho (Miller 1974) and as a threatened species in British Columbia in 1990 (Anon. 1990a).

14.2 Distribution

The white sturgeon is distributed along the Pacific Coast of North America from the Aleutian Islands of Alaska to Monterey, California (Scott and Crossman 1973). They are found in marine waters and in river systems which drain into the Pacific Ocean, including the Fraser, Taku and Columbia systems. Their distribution in the Fraser drainage includes lower tributaries, such as the Harrison and Lower Pitt drainages, as well as upper tributaries such as the Nechako drainage (below Kenny Dam) where the highest adult densities are found in the vicinity of the Sinkut River confluence and immediately downstream of Vanderhoof (Dixon 1986). Nechako populations are not anadromous but resident (Envirocon 1984), perhaps because the river is 800 km from the Pacific Ocean, which exceeds the maximum recorded distance of migration, 320 km (Bajkov 1951).

White sturgeon are found throughout the Columbia River system, from the international border upstream to Keenleyside Dam. Historically, sturgeon were captured in the Columbia River upstream of Keenleyside Dam between Arrowhead (on Upper Arrow

Lake) and Mica Dam, with the last authenticated capture occurring in 1970. However, rumours of anglers hooking sturgeon in recent years are common (K. Dobert, Revelstoke Fish and Game Club, pers. comm. 1990). The free-flowing section of the Columbia River between Revelstoke Dam and the north end of Upper Arrow Lake varies in length between 5 and 36 km, depending on the height of the Arrow Lakes Reservoir, and may provide adequate habitat for sturgeon. Sturgeon are also found in the Kootenay River between Castlegar and Kootenay Lake, and upstream from Kootenay Lake to the international border. Figure 34 shows white sturgeon distribution in the Columbia drainage; they are not found in the Peace or Liard river drainages. (Scott and Crossman 1973).

14.3 Life History and Habitat Requirements

14.3.1 General

White sturgeon are predominantly freshwater fish of large rivers preferring deep, low velocity areas with fine substrate. Individuals can also be found in marine environments but the species is considered semi-anadromous because the majority of individuals remain in fresh water even when ocean access is available (Haynes and Gray 1981; McEnroe and Cech 1985).

Adult sturgeon typically spawn from April to July in rapidly flowing areas of stream and rivers with bedrock, boulder, cobble, or gravel substrate. Most eggs are deposited on the substrate, however some drift downstream immediately after spawning. Eggs are brown, sticky and demersal and adhere to the bottom after they are laid (Scott and Crossman 1973). Larval development (incubation, hatching, and metamorphosis) is temperature dependant and occurs over one or two months, after which fry disperse.

Sturgeon distribution within drainages is a function of body size, sexual maturity, proximity to productive feeding areas, season, time of day, and water temperature as well

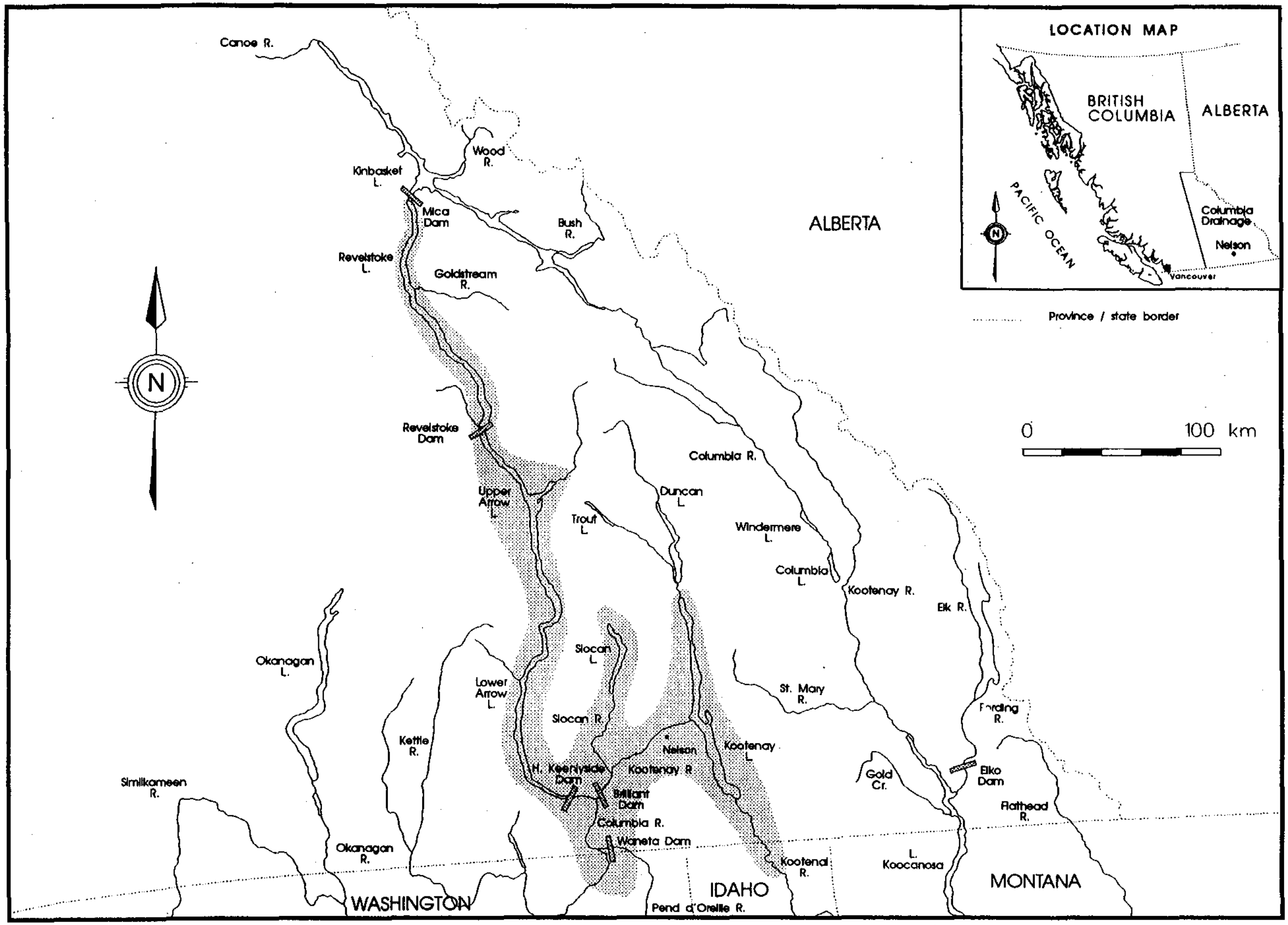

Figure 34: White Sturgeon Distribution in the Columbia Drainage, British Columbia

as the presence or absence of migratory blockages and lakes. Sturgeon are bottom feeders, as indicated by morphological adaptations that include ventral barbels, and a ventral, protrusible, sucker-like mouth. The digestive system structure indicates they are carnivores (Buddington and Christofferson 1985). Juveniles rear in deep areas of rivers on the benthos, feeding on invertebrates and fish. Fish prey typically become a more significant part of the diet as white sturgeon grow. As they grow, sturgeon enter the commercial and sport fisheries and the majority of data available regarding distribution, size and age are obtained from these sources. They become sexually mature after ten or more years. White sturgeon life history is shown in Figure 35. Observed habitat use and selected biological characteristics of white sturgeon are presented in Table 19 and discussed throughout the text.

14.3.2 Eggs and Incubation

The eggs are adhesive and attach to any substrate they contact (Brannon et al. 1985) which in the wild promotes retention in areas of high water velocity. In the hatchery, however, eggs tend to aggregate, which causes reduced oxygen supply and mortality, which in turn causes fungal growth and further mortality.

White sturgeon in California's Sacramento River have the greatest incubation survival at temperatures of 14 to 17°C, but eggs die at temperatures of 20°C and above (Wang et al. 1985). Temperatures between 18 and 20°C cause mortality during the most sensitive, early development stages. Temperatures from 10 to 13°C do not affect survival (Wang et al. 1985). Incubation time is inversely related to temperature and developmental time is greatly extended at temperatures below the optimum (Wang et al.1985). For example, embryos emerge 230 to 311 hours (9.5 to 13 days) post-fertilization at 11°C and 112 to 131 hours (4.6 to 5.5 days) post-fertilization at 17°C. In the wild, low water temperatures may increase mortality by extending the duration of the egg and larval stages, which are probably more prone to predation because of their small size. Recommended oxygen concentration during incubation is 5.5 mg/L or greater (Davis 1975).

FIGURE 35 - WHITE STURGEON LIFE HISTORY

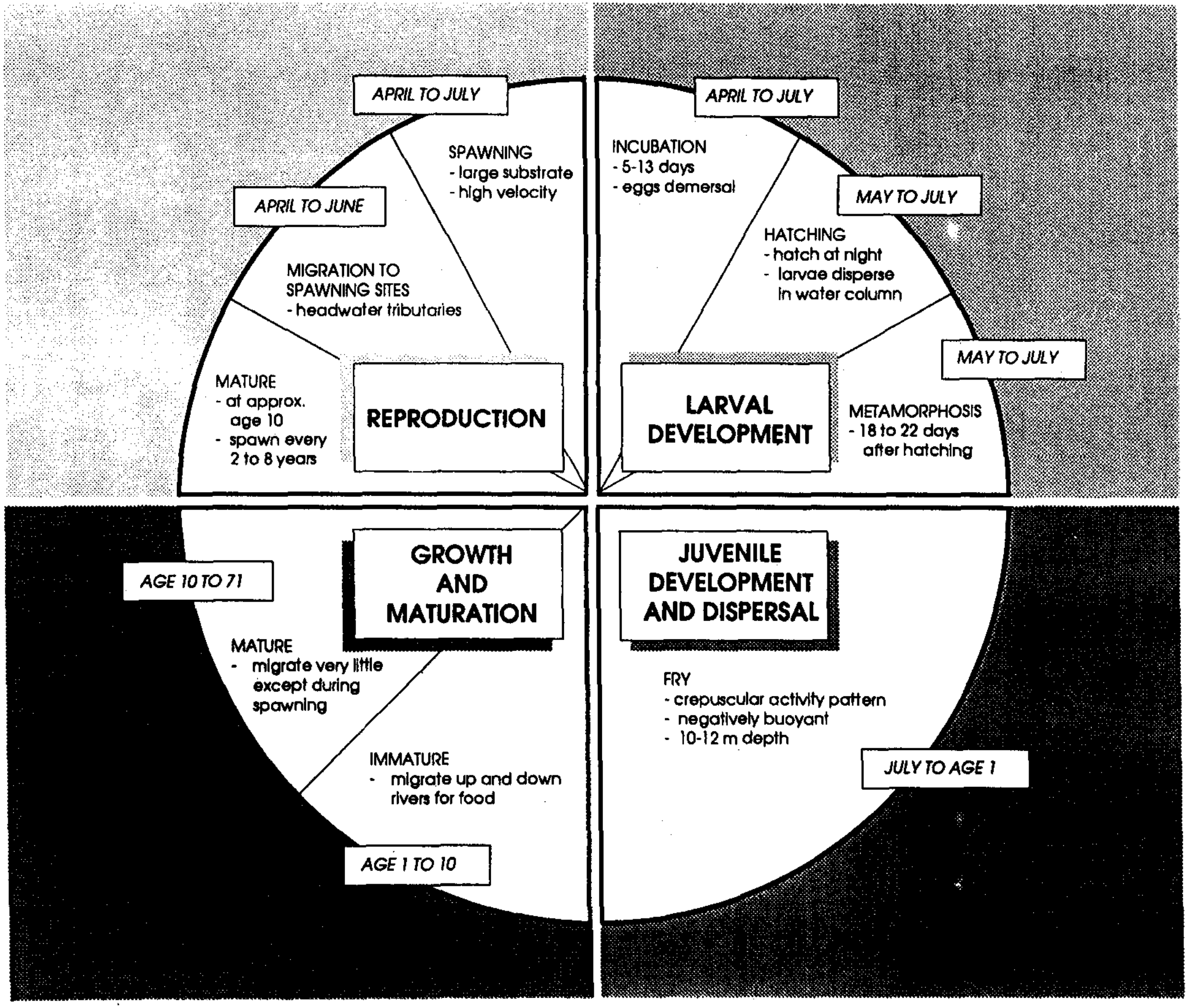

Table 19. Observed habitat use and selected biological characteristics by life stage for white sturgeon (for sources refer to text, NA- data are not available).

Eggs

Temperature tolerance range	NA to 20°C
Optimum incubation temperature	14 to 17°C
Recommended oxygen concentration	> 5.5 mg/l
Lower lethal oxygen concentration	NA
Habitat type	boulder/cobble/gravel substrate
Depth preference	3 to 21.3 m
Preferred current velocity	1.2 to 2.8 m/s
Substrate	boulder/cobble/gravel
Cover	substrate interstices
Range of incubation time	5 to 13 days
Incubation time at optimum temperature	approximately 8 days
Lower lethal pH	NA
Observed current velocity (for spawning in Columbia R)	1.2 to 2.8 m/s

Larvae

Temperature tolerance range	NA
Optimum temperature for growth	NA
Recommended oxygen concentration	9.5 mg/l
Lower lethal oxygen concentration	<5 mg/l
Habitat type preference	pools
Optimal depth	4.3 to 20.4 m
Preferred current velocity	1.1 to 2.3 m/s
Substrate	sand
Cover	gravel, cobble, plants, detritus
Observed turbidity tolerance range	<6.5 NTU
Primary food type	none
Secondary food type	none

Fry /Juveniles

Temperature tolerance range	NA
Optimum temperature for growth	NA
Recommended oxygen concentration	7.5
Lower lethal oxygen concentration	<5 mg/l
Habitat type preference	pools in large rivers
Observed depth preference in one study	10 to 11 m
Preferred current velocity	NA
Cover	debris and darkness
Turbidity tolerance	NA
Primary food type	benthic crustaceans
Secondary food type	benthic insects

Table 19 contd: Summary of general habitat requirements by life stage for white sturgeon (for sources refer to text, NA- Data not available).

Adults

Temperature tolerance range	0°C to 25°C
Optimum temperature for growth	NA
Recommended oxygen concentration	NA
Lower lethal oxygen concentration	NA
Habitat type preference	pools in large rivers
Depth preference	13 m (range 5 to 54 m)
Preferred current velocity	0.19 m/s
Substrate	varies
Cover	depth and darkness
Turbidity tolerance	NA
Primary food type	fish
Secondary food type	benthic invertebrates
Form of reproduction	iteroparous
Nest construction	no
Spawning habitat type	rapids and canyons in large rivers
Preferred spawning temperature	14°C
Preferred spawning depth	13 m
Preferred spawning substrate	bedrock/boulder/cobble
Preferred spawning current velocity	0.9 to 1.6 m/s
Range of first age-at-maturity	males age 11 to 22 years females age 11 to 34 years
Range of fecundity	approximately 5900 to 7000 eggs per kg

The incubation period of white sturgeon larvae ranges from five to 25 days (mean = 12.4 days) on the Sacramento River (Kohlhorst 1976). The yolk is consumed within 12 days (Conte et al. 1988), and sturgeon larvae can be free swimming within 18 days of spawning. Newly hatched larvae are 10 to 11 mm long (Monaco et al. 1981) and photophobic (Brannon et al. 1985).

The mechanism by which sturgeon larvae disperse has not been documented in the field. However, laboratory investigations show that sturgeon larvae move up into the water column immediately after hatching, behaviour which could facilitate their distribution in the wild (Brannon et al. 1985). This mechanism is used by Siberian sturgeon (*A. baeri*) larvae, which, although primarily benthic in habit, move downstream by moving up into the water column, catching the current, and then descending (Votinov and Kas'yanov 1978). In experimental aquaria, sturgeon larvae are photophobic and congregate under rocks, between pieces of gravel, among plants, and beneath detritus.

The transport of newly hatched larvae in the Sacramento River is greatest during years of high run-off (Stevens and Miller 1970; Kohlhorst 1976). As a result, in years of low flow the river is more important to rearing juvenile sturgeon than the delta and estuary areas than in years of high flow. Sturgeon larvae compensate for variation in flow and control dispersion by remaining in the water column longer when flow is low (Brannon et al. 1985).

Young larvae are sensitive to temperature changes. Brannon et al. (1985) found that two-day old sturgeon larvae left the substrate and swam freely when temperature was increased from 16.5 to 21.9°C. In contrast, when the temperature was decreased from 16.5 to 11.7°C, the larvae were less active. This effect of temperature on behaviour is time-limited as the effect was not evident in larvae 12 days old.

The larvae return to the substrate where they congregate under cover (Brannon et al. 1984) and remain inactive until 14 days old, when they resume activity during darkness. Daytime activity is first observed at 18 days, at which time the yolk sac has been absorbed and the photophobic response has diminished. The increased activity from 14 days onward coincides with the initiation of feeding as larvae begin feeding 9 to 11 days after hatching in water temperatures of 16 to 17°C (Monaco et al. 1981). By the onset of external feeding fry are 17 to 20 mm long (Monaco et al. 1981). After day 13, sturgeon movements are related to the presence of food. In the Columbia River downstream of Bonneville Dam, sturgeon larvae are found in mean water column velocities of 1.1 to 2.3 m/s, water velocities at substrate (0.6 m above the substrate) of 0.8 to 1.6 m/s, depths of 4.3 to 20.4 m, and bottom water turbidities of 3.4 to 6.5 nephelometric turbidity units (NTU). Between 18 and 22 days after hatching, sturgeon metamorphose; the rostrum elongates, the ventral portion of the body flattens and rows of scutes appear on the dorsal, lateral, and ventral aspects of the body (Monaco et al. 1981). Table 20 summarizes behavioral characteristics of white sturgeon early life history.

Table 20. Major behavioral events characterizing the early life history of Columbia River white sturgeon in a 16°C environment (Brannon et al. 1985).

Days post hatch	Activity
hatch	hatch during darkness
0	yolk sac larvae enter water column
1	larvae in high velocity areas begin to settle upon substrate under cover
5	larvae in low velocity areas begin to settle upon substrate within cover
9	yolk sac almost depleted, fry move onto open substrate, feeding begins
13	yolk sac depleted, all fry on open substrate actively feeding

14.3.3 Rearing, Food and Growth

After sturgeon larvae metamorphose to fry, they resume activity and show a weak preference for sand over mud, gravel, or detritus (Brannon et al. 1985), possibly because it harbours more potential prey than other substrates. The fry exhibit territorial behaviour when holding on sand (Brannon et al. 1984). By day 55, the fry display continuous rheotactic behaviour on the substrate (Brannon et al. 1985) aided by their negative buoyancy (Gordon et al. 1982).

From the fry stage to age 2 years, sturgeon are infrequently captured and their habitat requirements are poorly understood. At this age they may hold in large substrate in high velocity areas where sampling by conventional techniques is ineffective (R. Beamesderfer, Oregon Department of Fish and Game, Corvallis, pers. comm. 1991).

Sturgeon fry avoid low oxygen levels (5 mg/l) but neither avoid nor are attracted to supersaturated water (Brannon et al. 1985). Such an avoidance reaction is sufficient to draw them from their refuges, possibly increasing mortality by predators (Brannon et al. 1985).

Acute mortality to sturgeon fry from salinity occurs between three and 12 hours at 15.4 ppt and within three hours at 35 ppt (Brannon et al. 1984). Furthermore, sturgeon larvae and fry are intolerant of salinity above 16 ppt, tolerant of 11 ppt with some mortality and avoid salinity over 10 ppt if possible during their early life history (Brannon et al. 1985). Salinity of 11 ppt or less may induce indirect mortality through predation.

As mentioned above, juvenile sturgeon rear in deep areas of rivers on the benthos; they are negatively phototactic and associate with debris accumulations at depths of 10 to 11 m, which makes them difficult to catch (B. McConnell, pers. comm., in Brannon et al. 1985).

Sturgeon move in a diel pattern in response to light intensity during the summer months, although this pattern is inconsistent (Haynes and Gray 1981). During the day they hold in deep areas with cooler water and prior to sunset they move to shallow areas, possibly to feed (Haynes and Gray 1981; Apperson and Anders 1990). They display similar crepuscular behaviour in aquaria, remaining on sand substrate during the day and swimming into the water column in the morning and evening (Brannon et al. 1984).

Juveniles locate their prey by olfaction and rheotaxis rather than by vision, hence turbidity is less likely to reduce growth than it does in some salmonid species (Brannon et al. 1985; Buddington and Christofferson 1985). As a result, they are most effective when preying on visually-oriented prey in turbid water (Miller 1978).

The amphipod *Corophium* is an important part of the diet of young sturgeon, but becomes less important as sturgeon age (Bob McConnell, pers. comm. in Brannon et al. 1985). Larger sturgeon (>48 cm) can be piscivorous and feed principally on fish (lamprey, eulachon, sculpins, three-spine stickleback), crayfish (*Pacifastacus* spp.) and chironomids. The primary diet component of sturgeon less than 15 years old in the Columbia River downstream of the Bonneville Dam is the tube-dwelling amphipod *Corphium salmonis* (McCabe et al. 1989), reflecting the importance of benthic prey to the sturgeon diet. *Corphium* are also dominant in sturgeon in their first year of life from the Old River in California, but shrimp (*Neomysis*), and midge (*Tendipedidae*) larvae are also food items for these fish (Schreiber 1962).

Sturgeon in the Fraser River are mostly piscivorous (Semakula and Larkin 1968). During May most of the diet is based on eulachon (*Thaleichthys pacificus*) with less importance on sculpins (*Cottus* spp.), sticklebacks (*Gasterosteus aculeatus*), and lampreys (family Petromyzontidae). The non-fish component of the diet is composed of invertebrates, including chironomid larvae, crayfish (*Pacifastacus* spp.), stonefly larvae, Ephemeropteran larvae, mysids, *Daphnia* sp., and freshwater copepods.

In San Pablo and Suisun Bays, the estuary of the Sacramento and San Joaquin Rivers, white sturgeon feed predominantly on benthic invertebrates including shrimp (*Crago* sp., *Palaemon* spp.), isopods (*Synidotea* sp.), amphipods, barnacles (*Balanus* sp.), and crabs (*Rhithropanopeus harrisii*, *Cancer magister*) (McKechnie and Fenner 1971). Clams are the most consistent important diet item while barnacles, crabs, and shrimp are also important components of the diet at some times of the year. Crabs make up 30% of the volume of the diet during fall and winter; although abundant, annelids are not important. Herring (*Clupea harengus pallasi*) eggs are an important part of the diet during winter and spring. Fish, including striped bass (*Morone saxatilis*), starry flounder (*Platichthys stellatus*), goby (Gobiidae) and herring, comprised approximately 10% of the diet during fall and winter. Most animals in the diet of Sacramento sturgeon live and reproduce on mudflats in estuaries (McKechnie and Fenner 1971). Occasionally salmonids, even 30 cm or larger, comprise a significant part of the diet (Merrell 1961), as evidenced in Inch Creek sturgeon which easily eat larger salmonids on a regular basis (M. Rosenau, Fish and Wildlife Branch, B.C . Environment, Surrey, pers. comm. 1992).

Stomachs from sturgeon in the Kootenai River contained mostly plants and chironomidae, with clams, fish, plecoptera, ephemeroptera, and leeches making up the rest of the diet (Partridge 1980). Plant material found in sturgeon stomachs is probably the result of feeding on insect larvae living on plant material rather than feeding on plants themselves, as plant material undergoes little visible decomposition in the sturgeon gut.

Sturgeon growth is controlled by temperature, food supply, and sex. For example, juvenile growth is faster at 15°C than at 20°C but no different between 20°C and 25°C (Cech et al. 1984). Growth pattern comparisons between the lower Columbia River, Snake River, Fraser River, and San Pablo River demonstrate that anadromous sturgeon grow at a more constant rate than those landlocked by dams (Malm 1980 cited in Galbreath 1985). However, Malm's assessment assumes that Fraser River sturgeon are anadromous, but there is no documented evidence to confirm this (McDonald et al. 1989).

In the lower Columbia River, sturgeon grow an average of 3.4 cm per year from age 3 to 12, 16.9 cm per year from age 12 to 18, and 8.1 cm per year from age 19 to 28 (Malm 1980 in Galbreath 1985). In the Sacramento River in California sturgeon larvae grow in size from 10.9 mm in March, to 11.7 mm in April, to 12.2 mm in May (Kohlhorst 1976). Sturgeon size at age in the Columbia River is presented in Table 21.

Table 21. Length at age of white sturgeon captured in the Columbia River at the Dalles reservoir (Beamesderfer 1989).

Age	Fork Length (cm)	Age	Fork Length (cm)	Age	Fork Length (cm)
1	26.9	11	88.7	21	143.9
2	36.8	12	98.9	22	180.1
3	44.4	13	101.4	23	168.4
4	52.2	14	107.4	24	166.1
5	65.5	15	114.1	25	158.0
6	69.7	16	120.9	26	183.0
7	71.8	17	128.6	27	187.0
8	90.3	18	134.5	28	170.8
9	90.3	19	141.0	29	194.8
10	84.5	20	151.8		

In the Snake River, sturgeon range in length from 48.5 to 66.5 cm at age five, from 59.5 to 82 cm at age 10, and from 60.5 to 94 cm at age 15 (Coon 1978). These sturgeon were predominantly between 7 and 12 years old, with the oldest 56 and 255.5 cm long (Coon 1978). Snake River populations grow most rapidly in the first four years of life, at a slower but constant rate from six to twelve, and then at an increasing rate (Coon 1978). Sturgeon from brood years in different decades grow at different rates, presumably as a result of differences in habitat productivity and population size. In contrast to the Snake River, growth in the Fraser River is rapid from ages 1 through 10 after which it slows (Semakula and Larkin 1968).

The growing season is shorter in the Nechako River than in the Sacramento-San Joaquin Rivers or the lower Fraser and, as a result, Nechako sturgeon grow more slowly (Kohlhorst et al. 1980; Semakula and Larkin 1968; Dixon 1986). Sturgeon in the Kootenai River grow at a rate similar to those in the Nechako River, possibly because of similar physical characteristics of the rivers such as discharge, channel width and depth, gradient, and reduced nutrient levels and productivity resulting from upstream impoundment (Dixon 1986).

Juvenile sturgeon migrate actively, possibly in search of food (Brannon et al. 1985). Coon (1978) estimated that 46% of small sturgeon(< 92 cm) in the mid-Snake River moved an average 7.1 km downstream within a single year, primarily during August and April. Sturgeon greater than 183 cm did not move long distances up or down river. Haynes et al. (1978) observed that in the mid-Columbia River, sturgeon averaging 87 cm moved downstream an average 39 km. Older juveniles moved less frequently. Individuals averaging 131 cm remain within a single pool, and mature sturgeon (average 176 cm) move upstream (Haynes et al. 1978).

Immature sturgeon (41 to 112 cm) move upstream during September, October, and November in the Columbia River from Portland and upstream where they congregate at the base of the impassable Bonneville Dam (Bajkov 1951). They then migrate downstream through the late winter, spring and summer. The migratory speed of immature sturgeon was observed to be 0.8 km/day. These migratory patterns of immature sturgeon may be for feeding purposes.

Sturgeon movements coincide with water temperatures and they remain active throughout the year in water temperatures between 2.2 to 22.2°C (Coon 1978). They are most active during early spring and summer when mean water temperature rises from 7.5 to 18.5°C and are least active during late fall and winter when temperatures are dropping (Coon 1978). Movements of sturgeon in the mid-Columbia River begin in mid-June at water temperatures of 13 to 14°C and cease in mid-October when water temperatures are 15°C (Haynes et al. 1978). Sturgeon in the Kootenai River continue to move when water temperatures drop below 13°C to 6°C.

Haynes and Gray (1981) found that photoperiod does not directly influence the timing of sturgeon migrations greater than 2 km and river flow had no influence on the distance of sturgeon migration (Haynes and Gray 1981).

Sturgeon also move between areas of flowing water in the mid-Columbia reservoir, and may prefer this habitat (Haynes et al. 1978). They congregate in deep holes during the winter and move into shallow areas during the spring (Bajkov 1951; Haynes et al. 1978); in the Kootenai River sturgeon move into deep holes in the fall and travel more widely during early summer and fall (Apperson and Anders 1990).

Juvenile sturgeon greater than age 2 years have been captured at depths of 10 to 11 m coincident with debris accumulations (Bob McConnell, pers. comm., in Brannon et al. 1985) which they may use as cover. However, in the laboratory they do not hide in debris or substrate even though they are photophobic (Brannon et al. 1985). Sturgeon have been captured over a wide variety of substrates including fines, gravel and bedrock. During winter, juvenile sturgeon live in deep pools; in the summer they live in shallower areas (Haynes et al. 1978). Shallow areas with moderate current are believed to be sturgeon feeding sites in the Nechako River (Aitken 1981).

The preference of juvenile sturgeon for fine substrate suggests they might use backwaters and sloughs. Although use of these habitats has not been confirmed among white sturgeon, Siberian sturgeon juveniles use low velocity areas of the river including side channels, oxbow lakes and inlets (Votinov and Kas'yanov 1978).

Sturgeon less than 15 years of age rear in a wide variety of habitat types, but tend to rear in deeper water. For example, downstream of the John Day Dam, juvenile sturgeon between the lengths of 265 and 831 mm have been captured at a modal depth of 17 m (Parsley et al. 1989). Downstream of the Dalles Dam, juvenile sturgeon between the lengths of 311 and 850 mm have been captured at a modal depth of 26 m (Parsley et al. 1989). Downstream of the Bonneville Dam, sturgeon between 50 and 600 mm in length are most abundant at depths greater than 18.2 m.

Decreasing oxygen saturation from 160 torr Po_2 (100% saturation) to 90 torr Po_2, (56% saturation) (Burggren and Randall 1978) reduces the aerobic metabolism of adult white sturgeon, and probably juveniles as well. When oxygen levels are reduced below ambient, sturgeon become oxygen conformers and reduce metabolism, rather than shifting to anaerobiosis as do other vertebrates (Burggren and Randall 1978). As a result, sturgeon may be able to venture into deoxygenated benthic regions of lakes, ice covered waters and stagnant regions of estuaries. However, at 15, 20 and 25°C, environmental hypoxia (90 torr Po_2, 56% saturation) reduces sturgeon growth rate (Cech et al. 1984).

White sturgeon are hyposmotic in seawater and hyperosmotic in fresh water. Their tolerance to salinity increases with body size (McEnroe and Cech 1985). Juveniles have limited ability to regulate plasma osmolality and consequently their tolerance for high salinity is poor: upper salinity tolerance is 5-10 ppt for 0.4 to 0.9 g fish, 10-15 ppt for 0.7-1.8 g fish, and 15 ppt for 4.9-50.0 g fish (McEnroe and Cech 1985). Juveniles weighing less than 56 g die when exposed to salinity of 25 ppt or greater (McEnroe and Cech 1985).

Adult sturgeon migrate between streams along the Pacific coast, as evidenced by a Columbia River fish recovered in another coastal stream in Washington (Bajkov 1951). Furthermore, sturgeon tagged in the Sacramento River estuary were recovered over 1000 km north in the Columbia River estuary (Chadwick 1959). Restriction enzyme analysis, a method of characterizing DNA molecules and thus genetic relatedness, demonstrates recent past and perhaps contemporary migrations of sturgeon females between the Columbia and Fraser Rivers (Brown et al. 1991). In the Sacramento River, sturgeon greater than 102 cm long migrate upstream from the estuary in the winter or spring and migrate back downstream during the summer (Pycha 1956); sturgeon less than 102 cm long live in the lower river and estuary year-round (Pycha 1956). Sturgeon greater than 114 cm in length migrate upstream from San Pablo Bay, California to spawn in the Sacramento River during late winter and spring (Stevens and Miller 1970). The spawning migration of white sturgeon may consist of spawning and non-spawning individuals as is found with the Atlantic sturgeon *Acipenser oxyrhynchus* (Smith 1985).

Large sturgeon exhibit considerable movement within restricted areas in the Nechako River (Envirocon 1984; Dixon 1986). The greater movement of smaller fish suggests that the Nechako population mixes with the upper Fraser River and Stuart River populations through recruitment of juveniles.

White sturgeon in the Snake River avoid areas of slack water in reservoirs and this response appears to be both innate and immediate (Coon 1978).

14.3.4 Maturity, Adult Migration and Spawning

After ten or more years sturgeon reach sexual maturity. Age at first spawning is variable; in the Fraser River males first spawn between ages 11 and 22; however, some may have spawned twice by age 17 and three times by age 22 to 33. Females reach sexual maturity later than males - between ages 11 and 34, and a few have spawned twice by age 36. After maturity, males spawn every two to five years whereas females spawn every three to eight years (Semakula and Larkin 1968).

Male sturgeon in the Columbia River mature at 12 years at a length of 122 cm whereas females mature at 15 to 20 years and a length of 168-183 cm (Galbreath 1985). Sturgeon captured in the sports fishery in the Columbia River near Castlegar during the period 1978 to 1989 ranged from 14 to 37 years of age, with corresponding weights of 8.2 to 210 kg (L. Fleck, Fish and Wildlife Branch, B.C. Environment, Nelson, pers. comm. 1991).

White sturgeon migrate upstream to spawn in the Columbia but in the Nechako River sturgeon are rumoured to spawn at the confluence of the Fraser and Nechako Rivers, indicating a downstream migration (D. Cadden, Fish and Wildlife Branch, B.C. Environment, Prince George, pers. comm. 1991).

White sturgeon spawn between April and July in the Columbia River. In 1988, they spawned from April 19 to June 20 downstream of the Bonneville Dam, based on the back-calculation of spawning dates from the date of capture of eggs and larvae (LaVoy et al. 1989). Physical factors influenced spawning; sturgeon spawned ten days after the water temperature exceeded 10°C and nine days into a period of increasing flow (LaVoy et al.

1989). Spawning was not continuous but occurred in distinct episodes; for example, on May 30 to 31, June 8, and July 11 to 12 in the Columbia River downstream of the John Day Dam during 1988 (LaVoy et al. 1989). Spawning activity was observed during the day between 1200 and 1345 h in the Columbia River downstream of the Dalles Dam (Parsley et al. 1989), however, downstream of the Bonneville Dam the majority of eggs were captured between 1800 and 0500 h, suggesting that white sturgeon spawn in darkness (LaVoy et al. 1989). Although not directly observed, in one case egg releases coincide with breaching and rolling of 20 or more sturgeon at the surface (Parsley et al. 1989).

The distribution of sturgeon eggs in the wild reflects the location of spawning and the effects of dispersion by the river. In the Columbia River near the John Day and Dalles Dams, sturgeon spawn in tailrace areas of highest water velocity (Parsley et al. 1989). Water velocity may be a cue for spawning and may also influence survival of yolk-sac larvae by determining oxygen supply to the eggs or by preventing access by predators (Parsley et al. 1989). In the Columbia River downstream of Bonneville Dam, sturgeon eggs are found at mean water column velocities from 1.2 to 2.8 m/s, water velocities at substrate (0.6 m above the substrate) of 0.8 to 1.6 m/s, depths of 3 to 21.3 m, and bottom water turbidities of 2.6 to 6.5 NTU (McCabe et al. 1989).

During spawning the distribution of sturgeon changes. Spawning sites in the Columbia River near the John Day Dam, identified through the recovery of eggs after spawning, are characterized by mean depths of 12 to 14 m, mean water column velocities ranging from 0.88 to 1.61 m/s, and water velocities at the substrate of 0.52 to 0.85 m/s (Parsley et al. 1989). Reproductively mature sturgeon in the Kootenai River occupy habitats with a mean focal point velocity of 0.19 m/s (range, 0.031 to 0.56 m/s), and a mean depth of 14 m (range, 4 to 54 m) (Apperson and Anders 1990).

Sturgeon spawn in the Sacramento River from mid-February to late May with 93% of the activity in March and April (Kohlhorst 1976). Spawning occurs when water temperatures range from 7.8 to 17.8° C, peaks at 14°C and has been observed up to 22°C (Kohlhorst

1976). In contrast to Columbia River sturgeon, flow has no effect on the intensity of spawning in the Sacramento River (Kohlhorst 1976), however, that unique effect may result from the artificial, low-flow regime of the Sacramento River.

Fecundity is approximately 7000 eggs/kg in the Columbia River; 47,000 at 100 cm fork length (8 kg, 5875 per kg), and 210,000 at 150 cm fork length (31 kg, 6774 per kg) (Beamesderfer et al. 1989).

White sturgeon are a long lived fish species. Scott and Crossman (1973) state that some individuals may live more than 100 years. A 71 year old female has been taken from the lower Fraser River (Semakula and Larkin 1968) and an individual estimated to be 82 was taken from the Columbia River.

14.4 Mitigation and Compensation Strategies

Throughout the world, recent declines in sturgeon abundance have been caused by overharvesting and industrialization (Doroshov and Binkowski 1985). The late age of maturity and the delay between spawning years increases susceptibility to overharvesting. The effects of overharvesting may outweigh all other factors limiting white sturgeon production, as is the case with the Atlantic sturgeon *Acipenser oxyrhynchus* (Smith 1985). However, natural reproduction has also been impacted by river impoundment, eutrophication of spawning areas, and water pollution. Although a freshwater species and frequently landlocked, sturgeon must be managed internationally because of their distribution. For example, sturgeon in the Kootenay (Kootenai) River move between British Columbia, Idaho, and Montana (Partridge 1980).

The effects of overharvesting can be mitigated through fishing regulations. In the Columbia River, exploitation of sturgeon from 1860 to 1890 caused severe depletion. These stocks are now recovering because of size and catch regulations, increased food supplies, and a reduced interception by salmon fisheries (Galbreath 1985). However, Columbia River populations currently fished at exploitation rates greater than 10% are at risk of collapse, even with the existing size at harvest regulations, because of declines in habitat productivity (Rieman and Beamesderfer 1990). Minimum and maximum size limits now used in the lower Fraser River and Columbia River protect both juvenile and reproductive adult sturgeon (Anderson 1987; British Columbia Ministry of Environment 1990). From 1984 to 1986 size limits were more effective than bag limits in regulating the rate of harvest in the John Day Reservoir (Beamesderfer et al. 1990). The regulations applied vary between systems; for example, in the Sacramento River in California, a minimum size limit of 102 cm and a daily limit of one is required to prevent over exploitation (Miller 1978) whereas in the Nechako River, a minimum size limit of 120 cm is recommended (Dixon 1986).

Although heavily exploited during the late 19th century, sturgeon in the Columbia and Fraser Rivers have been resilient to exploitation (Rieman and Beamesderfer 1990). Conversely, in Idaho, sturgeon appear incapable of supporting exploitation, possibly a result of recruitment failure brought about by changes in habitat and extending over several years (Apperson and Anders 1990). Extensive diking along the Kootenai River has alienated backwaters and sloughs, possible rearing habitat of juvenile sturgeon, and may have promoted recruitment failure. Loss of backwater and slough habitats may be mitigated through channel alterations and the improvement of access to off-channel habitat areas. However, too little is known of the use of existing habitats to ensure effective design.

Dams affect sturgeon by blocking the migration routes of both adults and juveniles and by altering upstream and downstream water quality, quantity, and flow characteristics. Sturgeon may be lost to areas upstream of dams because of the habit of immature individuals to migrate downstream (Coon 1978). Dams may also reduce sturgeon growth by blocking the migration of the anadromous prey of sturgeon, including fishes such as salmon and lamprey (Coon 1978).

Hydroelectric projects that alter river flow and temperature during winter months may impact sturgeon by altering their normally docile winter behaviour. This in turn may influence egg maturation in gonadal tissue and cause resorption and a resultant decrease in fertility (Khoroshko 1972). As mentioned above, sturgeon eggs and larvae are sensitive to temperature (Wang et al. 1985) and this may have been the cause of the high mortality rate (87%) observed downstream of the John Day Dam during 1987, when flows were below average and the water reached lethal temperature (Palmer et al. 1988).

Hydroelectric dams may affect the genetic diversity of sturgeon populations. Populations upstream of hydroelectric dams in the Columbia River are less genetically diverse than those downstream and these isolated populations may be inbred. Sturgeon in the Kootenai River have a lower frequency of variant alleles than those of sturgeon in San Francisco Bay or the Columbia and Fraser Rivers, presumably because of the population bottleneck induced by natural barriers and the compounding effect of habitat loss from altered flow regimes (Cochnauer et al. 1985). Sturgeon in the Fraser River are in turn more genetically diverse than those in the Columbia River, where recent exploitation and habitat destruction may have created a genetic bottleneck (Brown et al. 1991).

Increased flow releases during the spring when sturgeon spawn and reduced flow releases during the winter when sturgeon are docile were recommended by Khoroshko (1972) to mitigate the effects of hydroelectric projects, although the effectiveness of these measures was not documented However, Votinov and Kas'yanov (1978) found that the rate of recruitment of Siberian sturgeon (*A. baeri*) to the Ob River increased with increasing flow during spawning. How increasing flow affects recruitment is unknown, but potential mechanisms include the flushing of spawning grounds prior to egg deposition, improved egg incubation, increased rearing areas, decreased predation, or decreased competition. Reducing flow during May and June when Siberian sturgeon spawn could impact on spawning success or egg survival and result in recruitment decline.

Spring flow releases are proposed mitigation measures for sturgeon on the Columbia River. A correlation between recruitment and flow has been documented but the mechanism is unknown (R. Beamesderfer, pers. comm. 1991). Evidence suggests that in most years flows are insufficient to initiate sturgeon spawning on the Kootenai River downstream of Libby Dam. However, an alternative explanation is that low flows force spawning on silt-laden substrate where survival is poor (K. Apperson, Idaho Department of Fish and Game, Coeur d'Alene, Idaho, pers. comm. 1991).

Fishways have limited success in promoting the passage of sturgeon over barriers. Sturgeon do not pass through the fish ladders at Bonneville Dam on the Columbia River; however, in an experiment conducted in the Sacramento/San Joaquin River delta, 20% of the sturgeon introduced successfully passed through an experimental vertical baffle fishway 14.6 m long with water velocities of 0.6 to 1.5 m/s (Fisk 1959). This experiment was conducted in brackish water and the results may not apply to landlocked sturgeon.

The impacts of hydroelectric projects have been compensated with artificial spawning grounds for European anadromous sturgeon since 1966 (Khoroshko and Vlasenko 1970). These are ridge-like structures, 10 to 12 m wide, one km long, 0.3 m thick, and composed of 5 to 8 cm diameter gravel, chipped quarrystone and sand. Within these grounds, stellate sturgeon (Sevryuga, *Acipenser stellatus*) prefer those areas with linear flow characteristics, water velocities between 0.7 and 1.1 m/s, and depths of 4 to 5 m. The artificial spawning grounds are used provided they are placed immediately downstream of blockages to upstream spawning migration; when placed too far downstream of the blockage, the fish do not use them. The survival of eggs deposited on these spawning ridges was not assessed. Artificial spawning grounds are not considered a viable compensation measure in the Columbia River because spawning habitat is limited by flow rather than substrate (R. Beamesderfer, pers. comm. 1991).

Sturgeon culture can compensate for habitat lost through hydroelectric developments. European sturgeon culture has been successfully practised for over 100 years, and today large scale ranching of wild stocks is the key element to sturgeon management (Kozin 1964, in Doroshov and Binkowski 1985; Doroshov and Binkowski 1985). Sturgeon culture is limited to ranching - i.e. the artificial spawning of wild-caught adults. Commercial growout of sturgeon is not considered a practical farming technique in Europe (Doroshov and Binkowski 1985).

White sturgeon have been cultured at the University of California, Davis, and brood stock is maintained for breeding (Doroshov and Binkowski 1985). On the Kootenai River a sturgeon hatchery is operating downstream of the Libby Dam. In British Columbia, sturgeon are being experimentally cultured at Malaspina College (Dave Lane, Malaspina College, Nanaimo, pers. comm. 1991).

Potential compensation measures for Columbia River sturgeon in the United States include transplants of juveniles from populations at carrying capacity to populations with low recruitment and sturgeon culture with subsequent stocking of juveniles (R. Beamesderfer, pers. comm. 1991).

Sturgeon in the Kuban River and Azov Sea of the U.S.S.R. have been impacted by hydroelectric development and these losses are compensated with sturgeon culture to offset losses in productive capacity. However, the short duration of the reproductive season limits egg quotas (Savelyeva et al. 1982). Subsequently, measures to mitigate habitat losses were implemented including increasing river flow so that upstream migration of sturgeon can be made safely, and erecting screening devices at water intakes to prevent mortality. Sturgeon farms were still required to maintain spawners in the Kuban River, with sturgeon fry being reared in lagoons to allow their adaptation, again emphasizing the importance of juvenile habitat.

Water pollution from pulp mills may also affect the survival of sturgeon. In the Fraser River downstream of Prince George near Stone Creek, the Department of Fisheries and Oceans measured concentrations of two known pulp mill wastes in sturgeon. Tetrachlorodibenzo-para-dioxin concentrations were 3.9 ppt in the muscle and 17.0 ppt in the liver, and tetrachlorodibenzofuran concentrations 77.0 ppt in the muscle and 320 ppt in the liver. These concentrations were sufficient to warrant eating restrictions (Anon. 1990b).

Copper concentrations in sturgeon oocytes sampled in adult sturgeon from the Kootenai River were 1.18 to 12.8 µg/L (Apperson and Anders 1990), 100 to 250 times greater than levels found lethal to larval white sturgeon (9 µg/kg) (Joel Van Ecnennann, University of California at Davis, pers. comm., in Apperson and Anders 1990). Levels of organochloride residues in Kootenai sturgeon were generally higher than levels harmful to rainbow trout (*Oncorhynchus mykiss*), however, successful sturgeon reproduction in the lower Columbia River where organochloride concentration in sturgeon ova is also high suggests that sturgeon may be more tolerant of organochlorides than salmonids. Similarly, sturgeon in the Sacramento River also bioconcentrate polychlorinated biphenyls in their tissues (Kohlhorst et al. 1980). Polychlorinated biphenyls and chlorinated pesticides have been found in sturgeon in the Columbia River (Bosley and Gately 1981). Concentrations of these chemicals are positively correlated with lipid content of the tissue and age of the fish. The concentration of phenol in an adult sturgeon from the Columbia River measured 56 ng/g, a concentration greater than that found in any other fish species sampled (Campbell et al. 1982). Whether phenol at this concentration has sublethal effects is unknown. The high body burdens relative to other species suggests that adult sturgeon are resilient to these pollutants. In contrast, sturgeon fry are more sensitive to chlorine than salmonids and die at levels of 0.45 ppm (Brannon et al. 1984).

The effect of water pollution on white sturgeon may be mitigated through improved waste treatment or increased dilution of wastes through increased flow. No evaluation of these strategies has been performed. Sturgeon may be more adaptable when faced with water pollution than other species; Columbia River sturgeon moved into other systems in response to elevated suspended solids resulting from ash released by the eruption of Mt. St. Helens in 1980 (King 1982).

In the Volga River dredgers remove water and sediment from the river bottom and entrain European sturgeon (*A. guldenstadii*) larvae and fry occupying the lower 3 m of the water column. This can result in 68 to 77% mortality of the entrained fry (Veshchev 1981). The number of sturgeon juveniles killed is proportional to their abundance in the river, and is related to season, since sturgeon juveniles are transported downstream from the spawning area during spring. The impacts of dredging can be mitigated by prohibiting dredging during the period 15 May to 10 June when European sturgeon are most abundant in this area.

The foremost requirement for effective mitigation and compensation of losses to sturgeon habitat is continued research. The British Columbia Ministry of Environment began a study in 1986 to address degradation of habitat, bioaccumulation of toxic substances, and overfishing (V. Swiatkiewicz, Fish and Wildlife Branch, B.C. Environment, Surrey, pers. comm. 1991). The study has shown that sturgeon move extensively in the lower Fraser River and its larger tributaries, emphasizing the importance of this habitat (Ian Whyte, Envirowest Consultants Ltd., pers. comm. 1991). Similar studies should be conducted throughout British Columbia to identify spawning sites and critical habitats for the rearing of larvae and fry.

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