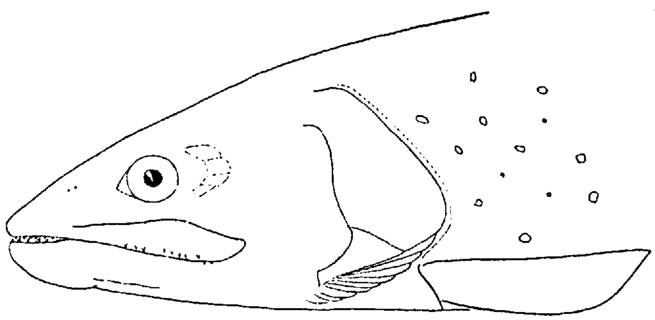
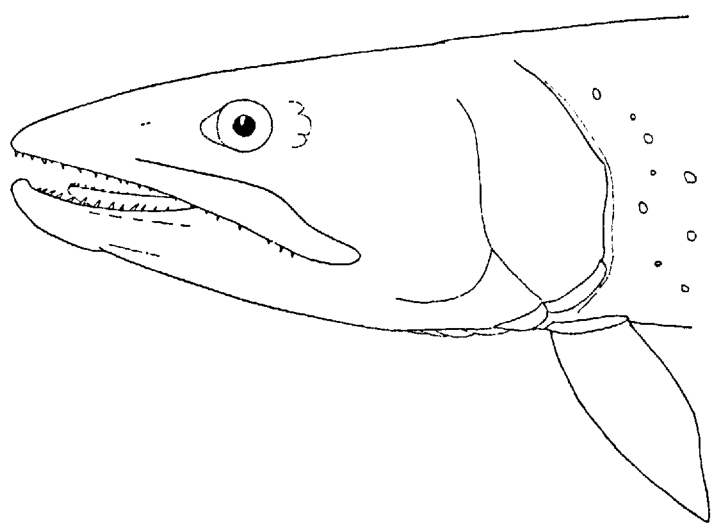
# *A Preliminary Assessment of the Native Fish Stocks of Jasper National Park*

David W. Mayhood





***Part 3 of a Fish Management Plan for Jasper National Park***

Freshwater Research Limited

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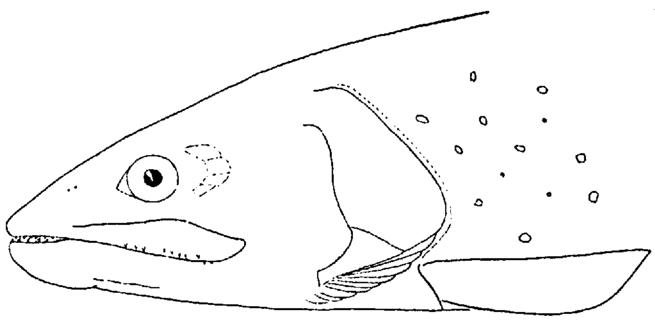

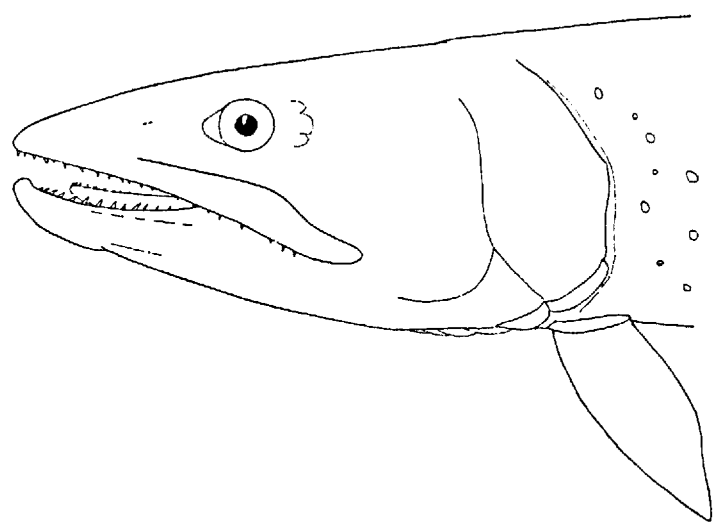

Prepared for
Canadian Parks Service
Jasper National Park
Jasper, Alberta

***Part 3 of a Fish Management Plan for Jasper National Park***

July 1992

**Cover & Title Page.** Alexander Bajkov's drawings of bull trout from Jacques Lake, Jasper National Park (Bajkov 1927:334-335). **Top:** Bajkov's Figure 2, captioned "Head of specimen of *Salvelinus alpinus malma*, [female], 500 mm. in length from Jaques [sic] Lake." **Bottom:** Bajkov's Figure 3, captioned "Head of specimen of *Salvelinus alpinus malma*, [male], 590 mm. in length, from Jaques [sic] Lake." Although only sketches, Bajkov's figures well illustrate the most characteristic features of this most characteristic Jasper native fish. These are: the terminal mouth cleft bisecting the anterior profile at its midpoint, the elongated head with tapered snout, flat skull, long lower jaw, and eyes placed high on the head (Cavender 1980:300-302; compare with Cavender's Figure 3). The head structure of bull trout is well suited to an ambush-type predatory style, in which the charr rests on the bottom and watches for prey to pass over.

# ABSTRACT

I conducted an extensive survey of published and unpublished documents to identify the native fish stocks of Jasper National Park, describe their original condition, determine if there is anything unusual or especially significant about them, assess their present condition, outline what is known of their biology and life history, and outline what measures should be taken to manage and protect them.

Sixteen species and subspecies are native to the park, three more are known from questionable records, and as many as 22 others occupy adjacent drainages, so ultimately may be found, with various degrees of probability, in park waters. One proposed subspecies, the Jasper longnose sucker, is endemic to Jasper National Park (i.e., found nowhere else); two other proposed endemic subspecies, a rainbow trout and a pearl dace, were described long ago but require taxonomic confirmation. The Talbot Lake stock of lake whitefish is genetically unusual (unique in the presently available dataset), as is a stock of rainbow trout immediately adjacent to the park and probably native also to Jasper waters. Pygmy whitefish, apparently rare in Alberta, are found in the Snake Indian River. Lake trout populations in two Jasper lakes were among fewer than a dozen that were native to the Rocky Mountains in Canada. A morphologically peculiar stock of lake whitefish may once have inhabited Lac Beauvert. Evidence is examined suggesting that some Alberta fish stocks could have survived in the vicinity of Jasper National Park in local glacial refugia (e.g., the Ice-free Corridor between the Continental and Cordilleran ice sheets, and associated ice-free areas) since the recession of the early Wisconsinan ice sheets more than 64,000 years ago. If true, we should expect to find other unusual fish stocks in Jasper National Park.

Native stocks of rainbow trout, bull trout, lake trout, northern pike, mountain whitefish and lake whitefish are (or were) actually or potentially important sport fish. Stocks of bull trout, mountain whitefish, longnose sucker, burbot and spoonhead sculpin are valuable as representative fish stocks characteristic of the East Slopes Rocky Mountain region in Canada. All native fish stocks in the park are of scientific importance as carriers of information concerning the zoogeography of the region. Fish in general must be important in the ecology of Jasper National Park as a supplemental or critical food supply for fish-eating wildlife such as otter, mink, mergansers and several other ducks, loons, ospreys, kingfishers, terns, bald eagles, garter snakes and many others.

Historical evidence suggests that trout, whitefish and northern pike were locally abundant (i.e., in certain waters) in the lower Athabasca valley and tributary waters accessible to fish, the area to which most native stocks are restricted. Native rainbow, lake and bull trout were abundant in certain waters in the early days of the park. The condition of the stocks at the time the park was formed would have reflected the influence of thousands of years of at least light use by aboriginal peoples, and

approximately 100 years of perhaps locally significant domestic fishing to supply nearby fur trade posts.

Firm data are not available on the status of any native stock, but some general assessments can be made. Native lake trout probably have been **extirpated**, as have certain stocks of native lake whitefish. Native rainbow trout are **endangered**, possibly extirpated, by introgressive hybridization with introduced non-native stocks. The Jasper longnose sucker, a proposed endemic subspecies, is considered **threatened** on the evidence of low recent catches. Bull trout are recognized as **vulnerable** throughout their range, primarily because of their many biological and life history characteristics that render them especially sensitive to overfishing. Several highly migratory species are of **special concern** because of potential toxic contamination from a pulpmill outside the park.

The biology, life history and critical habitat of native fish stocks is almost completely undocumented within the park. Abundant evidence in the literature supports the view that separate stock development is common in many species, and that stocks have different biological and life history attributes and different habitat requirements. An important element of fish conservation and management in Jasper National Park will be to identify the stocks that are present, and obtain basic data on their biology, life history and critical habitat requirements.

More detailed summaries of these points are available in the Conclusion to each section, in the Summary of each species account, and in the General Discussion.

# ACKNOWLEDGEMENTS

I am greatly indebted to the many individuals who gave me ideas, unpublished material and other assistance for this report. Most are acknowledged individually in the text and in the list of Personal Communications at the end of the volume. In particular, L. M. Carl, D. B. Donald, C. Hunt and B. Gadd were especially helpful and patient in answering requests for information. D. E. McAllister generously provided his important unpublished manuscript concerning the Jasper longnose sucker. L. M. Carl and C. Hunt allowed me to use their initial biochemical genetic data on the Wampus Creek rainbow trout. B. Coad provided valuable information on Jasper fishes in the collection of the Canadian Museum of Nature. R. Saunders permitted me to use his *Salmasellus* records. J. Taylor and W. Bradford, Project Manager and Acting Project Manager, respectively, did their level best to manage the unmanageable. They and the remaining members of the Advisory Committee for this project (D. B. Donald, P. Galbraith, M. Gilmour, C. Hunt and P. Wiebe) tested my ideas in numerous discussions. D. B. Donald and C. Hunt reviewed the draft, contributing many detailed written criticisms and observations which improved this final version. H. Johnson and D. Palmer helped with literature searches. The maps were drafted by M. Croot of Sun Mountain Graphics Services. This report was prepared under Canadian Parks Service contract number KJP-01290.

The views expressed herein are mine and are not necessarily shared by the Canadian Parks Service, the Advisory Committee or the reviewers. Any errors of fact or omission are mine.

*J. C. (Cliff) Ward, retired since 1972, was Western Region fisheries biologist for two decades, and held a special fondness for Jasper. A more decent and amiable colleague would be difficult to find: in 1967, Cliff helped me get my first job in fisheries. I have referred frequently in these pages to his work, especially his many important observations on the distribution of the park's native fishes. This volume is dedicated to Cliff Ward.*

# CONTENTS

# TABLES, FIGURES & MAPS

## Tables



## Figures



## Maps

The following maps are located in the map pocket at the back of the volume.

# GENERAL INTRODUCTION

This report is the third in a series leading to a comprehensive fish management plan for Jasper National Park. The first reviewed the legal and policy limits to the plan, and the principal biological concepts that must govern it (Part 1). The second surveyed approaches to fish management in a large number of parks and similar reserves in North America, to place Jasper National Park in context, and to discover pitfalls and benefits of various approaches that have been used by others in similar situations (Part 2).

The present report deals exclusively with native fish stocks. It is the native stocks that the current National Parks Act and Canadian Parks Service policies are intended to protect (Part 1). The significance of the many stocks that have been introduced to Jasper National Park over the years is reasonably well understood by resource managers and the public, because it is these fish that support most of the present-day sport fishery. These are the populations that have been documented in the stocking records and in the numerous reports and publications on Jasper Park fisheries. In contrast, the value and requirements of the native fishes are poorly appreciated; thus the crucial native stocks have been almost completely ignored in the past. There are presently few data on native fishes to guide the design of a suitably protective management plan. The information needed to build a wide public understanding or appreciation of the ecological, recreational or educational value of native stocks; i.e., the value of conserving native fishes within the national park system, has not been compiled.

It is the goal of this report to identify what is significant about the native fish stocks to Jasper National Park, and to outline what must be done next to begin protecting adequately the native stocks as required by the Act and national parks policy. This will give direction to the fish management plan, and will provide the basic information required to build understanding of and support for it. Its specific objectives are

1. to determine what the native stocks of fishes in Jasper National Park were, and what their natural condition or status was;

2. to establish what is significant about the native stocks in the park; in particular, whether there is anything unusual or especially valuable about them;

3. to assess the present status of the fish stocks native to the park;

4. to outline what is known of the basic biology and life history of native stocks as a basis for their management; and

5. to specify what action is required next to begin protecting native stocks adequately.

The body of the report is in three parts. Section I describes the origins of Jasper fish stocks by examining the glacial history of northwestern North America and the postglacial dispersal of fishes into the Jasper region. This section helps to establish the distinctiveness and geographic representativeness of the indigenous fish stocks in our area. Section II considers the use of fish by the original peoples of the Jasper area, and presents an annotated list and discussion of historical records of fishes in the vicinity of Jasper Park as another way to document the original condition here. Section III, the largest and most important part of the report, summarizes the status, significance and biology of native fishes, and the action required to properly manage them in Jasper Park, in individual accounts for each species.

The common and scientific names for all fishes mentioned in this report are listed in Table 1. The genetic nomenclature used is that of the original publications cited. I did not attempt to translate the protein and locus names to the standard recently recommended by the American Fisheries Society's Genetics Section (Shaklee et al. 1990) because in several older publications it was not clear what the correct translation would be, and I did not want to introduce further confusion for those wishing to check the original references.

**Table 1.** Common and scientific names of the fishes mentioned in the report. Taxonomy, nomenclature and listing order from Robins et al. (1991), except where noted otherwise. Family names in bold print. *–JNP native, ?–questionable JNP native. Fishes native to adjacent drainages that should be looked for in Jasper National Park are indicated as follows: A–Athabasca, S–Smoky, B–Brazeau, F–Fraser.

| COMMON NAME | SCIENTIFIC NAME | |
|---|---|---|
| **Sturgeons** | **Acipenseridae** | |
| lake sturgeon | *Acipenser fulvescens* Rafinesque | **B** |
| | | |
| **Mooneyes** | **Hiodontidae** | |
| goldeye | *Hiodon alosoides* (Rafinesque) | **?** |
| mooneye | *Hiodon tergisus* (Lesueur) | |
| | | |
| **Minnows** | **Cyprinidae** | |
| longfin dace | *Agosia chrysogaster* Girard | |
| lake chub | *Couesius plumbeus* (Agassiz) | ***** |
| brassy minnow | *Hybognathus hankinsoni* Hubbs | **S** |
| pearl dace | *Margariscus margarita* Cope | **A** |
| Jasper pearl dace | *Margariscus margarita athabascae* (Bajkov)[1] | **?** |
| peamouth | *Mylocheilus caurinus* (Richardson) | **F** |
| emerald shiner | *Notropis atherinoides* Rafinesque | **A** |
| spottail shiner | *Notropis hudsonius* (Clinton) | ***** |
| northern redbelly dace | *Phoxinus eos* (Cope) | **A** |
| finescale dace | *Phoxinus neogaeus* Cope | **A** |
| fathead minnow | *Pimephales promelas* Rafinesque | **A** |
| flathead chub | *Platygobio gracilis* (Richardson) | ***** |
| northern squawfish | *Ptychocheilus oregonensis* (Richardson) | **F** |
| longnose dace | *Rhinichthys cataractae* (Valenciennes) | **A** |
| Banff longnose dace | *Rhinichthys cataractae smithi* Nichols[2] | |
| leopard dace | *Rhinichthys falcatus* (Eigenmann & Eigenmann) | **F** |
| speckled dace | *Rhinichthys osculus* (Girard) | |
| redside shiner | *Richardsonius balteatus* (Richardson) | **F** |
| | | |
| **Suckers** | **Catostomidae** | |
| quillback | *Carpiodes cyprinus* (Lesueur) | |
| longnose sucker | *Catostomus catostomus* (Forster) | ***** |
| Jasper longnose sucker | *Catostomus catostomus lacustris* Bajkov[3] | ***** |
| bridgelip sucker | *Catostomus columbianus* (Eigenmann & Eigenmann) | **F** |
| white sucker | *Catostomus commersoni* (Lacépède) | ***** |
| largescale sucker | *Catostomus macrocheilus* Girard | **FS** |
| mountain sucker | *Catostomus platyrhynchus* (Cope) | **B** |
| | | |
| **Pikes** | **Esocidae** | |
| northern pike | *Esox lucius* Linnaeus | ***** |

Continued…

1 this study, re Bajkov (1927)

2 Renaud and McAllister (1988)

3 McAllister and Camus (1984), this study

Table 1 (concluded)

| COMMON NAME | SCIENTIFIC NAME | |
|---|---|---|
| **Trout & allies** | **Salmonidae** | |
| lake whitefish | *Coregonus clupeaformis* (Mitchill) | * |
| broad whitefish | *Coregonus nasus* (Pallas) | |
| golden trout | *Oncorhynchus aguabonita* (Jordan) | |
| cutthroat trout | *Oncorhynchus clarki* (Richardson) | |
| westslope cutthroat trout | *Oncorhynchus clarki lewisi* (Richardson) | |
| rainbow trout | *Oncorhynchus mykiss* (Walbaum) | * |
| chinook salmon | *Oncorhynchus tshawytscha* (Walbaum) | |
| pygmy whitefish | *Prosopium coulteri* (Eigenmann & Eigenmann) | * |
| mountain whitefish | *Prosopium williamsoni* (Girard) | * |
| Arctic charr[4] | *Salvelinus alpinus* (Linnaeus) | |
| bull trout | *Salvelinus confluentus* (Suckley) | * |
| brook trout | *Salvelinus fontinalis* (Mitchill) | |
| Dolly Varden | *Salvelinus malma* (Walbaum) | |
| lake trout | *Salvelinus namaycush* (Walbaum) | * |
| Arctic grayling | *Thymallus arcticus* (Pallas) | **?** |
| Montana grayling | *Thymallus arcticus montanus* Milner | |
| | | |
| **Trout-perches** | **Percopsidae** | |
| trout-perch | *Percopsis omiscomaycus* (Walbaum) | * |
| | | |
| **Codfishes** | **Gadidae** | |
| burbot | *Lota lota* (Linnaeus) | * |
| | | |
| **Sticklebacks** | **Gasterosteidae** | |
| brook stickleback | *Culaea inconstans* (Kirtland) | **ABS** |
| ninespine stickleback | *Pungitius pungitius* (Linnaeus) | **A** |
| | | |
| **Sculpins** | **Cottidae** | |
| prickly sculpin | *Cottus asper* Richardson | **F** |
| mottled sculpin | *Cottus bairdi* Girard | |
| slimy sculpin | *Cottus cognatus* Richardson | **AFS** |
| shorthead sculpin | *Cottus confusus* Bailey and Bond | |
| torrent sculpin | *Cottus rhotheus* (Smith) | |
| spoonhead sculpin | *Cottus ricei* (Nelson) | * |
| deepwater sculpin | *Myoxocephalus thompsoni* (Girard) | |
| | | |
| **Perches** | **Percidae** | |
| Iowa darter | *Etheostoma exile* (Girard) | **A** |
| yellow perch | *Perca flavescens* (Mitchill) | **A** |
| walleye | *Stizostedion vitreum* (Mitchill) | **A** |

4 Morton (1980)

# THE STUDY AREA

Important features of Jasper National Park directly and indirectly relevant to fish, their habitats and sport fisheries are summarized in the Jasper National Park Resource Description and Analysis (Seel and Strachan 1987a), to which the reader is referred for additional information. The following summary is based on that document unless otherwise noted.

## History and Significance of Jasper National Park

Seel and Strachan (1987b) summarized the history and regional significance of Jasper National Park. Woodrow (1987a, 1987b) described past and present land use. Additional historical information is provided by Lothian (1976, 1977, 1979, 1981), and is available in various early annual reports dealing with national parks (e.g., Douglas 1912a, 1912b; Hervey 1914). The park management plan (Canadian Parks Service 1988) provides some of the most recent information available on these topics. The following account is based on these sources except where noted otherwise.

Jasper National Park was established by the Government of Canada in 1907. Originally encompassing almost 13,000 $km^2$, the park was reduced in area to less than 2600 $km^2$ (16 km on either side of the railway line) shortly after it was formed, then later was expanded to 11,400 $km^2$. The present boundaries give the park an area of 10,878 $km^2$, extending for more than 200 km along the east slopes of the Continental Divide in Alberta (Map 1), and protecting a representative cross-section of the Rocky Mountain natural region (Canadian Parks Service 1988:5).

The park was originally set aside as a facilities-oriented tourist playground. Current legislation and policy for the park gives primacy to protecting natural and cultural resources over all other uses (Part 1). Canada also has a formal international obligation to protect Jasper. Under the World Cultural and Natural Heritage Convention (UNESCO 1972), the country has committed itself to protect Jasper and the three other contiguous mountain national parks as a World Heritage Site, so designated by the United Nations in recognition of the outstanding universal value of its natural heritage to mankind. See Part 1 for a review and analysis of these and related policy questions.

Despite its current emphasis on protecting the natural environment, Jasper National Park continues to have a strong role in facility-oriented tourism, and contains nationally-important transportation facilities such as trunk pipelines and communications, transcontinental railway lines, and major highways. The town of

Jasper, wholly within the park, has a permanent population of 3500 permanent residents, 1500 short-term residents, and can accommodate on the order of 3600 visitors in permanent facilities, giving it an effective population of 8600 at peak times. Employment in the town is primarily in the government administration, tourism and associated service industries (Canadian Parks Service 1988:129).

Jasper National Park is a major tourism resource, both to the province of Alberta and the country as a whole. As of 1984 it was the third most visited national park in Canada, in the period 1977-85 regularly registering close to 2,000,000 visitors annually (Woodrow 1987b:500). That number of visitors is expected to continue, if not increase, in the foreseeable future (Woodrow 1987b:533, Seel and Strachan 1987b:8). Nearly one-quarter of all Canadian national parks fishing licenses are sold in Jasper, and the monetary value of the sport fishery to the local economy has been estimated at $600,000 to $700,000 annually (Terms of Reference, this study).

# The Park Environment

The following summary is based on the resource descriptions of Masters (1987, climate), Weir (1987, geology), MacDonald (1987, vegetation) and Ralf (1987, wildlife) unless otherwise noted.

## Weather and Climate

The lower elevations of Jasper National Park have a cold, snowy forest climate with no distinct dry season and cool, short summers (Dfc in the Köppen classification). the climate of high elevation areas in the park has not been classified, but would be generally more severe than that of the valley bottoms. The principal east-west passes and certain major river valleys such as the Snaring, Brazeau and Athabasca River valleys, because of their orientation, serve as conduits for Arctic and Pacific air masses, so experience a greater variation in weather than the rest of the park, the valleys and mountain ranges of which are oriented northwest-southeast.

Mean daily maximum temperatures at Jasper townsite (48 to 50 years of record) range from -7.8 °C in January to 22.5 °C in July; mean daily minima from -17.8 °C in January to 7.6 °C in July. Total annual precipitation is relatively low at 409.3 mm, of which about 68 percent falls as rain. These figures by no means represent the park as a whole, however, because of its large area and extremely varied topography. They are more likely near the warmer, drier end of the ranges found in the park. The comparable figures for the Columbia Icefields, for example, present a much cooler, wetter picture, perhaps near the extreme of the ranges for these features (5 to 13 years of record only). There, mean daily maximum temperatures range from -9.4 °C in January to 15.2 °C in July; mean daily minima range from -19.0 °C in January to 2.9 °C in July; and total precipitation is 930.1 mm, of which over 69 percent falls as snow.

## Geology

Jasper National Park lies mostly within the Eastern Main Ranges and Front Ranges of the Rocky Mountain Thrust Belt. A small area of the park between the Southesk and Brazeau rivers takes in a portion of the Foothills geological subprovince. Elevations in the park range from less than 1000 m at the confluence of the Athabasca and Fiddle rivers, to 3747 m at the summit of Mount Columbia. Drainage patterns are determined by the orientation of the mountain ranges, which run primarily northwest-southeast. Carbonates, especially limestone, dolomite and calcareous shales, and quartzite are the predominant mineral types exposed within the park. Low-grade phosphate deposits have been reported in association with the Fernie Group, Whitehorse Formation, Sulphur Mountain Formation and Rocky Mountain Group.

The park was heavily glaciated by Cordilleran ice during the Pleistocene, much of it flowing over the Continental Divide from the Rocky Mountain Trench. Current thinking (summarized by Gadd 1986:189-202) holds that the entire park, save the high mountain peaks, was completely covered by glaciers during the Illinoian. The Wisconsinan, however, appears to have been less severe with ice accumulating to much lesser depths, leaving greater areas ice free.

There is biological evidence suggesting that one or more ice-free refugia existed in the Jasper-Banff region (discussed elsewhere in this report). Although a corridor along the mountain front between the Cordilleran and Continental ice sheets is believed to have remained ice-free for much of the Pleistocene, it was closed in the vicinity of Jasper National Park for at least part of the Illinoian. Suspected unglaciated areas of small extent exist on the north boundary of the park near Glacier Pass (H. Geldsetzer, personal communication) and in the vicinity of Poboktan and Jonas creeks (Hughes 1955:113).

A glacial lake, Lake Miette, was supposed to have straddled the Yellowhead Pass at one point during deglaciation, extending for many kilometres within the park (Taylor 1960, Baird 1963, Prest et al. 1967). It was thought possibly to have been important in connection with the postglacial dispersal of fishes (McPhail and Lindsey 1970, Paetz and Nelson 1970, Lindsey and McPhail 1986). More recent geological interpretations reject or do not postulate the existence of Glacial Lake Miette (Mountjoy 1974, in Weir 1987; Roed 1975; Levson and Rutter 1989). This matter is taken up in more detail in Section I.

Numerous glacial landforms are found throughout the park. Of particular interest in connection with fish habitat and distribution are cirques, hanging valleys, kettles, meltwater channels, rock basins, lateral, terminal and ground moraine and outwash plains. Well-developed karst occurs in the Snaring and Maligne drainages.

## Water Resources

Jasper National Park is drained by three major river systems. By far the greatest proportion of the park area, 9023 $km^2$ or 82.6 percent, lies within the Athabasca River watershed (Mackenzie River system, Arctic drainage). A small area in the southeast, 1117 $km^2$ or 10.2 percent, is drained by the Brazeau River to the North Saskatchewan system (Hudson Bay drainage), and another smaller area in the extreme northwest, 780 $km^2$ or 7.2 percent, is drained by the Smoky River to the Peace River (Mackenzie River system, Arctic drainage).

The surface water resources of the park consist of nearly 800 lakes of a size large enough to appear on 1:50,000 topographic maps (Ward 1974), several of which are among the largest in the mountain parks; thousands of kilometres of flowing water in the form of one major river, 16 small- to medium-sized rivers and hundreds of small streams; and innumerable small ponds, temporary pools, and intermittent brooks. In addition, there are within the park numerous identified springs (both hot and cold), and one of the largest karst drainages in the world (Maligne Valley; Brown 1973). Surficial groundwater is abundant. Glaciers still cover five percent of the park area.

Waters are primarily of the calcium-magnesium-bicarbonate type, reflecting the dominant limestone-dolomite rock types in the park, and are generally of low to moderate salinity. Some extremely dilute waters (2-10 mg/l) occur in some high-elevation basins, especially those dominated by quartzite (Anderson 1969:21, 1971:313). At the other end of the scale, at least one distinctly saline pond[1] is known, ionically dominated by bicarbonates and sulphates of magnesium and sodium (Katrine Lake, 983 mg/l, Dumont et al. 1978:442). Water quality problems have been identified in association with sewage disposal and other human activities, but in at least one case (relatively high mercury content in some park waters) appear to be related to local natural lithology (Anderson 1979). Glacial streams are numerous, carry high sediment loads and, along with the many glacial lakes, are very turbid during periods of high melt.

Data on ice conditions in over 50 lakes show that ice-free periods range from less than 100 days (large, high elevation) to more than 165 days (small, low elevation). Freeze-up is usually in late October to early November in all of the lakes, but break-up can take place anywhere from late April-early May (a few small, low elevation lakes) to mid-June-late July (moderate to high elevation lakes). The Athabasca River at Jasper is usually free of ice cover for more than 200 days each year, from April to November.

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1 in the sense of Rawson and Moore (1944:145); i.e., >300 mg/l total dissolved solids. Waters of this salinity and above clearly show the concentrating effects of evaporation on waters in closed basins (lakes and ponds with no outlet).

## *Vegetation*

Four zones based on vegetation and elevation have been recognized in Jasper National Park, and have been found useful for purposes of limnological classification (Anderson 1969; see also MacDonald 1987:258). The montane zone occurs primarily in the Athabasca Valley below 1380 m as a dry savannah type characterized by interior Douglas fir *(Pseudotsuga menziesii)* often associated with lodgepole pine *(Pinus contorta)* and trembling aspen *(Populus tremuloides)*. The subalpine zone extends from 1380 m to approximately 2000 m or somewhat higher, depending on aspect, and is typified by stands of Engelmann spruce *(Picea engelmannii)* and subalpine fir *(Abies lasiocarpa)*. Two subzones are often recognized in the subalpine: the upper subalpine (more open forest) and lower subalpine (dense, continuous stands). Above the subalpine and extending from approximately 2000 m to 2200 m is the treeline zone, with patches of stunted and contorted trees (Krummholz), especially of subalpine fir, interspersed with open tundra patches. The zone above treeline is the true alpine, a region of herbs and low shrubs, often much bare rock, and lacking trees entirely. Much more refined and detailed vegetation classes have been mapped in the park (Holland and Coen 1982), but an attempt to associate limnological data with them did not give any gain in predictability or interpretability over simple classification (D. B. Donald, personal communication).

## *Wildlife*

Five amphibian species, including one toad, three frogs and a salamander, are found within Jasper National Park and rely on aquatic habitats at least for breeding. The only common one is the western toad, *Bufo boreas*. The wood frog *(Rana sylvatica)*, spotted frog *(R. pretiosa)* and long-toed salamander *(Ambystoma macrodactylum)* are uncommon in the park. The latter is at the eastern edge of its range (Stebbins 1985:Map 3), is known in Alberta from only a few disjunct populations, and is considered rare in the province (Roberts 1982). The boreal chorus frog *(Pseudacris triseriata maculata)* is considered rare in the park, but is very widespread outside its boundaries (Stebbins 1985:Map 40).

The range of another widespread amphibian, the northern leopard frog *(Rana pipiens)*, is known to approach Jasper National Park closely on the east (Stebbins 1985:Map 54) so may once have been native within park boundaries. Russell and Bauer (1991:125) show a much more restricted range for the species in Alberta, acknowledging that its distribution in northern Alberta requires further investigation. Roberts (1982) reported *R. pipiens* to have greatly declined in numbers within Alberta, stated that it was now absent from much of its range in the province, and described it as a threatened species here.

One reptile, the wandering garter snake *(Thamnophis elegans vagrans)*, is known from Jasper park but is considered rare. This subspecies is common elsewhere, is often associated with aquatic habitats and includes fish in its diet (Stebbins 1985:202-204). The range of *T. sirtalis parietalis*, the common redsided garter snake, broadly overlaps the park (Stebbins 1985:Map 157) and should be expected within its boundaries. It too is often aquatic, and commonly eats fish.

Only a few species of mammals are closely tied to aquatic habitats in Jasper National Park. Beaver *(Castor canadensis)* are common, being found most frequently in the montane and lower subalpine zones. River otter *(Lutra canadensis)* are seldom sighted and are considered very rare in the park. They once must have been common: as many as seven were said to have used Talbot Lake alone in 1939 (lake survey report, D. S. Rawson per W. C. Cable, JNP Warden Service lakes files). Mink *(Mustela vison)* are most abundant in the montane zone, favouring floodplain lakes with sedge and high shrub shorelines, and braided stream channels with herbmat or sedge bank vegetation. The water shrew *(Sorex palustris)* and Richardson's water vole *(Arvicola richardsoni)* are rare or uncommon. Muskrat *(Ondatra zibethicus)* are common but of restricted distribution in the park.

Bears, both black *(Ursus americanus)* and grizzly *(U. arctos)*, are not ordinarily thought of as aquatic mammals, but may consume fish on occasion (Soper 1964:280, 287; Banfield 1974:306). Other mammalian carnivore species that inhabit Jasper National Park are known to consume fish as an incidental part of their diet, including wolf *(Canis lupus)*, red fox *(Vulpes vulpes)*, fisher *(Martes pennanti)*, short-tailed weasel *(Mustela erminea)* and wolverine *(Gulo gulo)* (Banfield 1974).

Of the mammals in Jasper Park, the most significant to fish and their habitats is likely to be the beaver because of its abundance, diet of riparian vegetation and its dam-building behaviour. The mammals for which fish are of greatest importance are most likely otters and mink, which rely on them as a major part of their diet, and perhaps water shrews, which also eat fish, but to an unknown extent (Banfield 1974).

In contrast to the mammals, numerous birds are closely associated with aquatic habitats in Jasper National Park. Those most likely to be of at least some significance to fish populations because they are common and eat large numbers of fish are common loon *(Gavia immer)*, common merganser *(Mergus merganser)*, osprey *(Pandalon haliaetus)* and belted kingfisher *(Megaceryle alcyon)*. These and many other species of Jasper Park birds rely on fish for a substantial proportion of their diet, and are likely to be affected by changes in fish abundance, as might many other birds that may compete with fishes for invertebrate food. These food web and potential competitive relationships are completely undocumented in Jasper National Park.

# *Sources of Information on Fish and Their Habitats*

A record of fisheries use extending over 165 years has left a sizeable amount of fish-related information on Jasper National Park. Most of it is unpublished, and most of the unpublished information exists only as disorganized correspondence and data sheets in numerous old files held in Jasper, the National Archives in Ottawa, and Edmonton. A domestic fishery operated to supply Jasper House in the mid-1800s may be documented at least partially in Hudson's Bay Company archives in Winnipeg. Practically none of this file information has been compiled in a useful form. Many of the data are difficult to use because they lack such essential ancillary information as dates, species, locations, methods, or purpose of collection. The available information that has been published, or at least compiled into well-documented project reports, is listed below. A listing of the relevant files found so far has been submitted separately.

A few miscellaneous observations on fish in or near Jasper in the nineteenth century were noted by early travellers and traders (e.g., Ross 1855, Drummond 1830, Hector 1863, de Smet 1847, Moberly and Cameron 1929, Cheadle 1931, Grant 1873). There are surprisingly few of these, however, given the importance of the Athabasca Pass fur trade route, and the then widespread use of fish as part of the staple diet in the Canadian west (McLeod, in McDonald 1971:97). Careful observers like Ross Cox (1831) Paul Kane in 1846 (Kane 1859) and David Thompson in 1811 (Thompson 1962) who described other western North American fisheries and published useful incidental observations on fish elsewhere did not do so for the area now included in the park, though they passed through it. The Earl of Southesk (Carnegie 1969), the earliest sportsman to hunt in the area (1859), did not comment on the fishing. Botanist David Douglas (Douglas 1914) confined his observations on his 1826 trip through the park to plants, partridges, landscapes, temperatures and stream drainages. Other notable early travellers through what is now Jasper Park, such as George Simpson in 1824-1825 (Simpson 1931), and Gabriel Franchère in 1814 (Franchère 1969), likewise made no mention of the fishes to be found there, although they frequently described the wildlife.

Incidental comments on fish and their habitats in the early twentieth century, at about the time that the park was established, are available in government annual reports (Douglas 1910, 1912a, 1912b; Hervey 1914; Rogers 1916; Sparks 1915; Driscoll 1918) and the report of a fisheries commission investigation at that time (Prince et al. 1912). A member of that commission published a brief anecdotal paper on the occurrence of fish in various East Slopes waters, including the Athabasca River and some of its major tributaries near the park (Sisley 1911).

It was not until the Jasper Park Lakes Investigations of 1925-26, however, that there was a serious attempt to scientifically document fish resources in and near the park (Bajkov 1927, Neave and Bajkov 1929). Other papers that were part of these investigations deal with organisms of various importance to the fish, or describe their habitats (McDunnough 1928, Bajkov 1929, Bere 1929, Neave 1929, Wallis 1929, Mozley 1926, 1930).

After an hiatus of a decade or so, in which there was apparently much activity but little rigourous reporting (Rodd 1930), scientific documentation of fish resources in Jasper National Park resumed with the studies of Donald Rawson. His initial investigation (Rawson 1940a) served as the guide to fisheries management in the park for many years thereafter, and formed the basis or impetus for numerous related scientific studies that included data on park waters in some of the classic publications in limnology and fisheries (Rawson 1941a, 1941b, 1942, 1947, 1951, 1953a, 1953b, 1955, 1958; Rawson and Elsey 1950). Other reports or publications based on Rawson's Jasper Park work or biological collections, or on that of his students or co-workers include Rawson (1940b) Elsey (1944), Rawson and Nursall (1947?), Brooks (1957) and Reed (1959).

Limnologists and fishery biologists of the Canadian Wildlife Service provided most of the new reported work on Jasper National Park fish after 1950. Vic Solman, Jean-Paul Cuerrier and Cliff Ward wrote most of the publications and reports in the early part of this period. Some of them made only passing reference to Jasper, or were relevant to this park only indirectly (Solman 1950, 1951; Solman et al. 1952; Cuerrier 1954, 1956; Cuerrier and Ward 1952, 1953, 1954; Cuerrier et al. 1967; Ward 1967a, 1967b, 1968a, 1968b, 1968c, 1969a, 1969b, 1971, 1972, 1974; Ward et al. 1961). Other documents on Jasper fish were produced in association with this group (Lepp 1966, Lemmen 1968, Kooyman and Wooders 1972). Many of these documents are informal reports not intended for distribution, but they are important as the main writings describing and explaining at least some of the fish management activities during this period. Brief file reports by William Cable, Superintendent of the Maligne River Hatchery in the 1940s and 1950s, are numerous in the files held in the Warden Office at Jasper, and likewise are an important source of coherent fisheries information.

The reports and publications of Canadian Wildlife Service researchers Stewart Anderson, and later David Donald, provide most of the data on fish and their habitats since the late 1960s (Anderson 1967a, 1968a, 1969, 1970a-d, 1971, 1973, 1974a-c, 1979, 1980; Anderson and Krochak 1972; Anderson and Raasveldt 1974; Anderson and Donald 1977, 1978a, 1978b, 1980; Anderson and Dokulil 1977; Anderson and de Henau 1980; Donald 1980, 1985, 1987; Donald and Alger 1986a, 1986b; Donald and Anderson 1978, 1979, 1982; Donald and de Henau 1981; Donald and Patriquin 1983; Donald et al. 1977, 1980, 1982, 1985). Other valuable studies on fish habitats or associated organisms were conducted in association with these authors, or relied on samples collected by them (Bowman 1975; Mudry and Anderson 1976, 1977; Dumont et al. 1977; Green 1979; Herzig et al. 1980).

Park personnel have authored a number of reports on fish management work in Jasper National Park in recent years (Miller undated, 1977; Miller and Dayman 1977; Strachan 1978; Strachan et al. 1978; Beswick 1982; Bradd and de Boon 1982; Antoniuk 1983, 1984; Antoniuk and Yasiansky 1983; Antoniuk et al. 1983; Ralf 1987;

Baraniuk 1989; Hunt 1989). Other government agencies have undertaken water quality studies in the park (Anonymous 1974a, 1974b; Water Quality Branch 1974; Curran 1975; Block and Gummer 1976; Lane et al. 1978).

A specialized body of fish research was conducted by consultants in connection with disease problems at the Maligne River Hatchery (Anonymous 1970; McDermott and Sonstegard 1971; Bell et al. 1972; Yamamoto 1972, 1974a, 1974b, 1975a-d, 1978, 1979; Yamamoto and Kilistoff 1979; Nielsen 1975a, 1975b). Other government agencies, university researchers and private consultants have published or reported on Jasper fish or their habitats independently (Ball and Fernando 1968; Brown 1970, 1972, 1973; Gilbert and Shaw 1981, Camus and McAllister 1984, McAllister and Camus 1984) or in connection with proposed development in the park (Mayhood 1980).

Collections of aquatic biota and habitat data from the park have been included in a large number of broader studies, and broad syntheses concerning fish and limnology often contain relevant data and comments. It would be exceedingly difficult to locate all of them, but a very incomplete list includes investigations by Needham and Claassen (1925), Ahlstrom (1943), Walker (1953), Livingstone (1963), Thomasson (1962), Northcote and Larkin (1963), Adshead et al. (1964), Paetkau (1964), Thomas (1964), Brooks and Kelton (1967), Nimmo (1970, 1971, 1974, 1977), McPhail and Lindsey (1970), Paetz and Nelson (1970), Saether (1970), Clarke (1973, 1977, 1981), Scott and Crossman (1973), Larson (1974, 1975), Nelson (1977), Nelson and Paetz (1976, 1982), Franzin and Clayton (1977), Cavender (1978, 1980), McAllister et al. (1985), Crossman and McAllister (1986), Williams et al. (1989) and Roberts (1989) as well as several others already cited elsewhere in this section.

There exist many popular accounts and guidebooks, especially angling books and articles, pertaining to fish and their habitats in Jasper National Park. These can be of considerable value when they contain new verified or verifiable data. Among the more useful recent ones are publications by Butler and Maw (1985), Gadd (1986) and Van Tighem (1988a, 1988b, 1989, 1991).

Useful technical bibliographies of fisheries and limnology that include Jasper Park waters have been prepared by Anderson (1974b), Anderson and Donald (1977), and Nicholson and Moore (1988a-c).

# SECTION I

# ORIGINS OF THE NATIVE FISH STOCKS

## Introduction

During the Pleistocene Epoch the great continental glaciers — the Cordilleran Ice Sheet over the western mountains and the Laurentide Ice Sheet centred over Hudson Bay — displaced the freshwater fishes from most of Canada and parts of the northern United States. Our fishes survived in refugia beyond the limits of the ice. When the ice retreated, the fish were able to invade our region as it became ice-free. The details of precisely how and when the ice retreated, the history of deglaciation, determined to a considerable degree the stocks of fish that were able to colonize the once-glaciated areas, including Jasper National Park.

In developing the fish management plan for Jasper, it is of interest to know where the present-day aquatic fauna of the park came from. Isolation for long periods in separate refugia during the Pleistocene allowed some fish species to evolve distinct stocks differing in their genetic properties, and therefore very likely in their behavioural, ecological and other attributes as well.

Suggestions have been made that fish may have survived glaciation in local refugia in western Alberta (McPhail and Lindsey 1970:13-14, Lindsey and McPhail 1986:661-2, Crossman and McAllister 1986); others have dismissed the possibility (Paetz and Nelson 1970:3, Nelson 1977:130). If fishes did survive glaciation in this province, populations native to the park should show genetic evidence of it. Some of our populations may have diverged significantly from populations that reinvaded from the larger refugia to the north and south of the continental ice. Other aquatic organisms, such as invertebrates, are even more capable than fishes of surviving in small local refugia. Any such isolated relict populations would have had an opportunity to evolve and diverge from populations that survived glaciation elsewhere, and may be uniquely adapted to particular local habitats. It is just such biological diversity that the fish management plan must be designed to protect (Part 1).

Published analyses of postglacial dispersal of fishes relevant to the study area include McPhail and Lindsey (1970:7-26) especially for the Mackenzie Basin and northward, and Paetz and Nelson (1970:3-6) and Nelson (1977) for Alberta. These have been supplemented by the detailed and more current work of McPhail and Lindsey (1986) for Cascadia, adjacent to the study area on the west; Lindsey and McPhail (1986) for the Yukon and Mackenzie basins; and Crossman and McAllister (1986) on the Hudson Bay drainage. Recent papers by Foote et al. (1992) and Bodaly et al. (1992) deal specifically with postglacial dispersal of lake whitefish. Several papers in the volume edited by Fulton (1984) synthesize views on the glacial history of the area. Gadd (1986) provides an excellent, up-to-date, popular-style account of Rocky Mountain glacial history that is both technically credible and understandable to non-geologists. Finally, the recent book by Pielou (1991) is an exceptionally lucid exposition of current views on Late Wisconsinan and postglacial ecology in the study area. The following account is drawn from these works except where otherwise noted.

## *Pleistocene Glaciation and Deglaciation*

The Pleistocene Epoch, beginning about 2 million years ago and extending to about 10,000 years ago, was a time of successive warm and cold periods. During the cold periods, two enormous sheets of glacial ice covered large areas of northern North America (Figure 1). The Cordilleran ice sheet covered the mountain region between the Pacific Coast and the Rocky Mountains from just south of the 49th parallel to the Yukon and Alaska. The Laurentide ice sheet extended over almost all of the rest of Canada east of the Rockies, and over much of the northern United States, especially in the east. As well, smaller isolated ice masses existed in the Brooks Range of northern Alaska and in the Yukon, and alpine glaciers south of the Cordilleran ice expanded considerably.

Table 2 shows the approximate timing of Pleistocene glacial and nonglacial periods in western Canada. The Canadian Rockies were subjected to at least two major advances of Pleistocene ice. (Evidence for earlier glaciations in western Canada is present, but is scarce and widely dispersed). The first recognizable advance was Illinoian, extending from approximately 240,000 BP (years before present) to about 128,000 BP. The most extensive glaciation of the southern Canadian plains occurred in this period, and it probably was the first time that the Laurentide ice reached the Rocky Mountains (Fulton et al. 1984:70). A warm ice-free period, the Sangamonian, followed the Illinoian advance, extending until the second recognizable glaciation, the Wisconsinan, beginning about 75,000 BP.

Three substages of the Wisconsinan are recognized in our area. The Early Wisconsinan was a period of heavy glaciation, though apparently significantly less extensive than the Illinoian. It lasted from 75,000 BP to 64,000 BP, and was followed by a warmer nonglacial period, the Middle Wisconsinan. The Late Wisconsinan (20,000 BP to 11,000 BP), once thought to have been a time of extremely strong glaciation in our area, is now considered to have been less extensive than either the Illinoian or Early Wisconsinan advances (Fulton et al. 1984:70).

**Figure 1.** Approximate maximum extent of the Late Wisconsinan glaciation (Prest 1984), showing known and potential refugia used by freshwater fishes. **E**- exposed Bering land bridge, **A-** Beringia (Yukon River and North Slope), **B-** Cascadia (Columbia River basin), **$C_1$-** upper Missouri River drainage, **$C_2$-** upper Mississippi River, **T-** Atlantic seaboard, **I-** Ice-free Corridor (the Nahanni Refugium of Foote et al. 1992 lies in the northern portion; i.e., the southwestern Northwest Territories). Modified from McPhail and Lindsey (1970:9).

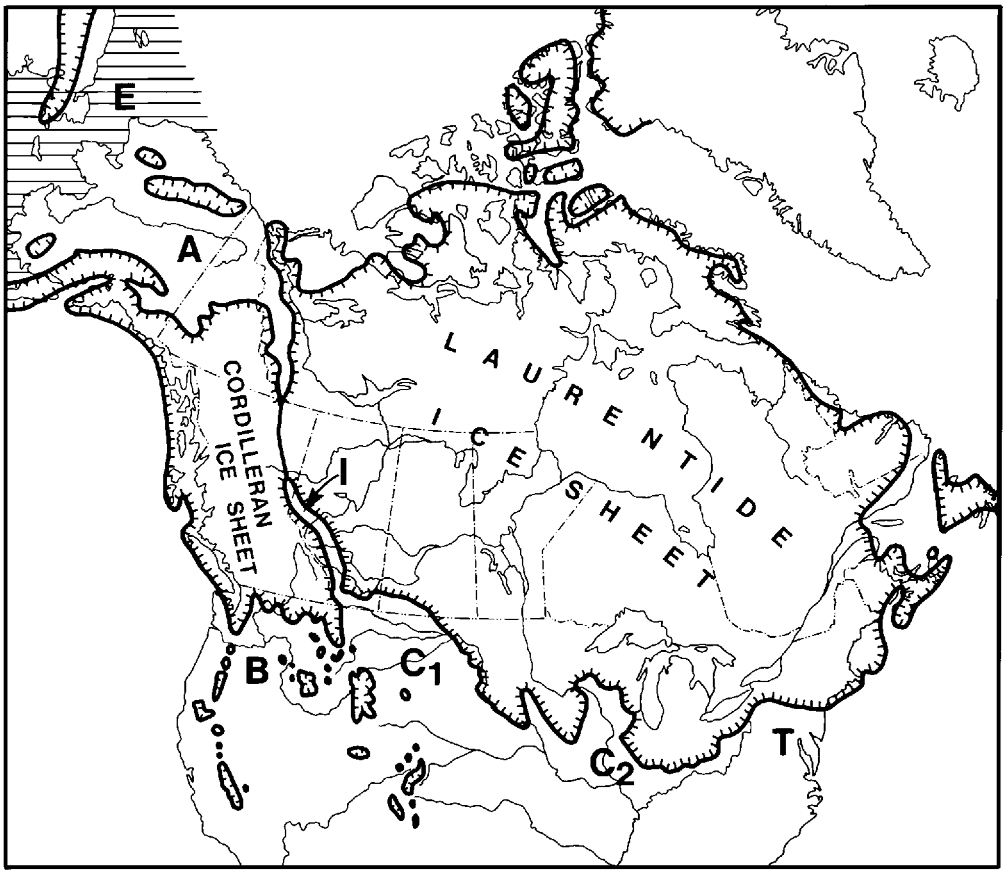



**Table 2**. Approximate timing of glacial and nonglacial periods in western Canada (adapted from Gadd 1986:189). BP: years before present, conventionally the year 1950.

| **Event** | **Began** | **Ended** |
|---|---:|---:|
| present nonglacial period | after 11,000 BP | |
| Late Wisconsinan glaciation | 20,000 BP | 11,000 BP |
| Middle Wisconsinan (nonglacial) | 64,000 BP | 20,000 BP |
| Early Wisconsinan glaciation | 75,000 BP | 64,000 BP |
| Sangamonian (nonglacial) | 128,000 BP | 75,000 BP |
| Illinoian glaciations (two separate advances?) | 240,000 BP | 128,000 BP |

The last deglaciation in western Alberta took place rapidly. The Cordilleran Ice Sheet of the Late Wisconsinan was retreating by 13,000 BP, and by 10,000 BP glacier cover was little more extensive than at present. The last Laurentide Ice Sheet was retreating by 13,500 BP and probably did not extend beyond the Canadian Shield by 11,500 BP (Fulton et al. 1984:70).

## *Refugia and Postglacial Dispersal*

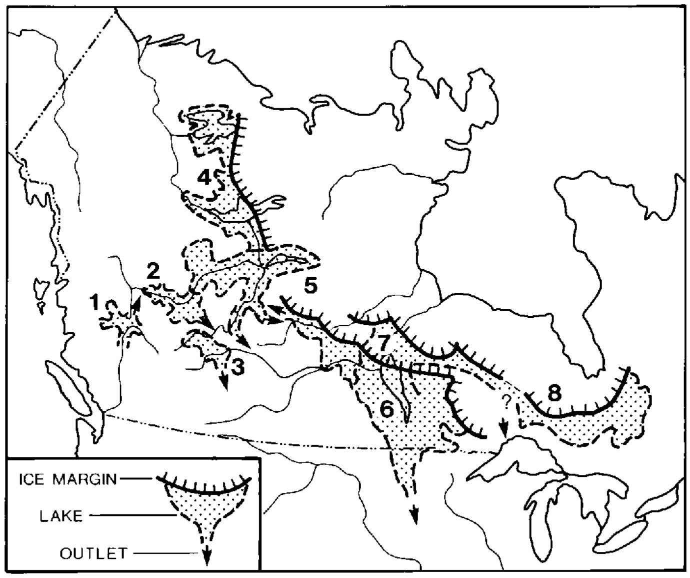
Four large unglaciated areas existed during the Pleistocene that served as refugia for freshwater fishes (Figure 1), three of them important to fishes of western North America. These were north of Cordilleran ice in the Bering Strait-Alaska-northern Yukon area (Beringia); south of the Cordilleran ice and west of the Rockies, centering on the Columbia drainage (Cascadia); and south of the Laurentide ice east of the Rockies in the Missouri and Mississippi river systems (McPhail and Lindsey 1970). The Missouri and Mississippi ice-free areas were at least partially isolated from each other, and represented separate refugia for some species. Smaller ice-free areas existed as well, especially during the Wisconsinan, and some of these may have served as refugia for fishes and other aquatic organisms. The largest and most important of these with regard to the native fishes of Jasper National Park was the Late Wisconsinan Ice-free Corridor that existed between the Cordilleran and Laurentide ice sheets.

Fishes are believed to have moved back into the glaciated regions mostly by following glacial lakes and waterways that formed along the margins of the retreating glaciers, but also by occupying waters that reversed their drainage as the land gradually rose or drainage routes became unblocked with the retreat of the ice, by following present-day drainage routes, and by taking advantage of local headwater captures.

Large Laurentide proglacial lakes thought to have been important dispersal routes for fishes that colonized the Jasper Park area are Lake Agassiz of Manitoba and northwestern Ontario, and Lake Tyrrell in northeastern Alberta (Figure 2). These two lakes together would have provided ready access for many fishes from the Mississippi River refugium to the North Saskatchewan, Athabasca and Peace river drainages. Smaller and earlier lakes Edmonton and Peace may have been locally important in providing dispersal routes between the North Saskatchewan and Athabasca, and between the Athabasca and Peace drainages, respectively. Many even smaller and more ephemeral proglacial lakes formed east of the mountain front from southern Alberta northward to the Hinton-Edson area (e.g., Taylor 1960, Prest et al. 1967, Alley and Harris 1974) that may have been part of dispersal routes to the Jasper area for fishes that survived the Wisconsinan in the Missouri River headwaters. In British Columbia, glacial lakes that connected the Okanagan valley with the upper Fraser system, and the upper Fraser with the headwaters of the Peace River near Prince George, are thought to have provided the means for fishes that found glacial refuge in

Cascadia (Columbia River basin) to move as far north as the Peace drainage.

**Figure 2.** Some of the large proglacial lakes that may have provided fishes access routes to the vicinity of Jasper National Park after retreat of the Late Wisconsinan ice. **1-** Prince George basin, **2-** Lake Peace, **3-** Lake Edmonton, **4-** Lake McConnell, **5-** Lake Tyrrell, **6 & 7-** two stages of Lake Agassiz, **8-** Lake Barlow-Ojibway. Modified from McPhail and Lindsey (1970:13).




In Jasper National Park itself, Glacial Lake Miette has long been supposed to have occupied the Athabasca valley for many kilometres, perhaps straddling the Yellowhead Pass (Taylor 1960 and earlier references therein, Baird 1963, Prest et al. 1967). This lake is often mentioned in connection with postglacial dispersal of fishes (e.g., McPhail and Lindsey 1970:14; Paetz and Nelson 1970:4, Crossman and McAllister 1986:57; Lindsey and McPhail 1986:667, 669; Tonn 1990:46). Recent interpretations of landforms and deglaciation here do not postulate the existence of Glacial Lake Miette (Mountjoy 1974, cited by Weir 1987:208; Roed 1975; Levson and Rutter 1989). Fish still may have moved over the Continental Divide at the Yellowhead Pass even in the absence of a glacial lake there, however. The pass is low, very flat and wet, with no significant barriers to fish movements from the Athabasca drainage on the eastern slope. There is a record of a natural small lake on the Divide with outlets to both the Fraser and the Athabasca drainages that existed as recently as 1913 (Rogers 1915:100).

> *"A new and beautiful lake was discovered by Warden Bigley, which I have called 'Summit lake', as it is on the divide between Alberta and British Columbia, with one stream flowing eastward to the Miette and another westward to the Fraser river. This lake is swarming with beaver, which have*

*a number of lodges around the lake shore."*

In the following paragraphs I will summarize the views of McPhail and Lindsey (1970) regarding the postglacial dispersal of fishes from the three major refugia and their invasion of waters in the Jasper area. This is still the most complete interpretation covering the region, even though newer information has caused these authors to change their views somewhat (Lindsey and McPhail 1986, McPhail and Lindsey 1986[1]), as discussed in the individual accounts for each species. It is the best-documented but most conservative interpretation, describing the most likely refugial origins of the fishes of western Canada assuming that the Ice-free Corridor did not exist, or at least did not serve as a refuge for fish. It will serve as a standard against which other proposals may be compared. When necessary to complete this standard view, I have interpreted in the most conservative manner new distributional records and taxonomic changes. The possibility that the Ice-free Corridor served as a local refugium for some Alberta fishes will be taken up in detail later. It is an idea that is particularly significant for managing the aquatic resources of the park, but one that has been given serious consideration only recently (Crossman and McAllister 1986).

McPhail and Lindsey (1970) listed the main refugial sources of the fishes known to occupy their study area, which included the upper Mackenzie drainage of which most of Jasper National Park is a part. Of the 32 native species and one subspecies known to occur in Jasper Park or near the park in waters draining it, the Missouri-Mississippi refugium was the only source for 17 species: goldeye, lake whitefish, flathead chub, northern redbelly dace, finescale dace, pearl dace, emerald shiner, spottail shiner, brassy minnow, fathead minnow, white sucker, brook stickleback, trout-perch, yellow perch, walleye, Iowa darter and spoonhead sculpin. Cascadia was the only source for rainbow trout and mountain whitefish. Three species — longnose sucker, slimy sculpin and burbot — could have invaded from any combination of the three major refugia. Lake trout, Arctic grayling, northern pike and ninespine stickleback could have been derived from either the Missouri-Mississippi refugium, the Beringian refugium, or both. Lake chub and longnose dace could have invaded from either or both Cascadia and the Missouri-Mississippi refugium.

Bull trout were not distinguished from Dolly Varden trout by McPhail and Lindsey (1970). It has been reported recently that bull trout occur in two drainages that are near or part of Beringia (Haas and McPhail 1991:2203, 2210; their collection numbers 307 and 308). On this evidence, these authors suggest that the species may be found even further north. The only major refugium certainly occupied by bull trout, however, is Cascadia (Cavender 1978, Haas and McPhail 1991); therefore this is the most likely refugial source for Jasper Park populations of this fish, according to the most conservative view.

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1 see also Foote et al. (1992) for Lindsey's current view of lake whitefish refugia and postglacial dispersal.

Pygmy whitefish had not been found in the Athabasca drainage at the time McPhail and Lindsey (1970) developed their view of postglacial dispersal. Only two specimens of pygmy whitefish have been reported from the Athabasca drainage in Jasper Park (Mayhood 1980). Others have been found in the upper Athabasca drainage outside the park (W. E. Roberts, personal communication), and in the Saskatchewan side of Lake Athabasca (D. B. Tripp, personal communication). The species has a highly disjunct distribution, and is found in all three major refugial areas. On this basis, the Jasper population(s) could have been derived from any of the three refugia. Morphological differences among the many disjunct populations, however, led Lindsey and Franzin (1972) to propose six separate refugia for this species.

Two species so far found near Jasper Park only in the North Saskatchewan drainage were outside McPhail and Lindsey's (1970) study area. Lake sturgeon probably survived Wisconsinan glaciation in the Mississippi-Missouri refugium, and mountain sucker conceivably could have entered our area from either or both Cascadia and the upper Missouri (Mississippi-Missouri refugium), judging from the present distribution of these species.

The conservative view just outlined of glacial refugia and postglacial dispersal of fish species now found in or near Jasper National Park is summarized in Table 3.

# The Ice-free Corridor and Local Refugia

The Ice-free Corridor idea has been the subject of much study and discussion by geologists and others since at least the early 1970s (e.g., Reeves 1973; Alley and Harris 1974; Rutter 1980, 1984; Stalker 1980; Jackson 1980; Mott and Jackson 1982; White et al. 1985). Its extent, chronology, varying location and significance continues to be a matter of disagreement, but its existence in at least some form is widely accepted.

## Glacial History

Current evidence suggests that all of Alberta was glaciated at some time, except for the top of the Porcupine Hills in the southwest, perhaps the tops of the Cypress Hills, and a few nunataks (mountaintops sticking up above the ice) in the Rockies. The Laurentide ice extended into Alberta as far as the Rockies, and Cordilleran ice flowed well out onto the prairies. The Ice-free Corridor existed because the two great ice sheets did not reach their maximum extent at the same time. Often the Cordilleran ice advancing from the west reached the foothills and prairies first, and already had retreated before the Laurentide ice from the east, flowing from a more distant and

**Table 3.** Two views of the origins of fish populations now inhabiting the East Slopes drainages in and near Jasper National Park. **+:** a conservative view based primarily on McPhail and Lindsey (1970), assuming that the Ice-free Corridor did not exist, or at least did not serve as a glacial refuge for fish; **•:** some species in which at least some populations may have survived the Late Wisconsinan glacial maximum in or near the Ice-free Corridor. Arguments in favour of the latter view are presented below and in the individual species accounts in Section III.

| Name | Mississippian | Beringian | Cascadian | Corridor |
|---|---|---|---|---|
| lake sturgeon | + | - | - | - |
| goldeye | + | - | - | - |
| lake whitefish | + | - | - | •[1] |
| brassy minnow | + | - | - | • |
| flathead chub | + | - | - | - |
| emerald shiner | + | - | - | - |
| spottail shiner | + | - | - | - |
| northern redbelly dace | + | - | - | - |
| finescale dace | + | - | - | - |
| fathead minnow | + | - | - | - |
| pearl dace | + | - | - | •[2] |
| white sucker | + | - | - | • |
| trout-perch | + | - | - | - |
| brook stickleback | + | - | - | - |
| Iowa darter | + | - | - | - |
| yellow perch | + | - | - | - |
| walleye | + | - | - | - |
| spoonhead sculpin | + | - | - | • |
| lake trout | + | + | - | • |
| Arctic grayling | + | + | - | • |
| northern pike | + | + | - | - |
| lake chub | + | - | + | • |
| longnose dace | + | - | + | - |
| mountain sucker | + | - | + | - |
| pygmy whitefish | + | + | + | • |
| longnose sucker | + | + | + | •[3] |
| burbot | + | + | + | • |
| slimy sculpin | + | + | + | - |
| rainbow trout | - | - | + | • |
| bull trout | - | - | + | • |
| mountain whitefish | - | - | + | • |

1 There is strong evidence from biochemical genetic studies that some elements of the northwestern Alberta lake whitefish fauna survived glaciation in the northern portion of the Ice-free Corridor (Foote et al. 1992).
2 Jasper pearl dace proposed subspecies
3 including the Jasper longnose sucker proposed subspecies

lower-elevation centre, arrived in the area. At other times, including the relatively weak Late Wisconsinan advance, ice from the two sources may never have reached the same locations (Prest 1984). To further complicate matters, movements of the margins of both ice sheets were not synchronous along their entire fronts. For example, the Cordilleran front at one place was advancing while at another it was retreating.

The Ice-free Corridor was closed at times at some locations. For a time during the Illinoian, from about the present City of Calgary northward, Cordilleran ice met Laurentide ice and deflected southward, closing much of the corridor but leaving a narrow ice-free zone extending into the unglaciated regions of Montana (Gadd 1986:193). This evidently happened during the latter part of the Illinoian. Gadd states that there were two Illinoian advances, during the first of which the Laurentide ice reached the mountain front throughout the area, while the second did so north of the Bow River, but barely reached the foothills in the south. In the Early Wisconsinan the corridor was open in the Waterton area, but the distance of northward extension is not known (Rutter 1984:51). The mid-Wisconsinan included a significant nonglacial period during which the Laurentide ice retreated perhaps as far as Hudson Bay and the Cordilleran ice may have largely disintegrated (Fulton et al. 1984:76), certainly leaving the corridor ice-free.

To summarize: during the Late Wisconsinan maximum, the currently-favoured interpretation is that the corridor was open north from unglaciated Montana at least to the Jasper-Hinton area, closed in northeastern British Columbia, and open again north of the 60th parallel (Rutter 1984, Prest 1984). Even this view of extensive closure in northeastern BC during the Late Wisconsinan may relax somewhat with further study. Gadd (1986:31-36,201,202) pointed to several features of the northern foothills landscape west of Fort Nelson that argue against Late Wisconsinan glacial activity in this area. He suggests that Wisconsinan glaciation in general was much lighter in the northern Rockies than it was further south (Gadd 1986:31). Prest (1984:Map 1584A) showed the maximum extent of the Ice-free Corridor to have reached far to the northwest of the Hinton area, well into northeastern BC.

The impression of the Ice-free Corridor gained from these descriptions is that of a long, rather narrow, northwest-southeast trending glacierless zone extending from the Yukon to Montana that undulated irregularly back and forth in an east-west direction with the ebb and flow of the ice sheets, fluctuating in width at various times along its length, and sometimes pinching out completely in the middle. Two current interpretations of the Corridor are illustrated in Figures 3 and 4. One could postulate the effect occurring also during the Illinoian before and after its maximum extent, and during the Early Wisconsinan, but the only direct evidence of it is from the Late Wisconsinan.

**Figure 3.** One recent view of the Ice-free Corridor in southwestern Alberta and Yukon-Northwest Territories. The Nahanni Refugium of Foote et al. (1992) lies in the extreme southern tip of the northern portion of the corridor. Modified from Rutter (1984:52,54).

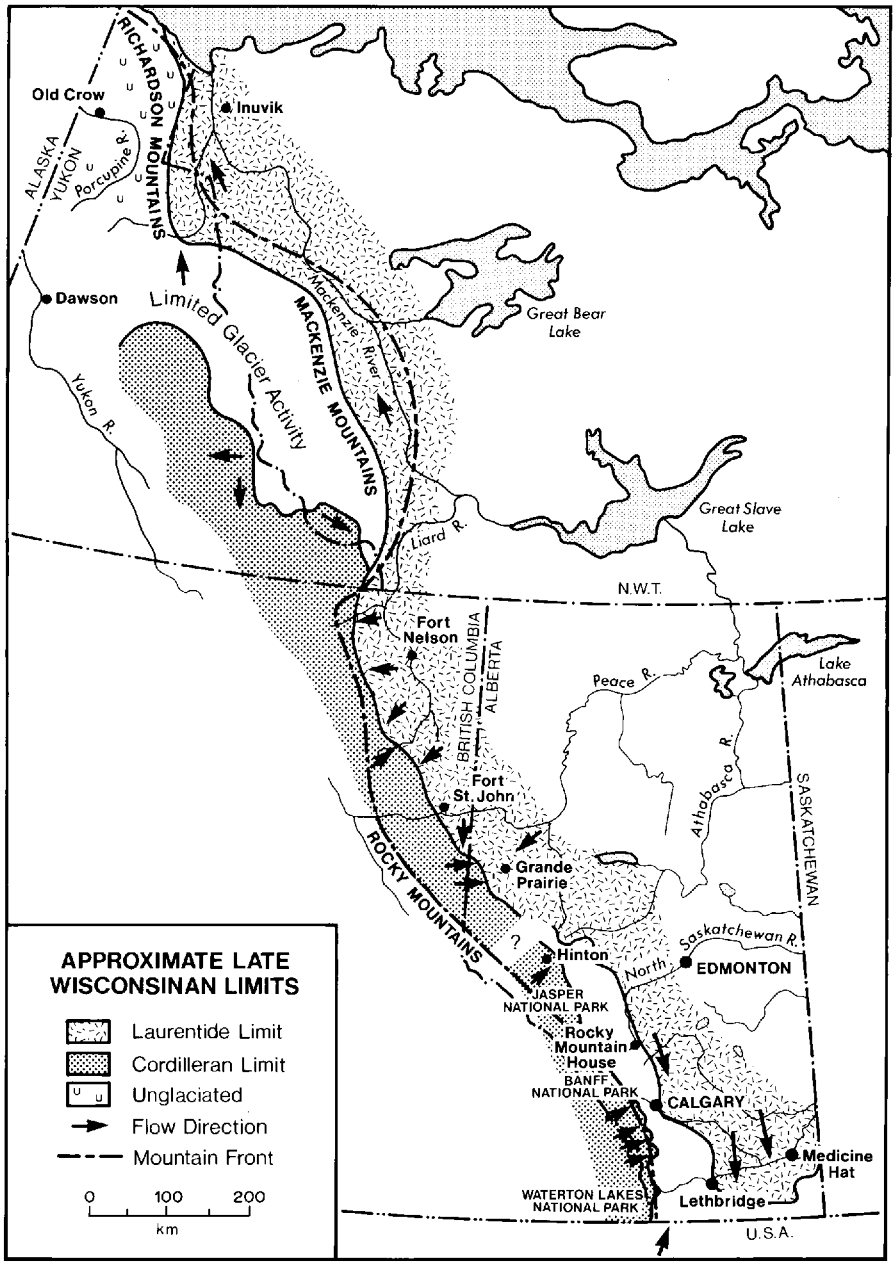
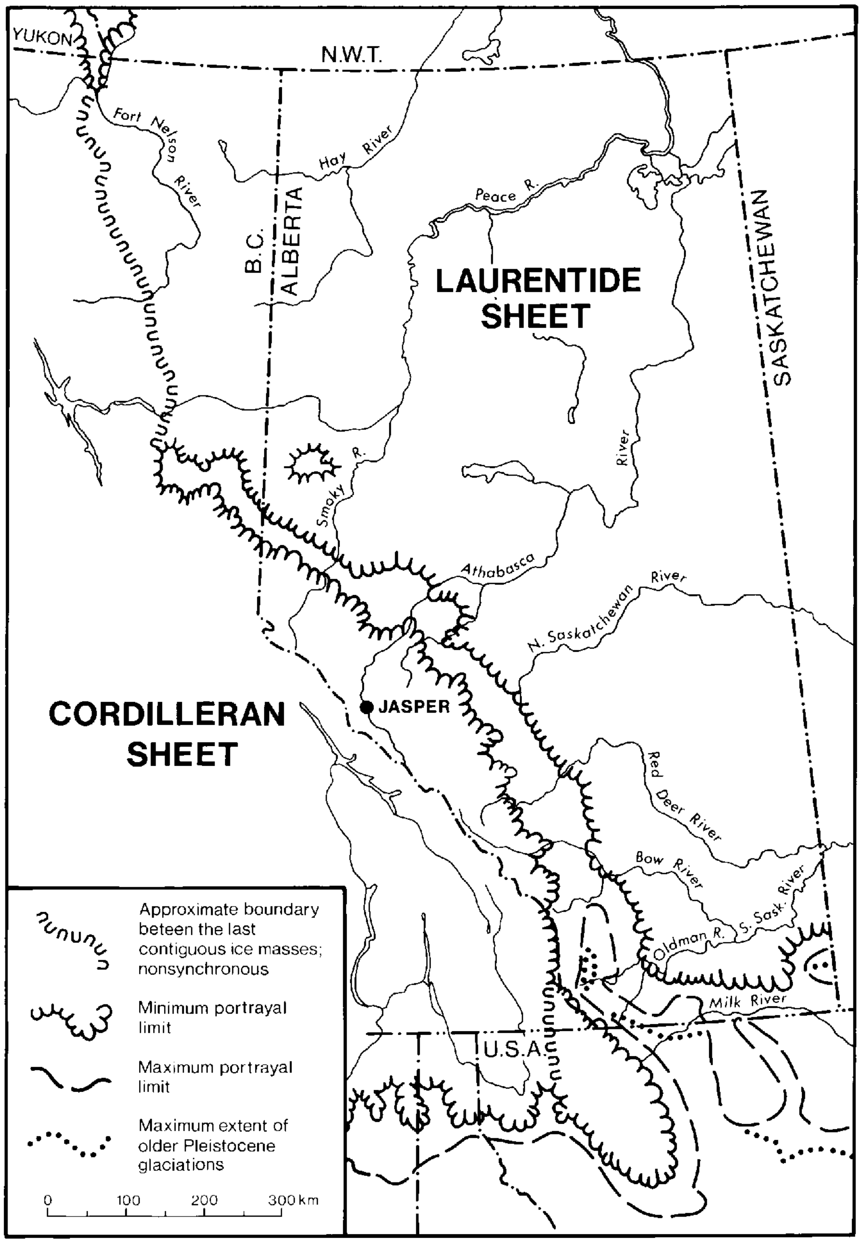


Figure 4. Another recent view of the extent of the Ice-free Corridor in western Alberta, showing maximum and minimum estimates of ice coverage in the region during the Late Wisconsinan advance. Modified from Prest (1984:Map 1584A).



The Corridor was wet (Reeves 1973:10-11, Pielou 1991:156), and perhaps supported a sparse, herbaceous tundra-like vegetation at the height of the Late Wisconsinan advance (Mott and Jackson 1982). Especially during ice retreat, numerous short-lived lakes formed along the ice front (proglacial lakes) as meltwater was blocked by the Laurentide sheet from draining eastward and northward with the slope of the land (e.g., Taylor 1960, Prest et al. 1967, Alley and Harris 1974). Instead, drainage of the southern half of the corridor was to the southeast, to Montana and the Missouri-Mississippi system; the northern half drained to the Yukon system. For this reason the north and south halves of the Corridor might be considered parts of the Beringian and Missouri-Mississippi refugia, respectively. The remoteness of the Corridor, however, would have partially isolated any fish populations living within it, and its rigourous tundra environment (Mott and Jackson 1982, Pielou 1991:156-157) would have given it a unique character as a semi-autonomous refugium on its own.

Smaller local ice-free areas of higher ground in the mountains would have been relatively common during the weak Late Wisconsinan advance, and these might be considered as part of the corridor refugium. At least two high valley areas in Jasper National Park are suspected to have been unglaciated during the Wisconsinan (valleys in the Jonas-Poboktan area, Hughes 1955:113; high pass near the Ancient Wall, H. Geldsetzer, personal communication). Biological evidence has been advanced in support of a hypothesized refugium in the Mountain Park area east of Jasper Park (Packer and Vitt 1974, Clifford and Bergstrom 1976). Crossman and McAllister (1986) referred to a possible Banff-Jasper Refugium, a term that might be applied to this combination of known and suspected ice-free lands.

The currently-favoured geological interpretations discussed above suggest that the Ice-free Corridor was unglaciated in the south (i.e., southwestern Alberta) and north (i.e., Mackenzie Mountains area) from at least the end of the Early Wisconsinan to the present, i.e., for at least the last 64,000 years. In the extreme south and extending an unknown distance northward, it was open at least since the end of the Illinoian 128,000 years ago, and perhaps for as long as 300,000 years (Rutter 1984:51, his Figure 1). It also had plenty of aquatic habitats in the form of glacial meltwater and proglacial lakes. If these views are correct, a significant portion of Alberta offered at least the minimal conditions in which coldwater fishes and other aquatic organisms could have survived *in situ* for at least the last 64,000 years, and in the extreme southwest at least for the last 128,000 years, rather than the approximately 13,000 years generally supposed. These time periods may have been sufficient to allow fishes surviving in the Corridor to diverge significantly from stocks that survived glaciation in other refugia.

## *Biological Evidence of a Corridor Refugium*

Refugia in or near the Ice-free Corridor were postulated some time ago for plants (Bird and Marsh 1973:273, Packer and Vitt 1974, Packer 1980) and subterranean aquatic invertebrates (Clifford and Bergstrom 1976, Bousfield and Holsinger 1981:1829). Although the idea often has been considered briefly by others (e.g., McPhail and Lindsey 1970:13-14, Nelson 1977:130, Lindsey and McPhail 1986:662,668), Crossman and McAllister (1986:86-87) are the only workers so far to attempt to make a case for a fish refugium in the Ice-free Corridor. In fact, they saw the possibility that the East Slopes might have held two separate refugia for fishes, a Banff-Jasper Refugium and a Bow-Oldman Refugium.

In the following discussion I examine Crossman and McAllister's suggestions at length by considering their biological evidence, and by adding some from the literature and a little from my own data. More detail on postglacial dispersal and distinctive stocks of fishes is provided in the accounts of individual species found in Jasper National Park.

I refer sometimes below to “endemics”. The word has a precise meaning, but frequently is misused to mean “indigenous” or “native” organisms. It is not synonymous with those terms. An endemic is any native taxon confined to, or exclusive to, a region (MacArthur and Wilson 1967:187). Endemics are of special interest in this discussion because in order to be different from other related organisms, they must have been isolated from them for a relatively long time. In our area, which is generally assumed to have been heavily glaciated very recently in evolutionary terms, endemics would usually constitute good evidence of a nearby glacial refugium. Endemics thus are valuable biogeographic markers as well as unique elements of regional biodiversity, and are often at risk of extinction because of their limited range.

### *Bow-Oldman Refugium*

The strongest evidence offered by Crossman and McAllister (1986:88) for a fish refugium in this area is their discovery of fossil scales of grayling (*Thymallus*, probably *T. arcticus*, Arctic grayling) from January Cave, Plateau Mountain. The scales were associated with fossil lemming remains dating from 22,000 to 23,000 BP (radiocarbon method, Burns 1980:1508); i.e., near or at the beginning of the Late Wisconsinan advance. There is geological evidence that Plateau Mountain was an unglaciated area (Beaty 1975:47-48, Burns 1980:1510). Radiocarbon dates of 18,300 and 18,400 BP have been obtained from near the bottom of a core taken from a Sheep River valley bog near Turner Valley (Jackson 1980:10, corrected for isotopic fractionation as reported by Mott and Jackson 1982:504). This site is 60 km north of Plateau Mountain; the dates are near or at the commonly supposed time of Late

Wisconsinan glacial maximum in the area. On the basis of this and other evidence, Jackson concluded

1. that the Sheep and other major foothills valleys in the area were ice-free at the height of the Late Wisconsinan stage; and

2. that the prairies and foothills above 1036 m in this region (effectively a corridor parallelling the East Slopes between southeastern Calgary and the mountain front) have remained ice-free since at least the Early Wisconsinan.

Stratigraphic and palynological analysis of the Sheep valley bog core shows a sparse, treeless, herbaceous, tundra-like environment existed in the general area at the time (Mott and Jackson 1982). Pollen of grasses, sedges, sage, a variety of other herbs and some shrub taxa (especially willow and alder) was present, but the total pollen influx was low, suggesting that total terrestrial vegetation was sparse. The immediate environment was able to support a variety of aquatic life. Fragments of two submergent aquatic moss species were found, one of them abundant. Snail and clam shells also were common. Pollen of vascular aquatic plants (*Potamogeton, Hippuris, Myriophyllum*) was present. The existence of these latter plants, which are generally absent from cold glacial mountain lakes in this region today (e.g., Anderson 1971, Mayhood and Anderson 1976:243-244), shows that aquatic habitats in the Ice-free Corridor at the Late Wisconsinan glacial maximum were not necessarily severely rigourous ones. The regional habitat perhaps was comparable to that of the tundra localities presently occupied by Arctic grayling in much of northern Canada and Alaska (Lee et al. 1980:120, Lindsey and McPhail 1970:124; cf. Rowe 1972:Pocket Map, Dansereau 1957:96,98).

These observations are strong evidence that at least one species of salmonid was present in the proposed refugial area at the beginning of the Late Wisconsinan, that both the local area and the general region were ice-free throughout the Late Wisconsinan, and that some aquatic environments were capable of supporting aquatic organisms, thereby providing the minimum conditions for salmonid survival. The problem is that, although many other cold-adapted fishes are native to the area in historical times, grayling are not (McIllrie and White-Fraser 1983, Sisley 1911, Prince et al. 1912). The crucial question now is: did grayling survive the Late Wisconsinan in a Bow-Oldman Refugium, becoming extinct there later for reasons unrelated to glaciation, or did the species fail to survive the postulated rigourous conditions of the Late Wisconsinan maximum? If the former, other fish species probably survived in the area also. The present evidence, however, is at least as consistent with the latter explanation.

Crossman and McAllister acknowledged that they knew of no endemics in the area that would constitute strong evidence of a refugium. They did note that several coldwater species are confined to the headwaters and do not extend into the South Saskatchewan even within Alberta, offering at least a suggestion that a refugium might have existed nearby. They suggested that Hudson Bay basin bull trout and mountain whitefish could have originated in this refugium as well as in Cascadia. They noted the remarkable occurrence of pygmy whitefish in the Oldman drainage (Waterton Lake) and the existence of isolated populations of lake trout and opossum shrimp *(Mysis relicta)* in Waterton Lake. All of these distributions they admitted could be as readily explained by the availability of coldwater habitat only in the headwaters, and postglacial invasion from elsewhere.

Of seven species they discussed as being restricted to the Oldman River above the South Saskatchewan, one (flathead chub) appears to have been included in error. It is well-documented as widespread in the Alberta portion of the South Saskatchewan and Red Deer rivers, but not in the Bow River (Paetz and Nelson 1970:135, Scott and Crossman 1973:485). Two species of sculpin previously reported for the Milk and St. Mary rivers and cited by Crossman and McAllister (1986) in support of a refugium (mottled sculpin and slimy sculpin) may have been misidentified in earlier literature. Roberts (1988a:121) recently found only shorthead sculpin in both rivers, out of 150 specimens examined. Roberts (1988a) also re-examined sculpins from Milk River identified as slimy sculpin, finding them to be shorthead sculpins. The four remaining species — pygmy whitefish, spoonhead sculpin, burbot and deepwater sculpin — are all coldwater forms that likely would be excluded by high temperatures from the South Saskatchewan, which beyond Lethbridge flows through one of the hottest, most arid regions in the prairie provinces (Longley 1972).

Apart from the Alberta records in the Milk and St. Mary rivers, the shorthead sculpin evidently has a very restricted distribution, being known outside of extreme southwestern Alberta only from the Puget Sound area (which includes the small, autonomous Chehalis refugium — McPhail and Lindsey 1986) and the Columbia basin, including the upper Flathead drainage in BC (Scott and Crossman 1973:836, Hughes and Peden 1984). Recently, Peden et al. (1989) found shorthead sculpin from southern Alberta to be morphologically distinct from most other known populations, resembling only specimens from the Flathead basin in British Columbia. Its apparently very restricted occurrence in the Milk (Missouri) and Oldman drainages could be explained by survival in an upper Missourian, Cascadian or Bow-Oldman refugium. Relying on distribution data for this species is risky because, as Roberts (1988a:121) and Peden et al. (1989) indicated, it is easily confused with mottled sculpin or other species, even by competent fish biologists, and requires taxonomic revision.

There is ecological evidence suggesting that western and northern populations of spoonhead sculpin differ from eastern populations. Distributional evidence suggests that western and northern populations may be derived from fish that survived Wisconsinan glaciation in the upper Missouri drainage or within the Ice-free Corridor. These matters are discussed in detail in the species account for spoonhead sculpin.

Waterton Lake pygmy whitefish are meristically distinct from numerous other populations in British Columbia, the north and Lake Superior, and possibly have been derived from a refugium in the nearby Missouri headwaters (Lindsey and Franzin 1972). The data of these authors also would be consistent with a refugium in the Bow-Oldman area.

It is worth noting that two other highly disjunct populations, both invertebrates, exist in upper Waterton Lake: the planktonic calanoid *Senecella calanoides* and the benthic amphipod *Pontoporeia hoyi* (as *P. affinis*, Anderson and Green 1975, 1976). Waterton Lake thus contains the common deepwater faunal assemblage (*Senecella, Pontoporeia, Mysis*, deepwater sculpin) characteristic of deep basins occupied by proglacial lakes during retreat of Wisconsinan Laurentide ice, or which received drainage waters from those lakes (Dadswell 1973). The one remaining freshwater member of this group not found in Waterton Lake, *Limnocalanus macrurus*, is thought to be competitively excluded from many waters by *Senecella* (Dadswell 1973:68), but may have had access to the lake originally. This species association in Waterton is evidence of a common origin with the many other Shield lakes having the same assemblage. The deepwater assemblage may be disjunct here only because there are no other suitably deep natural lakes between Waterton and the edge of the Shield.

A few native populations of lake trout exist in Montana immediately south of Crossman and McAllister's proposed Bow-Oldman Refugium. Lindsey (1964) reasoned that they either arrived there from the Yukon via the Ice-free Corridor, or survived glaciation in place, south of the ice. Khan and Qadri (1971) invoked the latter hypothesis, suggesting that lake trout moved northward from Montana with the retreating ice to found the morphologically distinctive populations they found in the Peace River drainage. They did not actually include the characters of the lake trout from the putative Montana refugium in their analysis, however, so it is not possible to judge whether the remnant Montana populations are distinctive.

Crossman and McAllister (1986:60) distinguished two groups of lake trout assignable to Beringian and Mississippian refugia, based on meristic differences. Two populations south of Waterton Lake in Montana (St. Marys Lake? and ?) fell into the group apparently derived from a Mississippian refugium, and all other populations surrounding the Waterton population were Mississippian as well. The Montana grouped data, however, were an extreme within the Mississippian cluster, suggesting they might at least form a subgroup. This subgroup, if real, would constitute evidence supporting the existence of the Waterton Lake-Montana Refugium considered by Black (1983a).

The presence of the airbladder nematode *Cystidicola stigmatura* in lake trout from Waterton Lake would offer strong evidence supporting a Mississippian origin for this population, but it is absent (Black 1983a:1247-1248). Similarly, the presence of the strain of *Cystidicola farionis* able to reach sexual maturity in lake trout in the Waterton population would offer strong evidence of a Beringian origin (as suggested by Lindsey 1964), but only immature worms were found (Mudry and Anderson 1977, Black 1983b:2037). The absence of these features in the Waterton Lakes population of lake trout does not constitute evidence for a separate refugium, it simply fails to refute that hypothesis.

The lake whitefish of Waterton Lake is genetically unusual with respect to at least one enzyme system. This population has by far the highest frequency of *G3PDH-1*b* allele, and the second-lowest frequency of the *G3PDH-1*a* allele, of more than 74 North American populations and subpopulation stocks studied outside the Maine-New Brunswick region (Franzin and Clayton 1977:625, Foote et al. 1992:768, Bodaly et al. 1992:771[2]). It is clearly anomalous in its immediate region in this respect. Although this population is identified as transplanted by Lee et al. (1980:80), it almost certainly is native. "Whitefish", as distinct from "grayling" (mountain whitefish), were present in 1890 in lakes of the Pincher Creek district (which included Waterton Lakes; McIllrie and White-Fraser 1983:38; see also Ward 1974:22). There is no record of lake whitefish stocking (Waterton Lakes National Park fish stocking records), and Paetz and Nelson (1970:72) considered this population as "probably native." Even large frequency differences among small numbers of alleles on their own do not prove great genetic isolation and divergence among stocks (Allendorf and Phelps 1981). Frequencies of isozyme alleles are prone to chance variation and perhaps sometimes to selective pressures. The advent of new alleles, however, must be a rare occurrence. If the Waterton Lake population survived the Wisconsinan in a Bow-Oldman Refugium, an allele unique to Waterton lake whitefish would be good evidence of it, but none has been found in the ten enzyme systems studied to date. The distinctive allele frequencies observed might have arisen in Waterton lake whitefish during relatively long isolation *in situ*, as could have happened in a Bow-Oldman refugium, but are not strong evidence of such a refugium.

Donald and Patriquin (1983) studied wing length in three lake-dwelling species of stonefly from the Continental Divide region of Alberta, British Columbia and Montana. They observed that shorter wing lengths were associated with greater lake age, and suggested that selection might have produced short-wingedness (brachypterism) over recent millennia. The shortest wing lengths for two species in their study samples, *Capnia confusa* and *Utacapnia trava*, were found in Waterton Lakes and nearby Upper and Lower St. Mary lakes, Montana, all part of the Oldman drainage in the extreme southern end of the Ice-free Corridor (Prest 1984:Map 1584A). Both sets of lakes were estimated to have been ice-free since before 50,000 yr BP (i.e., since at least the mid-Wisconsinan nonglacial period, Table 2). Their interpretation, if correct, implies that these lakes served as refugia for at least these two species through at least the latter portion of the Wisconsinan.

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2 The symbol for Waterton Lake in Figure 1b of Bodaly et al. (1992:771) is incorrect. Reference to the original published data (Franzin and Clayton 1977:625; cf. Foote et al. 1992, their Table 2 and Appendix 1) shows that the clear sector coding for the a allele should be hatched to code for the d allele.

Significantly *U. trava* in Crowsnest Lake, also part of the Oldman drainage in the same region, did not have especially short wings. This lake lies on the edge of the Ice-free Corridor, but was judged to be much younger than the St, Mary or Waterton lakes. It lies nearly on the Continental Divide in a major low pass, where it would have been highly susceptible to glaciation by eastward-flowing Cordilleran ice.

In a similar study of a stream-dwelling stonefly in the mountains of Alberta and British Columbia, Donald (1985) showed that in small streams, *Sweltsa revelstoka* had shorter wings in Waterton Lakes National Park than in an icefields area further north. He suggested that short wing length in small headwater streams was due to the absence of any functional value for wings in such habitats, and that there would be selection against individuals that have long wings and fly. The Waterton populations had been able to evolve shorter winglengths than the icefields populations because the Waterton area had been free of ice for much longer. He suggested that his Waterton study area had been ice-free since at least the Late Wisconsinan, and quite possibly since the Early Wisconsinan glacial maximum (Donald 1985:234). The short-winged populations of *Sweltsa revelstoka* thus may constitute evidence of a refugium for the species in Waterton Lakes National Park.

A rare calanoid, *Hesperodiaptomus victoriaensis*, is known within the Ice-free Corridor zone from a single pond in the Willow Creek drainage headwaters, Oldman River basin (Anderson 1967b, 1968b). The pond is on the northeast flank of Plateau Mountain approximately 4.5 km north of January Cave, where Crossman and McAllister (1986) reported finding the grayling scales described above. There is geological evidence that this mountain was unglaciated (Beatty 1975:47-48, Burns 1980:1510).

When found, this was one of just four known populations, and the only one known outside of the Arctic (Anderson 1968b:8). More recent collecting over an extensive area of the Rocky Mountains, foothills and adjacent prairies (Anderson 1974c), has failed to locate any other southern populations. Whether the species produces resting eggs is unknown, but they are common among calanoids. The Alberta habitat, a pond with widely variable water levels, might require that the species overwinter as resting eggs. Resting eggs potentially give a species great ability to disperse, so it is possible that long-distance transport of resting eggs by migrating Arctic birds could have produced the Alberta population. The rarity of the animal in the proposed source area makes this explanation unlikely, and its restriction to waters in or near known glacial refugia suggests its dispersal or colonization abilities in fact are weak.

Its apparent confinement to or near known ice-free areas suggests that *H. victoriaensis* is a true glacial relict. Its habitat holds no fish: the widely fluctuating water level renders the pond unsuitable for fish, and *Hesperodiaptomus* probably could not survive in the presence of fish in such a simple environment ( see evidence discussed in Part 1). Thus even if this interpretation is correct, the presence of *H. victoriaensis* does not constitute direct evidence that the area was a refugium for fish.

For theoretical reasons discussed at the end of the next section, however, it does suggest that the ice-free refugium in which it survived either was associated with others (i.e.; it probably was not extremely isolated from similar ice-free areas), or was large rather than small. In either case, a nearby refugium for fish is more likely than this single relict occurrence of a fish-intolerant organism might at first suggest.

The biological evidence still is insufficient to reject the conservative hypothesis that fishes and aquatic invertebrates in the southern Ice-free Corridor area survived glaciation elsewhere and invaded the area postglacially. The grayling fossil possibly of late Wisconsin age, the number of disjunct or otherwise distributionally unusual aquatic populations, and certain meristic and genetic peculiarities of fishes in the area all are consistent with the idea of an Ice-free Corridor refugium in southwestern Alberta, but most also can be explained without invoking a Bow-Oldman Refugium for fishes. The geological and biological evidence considered so far is stronger for a Montana (upper Missouri) refugium of which the proposed Bow-Oldman Refugium would have been an extension by virtue of its drainage and proglacial lakes. A careful study of intraspecific variation in western Alberta taxa throughout their ranges could cast light on the degree of isolation these populations have experienced in the region.

### *Banff-Jasper Refugium*

Crossman and McAllister (1986) point to the Banff longnose dace, and Bajkov's (1927) reports of distinctive longnose sucker, rainbow trout, and pearl dace as fishes that may be endemic to the Banff-Jasper region, but that all required taxonomic confirmation. They also cited the existence of three subterranean aquatic Crustacea and two gastropod molluscs that were endemic to the region as evidence favouring a refugium for fishes and aquatic invertebrates in the Banff-Jasper area.

Renaud and McAllister (1988) have since presented meristic evidence that, in their view, establishes the Banff longnose dace as a distinct subspecies endemic to Banff, a subspecies they believe is now extinct. Their data show that the Cave and Basin population of longnose dace originally described as the Banff longnose dace subspecies (Nichols 1916) had substantially fewer pored lateral line scales, on average, than do longnose dace populations in the adjacent Bow River, the rest of southern Alberta, British Columbia and Wyoming[3]. The original Banff longnose dace population also typically had seven dorsal rays, one fewer than the comparative populations, none of which had any specimens with so few dorsal rays. Finally, the original Banff longnose dace may have been substantially smaller than the typical form: the lack of information on collecting methods for the original specimens makes this conclusion uncertain.

The validity of the subspecies designation for the original Cave and Basin population

3 The Banff Cave and Basin population had 11.86 fewer scales, on average, than the typical form, or 18.1% fewer in proportional terms.

is disputed by some, who feel that the observed differences may not be genetically determined, but instead may be due to the effects of living in a high-temperature habitat (e.g.; P. Wiebe, personal communication). Meristic characters in fish are strongly influenced by environmental factors, especially temperature during early development (Strauss and Bond 1990:117). Temperature may act differently on different meristic traits, and intermediate temperatures can have greater effects than either high or low temperatures on some meristic traits (Lagler et al. 1977:309). Some meristic characters are also positively correlated with size (Lindsey 1975).

Renaud and McAllister (1988:104-105) acknowledged that sometimes lower dorsal ray and lateral line counts *are* found in hotspring populations of *Rhinichthys* (the genus in question) than in those living in nearby cool streams. They argued, however, that to account for the observed changes in dorsal ray and scale counts and their variance with time in the Cave and Basin population, any environmental factor must have shifted also, and must have been most variable during an intermediate period. They were unable to find any such trends in the temperature and water chemistry data available to them, so concluded that the available data do not support the hypothesis that the lateral line and dorsal ray counts were primarily determined by environmental conditions during development. Renaud and McAllister conceded that “some unknown sequence of environmental events” might have produced the observed meristic changes in the population, ruling it out only on the grounds that this interpretation required additional assumptions.

These arguments and others made by Renaud and McAllister (1988) in support of the taxonomic distinctiveness of the Banff longnose dace are reasonable given the available information. Their principal problem is that they are forced to rely heavily on the *lack* of adequate data supporting other interpretations. Particularly important is the absence of continuous temperature data and detailed reliable observations on other changes to the physical environment of the pond and hotsprings at the Cave and Basin. We know many other environmental changes have occurred that could have affected, for example, the temperatures to which the dace population was exposed, but the necessary details apparently are undocumented. (Renaud and McAllister use what is generally known about such changes in interpreting the causes for the population’s decline.)

Until less equivocal evidence is available that the observed differences were genetically determined, or that there are other genetic differences between the Banff longnose dace and the typical form, the taxonomic status of this proposed endemic will remain in question. Biochemical genetic studies on museum specimens are now being considered to help resolve this issue (T. Hurd, personal communication). Experimental work on the effects of temperature on the meristics of longnose dace, especially the present Cave and Basin population, likewise could assist in settling the dispute. In any case, whether the Banff longnose dace constitutes evidence of an East Slopes refugium for fish remains uncertain. Renaud and McAllister (1988:110) suggested that this fish might have either evolved postglacially from populations that survived the Wisconsinan in southern Alberta or Montana, or survived in place in a local or larger East Slopes refugium.

Evidence for the existence of an endemic subspecies of longnose sucker presently known from only a single Jasper lake has been presented at a scientific meeting (Camus and McAllister 1984), and is available as an internal manuscript of the Canadian Museum of Nature (McAllister and Camus 1984), but has not been published. Data and photographs presented by Bajkov (1927) describing a new subspecies of longnose sucker from four Jasper lakes were re-examined in this report (Section III). These data suggest that Bajkov's Jasper longnose sucker differed from typical longnose sucker (and from two other sucker species with which it might be confused) in several taxonomically-important respects. The available data tend to support the view that the Jasper longnose sucker is a valid subspecies endemic to Jasper National Park.

The existence and distinctiveness of the Athabasca pearl dace remains to be confirmed. As is discussed in the individual account of this species, Bajkov's (1927) scale counts suggest that if it is a pearl dace it is a distinctive form, quite different even from the typical population in nearby Obed Lake.

Jasper native populations of rainbow trout have not yet been examined to confirm Bajkov's (1927) distinctions in this species. Certain genetic data recently made available for one rainbow trout population in the Athabasca headwaters, however, are consistent with a refugium in or near the Ice-free Corridor for this species. The evidence is discussed in detail in the species account for rainbow trout. Briefly, an apparently pure native stock of rainbow trout in Wampus Creek immediately east of Jasper Park lacks two alleles that are common in rainbow/steelhead stocks of the middle and lower Columbia River drainage, and carries one allele at reasonably high frequency that is absent from Columbia River stocks. This is strong evidence that the Wampus Creek stock was not derived postglacially from a refugium in the Columbia drainage as prevailing hypotheses of postglacial dispersal in this species suggest (e.g., McPhail and Lindsey 1970:161, Behnke 1972:652). The stock must have come from some other refugium.

In the data made available to me for this report, there is some genetic similarity between steelhead stocks in the Skeena drainage and the Wampus Creek rainbow stock, which suggests that they may have been derived from a common source. Perhaps Wampus Creek rainbows were derived from a stock that survived glaciation north of the Alaska Peninsula, reaching the Athabasca headwaters via the Skeena by means of a series of headwater transfers. The problem with this interpretation is that the LDH-4(76) allele, which is absent from the Wampus Creek stock, is said to exist in the Skeena rainbows (L. Carl, personal communication). Furthermore, this hypothesis is not well supported by the present distributional evidence, which instead supports McPhail and Lindsey's (1970:161) view that rainbows from the Alaskan refugium dispersed very little postglacially.

The only remaining known area free of Late Wisconsinan ice that could have served as a refugium for rainbows is the Ice-free Corridor east of the Canadian Cordillera. But if rainbow trout did survive in the Corridor, it is not clear why they did not spread more widely along the East Slopes or eastward, taking advantage of the many proglacial lakes. Additional work on geographic variation in this species is needed to sort out these problems.

The two endemic molluscs cited by Crossman and McAllister (1986:87) as evidence of a Banff-Jasper Refugium are snails known as the Banff Springs physa, *Physa johnsoni*, and the blunt albino physa, *Physa jennessi athearni*. Alternative explanations for their endemicity are considered below.

*P. johnsoni* is known only from several hot springs, one cold spring, and their outlets in the immediate vicinity of Banff townsite (Clarke 1973:382, 1981:165). It is obviously distinct from, but apparently most closely related to, *P. gyrina*, also found locally (Clarke 1973:368, 376-377, 382-383). There is presently no evidence of gene flow between *P. johnsoni* and *P. gyrina*, according to Clarke (1973:368). The close association of *P. johnsoni* with hotsprings at Banff suggests that the hotsprings themselves served as a Wisconsinan refugium for this species, where it evolved in place.

It might be argued that the highly unusual hotspring habitat could have induced rapid speciation in *P. gyrina* to produce *P. johnsoni* in postglacial times. If so, a local Wisconsinan refugium need not have been present to allow this particular endemic to evolve. The problem with this explanation is that it requires an additional hypothesis to explain how *P. gyrina* populations became reproductively isolated, even though they were readily accessible to each other in adjacent hotspring and normal habitats. It is therefore less likely to be true than the hotspring refugium hypothesis.

*P. jennessi athearni* has been recorded only from Johnson Lake, Banff National Park; Horseshoe Lake, Jasper National Park (the type locality); and a marsh “1 mi W of Dapp Creek, 4.5 mi W of Rochester, Alta.” (Clarke 1973:367, 1981:162). The latter site is in the Pembina River-Athabasca River drainage halfway between Edmonton and the town of Athabasca, and appears to be the record thought by Crossman and McAllister (1986:87) to be in a marsh 16 km downstream of Jasper in the Athabasca system. The subspecies still is endemic to the general vicinity of the Ice-free Corridor.

The type locality for this endemic is also the type locality for the subterranean isopod *Salmasellus steganothrix* (see below). Like *S. steganothrix*, *P. jennessi athearni* is albinistic, characteristic of organisms that occupy subterranean habitats. A few other subterranean snails, especially *Physa*, are known (Pennak 1989:554, as *Physella*). Clarke (1973:367), however, described what was known of the habitat of *P. jennessi athearni* as small to medium-sized lakes and marshes with open water, on rock and gravel. If it also uses subterranean habitats, it might have survived the Wisconsinan there, as has been suggested for other subterranean organisms (Holsinger 1980, 1983; see discussion below).

The three endemic subterranean Crustacea cited by Crossman and McAllister (1986:87) as evidence of a Banff-Jasper Refugium are the isopod *Salmasellus steganothrix*, and the amphipods *Stygobromus canadensis* and *Stygobromus secundus. Stygobromus canadensis* is known only from Castleguard Cave, Banff National Park (Holsinger 1980, Holsinger et al. 1983), and *Stygobromus secundus* is known only from one spring 24 km southwest of Rocky Mountain House (Bousfield and Holsinger 1981).

Only *Salmasellus steganothrix* is known from more than one location. This small, blind, white isopod was described as a distinctive new genus and species from specimens in the stomach of a rainbow trout collected in Horseshoe Lake, Jasper National Park (Bowman 1975:349). It has since been reported from a cavespring immediately east of Jasper Park at Cadomin (Clifford and Bergstrom 1976), in Castleguard Cave, Banff National Park (identification by T. Bowman — J.S. Mort and A. D. Recklies, personal communication 16 May 1978), and in Deadhorse Cave, a large lava tube in Skamania County, Washington (J. J. Lewis identification, reported by Holsinger et al. 1983:545). It also occurs in Many Springs, Bow Valley Provincial Park, Alberta (D. W. Mayhood, unpublished data, identification confirmed by H. Clifford); and in a pond on Coronet Mountain, Jasper National Park (R. D. Saunders and D. W. Mayhood unpublished data, identification confirmed by F. Rafi). Specimens identifiable as *Salmasellus* sp. have been found in the stomach of a cutthroat trout captured in Peyto Lake, Banff National Park (R. S. Anderson and R. D. Saunders, unpublished data) and in groundwater adjacent to Wahkeena Creek, Multnomah County, Oregon (Bousfield and Holsinger 1989:968).

The Oregon and Washington records show that the genus *Salmasellus* is not endemic to the Banff-Jasper region. If the species identification by J. J. Lewis for Deadhorse Cave is accepted, then the species *Salmasellus steganothrix* is not endemic to the Banff-Jasper region either, although its known Alberta populations are disjunct from the others. Holsinger (1980, 1983) argued that the occurrence of this species and *Stygobromus canadensis* in Castleguard Cave, which lies beneath a present-day icefield and drains its meltwaters, constitutes strong evidence that groundwater itself could have served as a glacial refugium for subterranean aquatic organisms. In other words, these three species may have been capable of surviving beneath the Pleistocene glaciers and may not have required an area on the surface that was free of ice. For this reason their presence is not especially strong evidence of an ice-free glacial refugium for fishes in the Banff-Jasper area.

To the biological evidence of a Banff-Jasper Refugium mentioned by Crossman and McAllister (1986) might be added some other considerations. There is evidence that lake whitefish in most of British Columbia are members of a race distinct from those that survived in Beringia and the Missouri-Mississippi refugium (Foote et al. 1992). This stock, termed the Nahanni race, is thought to have originated in the vicinity of the South Nahanni River in the extreme southwestern corner of the North West Territories within the northern portion of the Ice-free Corridor (Figures 1, 3 and 4). Foote et al. (1992:768) assigned the Talbot Lake population of Jasper National Park to this stock, and identified the populations just to the east in Utikuma (Peace drainage), Lesser Slave (Athabasca drainage) and Wabamun (North Saskatchewan drainage) lakes as introgressed stocks of Mississippian and Nahanni origin. Foote et al. (1992:763,765) suggested that the Talbot stock (and by implication the Utikuma, Lesser Slave and Wabamun stocks, in part) arrived from the Nahanni refuge either during the Wisconsinan or early in deglaciation by dispersing southward along the Ice-free Corridor.

The Talbot Lake population, however, is distinguished by a unique allele, *LDH–A–2*b* , which is not present in any of the other 23 populations examined for it, including 10 pure or introgressed Nahanni race populations (Foote et al. 192:768, Bodaly et al. 1992:770). This suggests that the history of the Talbot Lake stock differs from the rest of the Nahanni race examined to date for *LDH–A–2** alleles. (Data on *LDH–A–2** alleles in other populations to which Talbot lake whitefish may be closely related, including those nearby in the headwaters of the Fraser, Peace and North Saskatchewan systems, have not been published as yet.) These observations are consistent with the view that the Talbot Lake stock may have survived at least the latter part of the Wisconsinan in a refugium separate from the rest of the Nahanni race. The nearest possible location for such a refuge is the Ice-free Corridor in western Alberta. Alternatively, it is conceivable that the *LDH–A–2*b* allele arose more recently in the Talbot Lake population or its progenitors. Bodaly et al. (1992:778) supported Behnke (1972) in suggesting that fishes might evolve rapidly over small geographic areas while colonizing recently deglaciated regions. It is not obvious on the available evidence which of these alternative explanations is the more probable.

Paetz and Nelson (1970:242) drew attention to Bajkov's (1927:24) record of a sculpin having palatine teeth, *Cottus punctulatus* (Gill), in the Athabasca and Maligne rivers in Jasper National Park. They state that this species is now recognized as a subspecies of *Cottus bairdi*, the mottled sculpin, a species that otherwise is not known from Alberta — Roberts (1988a) recently reidentified the only reported populations as *C. confusus*, the shorthead sculpin. The only sculpin reported for the upper Athabasca system in or near Jasper Park is the spoonhead sculpin, *Cottus ricei* (Ward 1974:32, Roberts 1988a), a species that lacks palatine teeth (Paetz and Nelson 1970:247). The slimy sculpin, *Cottus cognatus*, occurs in Smoky River headwaters immediately north of the Athabasca drainage near Jasper Park, but rarely has palatine teeth, and then only a few (Roberts 1988a:122).

Bajkov (1927:26) actually stated that his sculpin was found on “both slopes of the Rocky Mountain region”. He gives a description of a single specimen, but it is insufficient to determine species. There are several species with palatine teeth on the Pacific slope, but only two known in the Fraser drainage (Scott and Crossman 1973): *C. asper*, the prickly sculpin, below Prince George; and torrent sculpin *C. rhotheus* in the North Thompson River. The presence of a sculpin with palatine teeth in the upper Athabasca drainage might have significance for the hypothesized Banff-Jasper Refugium, but requires confirmation.

Some distributional and ecological evidence suggests that spoonhead sculpin stocks on the Rocky Mountain East Slopes may have survived the Wisconsinan in the Ice-free Corridor. The idea is discussed in detail in the individual account for this species.

Short-wingedness (brachyptery) in stoneflies is related to time since deglaciation in the Cordillera of Alberta, British Columbia and Montana (Donald and Patriquin 1983, Donald 1985). Short-winged populations of at least three species in the region typically are associated with lakes or streams that have been unglaciated for a relatively long time; thus short-winged populations may constitute evidence of ice-free refugia in the immediate area.

Donald and Patriquin (1983:924) published wing length data for *Capnia confusa* and *Utacapnia trava* from nine lakes in or near Banff and Jasper national parks: Rock, Yellowhead, Twintree, Hector, Moraine, Maligne, Bow, and two Geraldine lakes. None of these populations was especially short-winged, suggesting that their lakes were not part of the postulated Banff-Jasper Refugium of Crossman and McAllister (1986). The time of deglaciation for all of these lakes based on independent geological evidence ranged from 12,500 to 10,000 BP; i.e., all were known or suspected to have been glaciated during the Late Wisconsin. Donald (1985) included the Banff-Jasper region in his analysis of short-wingedness in *Sweltsa revelstoka*, but his analysis grouped these populations with many others in British Columbia (his "icefields" group). One of the icefields populations had relatively short wings (Donald 1985:236), but the site was not identified.

Two arctic fairy shrimps have disjunct distributions in the proposed Banff-Jasper Refugium in Alberta. Hartland-Rowe and Anderson (1968) recorded *Artemiopsis stefanssoni* from Dolomite Pond in Banff National Park. This species is widely distributed in coastal ponds of the Arctic Archipelago and the west coast of Greenland. The Dolomite Pond population, the only inland one known, lies approximately 1800 km south of its nearest neighbour at Bernard Harbour on the Arctic coast (Daborn 1977:281). All but one of the 15 Arctic locality records for this species are from coastal, ice marginal or Wisconsinan unglaciated areas (Daborn 1977:281, cf. Prest 1984:Map 1584).

The second fairy shrimp, *Polyartemiella hazeni*, is a rare species recorded from the stomach of a rainbow trout at Wampus Creek, immediately east of Jasper Park (Daborn 1976). Other than this record more than 1600 km south of its next occurrence, the species has "a strictly western Arctic distribution, … occurring primarily above the tree line" (Daborn 1976:2027). In fact, all but one of the six northern records lie in or immediately adjacent to areas that never have been glaciated (Daborn 1976, cf. Prest 1984:Map 1584A); i.e., in Beringia. The sixth, an island in Great Bear Lake that definitely was glaciated, lies over 400 km east of the northern arm of the Ice-free Corridor, a geographic extension of Beringia. Glacial Lake McConnell inundated Great Bear Lake and the island during deglaciation (Prest et al. 1967:Map 1253A). The western extremity of this lake lay about 75 km from an unglaciated (Late Wisconsinan) highland that drained into it, and about 100 km from the Ice-free Corridor on the east slopes of the Mackenzie Mountains (Prest 1984:Map 1584A).

Migratory waterfowl have been invoked as the agents responsible for dispersal to the disjunct Alberta locations in the case of both fairy shrimp species (Hartland-Rowe and Anderson 1968:425, Daborn 1976:2027). The confinement of Arctic *Polyartemiella hazeni* to a known Pleistocene refugium or to adjacent areas readily accessible via drainage during deglaciation suggests that its ability to disperse is very limited, arguing in favour of survival of the Wampus Creek population in a nearby ice-free area. The proposed refugial area of Mountain Park or the Ice-free Corridor are the obvious choices. Similarly, the fact that the Arctic populations of *Artemiopsis stefanssoni* are apparently confined to coastal, ice-marginal or Wisconsinan ice-free areas, with no known inland populations apart from that in Banff Park suggests that it lacks the ability to disperse inland, perhaps for reasons related to its unique habit of retaining its eggs within the female until hatching (Daborn 1977:283). *A. stefanssoni* probably survived the Wisconsinan in a nearby ice-free refugium, i.e., in the postulated Banff-Jasper Refugium.

Like *Hesperodiaptomus victoriaensis*, both fairy shrimp species typically occupy ponds that would probably be incapable of supporting fish, and their populations are probably incapable of sustaining themselves in the face of predation by fish. The existence of refugia for these species is therefore not direct evidence of refugia for fish, but may constitute indirect evidence of refugia for other aquatic organisms (including fish), for reasons discussed in the next paragraph.

It might be argued that refugia for all three species need not have been large: possibly even a single pond for each could have sufficed. In theory, however, larger refugia are more likely because extinction rates are much higher on very small “islands” than on larger ones (MacArthur and Wilson 1967). Species with weak dispersal or colonization abilities are particularly susceptible to extinction, and the distributional evidence suggests this applies to the three species discussed here. Put another way, the survival of these three species over thousands of years in ice-free refugia is evidence in itself that the refugia were not merely tiny isolated enclaves. If tiny, they most likely were not isolated, but close to other similar habitat islands (thus were large refugia, in effect); if truly isolated, they most likely were large contiguous ice-free areas. Furthermore, their wide distribution over nearly 400 km of the East Slopes suggests that the region generally was a Late Wisconsinan ice-free refugial area, consistent with the most widely favoured geological interpretation. In any case, the implication is that nearby refugia also may have existed for fish.

Though still as yet inconclusive, evidence is continuing to build that the Ice-free Corridor and perhaps associated ice-free areas in the vicinity of Jasper and Banff national parks served as a refuge from Late Wisconsinan glaciation for some aquatic invertebrates and fishes. Among the aquatic invertebrates, at least three species *(Physa johnsoni, Stygobromus canadensis* and *S. secundus)* and one subspecies *(P. jennessi athearni)* appear to be endemic to the region, although the two *Stygobromus* species and *P. jennessi athearni* may not have required an ice-free surface refuge. Single populations of two other small crustaceans, *Artemiopsis stefanssoni* and *Polyartemiella hazeni*, are highly disjunct in this area, and there is reason to think they are relicts. Among the fishes, the Banff longnose dace and the Jasper longnose sucker may be endemic subspecies. At least one population of rainbow trout native to the Athabasca headwaters, the only one yet studied by the appropriate techniques, is highly distinctive genetically. It apparently was not derived from other known refugial stocks. The population of lake whitefish in Talbot Lake likewise is genetically unique, carrying one isozyme-coding allele not found in any other of the proposed refugial races of this species. Two other fishes said to be distinctive at the subspecies level have been described from Jasper National Park, but require confirmation.

## *Postglacial Dispersal in the Ice-free Corridor*

Even if some fishes found isolated refuge from Late Wisconsinan glaciation in the Ice-free Corridor of southwestern Alberta, they would have been exposed to introgression by invading stocks as the ice retreated from western Canada. This would have tended to homogenize the stocks, in particular making any divergent Corridor stocks less distinguishable from the invading types. But if introgression did occur, distinctive Corridor alleles will still be present, and Corridor stocks that were able to remain isolated from invading stocks should be expected in the region, although their ranges may be limited. The Nahanni race of lake whitefish, a northern Ice-free Corridor fish that may have used the Corridor to disperse southward, nicely illustrates this phenomenon in western Alberta (Foote et al. 1992).

With deglaciation, the first exposure of Corridor stocks in southwestern Alberta would have been to upper Missouri fishes. As McPhail and Lindsey (1970:14) observed, the rapid northeasterly retreat of Laurentide ice from the western plains would have given upper Missouri River fishes access to western and northern Canada before Mississippi River fishes could have reached the area. Paetz and Nelson (1970:4) pointed out that in the early stages of deglaciation there were many proglacial lakes and drainage shifts in northern Montana and southern Alberta that could have allowed upper Missouri River fishes access to waters of the East Slopes in Alberta. Also, much of the Ice-free Corridor may have been accessible to upper Missouri fishes even at the Late Wisconsinan glacial maximum, because drainage from the Corridor would have been southward to the Missouri at that time.

Northward postglacial dispersal of upper Missouri fishes via the waters in the Corridor region has been suggested to explain the existence of several native fish stocks in western Canada. This explanation sometimes requires one to assume that the species later became extinct in the upper Missouri, because it does not now occur there. Particularly in the latter cases a stronger argument can be made that these fishes survived the Late Wisconsinan in the Ice-free Corridor of Alberta.

## Conclusion

The most conservative and best supported view of fish biogeography in western Canada is that all fishes were forced out of what is now Alberta and British Columbia (including the Jasper area) by the advancing ice of the Wisconsinan glaciations. Under this hypothesis, most of Alberta's fishes survived the Wisconsinan in refugia in the Mississippi-Missouri river basins, moving northward with the retreating ice front to recolonize our waters. A smaller number of our fishes are thought to have survived in Cascadia in the middle and lower Columbia River basin south of the Cordilleran ice, and a very few are considered to have survived in a Beringian refugium in Alaska and/or the Yukon.

This view is founded on geological interpretations that considered the Late Wisconsinan to have been a time of intense glaciation in which all of Alberta and British Columbia were completely covered by glaciers except for a few isolated mountaintops. But more recent interpretations judge the Late Wisconsinan glaciation in our area as having been far less extensive than previously believed. Evidence is mounting that there existed at the height of the Late Wisconsinan a shifting Ice-free Corridor of variable width between the Laurentide and Cordilleran ice sheets. The Ice-free Corridor extended along the East Slopes in southwestern Alberta from unglaciated Montana northward to at least the Hinton area, and in the north from unglaciated Yukon southward along the eastern slopes of the Mackenzie Mountains to at least northern British Columbia. The Middle Wisconsinan was a nonglacial period in western Canada; thus in Alberta the Ice-free Corridor would have been unglaciated at least since the end of Early Wisconsinan times, or at least for the last 64,000 years. In extreme southwestern Alberta the Corridor was ice-free for an unknown distance northward from Montana at least since the end of the Illinoian 128,000 years ago, and conceivably for as long as 300,000 years.

Any fishes that survived in place in the Ice-free Corridor therefore would have had five times longer than previously believed, or more, to adapt to local habitats and perhaps to diverge from other stocks. Native stocks in this area thus may have unique characteristics not found in other stocks of the same species that survived the Wisconsinan elsewhere.

Evidence is accumulating to suggest that several types of aquatic organisms including fishes survived at least the Middle and Late Wisconsinan in and near the Ice-free Corridor in Alberta. The geological evidence is strongest for a refugium in the Corridor in the Montana-Waterton area, of which the postulated Bow-Oldman Refugium (Crossman and McAllister 1986) might have been a part by virtue of its drainage and proglacial lakes. Several pieces of evidence support the view that some fishes survived in or near the Corridor in the Banff-Jasper region, the Banff-Jasper Refugium suggested by Crossman and McAllister (1986). Table 3 lists some species that may have survived the Late Wisconsinan glacial maximum somewhere in the Ice-free Corridor.

Other explanations for certain unusual occurrences of aquatic animals in the vicinity of the Corridor cannot be ruled out. Especially important is the likelihood that the Corridor area was a major dispersal route during the early stages of deglaciation. Among the most likely to have used the route are species that survived the Wisconsinan in the upper Missouri, but have become extinct there postglacially, and others that survived in the northern Ice-free Corridor and used the Corridor to disperse southward. It is possible also that some distinctive Corridor fishes diverged since the end of the Wisconsinan during rapid deglaciation and colonization in the region.

Whatever the ultimate explanations may be, the region comprising the Ice-free Corridor and its adjoining areas, including Jasper National Park, appears to be highly significant in the biogeography of Alberta. It holds numerous aquatic organisms that are disjunct, genetically, morphologically or ecologically distinctive, or are otherwise unusual. For this reason alone (there are other important ones), preserving native aquatic biota, including native stocks of fishes, should be a major goal of resource management in this region.

# SECTION II

# HISTORY OF FISHES

# AND FISHING

# IN JASPER NATIONAL PARK

## Introduction

The National Parks Act and Canadian Parks Service policies require that in the fish management plan we give first priority to protecting the resources and maintaining the ecological integrity of Jasper National Park (Part 1). Ideally to meet these requirements, we must know what the fish stocks were like in their original undamaged condition: what species were present, and how abundant they were. It also would be helpful to know what intensity of human use the original stocks sustained, as a guide to what degree of use might be acceptable under present park conditions.

In this section I attempt to answer these questions by considering briefly what is known about the original peoples of the Jasper region regarding their use of fish. I then present an annotated listing and discussion of historical records mentioning fishes and fishing in the Jasper area.

## Aboriginal Fishing

The available evidence of prehistoric use of Jasper National Park by aboriginal people has been summarized briefly by Woodrow (1987a). The evidence is sparse, and is judged to be “very preliminary” (Woodrow 1987a:497). Woodrow does not mention whether any fishing-related prehistoric artifacts have been found within the park.

According to Woodrow (1987a:496), the existing data show more or less continuous occupation of the Jasper park area from approximately 11,000 years before the present. Peoples of the mid-prehistoric period (5500 BC to 750 AD) were said to have had a “well-organized, integrated hunting culture of substantial numbers…. On the eastern slopes of the Rockies, the focus was on spring fishing, and spring and fall elk and deer hunting” (Woodrow 1987a:479). He also quoted Reeves (1983), stating that early peoples probably “moved on a regular seasonal or multi-year basis between the eastern and western slopes of the Rocky Mountains.” It is likely that the Athabasca Valley–Yellowhead Pass route would have figured prominently in any such movements.

Gadd (1986:745), summarizing current knowledge in a popular-style account, stated that “major eastern-slope valleys seem to have been occupied, at least in summer, since the end of the Wisconsinan glacial period (20,000-11,000 BP).” He acknowledged that an ice-free corridor between the Cordilleran and Laurentide ice sheets most likely permitted access by prehistoric man to the eastern slopes at least through the late Wisconsinan, possibly during the period of ice retreat during the mid-Wisconsinan (64,000-20,000 BP), and perhaps even throughout the Wisconsinan. He pointed out that it most likely was closed by Athabasca valley glaciers contacting Laurentide ice east of the park during the early Wisconsinan (75,000-60,000 BP). During this time proglacial lakes and meltwater channels must have been abundant within the corridor (e.g., Reeves 1973:11, Alley and Harris 1974), providing much potential habitat for fish. The Ice-free Corridor idea is discussed in more detail in Section I.

Just prior to European contact (i.e., the late prehistoric period from 750-1730 AD), the Jasper area was used primarily by Dene (Athapaskan- speaking) natives, including Sarcee, Beaver and Sekani people (Rostlund 1952:305, Gadd 1986:745, Woodrow 1987a:478 -- Woodrow’s Maps A and B are transposed in relation to his caption). Shuswaps (Carriers) occupied the Rocky Mountain Trench west over the Yellowhead Pass, and there is said to be evidence of Shuswap occupation of the Athabasca valley near Jasper House (Gadd 1986:746). Kootenays used both western and eastern slopes of the Rocky Mountains at least as far north as the North Saskatchewan River, just south of the park (Gadd 1986:746).

After about 1730, the occupation by Europeans of eastern North America and their increasing trading activity in the west brought about large changes in the distribution of the aboriginal peoples. Assiniboines (now called Stoneys in Alberta) migrated from their home near Lake-of-the-Woods, ultimately arriving at the east slopes of the Rocky Mountains, including the Jasper area. They displaced the former occupants, especially the Kootenays, forcing them to remain on the western slopes. The Beaver people were displaced westward by the influx of Crees into much of northern and eastern Alberta, and the Sarcees moved southward out of the park area to the vicinity of present-day Calgary. In the 1800s small numbers of Iroquois, accompanying the fur trade westward, settled in the Jasper area (Woodrow 1987a, Gadd 1986).

Fishing figured most prominently in Shuswap subsistence. Shuswaps were known to have used nets made from Indian hemp, nettles, cedar bark or willow bark; weirs and traps; advanced fishing spears (harpoons, leisters) and spearing techniques (shading devices, carved decoys or lures, and spearing by torchlight at night from a canoe); and fish-hooks (Rostlund 1952:162-185, Cheadle 1931:164). They also used special clubs for dispatching fish, dried fish and roe for later use, and used advanced culinary techniques (at least two methods of partly decomposing fish parts before consumption) in preparing fish for meals (Rostlund 1952:193-199). The Kootenays, the southern neighbours to the Shuswaps on the western slope of the Rockies, were also accomplished fishermen (Rostlund 1952:164-198), but their country apparently did not extend as far north as Jasper National Park on the eastern slopes.

The Sekani and Beaver people were also known to have fished, but their fishing was not as elaborately developed as that of the Shuswaps. Both Sekanis and Beavers are known to have fished with nets, weirs and traps, fishing spears and fish-hooks (Rostlund 1952:162-195). Sekanis reportedly used nets of willow bark, leister type fishing spears, and to have dried fish for storage (Rostlund 1952:168,174,195). The Beavers are known to have used rawhide nets, but there is no record of them drying or smoking fish (Rostlund 1952:168,195). There is evidently no record that the other Dene people of the Jasper area, the Sarcees, fished; they are said to have lived entirely by hunting (Rostlund 1952:184,205).

Fishing also was indulged in by the Stoneys, the later principal inhabitants of the Jasper area. Although fish nets and fish-hooks apparently were unknown to them before contact with Europeans, and they are said not to have preserved fish by drying, it appears that they did use weirs and traps of stones, simple wooden spears, and bow-shot arrows to capture and kill fish (Rostlund 1952:164-196, Hector 1863:108). There is a modern assertion that they used sinew to snare trout and whitefish and, contradicting Rostlund (1952:196), that they dried and smoked these fish for winter use (Russell 1987:74). The Iroquois are known to have been well-versed in fishing in eastern Canada (Rostlund 1952:162-199), but their late arrival and small numbers in the Jasper area limit their relevance to fisheries in the region.

Direct evidence that aboriginal people actually fished in the Jasper area is limited. Shuswaps fished for trout in Yellowhead Lake, immediately adjacent to Jasper Park, and were observed in 1863 fishing in Talbot Lake (Cheadle 1931:164, 171).

## Historical Records of Fishes and Fishing

The earliest historic visits to the Jasper area were made by fur traders, adventurers and natural scientists. To the extent that these people were interested in fish at all, it was primarily as a supplementary food supply to the abundant big game in the area. They lacked the motives or the means for making wholesale transfers and introductions of fish, but conceivably their rates of exploitation were sufficient to reduce significantly, or even eliminate, certain local populations.

With the designation in 1907 of the national park, the motive to develop and maintain high-quality pleasure fishing for abundant trout became prominent. By this time large-scale fish culture methods had become well developed, and their lavish use was seen as the principal solution to fisheries problems (e.g., Whitcher 1887). The means for large-scale introductions and transfers, however, were unavailable until the first railway was completed through the park in 1911, and the Coal Branch spur line was finished in about 1913.

I examined numerous published historical records for the period up to and including 1916 for comments on fish or fishing to obtain evidence about the native distribution and abundance of the park's fish populations. There are definite records of fish introductions into park waters beginning in 1917, and comments in old file correspondence seem to suggest that official government introductions did not take place before that time. Still, records become increasingly less reliable as indicators of indigenous distributions after about 1910, because by 1911 rail workers already had built a road from the end of steel at "Prairie Creek" (Entrance?), the railway itself arriving in the park in summer of that year, reaching Fitzhugh (Jasper townsite) in August (Douglas 1912a, 1912b). A rapid and efficient means then was available for transporting fish from established hatcheries in the east, and short time later from those in British Columbia.

The value of historical records for determining the native ranges of fishes also is limited by the inability of most early observers, often including trained biologists, to accurately identify species of fish. They nearly always used common names that have only local application, or are so undescriptive as to refer potentially to many species.

The best known confusion of names is the use of "grayling" in southwestern Alberta and southeastern British Columbia for mountain whitefish, but other name confusions are less easily solved. For example, mountain trout, silver trout, brook trout and speckled trout were all widely used to describe the fish found in various waters of the East Slopes, though they do not appear to have been used consistently. Of those species possibly native to the study area, "mountain trout" is known to have been used to refer to *Salvelinus namaycush* (Scott and Crossman 1973:227), but it is obvious from many records that it has been applied to another species more commonly found in streams as well. "Silver trout" is a common name for rainbow trout (Bajkov 1927:11, Dymond 1932:17, Scott and Crossman 1973:191). Writing about two forms of rainbow trout in Jasper National Park, a dark spotted form and a silvery form, Bajkov (1927:11) stated "anglers usually distinguish trout by colour and call the first form rainbow trout and the second brook trout". Scott and Crossman (1973) do not list "speckled trout" for any fish possibly native to the study area; however, *Salvelinus fontinalis*, the brook trout native to eastern North America to which bull trout bear some resemblance, has been widely known as "speckled trout" for many decades. To further confuse the issue, western true (i.e., black-spotted) trouts have been called "speckled trout", even by ichthyologists (e.g., Jordan and Evermann 1905:191).

Perhaps the most reliable guide to the early meanings of common names is provided by McIllrie and White-Fraser (1983) in their 1890 report on fishing in the districts of Calgary and Pincher Creek. According to them, speckled and mountain trout were used interchangeably in their areas to mean the fish we now know as cutthroat trout (their description unequivocally identifies this species). For example, notes accompanying an old photograph of fish clearly identifiable as cutthroat trout describe them as "speckled trout" from the Bow River at Calgary (Glenbow Archives, photograph NA-33-22, no date). Cutthoat and rainbow trout were not distinguished as separate species by some biologists of the time (e.g., Macoun 1905), and are commonly confused by anglers to the present day. Speckled trout and mountain trout therefore most likely refer to black-spotted trout in these reports.

Some names probably are consistently reliable. I have taken "bull trout" always to mean *Salvelinus confluentus*. "Whitefish" I have assumed are always coregonids, though distinctions between lake and mountain whitefish seem to have been made rarely, if ever, prior to the Fisheries Commission report of 1912 (Prince et al. 1912). Mountain whitefish were not recognized as whitefish at all by some observers (e.g., McIllree and White-Fraser 1983:37). Likewise "pike" and "jackfish" are presumed always to be *Esox lucius* and "ling" is assumed to mean burbot, *Lota lota*. "Lake trout" usually can be assumed to mean *Salvelinus namaycush* in these records, but only when used by someone known to be knowledgeable about fish identification. "Trout" used alone presumably means either trout or charr, but might even have been used in reference to Arctic grayling. Small lake whitefish arguably might have been mistaken for "goldeye".

Another problem with historical accounts is that the waters in which fish were found are often not adequately identified. Frequently reference is made only to a general area which may include several drainages. The problem is confounded by the fact that many place names have fallen into disuse, or were made up by the observer for his own purposes, or were used for two to several different waters in the same general area. "Prairie Creek" seems to have been a special favourite in the Jasper area, apparently being applied to at least three streams east of the park, two of them adjacent (Grant 1873:223-224).

Despite the obvious limitations, these early records do provide valuable information that can be used to help guide fish management in Jasper National Park. They are descriptions of the fish and the fishery conditions that existed naturally in the park area before the earliest form of rapid transport, the railways, made it possible to introduce non-native fish widely throughout the region, and they may document the earliest introductions of fishes into the region as well.

In the following analysis, I included comments on waters outside the present park boundaries both to show park fish resources in regional context, and in some cases to note the presence of fish taxa outside the park that might have access to waters within the park. Sources examined include the published journals of several explorers, adventurers and fur traders (many of them are listed under the heading: "Sources of Information…" in the Study Area section), detailed reports of land surveyors published in the annual reports of the Department of Interior (1874-1931), incidental comments published in the same series by the various agencies administering the national parks; detailed reports by forestry officers in the above annual reports; and the detailed annual reports of the various agencies responsible for federal inland fisheries (1910-1939). My comments on the evidence are set in square brackets ([]).

**1825: Henry House (approximately opposite the present Jasper townsite)**

Spring: *"Here my old friend Joseph Felix Larocque, Esq., an old north-wester, and formerly of Columbia, was in charge; and with his usual kindness, treated us to a dish of very fine titameg, or white fish, the first of the kind I had ever seen. The white fish here is considered, in point of quality, in the same light as salmon on the Columbia, the finest fish in the country; and many an argument takes place whenever parties east and west of the mountains meet, as to which is the best. The Columbians, as a matter of course, argue in favour of the semetleck, or salmon; while the adverse party advocate as strongly the titameg, or white fish. Delicious, however, as we found the titameg, there was nothing either in the taste or flavour to induce me to alter the opinion I had formed. I give the preference to the good old salmon, as the king of all the piscatory tribes on either side of the mountains"* (Alexander Ross 1855:202-3).

[Scott and Crossman (1973:305) list "tittimeg" as a common name for Arctic grayling, *Thymallus arcticus*, not whitefish. They list a species with an apparently related species name, *Coregonus atikameg*, as a synonym of lake whitefish. McLeod (in McDonald 1971:97) used "Attehawmeg" in connection with the whitefish familiar to the fur traders, and Whitcher (1887:88) used "attihawmeg" as a synonym for whitefish. Michael Sullivan (personal communication) informs me that several similar variations are used by Woodland Cree of the La Biche area in referring to lake whitefish, including tittimug and uhtittimug (my phonetic spellings of his pronunciation).

Both fish apparently were considered excellent fare by the fur traders. According to Alexander Mackenzie, grayling are "a most delicious fish" (Mackenzie 1927:177). McLeod (in McDonald 1971:97) lavished on whitefish the most extravagant praise for its flavour. The weight of the evidence, however, suggests that Alexander Ross almost certainly was referring to one of the whitefishes rather than Arctic grayling, despite the possible confusion of native names.]

**1826** **at a little lake approximately half way between the first Jasper House (Brûlé Lake) and the beginning of the "Portage" (confluence of the Whirlpool and Athabasca rivers)**

May 6: "*They found me encamped near a small lake, about half-way between Jasper's House and the commencement of the Portage, living upon* White fish, *which, though small, are of an excellent quality and which I did not observe in any other lake among the Rocky Mountains*" (Drummond 1830:196).

[The first Jasper House was built on the northwest shore of Brûlé Lake in 1813, according to Woodrow (1987:482). Drummond (1830:192) previously estimated that the "Assinaboyne" (Snake Indian) River was about half way to the Portage. The context suggests that the lake was on the Snake Indian side of the Athabasca valley, but Talbot, Edna or even Jasper lakes also are possibilities. Drummond's observations on the size and unusualness of the fish suggests they were mountain whitefish, which are generally smaller than the lake whitefish he would have known well from his travels, and also are found in only a few mountain lakes, although they are abundant in rivers.]

**1846** **Athabasca valley, Jasper area**

"*By way of a dainty morsel, the Indians pluck out the eyes of fish with the end of the fingers and swallow them raw, likewise the tripes with their whole contents, without further ceremony than placing them an instant on the coals, from thence into the omnibus or general reservoir, without even undergoing the operation of the jaws*" (de Smet 1847:192).

**second Jasper House (present-day Jasper Lake)**
[Jasper House was moved from the northwest end of Brûlé Lake to the north end of Jasper Lake in 1830, according to Woodrow (1987:482).]

April-May: "*Provisions becoming scarce at the Fort, at the moment when we had with us a considerable number of Iroquois from the surrounding country, who were resolved to remain until my departure, in order to assist at the instructions, we should have found ourselves in an embarrassing situation had not Mr. Frazer come to our relief, by proposing that we should leave the Fort* [Jasper House] *and accompany himself and family to the Lake of Islands, where we could subsist partly on fish. As the distance was not great, we accepted his invitation, and set out to the number of fifty-four persons, and twenty dogs. I count the latter,* *because we were as much obliged to provide for them, as for ourselves. A little note of the game killed by our hunters during the twenty-six days of our abode at this place, will perhaps afford you some interest; at least, it will make you acquainted with the animals of the country, and prove that the mountaineers of Athabasca are blessed with good appetites. Animals killed — twelve moose deer, two reindeer, thirty large mountain sheep or big horn, two porcupines, two hundred and ten hares, one beaver, two muskrats, twenty-four bustards, one hundred and fifteen ducks, twenty-one pheasants, one snipe, one eagle, one owl; add to this from thirty to fifty fine white fish every day and twenty trout, and then judge whether or not our people had reason to complain; yet we heard them constantly saying; 'How hard living is here? The country is miserably poor — we are obliged to fast.'*" (de Smet 1847:196-7)

[There are two apparent candidates for "Lake of Islands." Talbot Lake, a waterbody with several islands, narrow points and an attenuated isthmus that periodically flooded every freshet (forming islands?) lies just 2 km from Jasper House and is known to have been fished for whitefish by provisioners for the post (see Moberly and Cameron 1929, and Cheadle 1931, below). Jarvis Lake, over forty-five kilometres by trail to the northeast, was described as "studded with islands" by Saint Cyr (1909:145; see entry below for 1907). De Smet (1847:197) reported that upon his departure from camp, his new Christian converts each "discharged his musket in the direction of the highest mountain… and… gave it my name." Roche De Smet (2539 m) is close to, and easily visible from, Talbot Lake and Jasper House. There are two mountain ranges with peaks exceeding 2300 m intervening between Roche De Smet and Jarvis Lake, which are separated by 34 km in line of sight. Talbot Lake is most likely De Smet's "Lake of Islands" because it best fits the criteria of being "not a great distance" from Jasper House, and being in a location from which Roche De Smet is readily visible.

Ralf (1987:372) cited Ens and Potyondi (1986) to note that Colin Frazer, factor at Jasper House, in 1850 requested a transfer to a post where provisioning was not such a problem. It should be recognized that these complaints do not necessarily reflect low natural abundances. As de Smet's listing shows, considerable numbers of game and fish could still be captured in the Jasper area even though it must have been heavily exploited by provisioners for Jasper House for more than a quarter of a century. Furthermore, heavy hunting and fishing to supply Jasper House may have reduced nearby fish and wildlife populations far below their original abundances.]

**1854-5 second Jasper House (present-day Jasper Lake)**

*"Streams and rivers were stocked with mountain, silver, and speckled trout…. One small lake ten miles north of the Mountain House* [Jasper House], *on the tip of a mountain, with neither inlet nor outlet, swarmed with trout. One had only to drop a hook when dozens would jump for it. They weighed three-quarters to a pound and a half"* (Moberly and Cameron 1929:54).

[There is no obvious candidate for the lake described. Moberly (his p. 97) refers to the Snake Indian River valley as extending northward from Jasper House for about 12 miles, and Rocky River as extending south for about 5 miles, his distances apparently meaning by line of sight. In fact these valleys extend northwest and southeast, respectively, but his distances appear to be accurate. There is on topographic maps, however, no lake about 10 miles up the Snake Indian valley, or in fact in any northerly direction from Jasper House near that distance, that is at all like the one Moberly describes. Celestine Lake matches the physical description and is "north" of Jasper House by Moberly's directions, but it is only about 5 miles by trail from Jasper House. Work in progress on the paleolimnology of this lake has provided strong evidence that it held no fish until quite recently (S. Lamontagne, personal communication).]

**1858 second Jasper House (present-day Jasper Lake)**

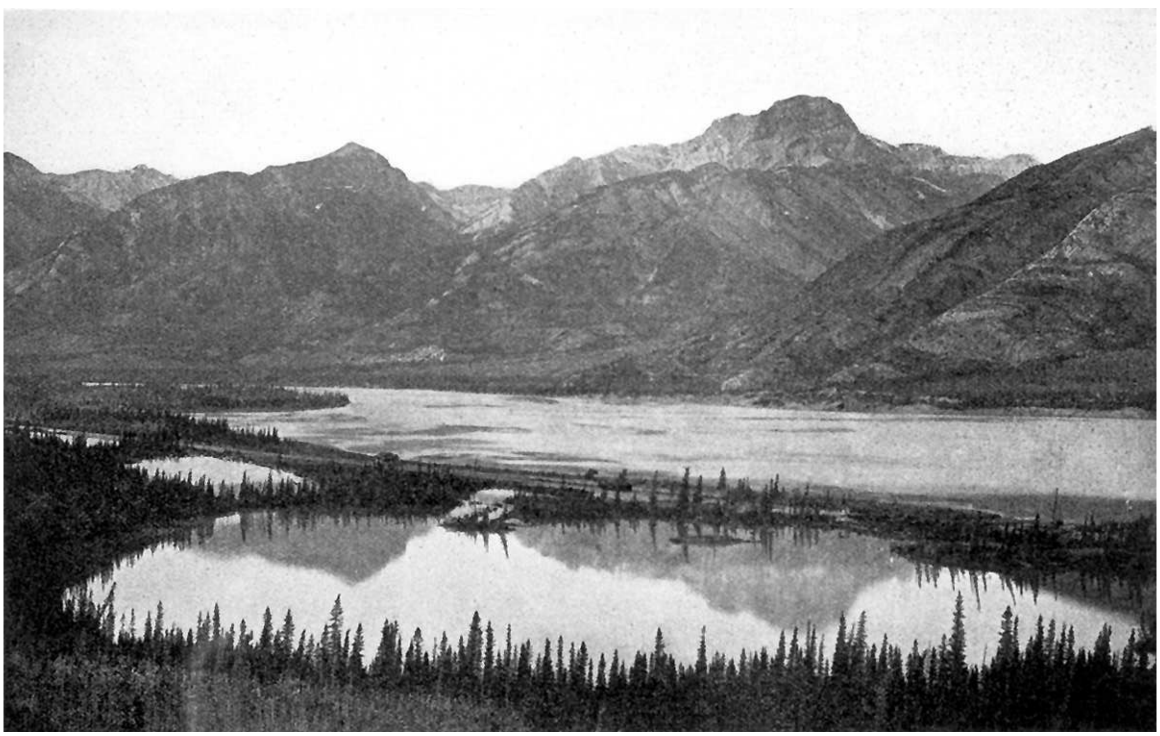
written in connection with description of 1858-59 season: *"Just above the houses the river at low water spreads into numerous channels separated by sandbars and at high water becomes considerable of a lake* [Jasper Lake]. *To the south of this lies a long sandy ridge a few yards wide, divided by a narrow channel. At high water this ridge is submerged and another beautiful lake is formed. During the freshet small whitefish enter this lake, remaining when the water recedes. They weigh from a pound to a pound and a half, and are delicious. The water in no place is more than eight feet deep and as clear as crystal. On a bright day, standing on the hill-top above, we could see every weed and fish"* (Moberly and Cameron 1929:97-98).

[Figure 5, a photograph of the south end of Talbot Lake, shows a location that matches Moberly's description of the lake south of Jasper Lake. Talbot Lake is generally clear, had a maximum depth in 1939 of 2.5 m (8 feet, Rawson 1940:64), and as Moberly describes, has a hillside observation point. Talbot Lake is almost certainly the lake to which Moberly referred.]

**1859** **second Jasper House (present-day Jasper Lake)**

February 8: *"Until a few years ago this trading post was not altogether abandoned during the summer, but the person in charge made a hunting tour for several months to accumulate provisions for next winter's support, and during these trips as many as 30 to 40 moose deer would be killed and several hundred big-horn sheep. In addition he always returned in time to secure a stock of fish before the frost set in and closed the mountain lakes, which abound in 'white fish' and trout"* (Hector 1863:128).

**Figure 5.** "Interlaken from High Hill to the Southeast, Jasper Park. Fish and Jasper Lakes in Foreground" (Bernard-Hervey 1915, no photo credit given in the original publication). This photograph probably dates from 1913 or earlier. The waterbody in the foreground is the southwestern end of Talbot Lake. Edna Lake is just visible beside the road at the extreme left-centre of the picture. The light patch between the two water bodies is a bare hillside locally known as Cinquefoil Ridge or Edna Knoll. I am grateful to K. Van Tighem for his assistance in interpreting this photograph.



**1863 small stream between Pembina and McLeod rivers**

June 14: *"… it struck me that there might be trout in the stream as it was very like a Yorkshire moor stream, & I therefore walked down to it. Saw a small fish rising and went back for tackle … Water very clear and brown; had recourse to a small spinner, & soon captured a small trout of some 2 oz. but could not get another run; the fish was very like an English burn trout, but instead of the red spots, it had a red line along each side about 1/8 inch broad; the black spots similar to the English variety; it ate like our own fish"* (Cheadle 1931:150).

[Van Tighem (1988a) should be credited for recognizing that this record is the first reliable observation showing that rainbow trout were native to the upper Athabasca drainage.]

**McLeod River near first Edmonton-Jasper crossing**

June 17: *"We crossed McLeod's River about 1/2 a mile above where we first struck it; here it was very shallow; water very low & clear. It is a pretty river, apparently as broad as the Saskatchewan, and the high banks handsomely clothed with fine pines & poplar. I had hoped to find trout in it but could find only some small fish like dace which were taking the fly"* (Cheadle 1931:153).

["Dace" could refer to almost any member of the minnow family (Cyprinidae) likely to be native to the area.]

**stream one to two days horse travel west of McLeod River crossing**

June 18 and 19: *"After camping for the night Baptiste went ahead & found moose & bear tracks & 2 small rivers in one of which were trout…. We kill several fish, some resembling dace, others small trout, & the boy kills a very fine large trout of 2 lbs with a partridge bait, & loses 2 or 3 more"* (Cheadle 1931:154).

**small stream at confluence with McLeod River, second crossing of this river on Edmonton-Jasper trail**

June 21: *"The young one fished for trout in one of the little streams with a gad-fly. But they were too lazy to eat, & I had to stand on one side of the stream to stir them up with a long pole, whilst he put the bait before their noses. In this way we caught two, but we both fell into the water with a* *great splash which however did not frighten away the fish"* (Cheadle 1931:155).

**near upstream end of Brûlé Lake**

June 28: *"I fish…. Caught no fish, water being too heavy"* (Cheadle 1931:160).

**Talbot Lake**

July 1: *"We therefore decided to go on two or 3 miles to a good feeding place for the horses, by a lake where there were plenty of whitefish, & a Company's fishery, & stay there for the day…. We camped by the fish lake, and went pike-fishing in a little river which flows out of it, in the afternoon. Water very thick, and killed nothing…. the* [lake] *water was very warm & beautifully clear. ..…In the evening the Company's men put out a net & caught a whitefish immediately, which they gave us. After dark the 2 Shuswaps went out in the canoe & speared fish by torchlight, a very pretty sight"* (Cheadle 1931:164).

July 2: *"The 2 Shuswaps brought us 11 fresh fish speared the preceding evening…"* (Cheadle 1931:166).

July 3: *"Before dinner I again tried fishing, but the water was too thick if there were any fish, which I doubt…. Just finishing dinner when Macaulay arrived…. Had killed 10 sheep, & at a lake nearly a day from here had killed 42 large trout in about 2 hours"* (Cheadle 1931:166).

[Cheadle must have been fishing in some other water body than Talbot Lake because he previously described Talbot as being clear and of supporting a fishery. Possibly he is referring to Athabasca River or Jasper Lake.

Macaulay was in charge of provisioning Jasper House, and like Cheadle and his party probably had remained on the right bank of the Athabasca. Cheadle's party was reluctant to cross the river because of very high water at the time; Macaulay's group was hunting to supply Jasper House. Had Macaulay been hunting off the left bank, north or west of the river, he presumably would have left his fish and game at Jasper House, but he had it with him when he camped near Cheadle. The lake he refers to must be south or east of Talbot Lake. Of the potentially fish-bearing lakes one day's journey distant in this area, Jacques Lake, 36 km up Rocky River or 26 km up Jacques Creek is a likely candidate, as is Mystery Lake, 32 km from

Talbot Lake via Fiddle River valley. Jacques Lake holds a native bull trout population (see below); Mystery Lake has native populations of mountain whitefish and bull trout (C. Hunt, personal communication; AWA 1973:117).

Taken literally, Cheadle's statement says that Macaulay caught the fish alone. But there were three others in Macaulay's party (Cheadle 1931:164); thus there were from two to eight fisherman-hours expended in capturing the 42 large trout, giving a capture rate of 5.25-21 trout per hour.]

**Miette River**

July 7: *". . . tried the Myette for trout last night but no success"* (Cheadle 1931:169).

**Yellowhead Lake**

July 9: *"Our guide* [a Shuswap] *told us this lake was a great fishing lake for the Shuswaps, and there were plenty of trout…. Here 2* [sic] *constructed a raft, & put out a long line into the lakes with many hooks, whilst Milton & I tried the spinner and fly from the raft, & the others fished from the bank; but it was no use; no trout to be had; great disappointment"* (Cheadle 1931:171).

[Lake trout are believed to be native to this lake (Carl et al 1959, Lindsey 1964). In July, lake trout probably would be in deep water and thus may have been inaccessible to the fishing methods used by Cheadle's party. In spring and fall they typically use near-shore shallow areas, and would be more vulnerable to the Shuswaps' well-developed fishing methods.]

**1872 stream tributary to McLeod River at "loop" west of Edson**

September 6: *"Here the McLeod sweeps away to the south and then back to the north, and the trail instead of following its long circuit cuts across the loop. This 'portage' is twenty miles long, and a muskeg in the middle — on one or the other side of which we would have to camp to-night — is the worst on the road to Jasper's. Halted for dinner at the bend of the river, having travelled nine or ten miles, Frank promising us some fish, from a trouty looking stream hard by, as a change from the everlasting pemmican…. Frank came back to dinner with one small trout, though Beaupre said that he and his mate last summer had caught an hundred in two hours, some of them ten pounds in weight"* (Grant 1873:211-212).

[While this statement has all the elements of a classic fisherman's lie, (nearly one fish caught per minute, monster trout, not repeatable, etc.), it cannot be dismissed entirely. There are so many similar reports of very large catches from the eastern slopes of the Rockies from this and later periods, some of them documented with photographs (e.g., Prince et al. 1912:65,66,67; Cavell 1984:136; Van Tighem 1988b; see also Cheadle's 3 July 1863 observation re Macaulay, above), that it is well within the bounds of belief at least as a rough indication of size and catch rate. The enormous previous catch could very well account for the poor results enjoyed by Fleming's party.]

**"Prairie" (probably Maskuta) Creek, about 10 km east of Brûlé Lake**

September 10: *"The Doctor in their absence had fished in most primitive style, with a tent pole and twine, and hook baited with pemmican, and had caught two fine trout…. supper without* richaud [a kind of stew made with pemmican] *was unanimously decreed, and Valad set to work at once on the beaver and Terry on the fish…. The trout were excellent…"* (Grant 1873:224-225).

**1889 Smoky River**

*"…and in Smoky River brook-trout and gold-eyes are found…. Near the mountains all the streams are said to abound in brook-trout"* (Thompson 1890:72).

[Thompson may be referring to a location far downstream from the park, near the Peace confluence. Scott and Crossman (1973:219) list "western brook trout" as a common name for Dolly Varden trout, and therefore for bull trout according to the most recent nomenclature. Macoun (1905, see next entry) called bull trout the "real brook trout" of the Rocky Mountains. Bajkov (1927:11), however, lists "brook trout" as another common name for rainbow trout. Although the species is native in the headwaters of the Peace drainage, possibly as far downstream as the British Columbia-Alberta border (Carl et al. 1959: MacCrimmon 1971:664), there is no firm evidence that rainbow trout are native to the drainage anywhere in Alberta.

Goldeye have not been reported from the Smoky River drainage by modern authors (Roberts 1989, Nelson and Paetz 1976, Scott and Crossman 1973, Paetz and Nelson 1970, McPhail and Lindsey 1970), but since the species occupies the Peace River at least as far upstream as the British Columbia boundary (e.g., Roberts 1989:135), its existence in at least the lower reaches of the Smoky River should not be surprising.]

**1905 Selkirk and Rocky Mountains**

*"The leading fish in all our inland waters are species of Salmonidae. The genera Salmo, Salvalinus* [sic]*, and Oncorhynchus give us our trout and salmon. Of the genus Coregonus, or whitefish, one, the* Coregonus Williamsonii*, is improperly named 'Grayling' by miners and others.*

*"In the Rocky mountains are three species of trout, which are respectively named the Great Lake Trout, the Bull Trout and the Rainbow Trout. The names given are applied in other districts to different species, so that the local name has no real significance.*

*"The 'Rainbow Trout' or 'Cut-throat Trout'* (Salmo mykiss) *is the black-spotted trout of the Rocky mountains, whose waters enter the branches of the Saskatchewan. This form is found in the Bow river at Banff and the Old Man river, farther south.*

*"…The Red-spotted Trout, Dolly Varden Trout or Bull Trout* (Salvalinus malma) [sic] *is the real Brook Trout of the mountains from the British Columbia boundary to Alaska. It is this species that gives zest to mountain fishing and real sport to the angler. Like its relative, the Brook Trout of the east, it is found in streams of all sizes, and, in consequence, weighs from a few ounces to over twelve pounds at the mouths of some of the northern rivers.*

*"The Great Lake Trout* (Cristivomer namaycush) …[is] *found in suitable localities… chiefly in the large lakes…"* (Macoun 1905:393).

**1907 Gregg Lake [called Whitefish Lake by one author] and Jarvis Lake**

November 13: *"Great numbers of whitefish, jackfish, etc., could be seen swimming around in the water beneath the ice. …Whitefish lake in range 26 abounds with whitefish, jackfish, trout, &c."* (Ross 1909:132-133).

[The record of trout in Gregg ("Whitefish") Lake is questionable. Ross did not mention it elsewhere in the same publication (see next entry), and the fisheries biologist for the region has no records of trout in the lake (C. Hunt, personal communication).]

*"This lake* [Gregg Lake] *contains great quantities of large whitefish and pike…"* (Ross 1909:350).

[Present-day whitefish in Gregg Lake are described as still abundant, but typically small (C. Hunt, personal communication).]

*"In this depression are many lakes; the two largest ones, three miles and a half apart are named Jarvis lake (altitude 3,875) and Gregg lake. The upper lake is the larger and is studded with islands, all wooded; the other one is very shallow; both are teeming with whitefish, pike, and ling"* (Saint Cyr 1909:145).

["Ling" is a commonly-used name for burbot, *Lota lota* (Scott and Crossman 1973:645).]

**McLeod, upper Athabasca and "Hay" (Wildhay) rivers and Carrot Creek along 14th Baseline between 5th and 6th meridians**

*"In McLeod and Athabaska rivers there are great numbers of jackfish, graylings, whitefish and a large species of trout. In Hay river, in range 27, there are great quantities of bull trout and Carrot creek in range 13 is teeming with speckled trout."* (Ross 1909:132-133)

[In this case the author lists "grayling" and "whitefish" as different fish. The mountain whitefish, *Prosopium williamsoni*, and the lake whitefish, *Coregonus clupeaformis*, even today are not distinguished by casual fishermen, so it seems likely that Ross really does intend "grayling" to mean *Thymallus*, not *Prosopium*. "Jackfish" is a widely-used name for northern pike, *Esox lucius*. "Speckled trout" most likely refers to rainbow trout, however see earlier comments regarding this common name, above.]

**waters near (mostly east of) the 6th meridian between the 13th and 16th baselines, including headwaters of the Little Smoky, "Baptiste" (Berland) and "Hay" (Wildhay) rivers, and Athabasca valley and tributaries in northeastern Jasper National Park**

*"…the lakes are teeming with whitefish and pike, and in the running streams trout of many species were caught"* (Saint Cyr 1909:150).

**Brazeau and "Little Brazeau" (Nordegg?) rivers approximately 50 miles below the park boundary at Tp 44 R 11 & 12 W5**

*"There is said to be an abundance of trout in both rivers"* (Hawkins 1910:434).

**McLeod River and creeks immediately W and SW of Edson**

*"Fish are plentiful in McLeod River and the creeks"* (Heathcott 1910:444).

*"The creeks and river abound with fish of every description"* (Heathcott 1910:445).

*"Sundance creek abounds with trout"* (Heathcott 1910:446).

**1908 Brazeau River and tributaries 30 to 50 miles below the park boundary at Tp 44 R 13-16 W5**

*"…trout, of which there are said to be several varieties, are plentiful in the Brazeau and its tributaries"* (Hawkins 1910:439).

**Brazeau River 10 to 30 miles below the park boundary at Tp 44 R 17-19 W5**

*". . . trout, of which there were said to be several varieties, were apparently abundant in the river"* (Hawkins 1910:443).

**McLeod River immediately west of Mercoal Tp 48 R 22 & 23 W5**

*"A number of bull-trout were caught in McLeod river"* (Hawkins 1910:449).

**vicinity of confluence of Athabasca, Rocky and Fiddle rivers, Tp 48 R 26-28 W5**

*"There are said to be jackfish in the Athabaska and trout in the smaller streams"* (Hawkins 1910:458).

**"Prairie" (Maskuta) Creek headwaters, Athabasca River, Brûlé Lake, Tp 49 & 50 R 27 W5**

*"There are mountain trout in Prairie creek and jackfish and goldeye in the*

*Athabaska"* (Hawkins 1910:459).

["Mountain trout" most likely refers to rainbow trout, but see the comments on the name in the introduction to the historical records.

Bajkov (1927:398) reported that some specimens of goldeye had been caught near Jasper in 1925, but that he had not examined any specimens from there. Roberts (1989) described the record as questionable because it is outside of the currently occupied range of the species and is not supported by specimens. Scott and Crossman (1973) pointed out that ciscoes in the Great Lakes have been referred to mistakenly as mooneye, so it is conceivable that Hawkins (or his local informant) mistook lake whitefish for the vaguely similar goldeye. On the other hand, it would be a mistake to dismiss Bajkov's and Hawkins' records solely because goldeye are no longer found in the area. Goldeye are recorded from the Athabasca River at least as far upstream as the mouth of the Pembina River (Roberts 1989; Franchère 1969:166 also recorded catching "5 or 6 lacaiches" — French: laquaiche — mooneye, very similar to goldeye, a congener, at the mouth of the Pembina River in his journal entry for June 1, 1814), and there are no barriers to their movement further upstream.]

**1909** **"Fish" [Talbot] and Jasper lakes**

*"East of Jasper lake from which it is separated by low sandy hills covered with jackpine, there is another narrow lake called by the natives 'Fish' lake…. Fish lake abounds with pike and whitefish"* (Saint Cyr 1910:195).

[Talbot Lake, identified in Figure 5 as "Fish Lake" in the original caption, is consistent with Saint Cyr's description.]

**Athabasca River and tributaries entering near Jasper Lake; headwaters of Wildhay River**

*"There is splendid trout fishing in the larger streams, and whitefish can be caught with nets in all the lakes. Pike is also caught in a few of these lakes, but they are more plentiful in the streams where the current is sluggish and the beds covered with aquatic plants"* (Saint Cyr 1910:198).

**circa 1910** **tributaries to Brazeau River (possibly including Brown and Chungo creeks and Blackstone River), about 10 miles east of the park boundary, Tp 41 & 42 R 19 W5**

*“The water is the very best, and along the larger branches of Brazeau River are to be found trout in abundance up to six pounds in weight”* (McFee 1911:108).

**Brazeau drainage immediately east of park boundary; headwaters of McLeod and Pembina rivers**

*“…mountain trout abound in the rivers”* (Rolfson 1912:140).

[If Rolfson intended to refer to a particular kind of trout with the term “mountain trout”, he most probably meant rainbow trout, which are known from other evidence to be native to the McLeod River drainage.]

**1910 North Saskatchewan and Athabasca drainages (Sisley 1911:113-116)**

*“These streams may be roughly divided into four groups, according to the kinds of fish indigenous to them, beginning from the south:*

*“…(c) North and South streams entering into the North Saskatchewan River. No thorough investigation has been made of these waters up to the present time, so that no definite statement can be made as to what fish are found in them.*

*“(d) Branches of the Athabasca River, such as the McLeod with its branches, the Embarras for example:*

*Grayling* (Thymallus)
*Rocky Mountain Whitefish* (Coregonus Williamsonii)
*Bull Trout* (Salvelinus Malma)

*and another valuable species of trout of which full particulars cannot be given at present.*

*“. . . (2) Grayling* (Thymallus montanus). *This is a very game fish and is not found in many Canadian waters. The upper jaw is short and square, while the lower one is slightly longer, which gives it somewhat of a bull-dog appearance, although it is not coarse in any way. The mouth is supplied with teeth of similar arrangement to that of the Cutthroat Trout. It is dark colored in the back and light underneath, with well marked scales. On each shoulder about a dozen dark spots are to be found. It has a dorsal fin peculiar to itself, which is longer than usually found in other fish and oval in shape. It is very similar in its habits to the Cutthroat Trout. It is not found south of the Athabasca River.*

*"(3) Rocky Mountain Whitefish* (Coregonus Williamsonii). *This is the fish that is usually and mistakenly called the Grayling. It is a true whitefish and is closely related to the Commercial Whitefish* Coregonus Clupeformis [sic]. *It is a very gamey fish, rises well to the artificial fly, has a small mouth with no teeth, the lower jaw being shorter than the upper. This fish is gray on the back, fading downwards to white underneath and has well developed scales. It lives wholly on insects, and spawns in September and October.*

*"(4) Bull Trout* (Salvelinus Malma). *This is not a very game fish and is not a true Trout, but belongs to the char species.… It is a dark colored fish with two rows of dull pink colored spots on each side. Mouth supplied with teeth but the palate is high and smooth and the vomer is free of teeth. It is a coarse fish with a large head, which is in the adult fish about one third of the whole.*

*"Besides the above game fish, some coarse fish are to be found, especially in the lower stretches of these streams and pretty universally over the whole territory. The principal ones are: (1) Pike —* (Lucius)*, (2) Suckers —* (Catastomus) [sic], *and (3) Ling —* (Lota Maculosa)*. Of the Suckers there are several varieties."*

**Lakes in Jasper Park**

*"Jasper Lake. Howard Douglas gave information as to the lakes in the Park; Jasper, Brule and Whitefish* [Gregg? — originally in the park?] *lakes; Maligne lake has no fish. The Commissioners visited Jasper Park. Found fish in Pyramid lake spawning on 23 September. Lakes are small"* (Prince et al. 1912:9).

[Later in this report (see below), the commissioners allude to lake trout in Pyramid Lake, a fall spawner; however another fall spawner, mountain whitefish, was common in the lake from an early date, and a third fall spawner, bull trout, is native to the drainage.]

*"Where lakes are near parks or other summer resorts and have fish that may be caught with hook and line and have few or no whitefish, they should be reserved for angling.*

*"The lakes in Jasper Park, such as Fish and Jack* [Jacques] *lakes …are instances of this class"* (Prince et al. 1912:11).

[Figure 5, a photograph of "Fish Lake" reproduced from a departmental report for 1913 (Bernard-Hervey 1915) unequivocally shows the waterbody now called Talbot Lake. A description by Rogers (1915:98) in the same publication describes a Fish Lake in the immediate vicinity of Edith and Beauvert lakes. Saint Cyr (1910:195, see entry for 1909 above) describes a Fish Lake east of Jasper Lake that is certainly Talbot Lake. Lakes in Switzer Park, once within Jasper's boundary and now just east of it, were referred to as the Fish Lakes also (C. Hunt, personal communication). Records of "Fish Lake" in Jasper National Park dating from this early period cannot be ascribed to any one waterbody unless accompanied by a description.]

**upper Athabasca drainage**

*"Two species of real trout are found on the eastern slope of the Rocky Mountains, the Cut throat trout* (Salmo clarkii) *in streams of the southern part of the Province of Alberta and the Rainbow trout* (S. irideus Athabasca) *in the upper tributaries of the Athabasca river"* (Prince et al. 1912).

*"3. The Rainbow Trout* (Salmo irideus Athabasca)*…. It is …a true trout, covered with black spots, but with the following differences: It has no red stripe in the skin on the inner side of the mandible, but has a well-marked lateral red band, reaching from behind the gills to the base of the caudal fin…. Apparently it is only found in the upper tributaries of the Athabasca river.*

*"4. The Grayling* (Thymallus Montanus *and* T. tricolor). *Cope. The fish usually called Grayling in southern Alberta is really the Rocky Mountain Whitefish, but there is a true Grayling, indeed apparently two if not three species in the waters reviewed and reported on by this commission…. a specimen forwarded in a dried condition from a tributary stream of the Athabasca west of Athabasca Landing is unquestionably* Thymallus tricolor*, while other specimens obtained by Dr. Sisley are identical with the specimens found in Montana and named by Mr. Milner,* T. Montana.

*"…The typical Alberta grayling is similar to the Montana species…. The Montana species which, as stated, is identical with the grayling most prevalent on the eastern slope of the Rocky Mountains …."* (Prince et al. 1912:18-19).

**North Saskatchewan and upper Athabasca drainages**

*"These streams may be divided into four groups according to the kinds of fish frequenting them. Beginning from the south:*

*"(c) North and south streams entering into the North Saskatchewan river. No sufficient evidence has been forthcoming as to what kinds of fish characterize these waters. The commission was not able to investigate further these streams.*

*"(d) Branches of the Athabasca river, such as McLeod river, and Embaras* [sic] *rivers with its branches:*

*Trout* (Salmo irideus Athabasca).
*Grayling* (Thymallus montanus).
*Rocky Mountain Whitefish.* (Coregonus Williamsoni).
*Bull Trout* (Salvelinus malma)*"* (Prince et al. 1912:43).

**Pyramid Lake**

*"In addition to the streams and rivers already mentioned there are a number of lakes in which are found the lake trout* (Cristivomer namaycush). *Several of these have already been reserved for fishing with hook and line, and may be known as sporting lakes in which netting operations are not allowed, viz: …Pyramid, &c"* (Prince et al. 1912:43)

**circa 1911** **extreme headwaters of McLeod River immediately east of park boundary; "North Branch Brazeau" (Cardinal) River**

*"Fish of the trout variety were obtained in the north branch of Brazeau river and the west branch of McLeod river"* (Francis 1913:90).

**Athabasca River and tributaries in the vicinity of Fiddle River confluence**

*"Athabaska river is but sparsely stocked with pike and rainbow and bull-trout, and the smaller mountain streams are probably too swift and rocky to carry even the mountain trout"* (Herriot 1913:98).

[These are the first records that actually mention rainbow trout and bull trout from within the boundaries of the park.]

**1911** **Jasper area**

[March: Tote road present within the park to service railway work camps (Douglas 1912a:17)

April: Grand Trunk Pacific Railway (GTPR) at "Prairie Creek" (probably Entrance), 183 miles west of Edmonton and three miles east of the then park boundary (Douglas 1912b:22)

June: GTPR crossed the Athabasca River west of "Prairie Creek" (Douglas 1912b:22-23)

August: GTPR reached Fitzhugh, present-day Jasper townsite (Douglas 1912b:23)]

**circa**
**1912** **Jasper Park lakes**

*"In many of the lakes, of which there are great numbers scattered throughout the park, trout are found and caught in large numbers"* (Douglas 1912b:26).

**1913** **"Jack" [Jacques] Lake**

*"From Medicine Lake the Forestry branch have cleared of windfalls a trail to Jack Lake, — the best fishing lake in or near the park as far as known …"* (Rogers 1915:96).

**Caledonia Lake**

*"There was also cut out by Warden J. A. Rootes, and graded, a good trail to Caledonia Lake, an excellent fishing point"* (Rogers 1915:96).

**Pyramid, Caledonia, "Jack" (Jacques) lakes**

*"Tourists visiting Jasper have had some enjoyable outings at Pyramid and Caledonia lakes, and excellent catches of large lake trout,* Salvelinus Namaycush, *and rainbow trout have been made, and visitors to Jack lake, that interesting lake on the Rocky river, have made such catches of Dolly Varden trout as to make one feel that this lake is possibly one of the best stocked in the mountains"* (Rogers 1915:97).

**1913-14 small lakes and major rivers near Jasper townsite**

*"One of the most noticeable features of the area is the large number of small lakes scattered over it…. Many of the lakes have no inlet or outlet, and are only large ponds, while others have outlets and inlets either on the surface or underground, and some of the latter contain fish. The best fishing is to be found in Caledonia lake, which in summer is visited almost daily by residents of Jasper and by tourists. Pyramid lake and Athabaska and Miette rivers also provide good fishing"* (Matheson 1916:135).

**1914 "Jack" [Jacques] Lake**

*"From Medicine lake to Interlaken a complete new trail has been built, passing Jack lake (an unusually good fishing lake) …"* (Sparks 1916:65).

**Lakes and streams in Jasper Park**

*"Good fishing is to be had in the various lakes and rivers"* (Sparks 1916:67).

**1916 Lakes and streams in Jasper Park**

*"Fishing is a feature of interest to nearly all visitors. Any true sportsman who visited this park last season and participated in this sport had no cause for complaint. The deeper lakes like Pyramid, Jack* [Jacques] *and others furnished their quota of 2-, 3- and 4-pound lake trout. The smaller streams and shallow lakes did well in the way of providing a good supply of that gamey little fighter, the rainbow trout, and the rivers, when they had become clear, a number of the Dolly Varden trout"* (Driscoll 1918:66).

[This is the only reference anywhere to lake trout in Jacques Lake, and probably refers to bull trout.]

## Conclusion

Fishing played at least some part in the subsistence of nearly all the native groups that used the Jasper National Park region. The evidence suggests that of these groups, fishing was most important to the Shuswap people. Even for them, however, hunting probably was the more important food source at most times (Rostlund 1952:206). The

Stoneys, relatively recent arrivals, commonly used fish as well, but the Beavers and Sekanis are said to have favoured game as food, fishing only when necessary to supplement meagre supplies of meat (Rostlund 1952:201,205). Nevertheless, the region was occupied for thousands of years before Jasper National Park was established, by people who are known to have subsisted at least in part by fishing. It therefore is reasonable to assume that low-intensity fisheries were conducted within the Jasper Park area for much of this time.

With the coming of the fur traders in the early 1800s, fishing in what are now Jasper Park waters must have intensified. Historical records examined in this survey show that fish were part of the provisions of Henry House, situated near the lakes across the river from present-day Jasper town, and the second Jasper House, located on the Athabasca River at the outlet of Jasper Lake. Probably fish also were part of the food supplies of the first Jasper House on Brûlé Lake. Talbot Lake, on which the Hudson's Bay Company operated a net fishery, certainly was a major source of fish for the second Jasper House, but other lakes and streams undoubtedly were fished for this purpose [e.g., the unidentified lakes and streams mentioned by Henry Moberly (Moberly and Cameron 1929), James Hector (Hector 1863) and by Walter Cheadle (1931)].

Although these posts as a rule were manned only seasonally, the numbers of people using them must have reached into the hundreds over a season, because they serviced the major northern trading and travel route to and from the Columbia. For example, De Smet's (1847) party of 54 people and 20 dogs comprised only a part of the occupancy of Jasper House during his 26-day stay in the vicinity in 1846. According to his account, his party consumed 780 to 1300 whitefish alone during that time, and perhaps as many as 600 trout, although his reference to numbers of trout is ambiguous. If these figures are typical of the numbers of fish consumed at Jasper House and environs, annual catches must have numbered in the thousands. A fishery of this size probably would have had little impact on populations in large systems, such as the Athabasca River, that are open to migrants. Prosecuted intensively over several successive years in small lakes and streams, however, it might have been of sufficient magnitude to severely reduce, even completely eliminate, some fish stocks.

Even after Jasper House was abandoned, settlers occupied the Athabasca valley within the original park boundaries (Douglas 1910:40). I did not find evidence of their use of fish, but presumably they would have continued exploiting fish stocks to some extent.

Whatever the effect these fisheries may have had on certain stocks, the anecdotal records convey a general impression of abundance. Many of the references quoted in this survey refer to large numbers of fish (trout and whitefish, but sometimes pike) in waters in and adjacent to the Athabasca valley of present-day Jasper National Park before the park was established (Moberly and Cameron 1929:54; Hector 1863:128; Cheadle 1931:164, 166), and shortly thereafter (Saint Cyr 1909:150; 1910:195, 198;

Douglas 1912b; Rogers 1915:96, 97; Matheson 1916:135; Sparks 1916:65; Driscoll 1918:66). Only one (Herriot 1913:98) stated that there were few fish in these waters. Herriot was referring specifically to the Athabasca River and steep rocky streams near the Fiddle River mouth, and his remarks contrast with those of others regarding the same general area (e.g., Saint Cyr 1909, 1910). The comments of the early park superintendents might be dismissed as mere boosterism, but they are consistent with those of the more disinterested observers. It is reasonable to conclude from these accounts that trout, whitefish and pike originally were abundant in many waters in and near the Athabasca valley in Jasper National Park.

The records for waters outside the park, but in its vicinity, consistently convey the idea of large numbers of fish when they comment on abundance. The words “plentiful”, “teeming” and “abound” are frequently used. From these accounts, it can reasonably be concluded that trout and whitefish in particular originally were abundant in the Berland-Wildhay, McLeod and Brazeau drainages, as well as in the mainstem Athabasca and its associated waters.

This historical analysis provided some helpful observations on the species of fish native to Jasper Park. Cheadle’s (1931:150) description of a trout he caught in 1863 shows conclusively that rainbow trout are native to the upper Athabasca drainage. There is also good historical evidence that lake trout were native to Pyramid Lake (Prince et al. 1912:43). Other observations confirm that several other species probably were indigenous to park waters. These include northern pike, “whitefish” (including a small form that most likely is mountain whitefish) and bull trout, the latter evidently reaching a considerable size, judging from some of the comments on large trout. The several references to trout in the Brazeau drainage are evidence that bull trout were abundant in Brazeau River and its major tributaries near the park boundaries, so presumably are native to the park in that drainage. Other observations have raised the likelihood that rainbow trout, and the possibility that goldeye and Arctic grayling were native to the park, but are inconclusive in themselves. Finally, the 1863 report of trout in Yellowhead Lake (Cheadle 1931:171) is evidence that unidentified trout were native to the Pacific drainage in the immediate vicinity of the Continental Divide, even though fishing at the time did not confirm it.

# SECTION III

# SPECIES ACCOUNTS

# OF THE NATIVE FISHES

## Introduction

The main purpose of the species accounts is to show what is significant and valuable about each of the fish species native to Jasper National Park, and to act as accessible summaries that can be used as a first guide to conserving and managing Jasper's native fishes. As will become evident, they will serve better to identify what we must learn about our native stocks in the future than to summarize what we know about them at present. In this sense they are preliminary, intended to document the need for research and management activities that will permit them to be replaced with a definitive work on the native fishes of the park.

The accounts have been compiled primarily from the major published works covering the fishes of our area. This information has been supplemented with data from more recently published studies, and whatever relevant unpublished material I have been able to locate, including records in parks files, unpublished reports, unpublished information contributed by others, and my own observations. The species accounts are not exhaustive reviews, however.

For reasons discussed at length in Part 1, I have made a special effort to identify the stocks that have colonized the area, and have emphasized differences among stocks in summarizing available information on habitat, biology, life history and conservation status. I have tried to avoid wild speculation while drawing attention to possibilities, supported by some evidence, that would have significance for conservation and management. The emphasis is on identifying features of Jasper's fish fauna that either are known to be, *or may be on the basis of preliminary evidence*, unique, unusual, especially representative or otherwise of special value for conservation. Many of its conclusions in this vein inevitably are disputable, and I draw attention to such problems where they occur. My intention is only to ensure that in future the possible existence of valuable but unrecognized stocks is properly taken into account, so that incompletely considered management actions do not wipe them out as has happened too often in the past.

Species accounts adhere to the following outline.

Common and scientific name
Status Flag: (where required)
Summary:
Nomenclature:
Description:
Distribution:
Refugia/Postglacial Dispersal:
Jasper Stocks:
Habitat:
Biology and Life History:
Ecological Significance:
Fishing:
Conservation Status (general):
Conservation Status (Jasper):
Required Action:

The contents of each section are as follows.

The left heading of each species account presents the common and scientific species names as currently listed by the American Fisheries Society's Committee on the Names of Fishes (Robins et al. 1991). Fishes are listed in the order used by Robins et al. (1991), but within the Salmonidae, species are listed in alphabetical order by subfamily and within subfamilies to keep similar fishes together. Subspecies names are not listed by Robins et al. (1991). When subspecies names are listed in this section, the justification for their use is discussed briefly under Nomenclature. The right heading lists the scientific and common names of the family to which the species belongs. In the Salmonidae only, the scientific and common subfamily names are included.

The following example illustrates the general format used.

| | |
|---|---|
| **Common name** | **Scientific Family Name** |
| *Scientific name* | Scientific Subfamily Name |
| | Common Family/Subfamily Name |

The conservation status is flagged in upper case boldface print if the species itself is, or if some of its stocks are, of some concern in the park. The terms and their definitions for the purposes of this report are listed below.

**Extirpated:** locally extinct, but existing elsewhere inside or outside the park

**Endangered:** in imminent danger of extirpation, soon may be lost if immediate action is not taken to reverse its decline

**Threatened:** declining, but not yet in imminent danger of extirpation

**Vulnerable:** possessing characteristics greatly increasing its sensitivity to damage, but not in any immediate danger

**Special Concern:** under some other threat, as yet not well defined, such as toxic contamination

**Rare:** known from only a few specimens within the park, despite adequate collection efforts

**Summary:** The most important points covered in the species account are noted in this section. They summarize briefly the significance of the species to Jasper National Park. The points are treated in detail in the rest of the outline.

**Nomenclature:** This section is used to list the alternate scientific and common names by which the species is or has been known. Scientific disputes and alternative views of the species' taxonomy also are outlined here in a few cases where the issue has some significance for the conservation and management of Jasper stocks.

**Description:** Usually the externally visible distinguishing features of the fish are described in terms that a knowledgeable sport fishermen would understand. The descriptions are summarized from accounts in standard identification manuals by Carl et al. (1959), McPhail and Lindsey (1970), Paetz and Nelson (1970) and Scott and Crossman (1973) unless noted otherwise, supplemented in some cases by my own observations. Much more elaborate descriptions are given where I felt it necessary, such as in describing subspecies purported to be unique to the Jasper area.

**Distribution:** The distribution section outlines the range of the fish in North America, Canada, Alberta and (when applicable) British Columbia. The main sources of distribution information are the atlas of Lee et al. (1980), and the manuals of Carl et al. (1959), McPhail and Lindsey (1970), Paetz and Nelson (1970), and Scott and Crossman (1973). The purpose of the section is to show how widespread or localized the species is outside the park, and to form a basis for the discussion of refugia and postglacial dispersal, below.

**Refugia/Postglacial Dispersal:** The various published interpretations of the Wisconsinan refugia used by the species, and its range expansion since the retreat of the ice sheets are discussed here. The views most frequently discussed are those of McPhail and Lindsey (1970, 1986), Lindsey and McPhail (1986) and Crossman and McAllister (1986). Where appropriate, the possible role of the Ice-free Corridor as a local refugium is considered. This section is intended to identify the possible geographic stocks that may have formed the complement of fishes native to JNP.

**Jasper Stocks:** This section lists the lakes and streams occupied by the species within the park. Local stocks are distinguished here.

**Habitat:** The kinds of habitat used by the various life history stages of the fish are described under this heading. Whenever possible, critical habitat is described; that is, the characteristics of migration routes and of spawning, rearing, overwintering and feeding places. I described the critical habitat used by Jasper stocks whenever possible, but information was available only for other stocks in most cases. Information on critical habitat is essential for guiding habitat protection and reclamation work.

**Biology and Life History:** Whenever possible this section describes the life history of local stocks of the species. This information is supplemented with generalized life history accounts from the literature, with emphasis on stocks most likely to resemble those in Jasper. Aspects of the biology of the species relevant to its conservation and management in the park are also detailed here. Like data on critical habitat, information on critical life history events is essential for guiding conservation and management activities.

**Ecological Significance:** Under this heading I speculate on the role the species may play in the ecology of Jasper National Park. Speculation is all that is possible in most cases, because the function of fishes in the broader ecology of the park has not been investigated for any native species.

**Fishing:** The history and degree of exploitation of Jasper stocks of the species is outlined here. The sportfishing potential of some species not normally considered as sport fish is also considered under this heading, because it may prove to be the only workable way of enabling park visitors to see, learn about and enjoy certain fish species that are accessible by no other means.

**Conservation Status (general):** This section describes the health of the species throughout its range according to jurisdiction; i.e., in North America, Canada and Alberta. Any status designations by formal bodies such as the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the American Fisheries Society's Endangered Species Committee are discussed here. The status of subspecies, distinct geographic forms and local stocks is emphasized because it is critical to preserve genetic diversity to protect the species. The result provides a basis for judging what role Jasper National Park and its local stocks must play in conserving the species as a whole. Conclusions from this analysis form the basis of the status designation given in the heading to the species account.

**Conservation Status (Jasper):** The condition of the stocks within Jasper National Park is considered in this section, and conservation problems are identified. Here also

I discuss the value of the stocks for conservation purposes.

**Required Action:** The initial work needed to address problems identified in the above sections is presented in point form under this heading. Emphasis is placed on outlining what is immediately required to protect the species properly as called for under the National Parks Act and Canadian Parks Service policies, and interpreted in the first report in this series (Part 1).

## ***Goldeye*** — ***HIODONTIDAE***

*Hiodon alosoides* (Rafinesque) — Mooneyes

**Summary:** The status of this highly migratory and ecologically intriguing fish in Jasper National Park is unknown. Only two anecdotal records exist, and it is possible that it may not enter the park or may use it only occasionally. It is known from the Athabasca River further downstream, and there are no significant physical barriers to its movement as far upstream as Athabasca Falls. This fact raises the concern that this highly migratory fish might carry pulp mill contaminants into the park. An intensive survey is required to determine the status of goldeye in Jasper Park waters.

**Nomenclature:** There have been no recent name changes. Bajkov (1927:22) spelled the generic name "*Hyodon*."

**Description:** A distinctive very thin (laterally compressed), deep-bodied silvery fish, with large eyes, a long anal fin, dorsal fin set far back toward the tail, and without an adipose fin. It is easily confused with the closely-related mooneye, which is not known from the Athabasca, Smoky, or Brazeau river drainages (Roberts 1989:135). It conceivably might be confused with certain ciscoes (e.g., Scott and Crossman 1973:336) or — less likely — with small, thin lake whitefish. The capacity for misidentifying this species should not be underestimated. Roberts (1989:138) reported that the Alberta angling record "goldeye" was actually a quillback, a distinctive laterally-compressed sucker with a very large pointed and elongated dorsal fin.

**Distribution:** Goldeye are widely distributed over the Great Plains from the lower Mackenzie River to near the mouth of the Mississippi. There is a small, disjunct group of populations in part of the James Bay drainage of Ontario and Quebec. In Alberta goldeye are common to abundant in the plains portions of the North and South Saskatchewan river systems, in the Peace River as far upstream as the British Columbia boundary, and in the Athabasca River upstream at least as far as the confluence with the Pembina River (Roberts 1989:135). There is an anecdotal record of goldeye in the Smoky River (Thompson 1890:72).

**Refugia/Postglacial Dispersal:** All Canadian goldeye populations are believed to be derived from stocks that survived glaciation in a Mississippi-Missouri Refugium. The details of how this species dispersed to create its present peculiar distribution in this country are uncertain. Various possibilities are discussed by McPhail and Lindsey (1970:66) and Crossman and McAllister (1986).

**Jasper Stocks:** There are only two records of goldeye in or near Jasper Park, both anecdotal. Hawkins (1910:459) reported in connection with his 1908 land surveys near Brûlé Lake that there were goldeye in the Athabasca River. Bajkov (1927:22) stated that some goldeye were caught near Jasper in 1925, but he had not examined specimens. These observations are discussed in more detail in Section II of this report. If this species uses park waters, it may do so only seasonally.

**Habitat:** Much habitat information for this fish has been collated in standard fisheries manuals (McPhail and Lindsey 1970:67, Scott and Crossman 1973:329), from which the following summary was prepared unless otherwise noted.

Goldeye most commonly frequent large, muddy rivers, the small lakes, ponds and marshes connected with them, and the turbid shallows of large lakes. Although they are often associated with slow-moving waters, they can be found in quite swift current also. The deeper water of lakes and large rivers provides suitable overwintering habitat. Spawning habitat is shallow and turbid water over firm bottom, apparently over gravel shoals in at least some cases. Spawning temperatures are relatively high at approximately 10 to 13 °C.

Newly-hatched fry use the open water, floating freely at the surface, and all stages feed at the surface. Underyearlings in the Peace-Athabasca Delta tend to remain for several weeks within a few hundred metres of shore near the areas in which they were spawned, and many immature goldeye stay in the delta for months after the adults have left for the Peace River (Donald and Kooyman 1977a). It has been suggested that older juveniles (age 4 to 6, but especially age 5) in lacustrine populations use rivers rather than lake habitat (Kennedy and Sprules 1967:17, Bond and Berry 1980a:30-32). In river populations, adults may proceed further upstream to feed after spawning. Discharge seems strongly to affect the extent of upstream movements of goldeye in the Red Deer River (Roberts 1989:136).

**Biology and Life History:** The following summary has been compiled from the descriptions of McPhail and Lindsey (1970:67) and Scott and Crossman (1973:329) unless indicated otherwise.

Spawning migrations and other movements vary widely depending on the stock. In the Peace-Athabasca Delta population, adults and juveniles move *downstream* in spring into the delta lakes from overwintering areas in the lower Peace River (Donald and Kooyman 1977a). Many juveniles either from this same stock or another possibly spawning in Lake Athabasca, move into the lower Athabasca River from the delta area to feed for the summer (Bond and Berry 1980a, 1980b; Tripp and McCart 1979, Tripp and Tsui 1980)[1]. In the North Saskatchewan and probably in the Red Deer rivers,

1 Adults are now frequently taken here as well (D. Donald, personal communication).

spawning migrations are *upstream* from overwintering areas in the lower river (see also Roberts 1989:136). The round-trip distances travelled by goldeye from overwintering to spawning areas may be as much as 800 km in some cases (Donald and Kooyman 1977a). Several individual movements of hundreds of kilometres have been recorded in tagging studies.

Spawning takes place in spring starting just after ice-out and continues for five to six weeks, apparently at night. The eggs are semibuoyant, a feature that would help to keep them from becoming smothered in silt on the bottom. The newly-hatched fry are planktonic, drifting at the surface. In rivers, this causes them to be displaced long distances downstream where they rear, and from whence they move upstream at older ages (Roberts 1989). Rearing juveniles and adults feed opportunistically at the surface on a very wide variety of invertebrates and vertebrates (see also Donald and Kooyman 1977b). Their eyes appear to be adapted to see in poor light, a characteristic that is presumably related to their night spawning habits and turbid water habitat.

Donald and Kooyman (1977a:12,16) provide evidence from life history characteristics that there are at least two distinct subpopulation stocks of goldeye using the Peace River. One occupies the river above Vermilion Rapids and Falls, the other, the Delta stock, uses the river below the rapids. The barrier, though difficult, is not impassable to goldeye moving upstream. There thus appears to be the potential for significant genetic exchange between the stocks. Bodaly et al. (1989:138) refer to unpublished evidence suggesting that the Peace-Athabasca population itself is subdivided into separate stocks, a view that would be supported by some of the characteristics of this population cited above.

**Ecological Significance:** Until the status of goldeye in Jasper National Park is clarified, its ecological role here will remain unknown. Its status and ecology here are of particular interest because if it does enter the park its highly migratory habits give it a possible role as a transporter of pulp mill contaminants into the Jasper ecosystem. Of five species of fish tested from the Athabasca River below Hinton in 1987 and 1989 for which data were presented (longnose sucker, mountain whitefish, burbot, bull trout and rainbow trout), all were contaminated with detectable, often dangerously high, concentrations of dioxin (2,3,7,8 T4CDD) and furan (2,3,7,8 T4CDF) (Alberta Government 1990). Because so many ecologically different species are known to be affected, there is good reason to suspect that other species occupying the river are contaminated as well.

**Fishing:** Fisheries that are known to have exploited goldeye as yet are undocumented in Jasper Park. Net fisheries were operated over many years in the 1800s on Talbot Lake and probably on other nearby lakes and streams to supply Jasper House. Other subsistence fisheries may have been conducted by settlers prior to the establishment of the park. Angling has been conducted since at least 1907. Presumably these fisheries would have captured goldeye had the species been present.

Although it is not widely considered to be a game fish, the goldeye is an outstanding sportfish when taken on light flyfishing tackle.

**Conservation Status (general):** Goldeye do not appear on most current threatened and endangered lists for North America (Ono et al. 1983, Williams et al. 1989), Canada (McAllister et al. 1985, Campbell 1991) or Alberta (Nelson and Paetz 1982). Local stocks have been lost in some areas (e.g., upper Tennessee River) where man-made changes, particularly impoundments, have modified natural conditions (Lee et al. 1980:74). Some jurisdictions on the periphery of its range have listed goldeye as of special concern (Mississippi, Wyoming) or have given the species legislated protection (Wisconsin) (Johnson 1987:4).

One reasonably well-studied and nationally-important stock under the partial jurisdiction of the Canadian Parks Service, the Peace-Athabasca Delta population in Wood Buffalo National Park, is threatened by a water level control structure intended to mitigate low water levels induced by the Bennett Dam (Donald 1989). Most other Canadian stocks are poorly documented, so the true status of this species is unknown.

**Conservation Status (Jasper):** It is unclear whether goldeye ever occurred in Jasper National Park. The present status of the species in the park is unknown. The lack of any certain record of this species being caught in the various park fisheries mentioned above (see Fisheries) does not constitute good evidence that the species does not (or did not) occur in the park, but does suggest that it is uncommon.

**Required Action:**

1. Further historical research should be undertaken to determine if goldeye formerly used the Athabasca River within Jasper National Park. Hudson’s Bay Company records for Jasper House, files held by the National Archives, and other historical documents should be searched for records of this species in the park.

2. The present status of goldeye in Jasper National Park needs to be determined as part of a detailed fish survey of park waters. An adequate fish survey of the major rivers in the park has yet to be conducted. The goldeye survey inherently would be part of a large river survey.

3. Further management action, if any is required, should be based on the results of the above work.

## ***Lake chub***

*Couesius plumbeus* (Agassiz)

## ***CYPRINIDAE***

Minnows

**Summary:** The lake chub is the most abundant and widely distributed minnow in Jasper National Park. In consequence, it probably plays a prominent role in many park aquatic ecosystems as both an important predator on aquatic invertebrates, and as a valuable prey of predaceous fish and waterfowl such as kingfisher, mergansers, loons and other consumers of small fish.

Native populations of lake chub in Jasper Park conceivably have been derived from as many as four separate refugial stocks, potentially differing in morphology, genetics, ecology, behaviour and other properties. Published data suggest that Jasper lake chub may differ slightly in morphology from other described specimens, but this needs to be verified by additional taxonomic study. There is also evidence in the literature of stock structure within single populations of lake chub, so it would not be surprising to find subpopulation stocks of the species in Jasper Park.

Several park populations of lake chub are suspected of being introduced, most likely from local sources. All of these, however, should be managed as native until it can be convincingly demonstrated that they are non-native. Several populations have been the target of poisoning programs, in most cases without success.

Studies are needed to delineate the distribution, abundance, life history and critical habitat of lake chub in Jasper National Park, and to determine the species' taxonomic status and stock structure. The results of these studies should be used to develop a comprehensive management and conservation plan for lake chub in the park.

**Nomenclature:** This is one of those difficult and variable species over which there seems to be perpetual disagreement as to the genus in which it should be placed. The problem is compounded by several subspecies designations, some of which were once recognized as full species. The synonym most likely to be encountered in references dealing with Alberta populations is *Hybopsis plumbea.* Various other names that have been used are discussed by Paetz and Nelson (1970:137), McPhail and Lindsey (1970:244), Scott and Crossman (1973:402, 406), Lee et al. (1980:150), and references cited by those authors. McPhail and Lindsey (1970:238-9) and Paetz and Nelson (1970:137) pointed out that many similarities exist between the monotypic genus *Couesius* and *Semotilus.* The species also has been referred to under the common names northern chub, northern lake chub, creek chub, chub minnow (Paetz and Nelson 1970:137, Scott and Crossman 1973:406) and chub.

As discussed below, the species identified by Bajkov (1927:24) and Neave and Bajkov (1929:19) as *Agosia nubila* (Girard) almost certainly was this species.

**Description:** The lake chub is variable throughout its wide range, as suggested by the many scientific names it has received. It is a small round-bodied fish in cross section, commonly less than 12 cm long in Jasper Park, but it may reach more than 20 cm elsewhere (Scott and Crossman 1973:405). It is often a leaden-grey colour dorsally, shading to silvery-grey on the sides and white on the lower sides and belly, with a dusky lateral band above the lateral line, increasing in intensity from the snout to the tail, or from the midbody to the tail in older fish, the band ending in a dark blotch on the base of the distinctly forked tail. The mouth is somewhat oblique and terminal or only slightly exceeded by the snout. Lake chub are easily distinguished from young whitefish and trout of similar size by their colour pattern (lateral band, no spots or parr marks) and lack of an adipose fin. Species identifications of minnows should be confirmed with the aid of taxonomic keys, which often require scale counts, measurements and examination of small or hidden parts under magnification.

Bajkov (1927:24) described a cyprinid he called *Agosia nubila* (Girard) ("dusky minnow") from "Yellowhead Lake (Mt. Robson Nat. Park). Lakes of Jasper National Park (Annette, Edith, Pyramid and Patricia Lakes, and creeks.)." The only fish now recognized in the genus is *Agosia chrysogaster* Girard, the longfin dace, known only in desert and grassland streams of Arizona, New Mexico and northern Mexico, and thought to be related to "*Rhinichthys*-like stock of western cyprinids" (Lee et al. 1980:141). Scott and Crossman (1973:502) list the names *Agosia oscula* (Girard) and *Rhinichthys nubilus* (Girard) as synonyms for speckled dace, *Rhinichthys osculus* (Girard). According to J. S. Nelson (personal communication), *Agosia nubila* definitely is a synonym of *Rhinichthys osculus.*

Bajkov's account is reproduced below.

*"Head 3 3/4-4 1/4, depth 4 1/4-5 1/4, eye 3 1/2-3 3/4; snout 2 3/4-3 3/4. Dorsal fin I,6-III,8; anal I,6-I,7; pectoral I,13-I,16; ventral I,6-I,8; caudal I,6-III,8. Scales usually* $58 \frac{10\text{-}12}{9\text{-}11} 64$. *Lateral line complete. Pharyngeal teeth usually 2,4-4,2 (rarely 1,4-4,2 or 1,4-4,1). Pharyngeal teeth strongly hooked, without grinding surface. Barbels are present on both sides. Body not compressed, mouth inferior, oblique, snout moderate, head short. Dorsal fin above ventrals. Pectoral in males larger than in females. Ventral nearly reaching the vent.*

*"In life the colour usually dark grayish-olive above, sides metallic blue, belly white, along both sides of body (just above lateral line) dark narrow stripe, at the end of caudal peduncle dark spot. Eye yellow. Fins tipped with yellowish brown. Caudal and dorsal dark. The gill rakers are very short and stubby, about 8 in number. Measurements are given in Table 10."*

The measurements tabulated were for 12 specimens from Annette Lake and 8 specimens from Pyramid Creek, and do not correspond exactly with the range of counts and proportions given above.

Bajkov (1927:24) stated: "This fish is very common in Lakes Patricia, Edith and Annette", and mentioned that it was found in Pyramid Lake. These lakes have been sampled numerous times since Bajkov sampled them, and the only cyprinid ever reported in the catches was lake chub (Rawson 1940a, Rawson and Elsey 1950, Ward 1974; Anderson and Donald 1978b:44,61,80,90; numerous catch records in JNP Warden Service lakes files). Rawson (1940a:8,50) described lake chub, *Couesius plumbeus*, as being present in Patricia Lake, present in large numbers in Edith Lake, and "many" in seine hauls from Pyramid Lake when he sampled these waters in 1939. He found no other species of minnow in any of these lakes. On the other hand, Bajkov (1927) did not report lake chub from these waters, but only *Agosia nubila*.

Bajkov (1927) did not describe exactly how he made his measurements and counts. For example, he does not state whether his body lengths are standard, fork or total measure, so proportions related to body length are only roughly comparable to other published data. Nevertheless his description, tabulated measurements and counts for his dusky minnow are generally consistent with lake chub when compared to published values (McPhail and Lindsey 1970:243, Paetz and Nelson 1970:136-7, Scott and Crossman 1973:401-2). They would not allow confident separation from published values for speckled dace (Carl et al. 1959:123, Scott and Crossman 1973:501) except in his comments regarding general form. Bajkov described his dusky minnow as being not compressed, whereas the speckled dace is said to be distinctly compressed laterally behind the dorsal fin (Scott and Crossman 1973:501).

The Jasper specimens appear to differ significantly from the published values for lake chub in two characters. Bajkov (1927:25) tabulated the following distribution for counts of principal dorsal rays (fin ray count followed by number of specimens in parentheses): 6(3), 7(12), 8(4), 9(1); and for principal anal rays: 6(9), 7(10), 8(1). In contrast, the publications above note an invariable count of 8 principal dorsal rays, and an almost-invariable count of 8 anal rays [Scott and Crossman 1973:402 list a distribution of 7(1), 8(83), 9(3) for anal rays]. Bajkov (1927:24) also described the dorsal fin as being above the pelvic fins. A dorsal fin originating slightly *behind* the origin of the pelvic fins is sometimes used as a diagnostic character for lake chub, but the dorsal origin may be over the insertion of the pelvics depending on the age, sex, or geographic location (Carl et al. 1959:121-2; McPhail and Lindsey 1970:243; Paetz and Nelson 1970:125, 136; Scott and Crossman 1973:402).

Paetz and Nelson (1970:131) stated that Bajkov (1927) recorded the longnose dace, *Rhinichthys cataractae* (Valenciennes) from Jasper Park as *Agosia nubila*. Longnose dace have not been reported in the locations Bajkov (1927:24) reported *Agosia nubila* to be abundant, despite numerous collections as noted above. In fact, they have not been reported from Jasper National Park at all. In general Bajkov's description is consistent with published descriptions of longnose dace, but differs from longnose dace in the measurements he reported for snout length and head length. Longnose dace are said to have snout length to head length ratios of 38.4 to 50.0 percent (Scott and Crossman 1973:494). Bajkov's dusky minnows had much shorter snouts, ranging from

28.6 to 42.0 percent (mean 34.6 percent) of head length, and with only 3 of 20 specimens falling within the range for longnose dace, one of those only barely (38.9 percent). All specimens fell within the range recorded for lake chub (26.6 to 40.0 percent — Scott and Crossman 1973:402). Finally, Paetz and Nelson (1970:131) stated that the name *Agosia* as used at the time of Bajkov implied that the fish lacked a frenum (a bridge of tissue connecting the upper lip to the snout). Longnose dace have a frenum; lake chub do not.

The reason for Paetz and Nelson's interpretation evidently lies in Bajkov's use of the genus name *Agosia* and in his description of the mouth of his dusky minnows as inferior (ventral to the terminal position, the snout usually overhanging the upper lip — Paetz and Nelson 1970:37). Where members of the genus *Agosia* have been synonymized, it has been with *Rhinichthys* species (e.g., Scott and Crossman 1973:500,502). Although other authors (Carl et al. 1959:122, McPhail and Lindsey 1970:243, Scott and Crossman 1973:402) note that the snout may project slightly beyond the upper lip in lake chub (thereby making the mouth inferior, although subterminal would be a better term), Paetz and Nelson (1970:136) describe the mouth as terminal in lake chub. A distinctly inferior mouth position is characteristic of *Rhinichthys* species, especially longnose dace.

**Distribution:** The lake chub is very widespread in northern North America (Scott and Crossman 1973:403, Lee et al. 1980:150), from the lower Yukon River in Alaska to Labrador, and from the southern Northwest Territories, Hudson's Bay and Ungava Bay south to the Missouri River headwaters (where it is widespread in Montana and Wyoming), the Great Lakes and the Maritimes mainland. A few isolated populations exist in the lower Fraser River- Puget Sound area (these records are absent from the summary of McPhail and Lindsey 1986:619, so require confirmation), and a single population is known from the upper Mississippi, where it is otherwise absent. It is absent from Alaska outside of the Yukon drainage, the Arctic Archipelago and the Arctic coastal region generally except in the Mackenzie Delta and Ungava Bay areas, the eastern Hudson's Bay and Labrador coastal areas, and the islands of the Gulf of St. Lawrence including the island of Newfoundland. In British Columbia its distribution includes Yellowhead Lake in the upper Fraser River drainage immediately adjacent to Yellowhead Pass and Jasper National Park (Carl et al. 1959:122). In Alberta it is known from every major drainage system in all parts of the province including the mountains (Paetz and Nelson 1970:138).

**Refugia/Postglacial Dispersal:** Like many other aspects of this fish, there is disagreement regarding the glacial refugia and postglacial dispersal routes used by lake chub. The wide present-day range of the lake chub includes only two areas that certainly were unglaciated — Alaska (Beringia) and the Missouri River basin — but its distribution suggests at least three others: Cascadia, the Mississippi and the Atlantic coastal area.

McPhail and Lindsey (1970:245) and Lindsey and McPhail (1986:651) believed that despite its presence in the unglaciated portions of Alaska, the species probably did not survive the glaciation there but entered the Yukon system from the Mackenzie postglacially. They argued that the lake chub should be more widespread in the Beringian Refugium if it had survived there. These authors noted that no morphological differences between the Yukon and Mackenzie populations had been detected, although such differences are known elsewhere that are probably related to origins in different refugia. For example, McPhail and Lindsey (1970:244) described two morphological forms in their study area of northwestern Canada and Alaska. They suggested that the two forms originated in separate refugia, one in the Columbia basin (Cascadia) and the other in the Missouri basin. The Cascadia stock expanded its range northward postglacially to the Fraser River, and from there to the Peace drainage in the Mackenzie basin. It became almost extinct in its refugial area south of the Cordilleran ice as a result of climatic conditions, they suggested (McPhail and Lindsey 1986:628-629).

Crossman and McAllister (1986:77, 80 footnote 5) advanced a different interpretation, stating it "seemed obvious" that lake chub in the Hudson Bay basin were derived from at least the Alaskan (Beringian) and Missourian refugia. If so, the Beringian stock must have entered the Athabasca drainage to reach the Hudson Bay drainage. They did not indicate Cascadia as being a likely source of lake chub to the Hudson Bay basin. They cited Stewart and Lindsey (1983) as considering that populations from the Churchill River to western Ontario entered the Hudson Bay basin via the Great Lakes (Crossman and McAllister 1986:77, 80 footnote 5).

Taking these data and informed opinions together, it appears that up to three different refugia may have contributed to lake chub stocks in the Jasper area, according to current views. There is evident agreement that lake chub from the Missouri River could have colonized Jasper waters. Because Cascadian lake chub appear to have penetrated northward as far as the headwaters of the Peace drainage via the Fraser River, a movement eastward to the Jasper area through Yellowhead Pass or southward from the Peace may have been possible. If Crossman and McAllister (1986) are correct that Beringia contributed a lake chub stock to the Hudson Bay basin, then Beringian lake chub could have colonized Jasper waters. This evidently would be disputed by McPhail and Lindsey. The Atlantic and perhaps the Mississippian refugia seem to be ruled out as a source of lake chub for our area if Stewart and Lindsey's view, above, is correct.

Finally, it is entirely possible that Jasper stocks are derived from lake chub that survived since at least the mid-Wisconsinan in the Ice-free Corridor of western Alberta. Populations exist today in the extreme glacier-fed headwaters of the Kananaskis (not native), North Saskatchewan, Athabasca and Fraser rivers (Nelson 1965:742-3, Paetz and Nelson 1970:138, Tebby 1974:64, Ward 1974:24, Carl et al. 1959:122). They clearly are able to survive the sort of near-glacial conditions that presumably prevailed in the Corridor at the late Wisconsinan glacial maximum.

**Jasper Stocks:** Bajkov (1927:24) reported lake chub (as *Agosia nubila*) from Yellowhead Lake (4 km west of Jasper National Park), Annette, Edith, Pyramid and Patricia lakes, the Athabasca River, "creeks", and Pyramid Creek (ibid., p. 25). More recent investigators have reported lake chub to inhabit the Athabasca River, its small tributaries and many of its floodplain lakes from the east park boundary upstream to Athabasca Falls (Ward 1974:distribution maps 10-12, Anderson and Donald 1978b, Mayhood 1980); Whirlpool River (Paetz and Nelson 1970:138); numerous West Block lakes (Ward 1974:distribution map 12, Anderson and Donald 1980); Miette River (Paetz and Nelson 1970:138, Mayhood 1980:154); Wabasso Lake (D. E. McAllister identification, Canadian Museum of Nature Catalogue number NMC 84-0304A); Celestine and Kidney lakes in the Snake Indian drainage (Donald et al. 1985); and Medicine, Beaver and Mona lakes in the Maligne drainage above the canyon (Ward 1974:distribution map 11, Donald and Anderson 1978). (Ward 1974:distribution map 11 showed lake chub in Mona Lake, but Donald and Anderson 1978:72 stated that lake chub had not been found in Maligne or Mona lakes as of 1978.) At least two populations are known to exist in lakes above Athabasca Falls (Buck and Long lakes), but there are no records of lake chub from waters above Sunwapta Falls (Donald and De Henau 1981).

The origin of many lake chub populations is in doubt. Many populations have been attributed to unauthorized introductions; for example, by sport fishermen using lake chub as live bait. Examples of such postulated clandestine, probably inadvertent stocking include: reintroductions after poisoning in Edith and Beauvert lakes (Ward 1974:24); introductions into Medicine and Beaver lakes (Donald and Anderson 1978:72); introductions into some or all of Cabin, Caledonia, Dorothy, Iris, Minnow, Riley and Saturday Night lakes, including reintroduction into some that were poisoned (Anderson and Donald 1980:183); intrductions into Honeymoon and Buck lakes, including reintroduction into the latter after poisoning (Donald and De Henau 1981:181); introduction into Celestine Lake, including reintroduction after poisoning, and possibly introduction into Kidney Lake (Donald et al. 1985:105).

Whether or not a population is native is a serious issue that affects how the population and its ecosystem should be managed. For this reason I will consider the problem at length.

It may very well be true that some or all of the above populations were the result of unrecorded introductions. Angling with live baitfish has long been contrary to regulations, but continues to be encountered by park enforcement personnel (W. Bradford, personal communication). A credible observer has told me that live baitfish were clandestinely maintained in Jasper and sold to anglers until recently (D. Donald, personal communications). In several of the cases mentioned above, earlier investigators did not report lake chub or any other minnow from lakes in which more recently they were found. In the Maligne drainage above the canyon, lake chub as of 1978 were restricted to Beaver and Medicine lakes (Donald and Anderson 1978). The very limited distribution of lake chub in the upper Maligne drainage, which appears to hold extensive suitable habitat, is good evidence that lake chub are not native above the canyon. Paleolimnological studies now being completed have provided good evidence that fish were absent until quite recently from one lake (Celestine) now holding lake chub (S. Lamontagne, personal communication).

There are in several cases, however, reasons not to accept the "unrecorded introduction" hypothesis on the basis of current evidence. First, it has been suggested that several lake chub populations have been introduced on the grounds that the species was found in a lake after Rawson (1940a) failed to report it from the same water body. Rawson (1940a) often did not describe his fish collection methods, in particular the gill net mesh sizes he used. He *may* have used standard gangs of gill nets of 38-, 51-, 76- and 102-mm mesh (22.9 m each) as his principal fish sampling method, as he reported for a later study in the park (Rawson and Elsey 1950:17). Even the smallest mesh is too large to catch efficiently all but the largest lake chub, which seldom exceed 10 cm in length in many Jasper Park waters. However, 38-mm mesh inevitably catches many of even the small lake chub where they are very abundant. Rawson (1940a) supplemented his gillnet sampling with minnow seining on occasion, but from his accounts he did not use a seine on many lakes. Large numbers of lake chub are very noticeable in the shallows of many lakes even to incidental observers, but small numbers are easily overlooked. In other words Rawson's (1940a) survey methods were not adequate *consistently* to detect fishes as small as lake chub, and there is a high probability that he overlooked them in some lakes, or simply failed to mention them in his report. Reasons such as these appear to have led him to miss lake chub in Annette Lake, for example, which were "very common" there in 1925-6 (Bajkov 1927:24, recorded as *Agosia nubila*) and were present in the 1940s, as mentioned incidentally (once only as "minnows") in several file reports by W. Cable dating from 1942 (JNP Warden Service lakes files, J.296 series).

Second, the appearance of a species some time after eradication has been attempted is not evidence of reintroduction by humans, because poisoning a lake with fish toxicants frequently does not kill all the fish in the lake. Some fish are especially likely to survive rotenone poisoning in lakes with inlet or outlet streams, spring areas, weedy shorelines, low water temperatures, thermal stratification, or alkaline pH (Foye 1964, Lennon et al. 1971:23). The failure rate of attempts at total eradication due to the presence of inlet and outlet streams and/or marshy shorelines alone may exceed 95 percent (21 of 22 lakes, Foye 1964:184). All of the reappearances of lake chub after reclamation attempts using rotenone in Jasper Park lakes could easily be due to incomplete eradication for one or more of the above reasons.

Third, the present-day inaccessibility of a lake or stream to fish (due to waterfalls or lack of a surface outlet, for instance) is not evidence in itself that lake chub could not have entered it by natural means. Many dispersal barriers, even including major waterfalls such as the Snake Indian, Athabasca and Sunwapta, probably have formed (more likely re-formed) in relatively late postglacial times as glacial debris deposited below them has eroded under fluvial action (V. Levson, personal communication 9 October 1990). Lakes that have no outlets now may well have had them in the relatively recent past under somewhat different climatic or geological conditions.

Fourth, current Canadian Parks Service policy requires that non-native species be removed from the park. Present evidence suggesting certain stocks are not native to certain park waters is too weak to support such drastic management action: there is too great a danger of mistakenly eliminating a population that really is native.

For these reasons, all present populations of lake chub in Jasper National Park, with the exception of those in Celestine Lake and the upper Maligne drainage, should be considered native until the hypothesis is convincingly refuted. The lake chub population in Celestine Lake is almost certainly not native on the paleolimnological evidence now available. Those populations in the upper Maligne drainage almost certainly are not native, based on historical records, the apparently limited distribution of the species within the drainage (as of 1978) and its presence above a canyon barrier that has blocked access by all other native fishes.

**Habitat:** In Jasper Park, lake chub have been found mostly in small low-elevation lakes on the floor of the Athabasca valley or on the Miette valley bench, but this probably reflects sampling bias in part, because few streams have been sampled for small fish. Bajkov (1927:24) reported lake chub from streams in the park, Pyramid Creek and the Athabasca River being the only ones specified. Mayhood (1980:148-50,154) captured lake chub in a small perennial inlet stream to Lake 496, an Athabasca River floodplain pond; in a small springbrook near the mouth of Pyramid Creek; and in deep (1 to 2 m), weedy (emergent sedges and submergent water milfoil), mud-bottomed, beaver-dammed channels ultimately connected to the Miette River approximately 19 km west of Jasper. In contrast, Donald et al. (1977) did not report them from the Fiddle River, a swift, stony, high-gradient stream. Mayhood (1980) failed to collect lake chub in sometimes swift, braided gravelly reaches of Moosehorn, Minaga or Clairvaux creeks, or the Snake Indian, Snaring and Miette rivers in extensive minnow seining in September and October 1980.

According to Scott and Crossman (1973:405), lake chub seem to resort to lakes whenever these are available, and appear to move into the deeper parts of lakes during summer. In Pyramid Lake, Rawson and Elsey (1950:21) stated that lake chub were abundant in shallow-water areas, based on seining and minnow trap collections. They did not specify the type of minnow trap used, times or locations fished, so it is not clear whether sampling bias could account for the apparent preference for shallow water. Scott and Crossman (1973:405) state that lake chub can successfully live in large rivers in the northern part of the range if large lakes are not available.

Critical habitat for lake chub has not been documented in Jasper National Park. Published information pertains to stocks derived from Atlantic or Mississippian refugia (referred to as eastern stocks here), and may not strictly apply to stocks in our area. This caveat should be kept in mind in this discussion and the one following on biology and life history.

An eastern stock of lake chub in Lac La Ronge, Saskatchewan spawned in at least on tributary stream as well as in the lake itself (Brown et al. 1970). The stream-spawning fish seemed to require, or at least to seek out strongly, cover among rocks in the deepest parts of the river channel. Actual spawning took place in about 5 cm of water over, among and under rocks near the banks, during which time cover was sought beneath rocks when there was a disturbance (ibid., p. 1010). Gravel and silt-leaf-wood fragment substrate were equally suitable substrates for successful egg incubation (ibid., p. 1012). Lake chubs that spawned in Lac La Ronge itself did so on shallow rocky shoals and along rocky shores of islands (ibid., p. 1009). Stream-spawning lake chub dwelt in the lake except during the spawning period (ibid., p. 1007).

**Biology and Life History:** Although the lake chub has been a target of numerous lake poisoning programs in Jasper National Park, its biology and life history in park waters are little known.

Bajkov (1927:24) observed that female lake chub (his *Agosia nubila*) contained yellow eggs about 1 mm in diameter when trapped in Annette Lake 3-5 June 1925 or 1926. This suggests that spawning likely would have occurred sometime thereafter. Ripe females and tuberculate males were collected from Caledonia Lake 15 May 1983, and a ripe female swollen with eggs was taken in Leach Lake 11 May 1983, by D. J. Alger and D. B. Donald (identifications and notes by D. E. McAllister — B. Coad, personal communication 26 September 1990). These observations suggest that lake chub spawn at least from mid-May to early June in Jasper waters.

The stomach contents of five lake chub specimens 56 mm to 90 mm in length taken from Pyramid Creek 25 June 1926 included caddisfly larvae and pupae, mayfly nymphs and adults, chironomid larvae and adults, and various terrestrial insects (Neave and Bajkov 1929:19). These authors also reported that many specimens of 50 mm to 67 mm in length collected from Annette Lake in 1925 and 1926 had consumed adult Diptera and beetles, caddisflies, mosquitoes, various crustacean zooplankters, plant remains, midges, ants, amphipods and even *Difflugia*, a protozoan. “Some specimens contained cestodes [tapeworms] and in some cases appeared greatly swollen by these parasites” (Neave and Bajkov 1929:19). Rawson and Elsey (1950:21) stated that the food of small lake chub in Pyramid Lake was mainly cladocerans and copepods, while larger specimens had eaten aquatic and terrestrial insects. The diet of lake chub elsewhere is said to consist largely of aquatic and terrestrial insects, zooplankton and algae, the latter sometimes a main food item (Scott and Crossman 1973:405).

Rawson and Elsey (1950:21) presented the following average fork length-age data for the Pyramid Lake population: 1 year, 28 mm; 2 years, 48 mm; 3 years, 71 mm; 4 years, 114 mm.

Lake chub spawning has been recorded as early as April in some southern populations in eastern Canada, while ripe males and females have been caught as late as August in the Northwest Territories (Scott and Crossman 1973:404), and gravid females were captured throughout the summers of 1966 and 1967 in Lac La Ronge, Saskatchewan, the latest on 13 September 1966 (Brown et al. 1970:1009). The latter authors cited references to other late-spawning populations, including references to August spawning in British Columbia and spawning throughout the summer in Montana. Nelson (1965:743) observed that many age 3+ females were reaching maturity in July in Upper Kananaskis Reservoir, and found ripe lake chub on August 8 and 9 in Lower and Upper Kananaskis Reservoirs, respectively.

Many lake populations spawn in inlet streams (Scott and Crossman 1973:404). Brown et al. (1970) described such a situation in detail in Lac La Ronge, Saskatchewan (Churchill River drainage). Some lake chub entered the river in early May, at least two weeks before spawning began. Most remained hidden in deeper parts of the river while water temperatures remained in the 4-8 °C range. Territories were not established and no nest was built. After break-up on an upstream lake on May 22, lake chub moved toward the banks to spawn. Most spawning took place in the afternoon, but some also occurred at night, mostly among or under rocks, where the nonadhesive eggs were simply broadcast over the bottom. Spawning was complete by May 27, after which almost all fish had returned downstream to Lac La Ronge. Lake chub fry first appeared in the first week of June. Eggs incubated in the laboratory at variable temperatures comparable to those in the river (8-19 °C) hatched in 10 days.

In Lac La Ronge itself, ripe lake chub were first found on 13-16 June when lake surface temperature had reached 10 °C. Ripe adults congregated on shallow rocky shoals and along rocky shores of islands in late June, where they undoubtedly spawned, and where fry were later found. Brown et al. (1970:1009) attributed to temperature the considerable time lag between spawning in the lake in comparison to spawning in the river. Lake chub were spawning in the inlet river at a time when most of Lac La Ronge was ice-bound.

Results of marking experiments showed evidence of substantial stock isolation, with virtually no mixing of lake-spawning and river spawning stocks within the study area. The study area comprised only a small part of the lake, so it is possible that there are many separate stocks of the species breeding in isolation in other inlet streams and shoal areas.

Female lake chub in the Lac La Ronge population reached sexual maturity at age 3, and probably spawned in successive years, significant numbers reaching age 5. Females reached larger sizes and probably lived longer than males.

**Ecological Significance:** Practically nothing is known of the ecological significance of this species in Jasper National Park. It generally has been considered a competitor of trout in park lakes (numerous comments in JNP Warden Service lakes files). This view was challenged by Anderson and Donald (1980:186), who pointed out that trout show a full range of growth, from poor to superior, in lakes harbouring lake chub, and that certain lakes in which lake chub were abundant (Mina, Riley and Patricia) also had the highest growth for rainbow trout found in four mountain parks during recent surveys. They conceded that lake chub might reduce overall trout production or might reduce trout growth in certain circumstances, but emphasized that all hypotheses regarding the effects of lake chub on trout needed to be rigourously tested. It should be added that competition can only exist for resources not available in excess, a condition that in most cases is very difficult to demonstrate, often requiring carefully controlled field experiments. The fact that two species eat the same type of food or live in the same lake is not in itself evidence of competition.

Lake chub are often abundant in park lakes, suggesting that the species may play a considerable role in their ecology, although abundance is not necessarily a measure of ecological significance. Too little is known of their food and feeding habits to judge whether they are significant predators on invertebrates, herbivores, or competitors of other fish. They are consumed by trout, at times forming a substantial part of the diet of some fish (e.g., Anderson and Donald 1980:151). They may form a significant part of the food supply of piscivorous birds such as loons, mergansers and kingfishers that swallow their meal whole, hence require small fish to pass down the gullet. W. C. Cable reported that at least six kingfishers were catching small fish, which he believed to be lake chub and rainbow trout, on Honeymoon Lake in 1951, apparently on 1 August (1951 investigation report for Honeymoon Lake in JNP Warden Service lakes files). Studies reporting predation by kingfishers and mergansers on lake chub were cited by Scott and Crossman (1973:405). The species is host to numerous parasites throughout its range, many of them intermediate forms that have other fishes or fish-eating birds as their definitive host (Scott and Crossman 1973:405).

**Fishing:** There is no known fishery for lake chub in Jasper National Park. If it is true that numerous lake populations in the park owe their existence to dumping of bait pails by anglers, there well may be a significant illicit baitfish fishery for the species. There have been attempts by fishery managers to eradicate many populations, as discussed below.

**Conservation Status (general):** As a species the lake chub is widespread, abundant, and is not considered threatened, endangered or of special concern (Nelson and Paetz 1982, Ono et al. 1983, Williams et al. 1989). A Canadian population thought to be distinctive at the subspecies level (McAllister et al. 1985:169), the Liard Hotsprings lake chub, for several years has been considered rare and of interest to COSEWIC for possible listing as vulnerable (Campbell 1988:85, 1990:5, 1991:155). Several local populations at the southern extremes of the species range, and of interest for that reason, may be extinct (Lee et al. 1980:150). Many states on the periphery of the range list lake chub as a species of special concern (Iowa, North Dakota, South Dakota, Washington) or grant it legislated protection (Massachusetts, Nebraska) (Johnson 1987:6). As long as the taxonomy of this species remains confused the potential for failing to recognize significant entities of concern, especially subspecies, remains.

**Conservation Status (Jasper):** Lake chub are widespread and often abundant in Jasper National Park, and the species does not appear to be in any danger at present. Despite this favourable picture overall, there are some areas of substantial concern.

1. The subspecies taxonomy and stock origin(s) are not adequately known for populations in the park. As discussed above with regard to the postglacial dispersal of this species, the lake chub of Jasper Park were derived from one or more of four potential refugia, the stocks of each potentially different in structure, genetics, behaviour, ecology or other properties. The taxonomy and biology of the species is so poorly known that it is impossible to judge the significance of the Jasper stocks or to know how to manage them at present.

2. There is evidence that at least three populations (those in Celestine, Beaver and Medicine lakes) are not native to those waters, suggesting that there may be other non-native populations in the park. Experience in Jasper has shown that lake chub are capable of forming large populations, and that some large populations seem to have appeared rather suddenly. Again, we do not know the role of lake chub in the ecology of the park, so we cannot judge what the significance might be of lake chub introductions into new habitat: it may be a serious problem or it may be inconsequential.

3. Lake chub populations were eradicated with poisons at least temporarily from Annette, Beauvert, Buck, Celestine, Christine, Dorothy, Edith, Hibernia, Honeymoon, Iris, Leach, Marjorie, Mile 16.5, Mina, Patricia and Riley lakes, and possibly from others. Populations have reappeared in all but Christine, Hibernia, Honeymoon and Marjorie lakes (Anderson and Donald 1978b, 1980; Donald and De Henau 1981; Donald et al. 1985; JNP fish stocking records; JNP Warden Service lakes files). The present populations may have arisen from fish that survived poisoning in refugia within the lakes or in the drainage basin. The surviving populations may have suffered a more or less severe reduction in genetic diversity, depending on the number of founders that survived and the degree of genetic diversity in the original stock. These populations now may be less viable in the long term, and the stocks may diverge in unpredictable ways from the parental type due to genetic drift.

**Required Action:**

1. A study of the taxonomy and basic biology of lake chub in the park is required to establish the origin(s) of the stock(s), and to detail the distribution, abundance, life history, critical habitat and ecological relationships of the species. No attempts should be made to manipulate any populations of lake chub until such a study has been successfully completed.

2. Where feasible and appropriate, paleolimnological studies such as those nearing completion on Celestine, Caledonia and Cabin lakes should be conducted on lakes suspected of holding introduced populations of lake chub. These studies use invertebrate fossils, some species of which are known to be intolerant of fish, to provide evidence of the presence or absence of fish in the past. In certain cases this information will help to determine whether present-day lake chub populations could have been native to particular lakes.

3. A comprehensive management and conservation plan for lake chub should be developed based on the results of the above studies.

## ***Pearl dace*** — ***CYPRINIDAE***

*Margariscus margarita* Cope — Minnows

**SPECIAL CONCERN**

**Summary:** The pearl dace is a common, widely distributed minnow in northern North America, closely resembling lake chub in general appearance. At least two common subspecies are generally recognized, being distinguished mainly by lateral line scale counts. Pearl dace were reported in 1926 from Jasper National Park, but the species has not been recorded here in the intervening 65 years, during which time there has been no adequate sampling for the species.

The Jasper stock was described as a new subspecies, *Leuciscus nachtriebi athabascae* Bajkov [=*Margariscus margarita athabascae* (Bajkov)]. Comparison of the original subspecies description with published data on geographic variation in pearl dace shows the putative *athabascae* subspecies to differ markedly in lateral line scale count from that expected in populations from the Jasper region. The taxonomic status of the Jasper stock remains to be confirmed, but if verified, *M. m. athabascae* would be a subspecies unique to Jasper National Park and would constitute further evidence of a local Wisconsinan refugium.

Slow, weedy streams and weedy lakes are the preferred habitat of pearl dace, which also require habitat secure from pike predation. Waters of this type are uncommon in the park, suggesting that the species is rare here. The type locality of the proposed subspecies apparently remains undamaged, but is close to the townsite and other developments.

In view of the potential significance of Jasper Park stocks and their possible rarity, pearl dace require immediate attention. A search for pearl dace in the type locality of the proposed subspecies should be conducted by qualified fisheries personnel using nonlethal means, and any specimens found should be forwarded to a taxonomic specialist for identification. Depending on the outcome, it may be necessary to develop a special conservation plan for this stock. Whatever the results of the special investigation, a survey of appropriate habitat in the park should be conducted to delineate the distribution, abundance, life history and critical habitat of pearl dace in Jasper National Park.

**Nomenclature:** The pearl dace has been referred to by many scientific names. Among those most likely to be encountered in reference to the fish in Jasper Park are *Leuciscus nachtriebi, Leuciscus margarita, Semotilus margarita*, and several subspecies variants of the above. Bajkov (1927:23) and Neave and Bajkov (1929:19) referred to it as a new subspecies by the name *Leuciscus nachtriebi athabascae*. The most frequently used common name synonym in western Canada is northern pearl dace.

**Description:** Paetz and Nelson (1970:139) described Alberta specimens as being dark green or grey on the back, dusky silver on the sides, the young bearing a distinct brownish-black lateral band that often is present posteriorly in adults. In breeding season the males typically have a bright red band below the lateral line. Internally the peritoneum (body wall lining) is silvery with a few black spots.

This species closely resembles lake chub in general appearance. It is distinguished by the tiny, flattened barbel usually hidden in the maxillary groove, or absent (barbels slender and more conspicuous in lake chub); usually by the smaller scales (see below — may not be applicable to Jasper specimens); by the upper lip extending slightly beyond the lower (mouth terminal or subterminal in lake chub); and internally by the pharyngeal teeth (usually 2,5-4,2 in pearl dace, 2,4-4,2 in lake chub). The bright red band in breeding males readily distinguishes pearl dace from lake chub, which at most develop separate bright red marks at the bases of the pectoral fins, corners of the mouth, opercula, and occasionally pelvic fin bases (McPhail and Lindsey 1970:244, Paetz and Nelson 1970:136, Brown et al. 1970:1010-1011).

Bajkov (1927:23) described a new subspecies, *Leuciscus nachtriebi athabascae*, from Jasper Park at Old Fort Point. The principal distinguishing feature of this fish was the relatively low lateral line scale count (55-62). Since this is also one of the most important characters separating the very similar lake chub from pearl dace, and the counts are within the range for lake chub (53-79, Scott and Crossman 1973:402), perhaps the most likely explanation is that Bajkov misidentified lake chub as pearl dace. This view is supported by the fact that Bajkov (1927) did not report lake chub from any park waters even though it is now common in many that he sampled. The evidence is strong, however, that Bajkov (1927) referred to lake chub in Jasper Park as *Agosia nubila* (see the species account for lake chub); therefore he presumably recognized his Old Fort Point specimens as being different from lake chub. The issue cannot be resolved on the available evidence. For conservation purposes it is safest to accept Bajkov's species identification provisionally until the Old Fort Point population can be sampled and properly identified.

McPhail and Lindsey (1970:230) examined the validity of Bajkov's (1927) *athabascae* subspecies, concluding that the *athabascae* scale count was intermediate between that of the Allegheny pearl dace *M. m. margarita* (49-62) and the subspecies of western Canada, the northern pearl dace *M. m. nachtriebi* (61-78). They did not consider distinctive any of the other characters given by Bajkov, nor did they consider specimens from nearby Obed Lake distinctive.

Scott and Crossman (1973:516-7) tabulated data tending to show clines in lateral line scale count and pectoral fin ray count of the northern pearl dace, the former increasing from east to west, the latter decreasing from east to west. The *athabascae* pectoral ray counts are low (10-15 principal rays, mean 13.4), fitting the clinal pattern for the character, but they are even lower than the range published for the species (14-19, most frequently 15-17; Scott and Crossman 1973:515). The low lateral line scale counts of *athabascae* definitely do not fit the clinal pattern (Table 4), being very low in a region where high counts are expected. Furthermore, the counts for lateral line scales and scales above the lateral line are decidedly lower in the *athabascae* specimens (8-9 above lateral line) than those published for specimens from nearby Obed Lake (lateral line scales 68-74, 11-13 above lateral line; Paetz and Nelson 1970:140). Obed Lake is also in the Athabasca valley just 100 km northeast of the Old Fort Point beaver dams, the type locality of *athabascae*.

**Table 4.** Geographic distribution of lateral line scale counts in pearl dace. Data from Bajkov (1927:23), Paetz and Nelson (1970:140), and Scott and Crossman (1973:516).

| Lateral line scales | Northern pearl dace | Nova Scotia | Ontario | Manitoba | Obed L. Alberta | proposed *athabascae* subspecies | Allegheny pearl dace |
|---|---|---|---|---|---|---|---|
| 49 | | | | | | | x |
| 50 | | | | | | | x |
| 51 | | | | | | | x |
| 52 | | | | | | | x |
| 53 | | | | | | | x |
| 54 | | | | | | | x |
| 55 | | | | | | 1 | x |
| 56 | | | | | | | x |
| 57 | | | | | | | x |
| 58 | | | | | | 1 | x |
| 59 | | | | | | | x |
| 60 | | | | | | 2 | x |
| 61 | | | | | | 2 | x |
| 62 | x | 1 | | | | 2 | x |
| 63 | x | | | | | | |
| 64 | x | 3 | | | | | |
| 65 | x | 1 | | | | | |
| 66 | x | 4 | 2 | | | | |
| 67 | x | | 3 | | | | |
| 68 | x | | 1 | | x | | |
| 69 | x | | 1 | | x | | |
| 70 | x | | 1 | | x | | |
| 71 | x | | | 2 | x | | |
| 72 | x | | 1 | 1 | x | | |
| 73 | x | | | 1 | x | | |
| 74 | x | | 1 | 2 | x | | |
| 75 | x | | | 2 | | | |
| 76 | x | | | 1 | | | |
| 77 | x | | | 1 | | | |
| 78 | x | | | | | | |

Scott and Crossman (1973:516) noted that northern Canadian populations will exhibit a lower scale count than southern ones, which might account for the lateral line scale counts from Obed Lake pearl dace being slightly lower than those for Manitoba fish, but it cannot account for the wide difference in scale counts on fish from populations in the same drainage, in the same locality and differing in elevation by less than 200 m.

Whether or not Bajkov's proposed *athabascae* subspecies deserves to be recognized, it appears to be highly anomalous for this geographic area, apparently most closely resembling a subspecies (the Allegheny pearl dace of Vermont and New York south to Virginia) to which it is unlikely to be closely related, judging from the current interpretation of postglacial dispersal in this species (below).

Bajkov did not refer to his fish by a common name, which if confirmed as a subspecies would be *Margariscus margarita athabascae* (Bajkov) under current nomenclature. I will use Jasper pearl dace in this report to distinguish it from typical northern pearl dace.

**Distribution:** The pearl dace occurs from the Peace River drainage of British Columbia to central Quebec and Nova Scotia, and from the Slave River mouth and the Hudson Bay — James Bay coast south to the Missouri River northern headwaters, the Great Lakes area and Virginia. Relict populations exist in South Dakota, Nebraska and Iowa (Scott and Crossman 1973:517, Lee et al. 1980:364). In Alberta pearl dace are widely but apparently sparsely distributed on the East Slopes and in the northern half of the province (Paetz and Nelson 1970:142, Nelson and Paetz 1976, Tripp and McCart 1979:105, Tripp and Tsui 1980:191).

**Refugia/Postglacial Dispersal:** According to McPhail and Lindsey (1970:231), the northern pearl dace (the subspecies *M. m. nachtriebi*) was probably continuously distributed in the upper Mississippi and Missouri systems during the Wisconsinan. Because of the timing and pattern of deglaciation, they believed the populations in the Missouri system had the first opportunity to disperse to the north and probably gave rise to the populations in the Mackenzie basin. Lindsey and McPhail (1986:667) described pearl dace as a species of Mississippian origin in connection with its distribution in the Peace River, but did not elaborate. Crossman and McAllister (1986:83) considered that pearl dace was one of numerous Hudson Bay basin species which originated in both the Mississippian and Missourian refugia. They drew attention to Bajkov's (1927) *athabascae* subspecies as possible support for their proposed Jasper-Banff Refugium, urging that it be restudied to determine whether it should be synonymized or recognized (Crossman and McAllister 1986:86-7).

**Jasper Stocks:** Bajkov (1927:23) reported the *athabascae* subspecies of pearl dace from "Athabasca, and Beaver dams at Old Fort Point near Jasper." Neave and Bajkov (1929:19) reported taking it at "Oldfort Point and from the Athabasca River during the summer of 1926." Ward (1974:27) mistakenly stated that Paetz and Nelson (1970) had reported Bajkov (1927) as taking pearl dace in the Athabasca River and adjoining beaver dams near the eastern park boundary and Jasper Lake areas. Pearl dace have not been reported since from waters in Jasper National Park.

**Habitat:** The comments of Bajkov (1927:23) and Neave and Bajkov (1929:19) quoted above are the only description available of the habitat for the Jasper pearl dace. Old Fort Point is not marked on the present-day 1:200,000 topographic map of the park, but three older topographic maps dated 1934-56 show it on the right bank of the Athabasca River at Jasper townsite, approximately halfway between the mouth of Tekarra Creek and Lac Beauvert. A perennial stream is shown at this location. The Old Fort Point area is undeveloped and the stream appears to be intact, with a large beaver dam approximately 1 km upstream from the mouth (recent air photo stereo pair, Levson and Rutter 1989:1327). A narrow road crosses it a few metres above the mouth. The Athabasca River is braided immediately above and below the mouth of the creek, forming several small side channels among vegetated islands. These channels and islands are persistent, appearing approximately in their present locations on 1:190,080 topographic maps printed in 1934, 1936 and 1956 (Department of Mines and Resources 1939a, 1939b; Canada Mines and Technical Surveys 1956).

In general in Alberta, pearl dace inhabit slow streams, and occur near cover along the margins of lakes (Paetz and Nelson 1970:141). The species inhabits Petite and Emerson lakes in the central Athabasca drainage (Robinson and Tonn 1989). Both are relatively small and shallow (7.5 to 11.25 ha in area, maximum depth 4 m to 7.25 m), and lack a surface outlet for part or all of the year.

Tripp and Tsui (1980) provide rare habitat information on pearl dace from their surveys in drainages tributary to the Athabasca River south of Fort McMurray. They discovered what appears to be a large population of pearl dace in Algar Lake, a relatively large (7.7 $km^2$), shallow (maximum depth 2.0 m), brownwater lake with a silty bottom “incorporating a large fraction of organic debris” (ibid., p. 55). Only a few small (immature?) pearl dace were found near shore, but large adults were abundant offshore. Pearl dace also were abundant in the Algar River, averaging 120.7 fish per hundred metres of bank seined (ibid., p. 112). The Algar River is a small (4-10 m wide, discharge 0.2 $m^3$ per second near the mouth), meandering, slow-moving, silt-bottomed, brownwater muskeg stream draining Algar Lake (ibid. pp. 19-20). Immature pearl dace only were abundant in the upper muskeg reaches of the river; in the lower swifter or wider reaches the species was less common. Tripp and Tsui found pearl dace in many other streams in their study area, but always in much lower numbers (0-11.2 per 100 m of bank seined, ibid. p. 112), even where the stream habitat resembled that in the Algar River. In streams overall, pearl dace were most frequent (35.7 percent) in small slow-moving muskeg reaches, less frequent (20.0 percent) in larger slow-flowing reaches with sandy substrate, still less frequent (10.3-11.1 percent) in small stream reaches with rubble substrates and moderate to fast flow, and absent from large stream reaches with boulder substrates and fast flow (ibid. p. 105). Pearl dace have been found in the Athabasca River in the general area of Fort McMurray, but only in very low numbers, once at the mouth of a small tributary (Tripp and McCart 1979:105).

Details of critical habitat required by this species are scarce. In a Michigan stream, spawning has been observed in clear water 46 to 61 cm deep on sand or gravel in a weak or moderate current (Scott and Crossman 1973:518). I have found no detailed description of rearing or overwintering habitat. The latter particularly is of interest because the habitat in which pearl dace are found in the open-water season must suffer severe dissolved oxygen depletion in winter.

**Biology and Life History:** Bajkov (1927:23) provided age-length data for the eight specimens of Jasper pearl dace he described. Age 2 fish (two of each sex) were 72-81 mm long; age 3 fish (three males, one female) were 98-102 mm long (total, fork or standard length not mentioned). Neave and Bajkov (1929:19-20) noted that Jasper pearl dace taken at Old Fort Point and from the Athabasca River in summer 1926 age 1-3 years ranged in length from 16-100 mm. Their guts contained a variety of diatoms, filamentous algae, the algal macrophyte *Chara*, harpacticoid and cyclopoid copepods, a cladoceran (*Alona*), and chironomid larvae. Jasper pearl dace were sympatric with rainbow trout, which were also found in the creek at Old Fort Point (Neave and Bajkov 1929:12). Flathead chub apparently were present in the Athabasca River at Old Fort Point (Bajkov 1927:24, cf. Neave and Bajkov 1929:19), so may have coexisted with Jasper pearl dace as well.

Robinson and Tonn (1989) found that pearl dace were part of an association of small fish species that was present in lakes of the central Athabasca drainage only when northern pike and/or yellow perch, both predatory species, were absent. Similarly, data published by Tripp and Tsui (1980) on fish and their habitats in Athabasca tributaries near Fort McMurray show that pearl dace were abundant only in a drainage (Algar River) in which predatory fish were completely absent from their collections.

The absence of predators does not fully explain the high abundance of pearl dace in the Algar drainage because piscivores also were absent from four other streams (Prairie, Saline, Saprae, Surmont) that either lacked pearl dace or held them only in low numbers. One of these (Surmont) consisted primarily of habitat in which pearl dace were scarce throughout the study area (small streams with fast water flowing over boulder, rubble and gravel substrates). The remaining three streams lacking piscivores provided extensive small muskeg stream habitat, the predominant type in the Algar drainage (see discussion of Habitat, above). The difference between the Algar drainage and the three drainages apparently favourable to pearl dace appears to be in the presence of a lake in the system (Algar Lake). Lakes were absent in the Prairie, Saline and Saprae drainages.

Very little is known of the life history of this fish. It is said to spawn in spring (Scott and Crossman 1973:517), from May to early summer in Alberta (Paetz and Nelson 1970:141). There is a record from Michigan of spawning on 12 June at a water temperature of 17 to 18 °C. Details of spawning behaviour are summarized by McPhail and Lindsey (1970:231) and Scott and Crossman (1973:517-8) from published observations of Langlois (1929) in Michigan. I have found no information on growth rates, age at maturity, sex ratio and other fundamental aspects of its life history.

**Ecological Significance:** The role of pearl dace in the ecology of Jasper Park is not known. As discussed below, the species probably is restricted here by a scarcity of secure habitat. Scott and Crossman (1973:518) cited a study noting its occurrence in the diet of kingfishers, and speculated that mergansers probably consume it. These and any of a variety of animals in the park known to prey upon small fish may rely upon it to an extent, particularly if for some reason they are restricted to its rather specialized habitat. It conceivably has a significant influence on invertebrate or even algal populations in the locations it does occupy.

**Fishing:** There is no fishery for pearl dace in Jasper National Park, although it is undoubtedly part of baitfish fisheries elsewhere (McPhail and Lindsey 1970:231, Scott and Crossman 1973:518).

**Conservation Status (general):** The pearl dace is widespread and sometimes abundant. It does not appear on any lists of endangered or threatened fishes for North America (Ono et al. 1983, Willams et al. 1989), Canada (McAllister et al. 1985, Campbell 1991) or Alberta (Nelson and Paetz 1982). On the southern margin of their range, pearl dace are of special concern in Montana and North Dakota. They are given legislated protection in South Dakota, Nebraska (both of which hold disjunct populations — Lee et al. 1980:364), and Iowa (Johnson 1987:9).

Certain subspecies would be of concern if they were to be recognized, but acceptance of two of four proposed subspecies seems to be awaiting a thorough study of the fish throughout its range (Scott and Crossman 1973:516). There is only a single known population of one proposed subspecies, the Harvey Lake pearl dace of Isle Royale, Lake Superior. Specimens of another proposed subspecies reported only from Jasper National Park have not been collected since 1926.

**Conservation Status (Jasper):** As discussed above, the pearl dace subspecies *M. m. athabascae* described by Bajkov (1927) from Old Fort Point, Jasper National Park, is clearly anomalous in at least two meristic characters, one of them presently used to distinguish subspecies. The type locality has not been sampled since the original 1926 collection, and it is possible that the original population no longer exists. The distinctiveness and taxonomic status of the Jasper pearl dace urgently require confirmation, because it may be a very rare fish unique to the park.

From the analysis of published information on the biology and habitat of pearl dace, it appears that this species will persist in substantial numbers only in slowly-flowing or lentic habitat from which piscivorous fishes, especially northern pike, are excluded. In Jasper National Park this type of habitat probably is rare. Candidate habitat perhaps occurs in a few isolated beaverdammed creeks in the Athabasca valley downstream from the town of Jasper to the park boundary, the Miette River valley, the West Block lakes area, some Prairie de la Vache streams, and possibly the Snake Indian valley between Deer Creek and Rock Creek.

In view of the potential significance of Jasper Park stocks and their possible rarity, pearl dace require immediate attention.

**Required Action:**

1. A search for pearl dace should be made in the type locality of the putative subspecies *M. m. athabascae*, the creek and beaver ponds at Old Fort Point and the Athabasca River. The search should be made by nonlethal means, preferably by live-trapping (careful use of a DC backpack electrofisher would be the second choice). A small number of specimens should be examined by a recognized fish taxonomist, the samples being prepared and shipped according to that person's instructions. Great care should be taken to ensure that the search and sampling themselves do not harm the population or its habitat.

2. Depending on the outcome of (1), a special protection plan may need to be developed for the pearl dace in Jasper Park.

3. A survey of appropriate habitat in the park should be conducted to delineate the distribution, abundance, life history and critical habitat in Jasper National Park, regardless of the outcome of the special investigation.

## *Spottail shiner* — **CYPRINIDAE**

*Notropis hudsonius* (Clinton) — Minnows

**Summary:** The spottail shiner is a widely distributed and often abundant little minnow of rivers and lakes in the north half of North America. There is a confusing array of morphological variants probably representing many different but as yet undefined geographic stocks. The species so far is known in Jasper National Park only from Talbot Lake, where it may be a significant part of the diet of juvenile northern pike and perhaps several species of waterfowl that consume small fish. A survey is needed to determine the distribution, abundance, life history and critical habitat of spottail shiner in the park.

**Nomenclature:** The spottail shiner has been known under a large number of different genus, species and subspecies designations. These have been listed and discussed by McPhail and Lindsey (1970:264), Paetz and Nelson (1970:166) and Scott and Crossman (1973:460, 463). Many subspecies have been proposed, but there is considerable clinal variation and confusing overlap of pigmentation characters throughout the range of the species, which probably require biochemical systematic studies to sort out (Lee et al. 1980:275). Common name synonyms often used in western Canada are spottail minnow, spottail and shiner.

**Description:** Spottail shiners are attractive laterally compressed little fish with dark blue-green backs, silvery sides, large eyes, large scales, a small mouth and a distinct black spot at the base of the caudal fin. Adults are commonly 8 to 10 cm long, but reach nearly 15 cm in this province (Paetz and Nelson 1970:165). McPhail and Lindsey (1970:263) list the absence of a barbel, the large scales and the prominent black spot at the base of the caudal fin as characters serving to distinguish this fish from others in their study area, which includes the Athabasca headwaters.

**Distribution:** The spottail shiner is found in a broad band from the lower Mackenzie River southward east of the Mackenzie and Rocky mountains and the Missouri River to southern Illinois, and eastward to Great Slave Lake, the Hudson Bay Lowlands and southern Quebec, the Great Lakes basin, and the Atlantic seaboard states from New England to Georgia (Lee et al. 1980:275-6). In Alberta it has been found in all major river drainages except the Hay and the Milk (Paetz and Nelson 1970:167), although it is known from the lower Hay River in the Northwest Territories (Lee et al. 1980:276). There are locality records for spottail shiners from points immediately east of Jasper National Park, apparently in the McLeod and upper Pembina drainages (McPhail and Lindsey 1970:262, Scott and Crossman 1973:461).

**Refugia/Postglacial Dispersal:** The present distribution of the spottail shiner includes two unglaciated areas, the upper Mississippi and Atlantic drainages (Lee et al. 1980:276). Citing evidence of subspecific differences of Atlantic populations and absence of the species from the upper Missouri drainage, McPhail and Lindsey (1970:264) argued that spottail shiners of the Arctic drainage probably were derived from the upper Mississippi drainage by postglacial dispersal via Glacial Lake Agassiz. In a later publication, the same authors described the spottail shiner as one of 13 species of Mississippian origin that populated the lower, but not the upper, Peace River (Lindsey and McPhail 1980:667). Crossman and McAllister (1986:83) differed, stating that spottails were one of 13 species showing evidence of invading the Hudson Bay basin from both Mississippian and Missourian refugia. They argued that records of the species from southwestern Alberta north to the Mackenzie suggested a Missourian origin for these populations (ibid., p. 80, footnote 9). There is thus no consensus as to the likely origin of spottail shiners in the Jasper area.

**Jasper Stocks:** Talbot Lake holds the only known population of spottail shiners in the park. Ward (1974:26) noted that it was collected in 1970 and the specimens identified by D. E. McAllister. A Canadian Museum of Nature collection of 30 specimens, catalogue number NMC 71-0676, collected by J. C. Ward on 26 August 1971 from Talbot Lake was identified by D. E. McAllister in September 1971 as spottail shiner (B. W. Coad, personal communication 26 September 1990). Handwritten notes in the Talbot Lake file (JNP Warden Service lakes files) dated 24 May 1984, apparently written by D. J. Alger (a Canadian Wildlife Service fish biologist working with D. B. Donald) note the capture by boatshocker of numerous spottail shiner in Talbot Lake.

It is possible that spottail shiners were introduced into Talbot Lake by fishermen using them as live bait, but it is impossible to judge the likelihood of this explanation from evidence presently available. Rawson (1940a:64) did not report spottails to be present when he sampled the lake 26 September 1939. He used gillnets (mesh size not reported), however, which may not have been efficient at capturing spottails. For conservation purposes it is best to consider this population as native until convincing evidence to the contrary is forthcoming.

**Habitat:** Talbot Lake (Figure 5) is approximately 336 ha in area, separated from Jasper Lake, a widening of the Athabasca River, by a sand isthmus carrying Highway 16. The original outlet to Jasper Lake was filled in and an artificial one was blocked by a dam at the time Rawson visited it. The present condition of the outlet is not recorded. The lake is shallow, with a maximum depth of 2.5 m, and the bottom is covered with the algal macrophyte *Chara* over much of its area. Winter dissolved oxygen is low throughout much of the lake, but springs are said to enter the lake along the south shore (JNP Warden Service lakes files). Details of habitat use by spottails in Talbot Lake are not known.

Paetz and Nelson (1970:166) described spottail shiners as common in lakes and streams, often being pelagic. It is the most northerly ranging species in its genus, according to McPhail and Lindsey (1970:264). These authors reported that some spottails have been taken in large turbid rivers in the north, although they are abundant in the shallows of large northern lakes as well. Scott and Crossman (1973:462) suggested that the view of the spottail shiner as usually a fish of larger rivers and lakes may simply reflect sampling bias, the myriad of smaller Canadian lakes having been inadequately collected.

Sandy shoals, the lower reaches of creeks and creek mouths have been reported as spawning habitat for spottail shiner (Scott and Crossman 1973:461). Other aspects of critical habitat required by this fish have not been summarized in standard references.

**Biology and Life History:** The biology and life history of spottail shiner in Talbot Lake has not been documented.

In Alberta spottail shiners are believed to spawn from June to August (Paetz and Nelson (1970:460), but the exact date of spawning may depend upon latitude and weather. McPhail and Lindsey (1970:265) reported that fish from Calling Lake, in the Athabasca drainage about 400 km northwest of Jasper Park, had large testes or very large ovaries on a 6 June collection date. In some locations (e.g., Lake Erie), spawning is thought to be either prolonged over a period of six weeks or more, or highly variable from year to year (Scott and Crossman 1973:460). Separate stocks could be involved also. In other places the spawning period may last only a matter of a day or two (data of Peer 1960, cited by Scott and Crossman 1973:461). Various sources already cited suggest that spottails reach maturity at age 3 and live only to age 4 as determined from scales.

Spottails feed on plankton, aquatic insects and bottom fauna, as well as filamentous algae and even small fish, including their own eggs and young (Paetz and Nelson 1970:166, McPhail and Lindsey 1970:264, Scott and Crossman 1973:462). Their populations often exhibit high rates of infection with the tapeworm *Ligula intestinalis*, the definitive hosts of which are usually fish-eating birds, including terns. Numerous other parasites are known to use spottail shiners as hosts.

**Ecological Significance:** The ecological role of this species has not been examined in Jasper Park. Spottail shiners may be an important prey species of northern pike in Talbot Lake. Juvenile pike in particular may rely upon the species because of its numbers and small size. There are few reports of stomach contents of pike from the lake, and those that exist have dealt with larger pike or have discovered empty stomachs (e.g., Rawson 1940a:64), whitefish or fish remains (file data, JNP Warden Service lakes files). Many fish-eating birds such as terns, kingfishers, loons and mergansers may make use of it as well. Depending on its abundance, the spottail shiner conceivably could influence the zooplankton and benthic invertebrate communities in Talbot Lake.

**Fishing:** There is no fishery for spottail shiners in Jasper National Park. The species is commonly used as a baitfish in other parts of its range.

**Conservation Status (general):** Spottail shiners are widespread and often very abundant. They do not appear on any current lists of species considered rare, endangered, threatened or otherwise of special concern (Nelson and Paetz 1982, Ono et al. 1982, McAllister et al. 1985, Johnson 1987, Williams et al. 1989, Campbell 1991).

Subspecies designations based on conventional morphological criteria have been widely proposed and often rejected because of clinal variation and a plethora of intergrading forms. The apparent survival of the fish in at least two and perhaps three glacial refugia, its existence in a wide variety of habitats that seem to depend in part upon the part of the range in question, and the pronounced variability throughout the range strongly favour the idea that the species is comprised of separate groups that may prove to be distinctive at the subspecies level. The status of subspecies cannot be determined until they are better defined, by using biochemical genetic techniques, for example.

**Conservation Status (Jasper):** Spottail shiners are said to be numerous in Talbot Lake. Whether the species occurs elsewhere in the park is not known, but they might yet be found in other small lakes associated with the Athabasca River from below Jasper townsite to the park boundary once adequate collections are made in suitable sites.

The relationship of the Talbot Lake population (and others in Jasper National park, if any) to other Alberta populations is of interest in view of the two contending views of postglacial dispersal of spottail shiners in this area. Examination of this question would have to be made as part of a broader study of geographic variation in the species, preferably using biochemical genetic techniques.

**Required Action:**

1. A survey is required to determine the distribution, abundance, life history, critical habitat and other biological characteristics of spottail shiner in Jasper National Park.

## ***Flathead chub*** — ***CYPRINIDAE***

*Platygobio gracilis* (Richardson) — Minnows

**Summary:** The flathead chub is a large predaceous minnow characteristic of the great turbid rivers of the North American plains from the Beaufort Sea to the Gulf of Mexico. It is known in Jasper National Park from a single record of nine small immatures taken at Old Fort Point in 1925. This record, if confirmed, suggests that the species spawns and rears in the park. Flathead chub may use the Athabasca River from the vicinity of Jasper to the east boundary, remaining unknown here perhaps only because the river has not been adequately sampled for them in the intervening 65 years.

Any park stock presumably represents the northern subspecies typical of our region, which was derived from fish that survived the Wisconsinan in a refugium in the upper Missouri River. Taxonomic verification is needed.

Habitat in the park probably is ecologically marginal for flathead chub. Such marginal populations are thought to be especially worth preserving as a source of new adaptive genes for the species as a whole.

**Nomenclature:** This species invariably is referred to in standard reference texts for our area as *Platygobio gracilis* (Carl et al. 1959, McPhail and Lindsey 1970, Paetz and Nelson 1970, Scott and Crossman 1973). Much literature published since about 1960 adopts the generic name *Hybopsis*, following the recommendation of the American Fisheries Society's Committee on Names of Fishes (e.g., Robins et al. 1980). The argument in favour of the *Platygobio* designation was made by McPhail and Lindsey (1970:238-9), and it is this name that has been recommended most recently (Robins et al. 1991).

Two subspecies are recognized by some workers. The northern flathead chub, *P. g. gracilis* (Richardson), is the subspecies likely to occur in the Jasper area (McPhail and Lindsey 1970:239).

**Description:** The flathead chub is a distinctive large minnow with a broad, flat head, large mouth with conspicuous barbels at the corners, falcate (sickle-shaped) dorsal, anal and pectoral fins and a deeply forked caudal fin. The colour is dusky or brown dorsally, changing abruptly at about the lateral line to silver on the sides.

**Distribution:** The flathead chub occurs from the Mackenzie River Delta in the north nearly to the Mississippi Delta in the south, and from the east slopes of the Mackenzie and Rocky mountains east to the western edge of the Canadian Shield, Lake Winnipeg, the Missouri River and the Mississippi River. There is a somewhat isolated group of populations in the headwaters of the Rio Grande and the Pecos, Arkansas and Canadian river drainages in New Mexico, Colorado, Kansas and Oklahoma (Lee et al. 1980:186). In Alberta flathead chub are widespread in every major river system, but apparently have not been reported from the Petitot (Liard drainage), Hay, Battle, or Bow river drainages (McPhail and Lindsey 1970:236, Paetz and Nelson 1970:135, Nelson and Paetz 1976, Scott and Crossman 1973:485, Lee et al. 1980:186).

**Refugia/Postglacial Dispersal:** McPhail and Lindsey (1970:240) argued that the absence of flathead chub from the upper Mississippi and the Great Lakes indicates that it survived glaciation in the Missouri and perhaps in large Mississippi tributaries to the south. They believed that stocks in the Mackenzie drainage were derived by postglacial dispersal from the Missouri River system. Lindsey and McPhail (1986:667) mentioned it without further comment as one of 13 species below the Peace River Canyon that originated from a Mississippian refugium. Crossman and McAllister (1986:83) described flathead chub as one of just four species that, on the basis of their distribution, appeared to have moved northward into the Hudson Bay basin from a Missourian Refugium only.

**Jasper Stocks:** Bajkov (1927:24) collected immature flathead chub from the Athabasca River at Jasper in 1925. Neave and Bajkov (1929:19) described the gut contents of nine specimens ranging in length from 21 to 58 mm caught at Old Fort Point in 1925. There are no other records of flathead chub in the park, and its present existence in the park requires confirmation.

**Habitat:** The habitat used by flathead chub in Jasper National Park has not been described. Juveniles of this species may rear in the river near Old Fort Point, and the species presumably spawns in the general area also. The Athabasca River in the park is cold and highly turbid from glacial silt during the summer, but runs clear from mid-autumn through early spring. Immediately above and below Old Fort Point, where juvenile flathead chub were collected in 1925 (Bajkov 1927:24, Neave and Bajkov 1929:19), the river is braided, divided by several persistent islands into side channels (see discussion of pearl dace habitat). The zooplankton stomach contents of these specimens suggest that the fish either had been feeding in a weedy, lentic habitat or had been feeding in a location a short distance below such a habitat.

Standard compilations of data on this fish (Carl et al. 1959, McPhail and Lindsey 1970:240, Paetz and Nelson 1970:134, Scott and Crossman 1973:487, Lee et al. 1980:186) unanimously describe flathead chub as inhabitants of large, muddy rivers almost exclusively. They are said to use the flowing waters of main channels, shallow to fairly deep water over mud or rocky bottoms, and backwaters or margins of large, turbid rivers, seldom being taken in clear or standing waters. Smaller streams may be entered in the spawning season.

Jones et al. (1978:8-10) caught flathead chub in the lower Clearwater River and in the Athabasca River from Fort McMurray upstream to Brûlé Rapids in fall 1977. Tripp and McCart (1979:40) reported flathead chub to be common throughout the Athabasca River and its major tributaries including the Clearwater River in spring 1978 in their study area, which encompassed that of Jones et al. (1978). Precise collection sites for this species were not given. In August 1978 flathead chub were caught only near, not in, the Clearwater River at its confluences with the Athabasca and the Christina rivers (the latter collection site yielded just 0.1 fish per 100 $m^2$), yet the species was common (40.9 fish per 100 $m^2$ of bank seined) in the Athabasca River at that time (Tripp and Tsui 1980:3, 217).

During Tripp and McCart's spring study period of late April to late June 1978 the Athabasca was turbid, exceeding 40 Formazin Turbidity Units (FTU) on 7 of 9 sampling occasions (ibid., pp. 15-16). In contrast the Clearwater River was clearer, exceeding 15 FTU only immediately following the period of ice break-up in early May. Tripp and McCart (1979:13) described the Athabasca River in the study area as flowing over mostly coarse gravel, and having several major rapids, at least two of which (Mountain and Cascade rapids) form a serious barrier to fish movements. In contrast the Clearwater River is slower, meandering over mostly sand substrate, eroding the outside curves of meander bends and being dotted with numerous islands. The side channels formed by the islands often had extensive growths of macrophytes.

I have found no details on the specific characteristics of the critical habitat required by this species.

**Biology and Life History:** The life history of this important and unusual minnow is poorly known. Spawning is thought to occur in July and August in Alberta (Paetz and Nelson 1970:134). McPhail and Lindsey (1970:240) reported that spawning probably was in progress 27 June in the Mackenzie River at 64 degrees N, because females with large ovaries containing almost free eggs, as well as spent females, were taken then. Tripp and McCart (1979:43) suggested that the spawning period for flathead chub in their area (Athabasca and Clearwater rivers near Fort McMurray) took place after the end of their study on 26 June 1978, because they captured no ripe fish during their late May to late June sampling period. Females taken at Fort Vermilion on the Peace River on 4 August reportedly were spent, so spawning must have ceased before that time (McPhail and Lindsey 1970:240). Scott and Crossman (1973:486) cite data providing evidence for a summer spawning time in the southern part of the Canadian range also.

Tripp and McCart (1979:40, 42) observed that their catches of flathead chub near Fort McMurray reached a maximum in late June at the end of their study. They suggested that there may be migrations of juveniles and adults between their study area and other parts of the Athabasca drainage. These workers caught many flathead chub ranging in fork length from 170 mm to 295 mm, and in age (scale determinations) from 3 to 8, noting also that juveniles of approximately 40 mm to 80 mm in length were abundant in minnow seine collections. Immature fish as old as age 6 (one male and one female) occurred in their collections, but most females at least were mature by that age (they had few males in their study sample). Other studies in the lower Athabasca area cited by them indicated that age of first maturity ranged from as low as age 2 to as high as age 5. Tripp and McCart also provided growth, sex ratio, and length-weight relationship calculations for flathead chub.

The flathead chub seems to be mostly predaceous. Paetz and Nelson (1970:134) reported its diet to be insects and occasionally fish. McPhail and Lindsey (1970:240) described the fish as shark-like in structure and to some extent in feeding habits, calling it an omnivorous and voracious feeder. They stated that its long, sickle-shaped fins, flat wedge-shaped head and flat belly adapt it to swift water, and that it located food primarily by smell with its prominent barbels. The list of food contained in northern specimens included large quantities of aquatic insects, terrestrial insects, berries, seeds, feathers, young suckers and other small fish, and even a young rodent. Scott and Crossman (1973:486) believed that flathead chub also fed by sight as well as by smell. Neave and Bajkov (1929:19) reported the gut contents of nine specimens 21 to 58 mm in length caught at Old Fort Point, Jasper National Park in 1925 contained several benthic and littoral species of cladoceran, a cyclopoid, a planktonic calanoid, a protozoan, a filamentous green alga, chironomid larvae and other larval and adult dipterans. As described under the Habitat heading for this species and pearl dace, the Old Fort Point area includes numerous side channels and a slow tributary with at least one beaver pond.

**Ecological Significance:** The ecological role of the flathead chub in Jasper National Park is not known. It is known to be abundant in other large, turbid Alberta rivers, including the lower Athabasca. It might be a significant bottom-feeding predator in turbid rivers, perhaps filling the niche more effectively than potential competitors that presumably feed mostly by sight, or complementing such surface-feeding predators as goldeye, with which they are sometimes sympatric.

**Fishing:** There is no fishery reported for flathead chub in Jasper National Park. Chumming for flathead chub by Indians is said to be widespread in the north, and they also are said to be angled by artificial fly and natural baits (McPhail and Lindsey 1970:240, Paetz and Nelson 1970:134, Scott and Crossman 1973:486).

**Conservation Status (general):** The flathead chub does not appear on most lists of rare, threatened or endangered species (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Williams et al. 1989, Campbell 1991). Kansas, Kentucky and Mississippi list it as a species of special concern (Johnson 1987:7). The latter two states are on the periphery of the range, and probably list flathead chub because of their limited occurrence in those jurisdictions. Kansas probably lists the species to protect the isolated populations mentioned under Distribution, above. Apart from these local concerns, the species evidently is common to abundant in appropriate habitat throughout its range.

The striking association of this species with large turbid river habitat suggests that it may be a species at risk below major dams on large turbid rivers. Impoundments act as settling basins, removing silt and clarifying the water released downstream. If flathead chub require turbid water (to protect them from predators or to allow them to compete successfully against sight feeders, for example), populations below dams eventually may be reduced or lost. It would be worth examining this question in connection with present or proposed dams on the Liard, Peace, South Saskatchewan and Milk rivers because park protection may be increasingly important to ensure survival of this species.

**Conservation Status (Jasper):** The present status of flathead chub in Jasper National Park is unknown. The species has not been recorded from park waters since Bajkov's (1927) original collection 65 years ago. It is entirely possible that suitable habitat has not been sampled by suitable means at the appropriate time of year. Certainly there are no records of fish collections from Old Fort Point since Bajkov's time.

Habitat in the park probably is ecologically marginal for flathead chub. It recently has been suggested that such marginal populations are especially valuable to species as a source of new adaptive genes, making them and their habitats particularly worth preserving (Scudder 1989).

**Required Action:**

1. Intensive spring, summer, fall and (if possible) winter surveys of the mainstem Athabasca River and major tributaries within the park are required to confirm the presence and taxonomic status of flathead chub in Jasper National Park, and to determine its distribution, abundance, critical habitat, life history and basic biology.

## Longnose sucker

*Catostomus catostomus* (Forster)

## CATOSTOMIDAE

Suckers

**SPECIAL CONCERN**

**Summary:** The longnose sucker is a widespread and often abundant species of coldwater lakes and streams on the mainland of northern North America. It is a characteristic member of the Alberta fish fauna. In the Athabasca River system it evidently exists in several separate stocks, most of which are as yet undescribed. Possibly two stocks distinct at the subspecies level occur within Jasper National Park. The Jasper longnose sucker (*C. c. lacustris*) is treated in a separate account. The typical form treated here occupies the Athabasca River and waters accessible from it, from below Athabasca Falls to the east park boundary. It may be representative of longnose sucker stocks typical of large East Slopes rivers.

Practically nothing is known about this stock in the park, except that it exists. Despite this ignorance, many attempts have been made to eradicate longnose suckers from selected lakes, with success in some cases. Suckers in general are often hated by sport fishermen and even some trained fishery workers, frequently suffering inhumane treatment at their hands. Depending on their abundance, longnose suckers may play an important role in the Jasper ecosystem as a source of food for several species of fish, bird and mammals; as a competitor of other vertebrates for benthic invertebrate prey; or conceivably as an element of the decomposition cycle. As a result of dioxin and furan contamination from a pulpmill outside the park, longnose suckers also may prove to be a significant transporter of these dangerous toxins into the Jasper ecosystem. This, plus the commonly-encountered irrational persecution of suckers in general, make the longnose sucker a species of special concern in the park.

A contaminant survey is required to ascertain the degree and extent of contamination, if any, of longnose suckers in Jasper Park. Also needed is a survey to delineate the distribution, abundance, life history, critical habitat and taxonomic status of the “typical” form of the species here. Finally, a comprehensive interpretive program needs to instituted to explain the biology and ecology of this and other species of sucker. The destruction of suckers should be forbidden within the park, and their protection strictly enforced.

**Nomenclature:** Literature pertaining to Jasper National Park has used the currently-recognized scientific name quite consistently. Other common names widely-used in the past are northern sucker, finescale sucker and sturgeon sucker.

**Description:** Bajkov (1927:21) described specimens from the Athabasca River in Jasper National Park.

*“Colour in life — back gray-olive, belly white, sides quite dark. Head dark. Dorsal fin gray. Caudal darker at tip. Anal and ventrals dull orange. Pectoral brownish or yellow.”*

He also recorded detailed measurements and counts, apparently for a single fish, and noted that the form in the Athabasca River "is quite indistinguishable from specimens from the Kolyma River system in eastern Siberia."

In general, the longnose sucker is a round-bodied fish with a somewhat pointed snout clearly extending beyond the ventral sucking mouth (Nelson 1973:557). It is black, grey or olive brown dorsally shading to white ventrally, spawning males with a burgundy to bright red band above a lateral black band, young fish often (Paetz and Nelson 1970:186) or occasionally (Carl et al. 1959:91) with three faint lateral dark blotches (said to be sometimes faint or absent in Alberta specimens — Paetz and Nelson 1970:186), juveniles mottled with a few irregular light blotches dorsally.

**Distribution:** Longnose suckers are found from northeastern Siberia to Labrador. In North America the species occupies fresh waters on the coast of the Beaufort Sea to the Columbia, Snake and upper Missouri river drainages in the west, and from fresh waters on the coast of Hudson Bay, Ungava Bay and Labrador to the Great Lakes and New England in the east. It is absent from the Arctic Archipelago, freshwaters along the central Arctic coast, southeastern Labrador, Nova Scotia, and islands off the east and west coasts, including the Queen Charlottes, Vancouver Island, Anticosti Island, Prince Edward Island and the island of Newfoundland. In Alberta longnose suckers have been reported to occur in every major drainage system, although there appear to be no records for the Battle River, a major central Alberta tributary of the North Saskatchewan (Paetz and Nelson 1970:189, Scott and Crossman 1973:533).

**Refugia/Postglacial Dispersal:** The present distribution of the longnose sucker includes at least three areas that never have been glaciated, and therefore could have served as Wisconsinan refugia: Beringia, Cascadia and part of the Mississippi basin (McPhail and Lindsey 1970:286). McPhail and Lindsey (1970:286) believed that the Mackenzie River system was populated from the Mississippian refugium, basing their view on the geographic variation in gill raker counts. Crossman and McAllister (1986:85) appear to disagree: they suggest that both Beringia and the Missouri basin were the source of longnose sucker stocks in the Hudson Bay basin. If so, the Beringian stock must have entered the Mackenzie drainage at some point. These same authors raised the possibility that the subspecies *C. c. lacustris* described by Bajkov (1927) from some waters in Jasper National Park survived in a Jasper-Banff Refugium (Crossman and McAllister 1986:87). This issue is taken up in the separate account for the subspecies.

Neither pair of authors discussed the possibility that Cascadia was the source of any longnose sucker stocks east of the Continental Divide, but this alternative cannot be ruled out. McPhail and Lindsey (1986:633) indicate that the Fraser River above Hell's Gate was colonized by longnose suckers from the Columbia River (Cascadia), and longnose suckers are said to occur in the Fraser headwaters within Mount Robson National Park (BC Fish and Wildlife file data, fall 1980). Yellowhead Pass even today is a possible point for headwater transfer of fishes in both directions, a matter discussed in Section I of this report.

**Jasper Stocks:** Bajkov (1927:21) reported the longnose sucker from the Athabasca River in Jasper National Park. He described a separate subspecies, *C. c. lacustris*, from four park lakes. This subspecies recently has been redefined on the basis of Pyramid Lake specimens (McAllister and Camus 1984), and is considered in a separate account.

Rawson (1940a) reported catching longnose suckers in Annette, Beauvert, Pyramid, Patricia and Moab lakes. Paetz and Nelson (1970:189) show locality records for the species at Jasper, in the Whirlpool River, and at a location in the vicinity of Jacques Lake. The latter appears to be the only record of the species in the Jacques Lake area despite several collections (Bajkov 1927; Neave and Bajkov 1929; Cable 1950, 1951, 1953; Baraniuk 1989). Ward (1974:28) reported longnose suckers to use the Athabasca drainage as far upstream as Athabasca Falls and Moab Lake. He also stated that it occurred in Pyramid, Beauvert and Talbot lakes. His distribution maps 11 and 12 show it to occur in several backwaters and channel cutoffs from Jasper townsite downstream to the park boundary. I collected longnose suckers in one of these areas, a creek entering the south end of Lake #496, in October 1980 (Mayhood 1980:148). There appear to be no actual records of longnose suckers being caught in Talbot Lake despite many netting records in the JNP Warden Service lakes files. There is a single record of suckers (species not named) in the outlet of the lake on 19 May 1982 by Warden G. Antoniuk in a Warden occurrence report (Occ. No. 82-387).

Anderson and Donald (1980:183) collected longnose suckers from Dorothy and Iris lakes. Twenty-six specimens from the latter lake collected by D. Alger 11 May 1984 and forwarded to the present Canadian Museum of Nature (catalogue number NMC 84-0308) were identified by J. L. Camus as *C. catostomus*. Seventy-six suckers collected 1 June 1984 from an inlet to Pyramid Lake by G. Antoniuk (Canadian Museum of Nature catalogue number NMC 84-0306) were identified in September 1984 by J. L. Camus as *C. catostomus*. Previously in December 1983, nine suckers collected 22 May 1980 from Pyramid Lake by D. J. Alger and D. B. Donald (Canadian Museum of Nature catalogue number NMC 83-0390) were identified as *C. c. lacustris* by D. E. McAllister. It is not clear whether the Pyramid Lake inlet record, and perhaps the records for some of the other waters in the Athabasca drainage, apply to the common subspecies *C. c. catostomus*, or to the proposed Jasper endemic *C. c. lacustris*.

Longnose suckers evidently are native to Rock Lake just outside the park (Miller and Paetz 1953:101), so may be native in the Rock Creek drainage with the park boundaries. The longnose sucker has not been found in the limited sampling reported for the Brazeau drainage (Rawson 1940a, Yamamoto 1989, Baraniuk 1989). The nearest record for it in that system is far downstream near the Brazeau dam (Paetz and

Nelson 1970:189). Ward (1974:28) stated that longnose suckers occurred north of the park in the Smoky River, probably based on Paetz and Nelson's (1970:189) locality record there, but did not know if it entered the park in the Smoky drainage. Donald et al. (1985) did not collect any longnose suckers from Adolphus, Beatrix or Twintree lakes, all in the Smoky drainage, when they sampled them with gillnets in the period 1979-1984.

The possible native distribution of the longnose sucker in Jasper National Park is shown in Map 1 (map pocket).

**Habitat:** Details of critical habitat for longnose suckers in Jasper National Park have not been documented. Suckers (species not identified) are said to spawn below Highway 16 in a springbrook entering the Athabasca on the left bank within 100 m of the Pyramid Creek mouth (John Woodrow, personal communication fall 1980). I reported only underyearling and juvenile white suckers there based on sampling conducted 20 September and 19 October 1980 (Mayhood 1980:149, see species account for white sucker). Warden G. Antoniuk reported suckers (species not identified) spawning in the outlet of Talbot Lake on 19 May 1982 (Occurrence Report No. 82-387).

In general, longnose suckers occur in clear, cold water in large numbers in the northern part of its range, less abundantly in the south. They have been taken at depths over 180 m in Lake Superior. Longnose suckers use inlet or outlet streams for spawning where available, otherwise they will spawn in the shallows of lakes. Spawning in streams is said to take place in water approximately 150-280 mm deep, in a current 30-45 cm per second over gravel 5-10 cm in diameter (Scott and Crossman 1973:534). Young of the species in lakes evidently rear near shore (Paetz and Nelson 1970:188).

Habitat use differing significantly from the above has been documented in the Athabasca River and its tributaries in the Fort McMurray area for a major river-spawning population of longnose suckers (Tripp and McCart 1979). A migratory population spawns immediately below Cascade Rapids and Mountain Rapids in the Athabasca mainstem above Fort McMurray. At Cascade Rapids spawning apparently occurred in 2.8 to 4.5 m of water moving at 0.4 to 2.1 metres per second (surface) over bedrock and coarse rubble nearest the rapids, to rubble further downstream and gravel and sand near the river banks. At Mountain Rapids spawning took place in 3.0 to 5.0 m of water moving at 0.7 to 2.1 metres per second (surface) over rubble and boulders, with gravel and some sand near the banks. Eggs presumably incubate in the substrate and most fry drift downstream in midcurrent after emerging. Some fry remain to rear in slow water near the bank, but where the fry rear that drift downstream is not known, nor are the precise rearing and overwintering habitats for juveniles.

**Biology and Life History:** The biology and life history of longnose suckers in Jasper National Park has not been documented (see, however, the separate account for *C. c. lacustris*).

Elsewhere longnose suckers move upstream, mostly between noon and midnight, to spawn in streams in early spring (typically mid-April to mid-May) as soon as the water temperature reaches 5 °C. The eggs are deposited over the substrate and adhere to it, hatching in about two weeks, depending on the temperature. The newly-hatched fish remain in the gravel for one to two weeks before emerging and drifting downstream to rear in lakes (Scott and Crossman 1973:533) or in tributaries or slow water in major rivers (Tripp and McCart 1979:55, 65; Tripp and Tsui 1980:158).

There are thought to be at least two separate stocks of this species using the mainstem Athabasca River near Fort McMurray: one below the Cascade and Mountain rapids believed to migrate over 300 km from Lake Athabasca to spawn there, and a second resident population above and below the rapids (Tripp and McCart 1979:67). In addition, Tripp and McCart (1979:67) have presented evidence of a possible third stock in the Clearwater River, a major tributary entering below the rapids at Fort McMurray. Several other major tributaries near Fort McMurray are known to be important spawning streams for longnose suckers, but whether they represent separate stocks has not been investigated (Tripp and McCart 1979, Tripp and Tsui 1980, and references cited therein).

**Ecological Significance:** The role of the longnose sucker in the Jasper Park ecosystem is unknown, but could be substantial depending on its abundance and the particulars of its life history in the park. Although apparently omnivorous, it is well-adapted in its adult form to prey heavily on benthic invertebrates, so could strongly influence the composition of benthic communities in lakes and streams in which it is abundant. Depending on whether food supplies are limiting, their benthic feeding habits could make longnose suckers effective competitors of other species consuming benthic invertebrates, such as white suckers, mountain whitefish, rainbow trout, the juvenile size classes of several other fish species, or even swallows and bats, which probably eat the flying adult stages. The long, looped intestine of longnose suckers suggests that this species is in part a detritivore or herbivore, perhaps important in the decomposition cycle of streams and lakes. Juvenile longnose suckers could be an important prey of several piscivorous vertebrates, for example bull trout, burbot, pike, mergansers, loons, kingfishers and several other waterfowl species, mink and garter snakes.

Data released by the Alberta Government (press release 153, 27 July 1990) show longnose suckers in the upper Athabasca River to be contaminated with dioxin and furan. If the species migrates the long distances it is known to travel in the lower reaches of the river, longnose suckers may be important transporters of these dangerous toxins into the Jasper Park ecosystem. Predators (e.g., bull trout, burbot, northern pike) preying on contaminated suckers conceivably could concentrate the toxins to levels far above those found in the suckers themselves. These fish could then become a direct public health hazard.

**Fishing:** There is no record of longnose suckers being fished in the park, but they likely formed at least an incidental part of the catch of any Indian subsistence fisheries, and of the known domestic fishery conducted by fur traders to supply Jasper House in the 1800s. They also must be caught accidentally in the present-day sport fishery, but there are no records to confirm this.

**Conservation Status (general):** As a species the longnose sucker is very widespread and often very abundant; however there are many unstudied or little-studied forms throughout the range (Scott and Crossman 1973:532). The status of most of these is unknown. One, the Jasper longnose sucker, a proposed subspecies, is a Jasper endemic classified as being of special concern by the American Fisheries Society (Williams et al. 1989:5). The Jasper longnose sucker is discussed separately in this report.

The longnose sucker is absent from most current listings of rare and endangered fishes (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Williams et al. 1989, Campbell 1991). Along the southern margin of its range, however, many jurisdictions list it as a species of special concern (North Dakota, Washington, West Virginia) or give it legislated protection (Illinois, Ohio, South Dakota) (Johnson 1987:9).

Like all suckers, the longnose sucker is hated by many sport fishermen and is routinely destroyed by them when caught. Many are treated with a wanton cruelty that would earn criminal prosecution if it were directed toward other species of animals. Even some professional fishery workers behave in this fashion.

More significant from the point of view of conservation, however, is the deliberate wholesale extermination of suckers from lakes for management purposes. Typically in such cases there has been only perfunctory research into the relationships between the sucker population and the game fish population it is supposed to be damaging. There may be a case to be made for reducing or eliminating competitor or predator fish in certain circumstances even in national parks. That case must be made, however; it cannot simply be assumed.

**Conservation Status (Jasper):** The status of the longnose sucker in Jasper National Park is largely unknown. It was extirpated from Moab Lake by poisoning with toxaphene in 1958, and no longer occurs there (Donald and De Henau 1981:181), even though the lake is accessible to fishes from the Whirlpool River via the outlet. It also has been extirpated from Lake Annette by poisoning with toxaphene in 1957 (Anderson and Donald 1978b:44, JNP fish stocking records). According to Rawson (1940a), longnose suckers were abundant in both lakes when he sampled them in 1939.

The species has recolonized Lac Beauvert, presumably from the Athabasca River, since that lake was poisoned in 1964 (Anderson and Donald 1978b:51,155; JNP fish stocking records). The original stock there and in Patricia Lake may have been *C. c. lacustris* (Bajkov 1927). Patricia Lake, poisoned 7 September 1966 with rotenone, has regained a population of longnose suckers (Anderson and Donald 1978b:80). These fish might have survived in the lake, which may have been only partially poisoned (Lepp 1966:11); however Ward (1967b:9) believed that poisoning had been complete because repeated post-treatment gillnetting captured no fish. Alternatively, they may have entered from Pyramid Lake, which holds *C. c. lacustris*, according to McAllister and Camus (1984).

There is reason to think that migratory longnose suckers might have become contaminated by dioxins and furans from a pulpmill outside the park (Alberta Government press release 153, 27 July 1990). Such highly toxic compounds could pose a threat to the contaminated populations and, through the food web, to the general public. For this reason, and because suckers in general are often the subject of irrational persecution, the longnose sucker is a species of **special concern** in Jasper National Park.

**Required Action:**

1. In view of the potential hazard to public health and ecosystem wellbeing posed by pulpmill toxins in longnose suckers that may enter the park, an immediate contaminant survey is required to determine the degree of toxic contamination, if any, in longnose suckers of the Athabasca River system in Jasper National Park.

2. The taxonomic status, distribution, abundance, life history and critical habitat of the longnose sucker needs to be determined in Jasper Park.

3. A comprehensive interpretive program needs to instituted to explain the biology and ecology of this and other species of sucker. The destruction of suckers should be forbidden, and their protection strictly enforced.

## ***Jasper longnose sucker*** — ***CATOSTOMIDAE***

*Catostomus catostomus lacustris* Bajkov — Suckers

**THREATENED**

**Summary:** The Jasper longnose sucker may be a rare endemic subspecies known originally only from four small lakes in Jasper National Park. It was described as a distinct subspecies in 1927 from lakes Pyramid, Annette, Beauvert and Patricia. Its most obvious distinguishing feature was its usual small adult size. Until recently this subspecies was dismissed as being indistinguishable from the nominate subspecies, which is common throughout much of North America. Recent study of specimens from Pyramid Lake resulted in a proposal to redefine the Jasper longnose sucker on the basis of gill raker count, which is distinctly lower than that of the common subspecies. Additional evidence, discussed in this account, is present in the original description and published photographs showing that *C. c. lacustris* differs from the nominate subspecies. If confirmed by more complete taxonomic study, the existence of this endemic fish in Jasper Park may constitute additional evidence of a local Wisconsinan refugium. The Jasper longnose sucker is considered a separate entity for the purpose of conservation and management planning in this report.

The Jasper longnose sucker is threatened. The only population known still to exist is in Pyramid Lake. This population shows evidence of drastic decline in abundance since the 1940s, and perhaps even more recently. Patricia Lake may still have a population even though it was poisoned in 1969. Lakes Annette and Beauvert were poisoned, and no longer hold populations of the Jasper longnose sucker.

Immediate action is needed to establish the taxonomic and conservation status of this fish, and to ensure its safety. A description of the redefined subspecies needs to be peer-reviewed and published, which may require additional taxonomic and genetic research. Protection and enforcement activities should be reviewed and enhanced if necessary. Other park waters should be surveyed in an attempt to locate more populations.

**Nomenclature:** Alexander Bajkov (1927:22) described this subspecies from “the Lakes of Jasper Park”, evidently meaning lakes Annette, Beauvert, Patricia and Pyramid (ibid. p. 21). Rawson and Elsey (1950:20) rejected the subspecific designation, apparently because they collected many specimens from Pyramid Lake, the type locality, that were much larger than the 114-mm maximum length reported by Bajkov (1927). [Bajkov (1927) distinguished this subspecies primarily on the basis of its small adult size, although his published data provide other bases for separation as well, as will be shown below.] Paetz and Nelson (1970:188) concurred with Rawson and Elsey (1950) in considering the subspecific distinction unwarranted. In as-yet unpublished accounts, Camus and McAllister (1984, in McAllister et al. 1985:169) and McAllister and Camus (1984) accepted the subspecies after redefining it based on gill raker counts on specimens from Pyramid Lake. They referred to it as the Chinook longnose sucker, but in more recent publications it is called the Jasper longnose sucker (Campbell 1988:83, 1990:4, 1991:154; Williams et al. 1989:5).

**Description:** Bajkov's (1927:22) original description of this fish reads as follows (my comments are enclosed in square brackets).

*"In the lakes of Jasper Park: lower lip with 5-6 rows of tubercles; eye small, 6 in head, 3 in snout.*

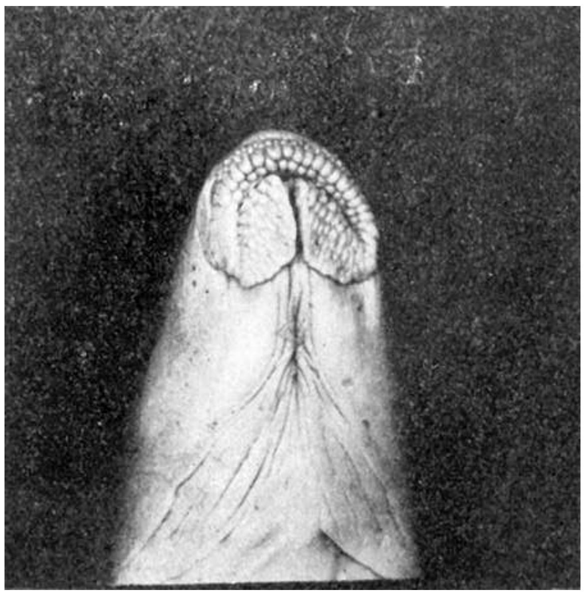
*"It is certainly a purely lacustrine form and must be called* Catostomus catostomus lacustris. *The following description applies to specimens from the Lakes of Jasper Park.*

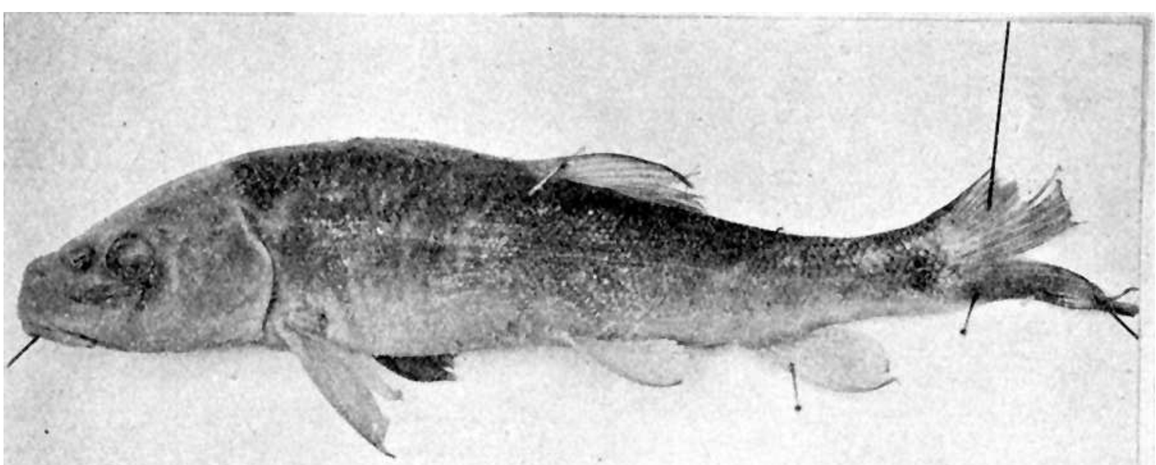
"Catostomus catostomus lacustris. *(Plates I, c; II, a* [Figure 6 in this report]*) Lacustrine, maximum size 4-4 1/2 inches* [102-114 mm]*. On the back the metallic colour is obscured by small spots and specks of dark olive. Sides dark gray with metallic shade. Belly white; dorsal and caudal fins are gray. Anal and pectoral brownish. Pectoral gray-brownish. Scales smaller than* Catostomus catostomus *from the Athabasca River (more than 100-110)* [presumably lateral line scale count]. *Upper lip thick, with 3-4 rows of tubercles (about 28 in medium rows). This fish never grows to a length of more than 4 1/2"* [114 mm].*"*

Bajkov's (1927:22) tabulated morphometric and meristic data for ten specimens, seven females and three males, differ from his description above in several respects. First, one of the specimens is 135 mm (5.3 inches) long, somewhat exceeding his stated maximum size. Second, the lateral line scale counts range only from 96 to 105 (mean 101), not "more than 100-110." Third, the eye diameter is closer to 5 in the head length (mean 5.0, range 4.0-6.0, standard deviation 0.61), not 6 as he stated. Finally, the eye diameter is closer to 2, rather than 3, in the snout length (mean 2.2, range 1.6-2.8, standard deviation 0.38).

There are other interesting features of his photographed specimens (reproduced in Figure 6). The snout clearly does not project much beyond the upper lip in either Plate Ic or Plate IIa. In typical longnose suckers the snout projects well beyond the upper lip except in the very young (Paetz and Nelson 1970:186, Scott and Crossman 1973:531). In Plate Ic the proportion of length to width of the lower lip is very close to 1:1; i.e., the lower lip is deep or elongate relative to its width. The lower lip of *C. c. lacustris* is very similar in proportion (but not papillation) to the lower lip of the largescale sucker (Scott and Crossman 1973:526). Typical longnose suckers have a much shallower lower lip with a length to width ratio near 1:2 (Paetz and Nelson 1970:176). In Plate Ic there are clearly at least three rows of papillae on the upper lip of the specimen, and (as quoted above) Bajkov described the upper lip as having three to four rows of "tubercles"; in typical longnose suckers there are only two rows (Paetz and Nelson 1970:176, Scott and Crossman 1973:525 — used as a key character). The specimen in Bajkov's Plate IIa lacks the overall distinctive fusiform shape of the young (89 mm standard length) or mature longnose suckers photographed by Paetz and Nelson (1970:186-7). Instead, Bajkov's specimen is blunt-nosed and relatively deep-bodied, with the point of maximum body depth much closer to the head than that of the juvenile or adult specimens photographed by Paetz and Nelson (1970:186-7). The general body form of the specimen in Bajkov's Plate IIa is more similar to the white sucker or largescale sucker in general appearance than it is to typical longnose suckers.

**Figure 6.** Bajkov's photographs of the Jasper longnose sucker, *C. c. lacustris* (Bajkov 1927). **Top:** his Plate Ic, captioned "*Catostomus catostomus lacustris* (subsp. nov.). Natural size." This reproduction has been magnified approximately 1.4× the original published photograph. **Bottom:** his Plate IIa, captioned "*Catostomus catostomus lacustris* (subsp. nov.)." This reproduction is approximately 1.2× Bajkov's original published photograph. Scales were not published with the originals.





McAllister and Camus (1984) described the Jasper longnose sucker as a small subspecies, usually less than 150 mm standard length, with 20-23 gillrakers (mean 21.6). They pointed out that this distinguishes it from the typical form of longnose sucker, which commonly exceeds 200 mm, and usually has 24-29 (mean 26.4) gill rakers, although extremes of 21-33 apparently are known.

The observations outlined above tend to support the view of McAllister and Camus (1984) that *Catostomus catostomus lacustris* should be recognized as a valid subspecies distinct from the typical form of the longnose sucker. The gillraker numbers, shape and structure of the lips (especially the papillation of the upper lip), blunt snout and general body form all suggest it is different from the typical form. The taxonomic distinctiveness of this fish needs to be confirmed by the publication in the primary literature of a full redescription and comparison to other longnose suckers from throughout the range of the species.

**Distribution:** If confirmed as taxonomically distinct, the Jasper longnose sucker would be a subspecies endemic to Jasper National Park (see Jasper Stocks, below).

**Refugia/Postglacial Dispersal:** It has been suggested that the Jasper longnose sucker may be a relict of a small fauna that survived the Wisconsinan in a montane-foothill (Jasper-Banff) refugium (McAllister and Camus 1984, Crossman and McAllister 1986:86). The typical form of longnose sucker is generally distributed in coldwater environments (Scott and Crossman 1973:534). It is widespread at lower elevations in the Alberta Rocky Mountains, and is able to tolerate some of the coldwater habitats that would have characterized the Ice-free Corridor. It is conceivable that a distinctive Jasper subspecies diverged in postglacial times from the normal type, but there is nothing obviously different about the Pyramid Lake environment, or aquatic environments in the Jasper area in general, that would encourage rapid divergence. Survival and divergence in isolation over a longer period seems a more likely explanation for an endemic sucker here, if such it is.

**Jasper Stocks:** The Jasper longnose sucker is presently known from only one location: Pyramid Lake in Jasper National Park (McAllister and Camus 1984). Seventy-six suckers collected in 1984 from an inlet to Pyramid Lake by G. Antoniuk were identified in the same year by J. L. Camus as *C. catostomus* (Canadian Museum of Nature catalogue number NMC 84-0306). Previously, however, nine suckers collected in 1980 from Pyramid Lake by D. J. Alger and D. B. Donald (Canadian Museum of Nature catalogue number NMC 83-0390) were identified in 1983 as *C. c. lacustris* by D. E. McAllister. It is not clear in this case whether these are the same subspecies, or whether both the common and endemic forms exist together at Pyramid Lake. It is possible that suckers identified only as *C. catostomus* in this and other park waters are

*C. c. lacustris*.

The populations reported by Bajkov (1927:21) to occupy Annette and Beauvert lakes were extirpated by poisoning with toxaphene in 1957 and an unidentified toxicant in 1964, respectively (JNP fish stocking records). McAllister and Camus (1984) recently examined previously-collected specimens from Annette and Beauvert lakes, but found them indistinguishable from typical longnose suckers.

McAllister and Camus (1984) were not able to study suckers from Patricia Lake, from which Bajkov (1927:21) had reported *C. c. lacustris*. This lake was poisoned with rotenone in September 1966, but has since regained a small population of longnose suckers (Anderson and Donald 1978b:80). There is some doubt that poisoning was complete in Patricia Lake (Lepp 1966:11); however Ward (1967b:9) believed that poisoning had been complete because post-treatment gillnetting attempts captured no fish. Some fish may survive rotenone poisoning in thermally stratified lakes (Foye 1964:184, Lennon et al. 1971:21-22), as Patricia Lake was at the time it was poisoned. Another possible recent source of the suckers in Patricia Lake is Pyramid Lake, which holds the proposed subspecies *C. c. lacustris* (McAllister and Camus 1984) and is connected to Patricia Lake by an intermittent creek flowing from the former to the latter (Anderson and Donald 1978b:157). Ward (1972:19) pointed out that suckers often spawn at the outlet of this creek in Pyramid Lake, and believed there was a "good chance" that suckers repopulated Patricia Lake from Pyramid Lake during high water overflows in 1971.

The locations from which Bajkov (1927) reported *C. c. lacustris* are shown in Map 1 (map pocket).

**Habitat:** Rawson and Elsey (1950:13-14) and Anderson and Donald (1978b:83) have described the main limnological features of Pyramid Lake. It is a 127.4-ha arc-shaped water body approximately 2.4 km long and 480 m wide lying at an elevation of 1186 m. It has a maximum depth of 19 m, a mean depth of 8.7 m, and 35 percent of its area is less than 5 m deep. There is a single small island connected by a short bridge to the eastern shore. The lake has at least four surface inlets, all on the west shore. One of these drains a muskeg with beaver dams, and is a significant spawning stream for the Jasper longnose sucker. The natural outlet is steep and impassable to fish, draining at the surface from the north end to descend approximately 150 m to the Athabasca River. There is a second artificial outlet at the south end that may overflow at high water draining to Patricia Lake approximately 500 m to the south (Rawson 1940a:43). The eastern shore is mostly rocky; the western and southern mostly sandy. Sediments at 5 m depth are black mud; at 16 m, flocculent and gelatinous. The macrophytic algae *Chara* and *Nitella*, and the vascular macrophyte *Potamogeton*, are found irregularly down to 3 m depth throughout the lake.

Pyramid Lake typically is ice-free from approximately mid-May to late November.

Thermal stratification becomes established in July, with a thermocline forming at anywhere from 5 to 9 m, persisting until the fall overturn in September. In the 1940s, dissolved oxygen was not found to decrease below 71 percent saturation in the hypolimnion; more recent data apparently are not available.

The transparency of Pyramid Lake may have decreased significantly since the 1940s. Four Secchi depth determinations in 1939 ranged from 6.5 to 9.5 m (Rawson 1940a:43). Rawson and Elsey (1950:15) reported Secchi depths of 7 to 10 m, apparently for the period 1939-45, Anderson and Donald (1978b:87) reported Secchi depths of only 2 m to approximately 5.8 m for 1972, and Anderson and Dokulil (1977:105) found a Secchi depth of 6.9 m in August 1974. Herzig et al. (1980:50) felt that there was no longterm difference in Secchi transparency, attributing the differences to year-to-year variations in weather.

Spawning habitat for the Jasper longnose sucker is the streams and certain shallow rocky parts of the lake, according to Rawson and Elsey (1950:20-21). Details of critical habitat for this subspecies have not been documented.

**Biology and Life History:** Rawson and Elsey (1950) described much of what is known of the life history of the Jasper longnose sucker based on observations and collections made in 1939-45. Spawning took place in spring in streams and certain rocky parts of Pyramid Lake beginning about 10 June, peaking in the third week of June, and ending by 1 July. Fish moved into the streams at 11 to 14 °C, but remained in the lake near the stream mouths when the water temperature was 9 °C or lower. In 1982 Pyramid Lake suckers also first moved into the principal spawning stream beginning on 10 June, reaching a peak on 15 June, and ending on 20 June — except for two fish each that entered the trap on 26 and 29 June, after which the trap was removed (G. Antoniuk, "Sucker Control Program, Pyramid Lake, JNP, 1982", MS report in file 9875-4: Fish Surveys & Studies, JNP Warden Service files). In 1982, stream temperatures at 0900 h ranged from 6.5 to 8.0 °C from 10 June to 20 June, and there was no apparent effect of temperature on fish movements in the data.

Rawson and Elsey (1950:21) reported that, in the Pyramid Lake population, forty percent of the males and 12 percent of the females reached sexual maturity in their fifth summer, 65 percent of the males and 20 percent of the females were sexually mature by their sixth summer, and all were sexually mature by their seventh summer (these are scale ages 4, 5 and 6, respectively). Furthermore, females constituted 99 percent of the fish over approximately 200 mm in length, a size reached at an age of seven years, on average (ibid. p. 20).

The fish grew very slowly in the 1940s (Figure 7), attaining a maximum age (as determined by scales, presumably) of 14 years (Rawson and Elsey 1950:24). The largest fish caught was 411 mm long (fork, total or standard length not specified) and weighed 822 g, and many were said to be 254 mm to 406 mm in length. It is evident from the age and size distribution data (ibid. pp. 20, cf. p. 24), however, that approximately 75 percent of the fish caught were shorter than 224 mm even when the population was relatively unexploited. The heavy fishing virtually eliminated fish older than age 6 or longer than approximately 180 mm by the end of Rawson's removal program in 1945. Essentially 100 percent of the population at that time consisted of fish age 8 or less; i.e., mean length less than 224 mm.

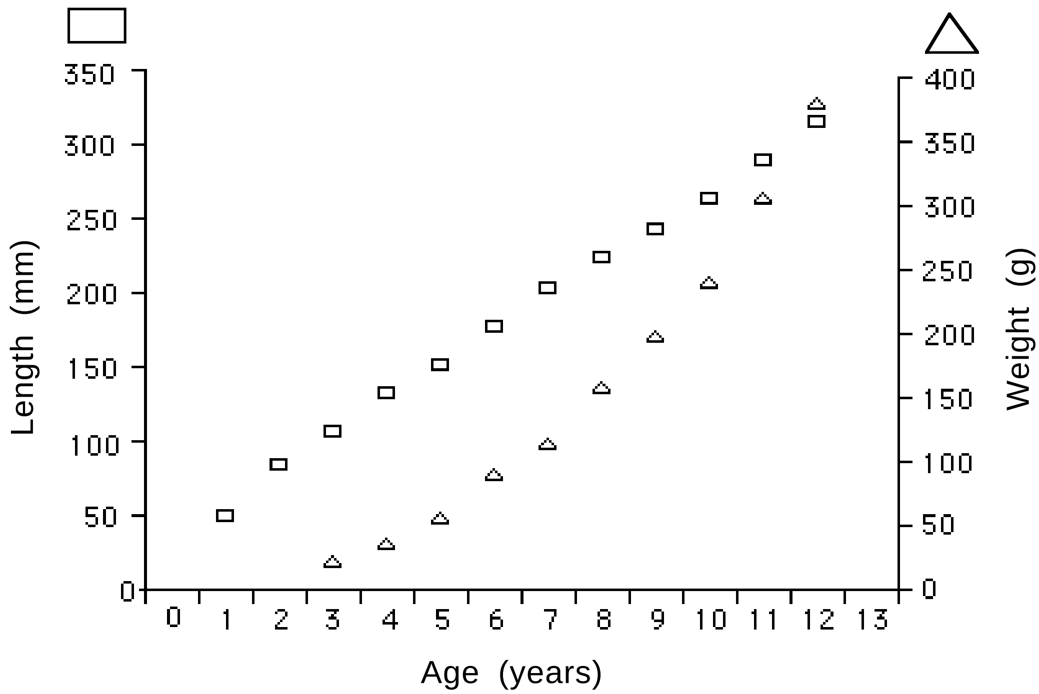



**Figure 7.** Age-length and age-weight relationships in Jasper longnose suckers, Pyramid Lake, sometime in the period 1939-45 (data of Rawson and Elsey 1950:20). Whether the lengths were fork, total or standard lengths was not specified, nor was the method of age determination.

In 1982 the size structure of the population appeared to have recovered little. Over 96 percent of the 226 suckers caught in the 1982 spawning run in the main inlet creek were less than 220 mm in length, although approximately 22 percent were longer than 180 mm, and one specimen exceeded 400 mm in length (G. Antoniuk, ibid.).

Longnose suckers less than about 50 mm long in Pyramid Lake fed mainly on zooplanktonic Crustacea (66 percent, apparently by volume) and terrestrial insects (23 percent). Suckers longer than this consumed mostly amphipods (72 percent) and chironomid larvae and pupae (19 percent), according to Rawson and Elsey (1950:21).

Bajkov (1927:22) stated that *C. c. lacustris* remains under stones during the day and in the evening comes to shore at shallow places. He caught large specimens at night in traps set close to shore. Neave and Bajkov (1929:19) described the fish as feeding entirely at the bottom, mainly at night in shallow water near shore. On four occasions Rawson and Elsey (1950:24) compared catches of suckers in day gillnet sets (0830-2030 h) to night gillnet catches (2030-0830 h) at the same locations. No suckers were taken in the day sets; the night sets in contrast took 44 to 78 suckers per net. These results must reflect in part the relative activity of the fish caught. They tend to support the statements of Bajkov (1927:22) and Neave and Bajkov (1929:19) suggesting that *C. c. lacustris* is inactive during the day and feeds actively during the night.

**Ecological Significance:** Despite the work of Rawson and Elsey (1950), there remains little understanding of the role of the Jasper longnose sucker in the ecosystem of Pyramid Lake. In view of its former great abundance, it may have directly influenced the structure and composition of the zooplankton and benthic invertebrate communities. In turn, it might have been a major source of food for native lake trout when that stock still inhabited the lake. Other vertebrate fish-eaters must rely on it to some extent as well. The fact that it reportedly enters shallow water at night suggests that such sight predators as kingfishers, terns, loons and other aquatic birds prey upon it. It serves as an intermediate host of the tapeworm *Ligula*, which Rawson and Elsey (1950:21) found in 18 percent of the fish they examined, and which uses fish-eating birds, including terns, as definitive hosts (Scott and Crossman 1973:462).

**Fishing:** There has never been a significant sport, commercial or domestic fishery for this small subspecies, but the Pyramid Lake population was fished very heavily from time to time to reduce the numbers of the subspecies in the lake (see below).

**Conservation Status:** The Jasper longnose sucker is threatened.

Rawson and Elsey (1950:26) estimated the population of nettable size (at least 127 mm in length — ibid. p. 22) in Pyramid Lake at 20,000 in 1943. This figure represented approximately 75 percent of the total number and 50 percent of the total biomass of all fish species except lake chub in Pyramid Lake at that time. Over 27,000 longnose suckers were removed from the lake in the seven-year period 1939-45 in an attempt to improve trout fishing, on the assumption that the suckers competed with trout for food. At the end of this period, the population of nettable suckers was estimated at approximately 11,000 to 16,000.

A similar program to reduce the sucker population is said to have been operated on Pyramid Lake by J. Kilistoff and others during the period 1960 to 1970 (J. Strachan, 21 July 1981: "Sucker Control Program", memo to file 9875-4 Fish Surveys & Studies, JNP Warden Service fisheries files). I have not yet found records of the numbers of suckers removed during this period.

In gillnetting conducted in 1973, 30 of 58 fish (51.7 percent) caught in Pyramid Lake were suckers (Yamamoto 1974b:34). In 1974, 76 of 171 fish (44.4 percent) caught by gillnetting were suckers (Yamamoto 1975a:29). In 1977, three nights of gillnetting yielded only 31 suckers out of a total 223 fish (13.9 percent) caught in Pyramid Lake (Yamamoto 1978:33). In 1980, at least 81 percent of the gillnet catch in Pyramid Lake was comprised of species other than longnose suckers (Donald 1987:551); i.e., no more than 19 percent of the catch could have consisted of longnose suckers in that year.

A trap and a Fyke net were set in two inlets to Pyramid Lake "shortly after break-up" (probably mid-May) in 1981 and from 26 May to 29 June 1982, removing 147 and 226 suckers, respectively (J. Strachan, ibid.; G. Antoniuk, "Sucker Control Program, Pyramid Lake, JNP, 1982", MS report in file 9875-4: Fish Surveys & Studies, JNP Warden Service files). The larger of these catches, which appears to have taken the entire spawning run in one inlet creek, is only 14.7 percent of the 1536 suckers (5-year mean) removed annually from two inlet creeks in the period 1941 to 1945, and only 6.4 percent of the total 3534 suckers removed during 1941, the first year of trapping the spawning runs (Rawson and Elsey 1950:23).

Obviously it is difficult to compare catches among these studies. In the more recent collections, times, mesh sizes, lengths of net, and other important variables were not reported. On the other hand, the general methods used are at least roughly comparable, and seem to have taken fish of a similar size range. What is of real concern is that recent collections have consistently failed to collect suckers from Pyramid Lake in anything like the large numbers previously reported by Rawson and Elsey (1950). It would be irresponsible to dismiss as artifacts such large differences in catches suggesting that there has been a moderate to large decline in a population of a possibly unique fish under park protection.

Concern for the Jasper longnose sucker was first raised by McAllister and Camus (1984), who rated it as "vulnerable." McAllister et al. (1985:169) downgraded its status to "rare, possibly threatened." Campbell (1988:83), in a listing of fishes for which status reports were in preparation or under review by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), gave it a proposed status of "rare"; more recently, COSEWIC listed its proposed status again as "vulnerable" (Campbell 1991:154). The Endangered Species Committee of the American Fisheries Society listed it as of "special concern" (Williams et al. 1989:5).

All of these status ratings appear to be based on the unpublished manuscript of McAllister and Camus (1984). Those authors in turn seemingly based their status assessment on their understanding that the Jasper longnose sucker in the 1980s was no longer the dominant fish in Pyramid Lake, citing in support D. B. Donald (*in litt.*) (now presumably Donald 1987). The several other recent catch records presented above suggest that there may have been a drastic decline since the 1940s (and possibly much more recently) in the last known population of this fish. In the face of these results, and in the absence of any other contradictory data, the Jasper longnose sucker must be considered as **threatened** pending a more comprehensive investigation of its status.

**Required Action:**

1. McAllister and Camus need to confirm the taxonomic status of the Jasper longnose sucker by completing any necessary additional research and publishing a complete description of the redefined subspecies in an appropriate scientific journal. Jasper National Park should provide whatever assistance is required to ensure that this is done.

2. Enforcement activities should be reviewed to ensure that they are adequate to protect the Pyramid Lake population of Jasper longnose sucker. This activity appropriately would be coupled with a professionally-designed public information program to inform park users of the significance of this fish and the action underway to protect it.

3. Other Jasper Park waters should be surveyed to locate other populations of this fish.

4. A detailed analysis of the life history, population biology and critical habitat of the Jasper longnose sucker in Pyramid Lake is required to determine its status there, and to provide the information necessary to monitor and protect it.

5. Direct genetic comparisons should be made between the Jasper longnose sucker, the local typical form, and among other potentially closely-related longnose sucker stocks, to establish the degree of distinctiveness of the Jasper longnose sucker and its relationship to other longnose sucker stocks. This study should employ electrophoretic analysis, mitochondrial DNA analysis or other sensitive genetic techniques. This may form part of (1), (3) and (4), above.

6. Depending on the results of (3) and (4), the Canadian Parks Service should make plans to establish other populations of Jasper longnose sucker in secure lakes in Jasper National Park. There should be no fewer than three secure populations of this fish; more certainly would be preferable. If the survey in (3) locates sufficient populations in other waters the conservation status of this fish could be upgraded, and it will not be necessary to establish any new populations.

## *White sucker* — *CATOSTOMIDAE*

*Catostomus commersoni* (Lacépède) — Suckers

**Summary:** The white sucker is widely distributed and often abundant in lakes and streams of central North America. In Alberta it is one of the province's most characteristic species. Despite its prevalence in provincial waters, it only rarely has been recorded from Jasper National Park, and there has been some question whether it actually exists here. Evidence summarized in this account confirms that it does occur in the park in certain waters accessible to the Athabasca River from near the townsite to the east park boundary, therefore presumably in the Athabasca River itself. Its distribution and abundance in the park are not documented, so a survey is needed to obtain this information.

The white sucker was one of the first species that fish zoogeographers suspected of having survived glaciation in or near the Ice-free Corridor, in addition to better-known refugia. Lying close to the Corridor, Jasper's waters are among the more likely ones to have been colonized by these fish, which would be expected to have diverged somewhat from stocks that survived in other refugia south of the continental ice. Evidence in the literature suggests that subpopulation stocks also may be common in this species, so future management should be sensitive to the possibility that white sucker stocks with differing genetic and ecological properties may coexist in the park. White suckers in Jasper Park probably exist in conditions that are ecologically marginal for them. Marginal populations are especially worth preserving as a source of genetic diversity for the species as a whole.

**Nomenclature:** There have been no recent changes in the scientific name. White suckers were often called common suckers until quite recently, and the name coarsescale sucker was often used to distinguish it from the longnose (finescale) sucker. The fur traders often referred to suckers as "carp."

**Description:** The white sucker is a round-bodied, large-scaled fish with a sucker mouth, coloured dark grey to black dorsally, shading to pewter grey on the sides and white on the belly. White suckers may be distinguished in the field from longnose suckers by the slightly oblique subterminal mouth, the snout not projecting beyond the upper lip (mouth near horizontal and clearly inferior, the snout obviously projecting beyond the upper lip in longnose sucker); the convex dorsal surface of the head in profile (nearly flat to concave — turned-up nose — in longnose sucker); white ventral colour ending at mouth, not entirely surrounding the sucker (white ventral colour entirely surrounds mouth in longnose sucker); and the obviously larger scales, especially on the front half of the body (scales relatively small and crowded on front half of body in longnose sucker) (McPhail and Lindsey 1970:281, Nelson 1973:558-9). Lateral line scale counts separate the species completely: 55-85 in white suckers, 91-115 in longnose suckers. Underyearling and juvenile white suckers have three dark, nearly circular blotches on their sides. White suckers can be distinguished from largescale suckers (known from the Fraser River headwaters in Mount Robson

Provincial Park, and possibly could occur in Jasper National Park) by the thicker caudal peduncle (obviously narrow in largescale suckers) and the elongate dorsal fin base of the largescale sucker.

**Distribution:** The white sucker is widely distributed in central North America, from central British Columbia to the lower Mackenzie River; south of the treeline to New Mexico and South Carolina; and east to the Atlantic Coast in the US. The species is absent north of the treeline, the Labrador coastal region, the island of Newfoundland, and the Gaspé Peninsula (Scott and Crossman 1973:540, Lee et al. 1980:376). In Alberta the species has been recorded in every major river system (Paetz and Nelson 1970:193).

**Refugia/Postglacial Dispersal:** The present-day wide distribution of the white sucker includes two large unglaciated areas: the Atlantic coastal area, and the Mississippi-Missouri basin (Lee et al. 1980:376). Current interpretations favour dispersal from a Missouri River refugium to account for populations of white suckers in the Jasper area. The existence of white suckers in the headwaters of the Peace, Liard, Skeena and Fraser systems has been taken as evidence of early postglacial dispersal into those areas, because barriers to dispersal developed later, and the Missouri basin is the closest area in which the species is certain to have survived the Pleistocene (McPhail and Lindsey 1970:282,1986:632; Nelson 1977). This interpretation of survival in a southern refugium and postglacial dispersal northward is consistent with evidence that the northern distribution of the white sucker may be limited by cold climate (see the discussion of Habitat, below).

On the other hand, the presence of white suckers in these headwater areas may be evidence of a much more local refugium. Nelson (1968:114) cited geologist W. H. Mathews in suggesting that lakes "probably persisted in the Peace area during the most recent glaciation, commencing about 25,000 years ago", implying that white suckers might have survived there. Nelson (1977:132) again alluded to this possibility, but considered it "perhaps less probable" than early access from the Missouri-Mississippi refugium. McPhail and Lindsey (1970:283) thought it conceivable that the species persisted throughout the Wisconsinan in a refugium in Glacial Lake Peace in Alberta, or in the Prince George region. McPhail and Lindsey (1970:282) and Lindsey and McPhail (1986:668) mention that there is an apparent difference in spawning colour on the two sides of the Continental Divide, which might suggest stocks with different origins. Write Lindsey and McPhail (1986:668): "a refugium somewhere along the [Ice-free] Corridor (in addition to others in the Mississippi and possibly on the Atlantic Slope) would be consistent with available information."

**Jasper Stocks:** Bajkov (1927) reported only longnose sucker, not any populations of white sucker, in Jasper National Park. On a lake survey form for 1939 (document in

JNP Warden Service lakes files), D. S. Rawson listed the sucker species he caught in Lac Beauvert as “common sucker”, describing its abundance as “moderate”, but in his project report on this work he reported only longnose sucker, not white sucker, in the waters of the park, including Lac Beauvert (Rawson 1940a:22). (At least in some cases these lake survey forms appear to have been filled out after the fact, probably by someone other than Rawson.) Numerous file reports on test netting done since then have reported only longnose sucker from this lake (JNP Warden Service lakes files), with one exception. A letter on file dated 31 October 1955 (Superintendent G. H. L. Dempster to Chief, National Parks Service, J. 296-12 and J. 296-13) stated, “There have been caught from the above noted lakes [Lac Beauvert and Lake Mildred] specimens of suckers which have been tentatively identified, from general conformation, scale count and size of scales, as being Common White Suckers. (Catostomus Comersonii Commersonii) (Lacepede).” Two specimens were caught in Lac Beauvert and one in Mildred Lake, and had been retained for the limnologist to confirm the identification. I have not found any record confirming the identification.

In a brief report to file on the 1955 rainbow trout egg collection in Edith Lake, W. C. Cable stated in passing: “Thirty-five common suckers were gilled in the seines and were destroyed.” All other references to suckers in this lake prior to poisoning in 1958 are to longnose suckers (e.g., Rawson 1940a:13, and numerous file reports by W. C. Cable and others), so it is likely that this is an erroneous identification.

Handwritten notes in the Talbot Lake file (JNP Warden Service lakes files) dated 24 May 1984, apparently written by D. J. Alger (a Canadian Wildlife Service fish biologist working with D. B. Donald) note the capture of one white sucker in Talbot Lake.

Paetz and Nelson (1970:193) show a single locality record for white sucker in the park on the Miette River. Ward (1974:29), apparently referring to this record, stated that he had found only longnose sucker in his work in Jasper Park, and mapped no locality records for the species. The only sucker reported in more recent fish surveys in park waters is longnose sucker (Anderson and Donald 1978b, 1980; Donald and De Henau 1981). Mayhood (1980:148-9), however, reported capturing both white and longnose sucker in a small stream entering Lake #496 (Ward 1974), a backwater of the Athabasca River, and white sucker in a springbrook approximately 100 m north of Pyramid Creek at the CNR crossing (hereinafter referred to as the Pyramid springbrook).

I have re-examined two white sucker specimens from the Lake #496 inlet.

specimen 1: fork length 100 mm, dorsal rays 11, lateral line scales 58, caudal peduncle scales at least 15 (damaged).

specimen 2: fork length 102 mm, dorsal rays 11, lateral line scales 62, caudal peduncle scales 18.

The low dorsal ray counts confirm that these fish are not largescale suckers (typically 13-15 rays). They also lack the distinctly narrow caudal peduncle of that species. The scale counts identify them as white sucker, not longnose sucker (lateral line scales typically 91-115, caudal peduncle scales typically 25-29). In addition, the snout of neither specimen projects beyond the upper lip, both have slightly oblique mouths, pigment touches the upper lip, and both fish have three large dark round blotches on each side. For comparison, a longnose sucker of 98 mm fork length from the same location had clearly more than 100 lateral line scales, 27 caudal peduncle scales, the snout projected obviously beyond the upper lip, the mouth was horizontal and inferior, the mouth was completely surrounded by the white colour of the ventral surface of the fish, and the fish was mottled overall.

White suckers would be able to enter the Athabasca River from this location. They may be widespread in the Athabasca drainage within the park, at least below major barriers to dispersal. They are probably much less abundant than longnose sucker and may be restricted to areas of particularly favourable habitat. In the Brazeau drainage there is one locality record for white sucker in the Brazeau Reservoir far downstream from the park (Paetz and Nelson 1970:193). There is no record of the species in the Brazeau drainage within the park.

**Habitat:** The Pyramid springbrook mentioned above is known as a spawning area for suckers (J. Woodrow, personal communication fall 1980). I found young-of-the-year and some juvenile white suckers there on 30 September and 19 October 1980 (Mayhood 1980:149), indicating that it is a spawning and rearing area for that species. The inlet to Lake #496 mentioned above also held juvenile white suckers (some very small, possibly young-of-the-year) on 1 and 18 October (Mayhood 1980:148), and likewise is probably a white sucker spawning and rearing area.

Elsewhere, white suckers use inlet or outlet streams or the shallows of lakes for spawning (McPhail and Lindsey 1970:283). The species is said usually to be a fish of warmer, shallow lakes or warm, shallow bays and tributary rivers of larger lakes (Scott and Crossman 1973:542). Lindsey and McPhail (1986:665) drew attention to the remarkable correspondence between the northern limit of distribution of this species and the treeline, suggesting that white suckers may be limited in their northern distribution by the cold climate.

**Biology and Life History:** Nothing has been reported regarding the biology or life history of white sucker in Jasper National Park.

I collected several metalarvae in the Pyramid Creek springbrook on 30 September 1980, the measurements of four of which are listed below. Percentages of total length are given in parentheses, and were calculated from the original measurements in ocular micrometer units. Measurements were made as described by Fuiman (1979:563) with the aid of a dissecting microscope at 10× magnification.

specimen 1: total length 20.20 mm, preanal length 13.97 mm (69.2%), eye diameter 1.12 mm (5.6%)

specimen 2: total length 20.40 mm, preanal length 13.67 mm (67.0%), eye diameter 1.12 mm (5.5%)

specimen 3: total length 19.38 mm, preanal length 13.67 mm (70.5%), eye diameter 1.12 mm (5.8%)

specimen 4: total length 19.89 mm, preanal length 13.36 mm (67.2%), eye diameter 1.12 mm (5.6%)

The percentage of preanal length to total length identifies these specimens as suckers, not cyprinid (minnow) larvae; the relatively small eye (less than 7.1% of total length) identifies them as white sucker larvae, not longnose sucker larvae (Fuiman 1979:563, Fuiman and Witman 1979:617). The fact that white sucker metalarvae were present at this location in late September is surprising, and suggests that spawning may occur late in this population, although low temperature (typical of such spring habitats) and crowding both could have retarded development.

White suckers spawn in April to June in Alberta, typically shortly after longnose suckers, starting at water temperatures of 10 °C (Paetz and Nelson 1970:192). Adults are said to home to certain spawning streams, and in some lakes a certain portion of the population spawns in the lake while another spawns in tributary streams (Scott and Crossman 1973:540). White suckers do not build a redd, but broadcast their eggs in shallow water with a gravel bottom, rapids, and the shallows of lakes. The eggs are demersal and adhesive, sticking to the substrate in place, or drifting downstream to adhere to bottom material in quieter areas. The eggs hatch in 8 to 11 days at 10 to 15 °C (laboratory).

The newly-hatched fry remain in the gravel for one to two weeks before emerging. In stream-spawning, lake-dwelling populations the fry drift downstream to rear in the lake. The young at first have terminal mouths and are predaceous on zooplankton, but the mouth moves to a subterminal or inferior position within a few weeks and the fish then become bottom feeders, consuming benthic invertebrates. Sexual maturity is reached at anywhere from 3 to 8 years with males maturing typically one year before females (Scott and Crossman 1973:541); an Alberta publication states that maturity is first reached at age 5 (Paetz and Nelson 1970:192).

There is considerable evidence suggesting that separate stocks develop within some populations. Mention already has been made of adults homing to particular streams to spawn, and to the occurrence of separate lake- and stream-spawning groups in certain lakes, features both favouring and suggesting separate stock development. Scott and Crossman (1973:543) report that dwarf populations may coexist in lakes with a normal population. The existence of geographic stocks or distinct races is suggested by the many variants of the species that have been described throughout its range (McPhail and Lindsey 1970:282, Scott and Crossman 1973:539).

**Ecological Significance:** It is not reasonable even to speculate on the role of white suckers in the ecology of Jasper National Park until more is known about its distribution, abundance and ecological relationships here.

**Fishing:** No fishery has operated in the park specifically to capture white sucker, although the species may have been captured incidentally in whitefish and trout fisheries operated to supply Jasper House in the 1800s. It also may be captured inadvertently in the sport fishery in the park, especially by fishermen using bait. They are said to strike spinners and wet flies as well, providing good sport (Scott and Crossman 1973:543).

**Conservation Status (general):** White suckers are widespread and abundant throughout most or all of the range of the species. Neither the species nor any subspecies are listed as endangered, threatened or of special concern (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Johnson 1987, Williams et al. 1989, Campbell 1991). There is some reason for skepticism regarding this generally rosy picture, however, because the many apparent geographic variants have not yet been adequately studied.

**Conservation Status (Jasper):** Other than that it exists here, the status of the white sucker in Jasper National Park is undocumented. It is probably near its ecological limits in park waters. It has been proposed that ecologically marginal populations are a major source of genetic diversity, bearing a high adaptive significance for the species as a whole (Scudder 1989).

**Required Action:**

1. A survey is required to determine the distribution and abundance of white sucker stocks in the park, and to assess the taxonomic and conservation status of Jasper stocks.

# Northern pike

*Esox lucius* Linnaeus

# ESOCIDAE

Pikes

**Summary:** Northern pike are native to Jasper National Park, inhabiting a few small lakes and slow-flowing weedy streams from the lower reaches of the Miette River downstream in the Athabasca valley to the east boundary. Much of its habitat within the park is marginal, and populations in marginal habitat are believed to be important sources of genetic diversity for species as a whole. Pike apparently have been extirpated from two lakes, Edna and Beauvert. A survey of the distribution, abundance, life history and critical habitat of this species should be conducted, and a comprehensive conservation and management plan should be developed based on the results.

**Nomenclature:** Although the scientific name has remained stable for many years, several common names are in wide use among anglers. This species is variously known in western Canada as pike, jackfish, jack and snake. Smaller specimens of around 40 cm in length often are referred to as "hammerhandles".

**Description:** This species resembles no other in western Canada: it is unmistakable even when very young. The northern pike is a decidedly elongated fish with a flattened, duckbilled snout that looks pointed in profile, and with the dorsal and anal fins set far back on the body. The colour is usually green densely flecked with whitish to yellow oblong spots along the flanks, and with heavy black bars and spots on amber-coloured fins. In young fish and smaller adults, oblique whitish to yellow lines or narrow bars sweep up and back from the belly across the flanks. An unspotted silvery to steel-blue colour variant (sometimes called silver pike) is rare but widespread throughout at least the northern part of the range of the species (Crossman 1978:16). In two Alberta populations, those in Cold and Primrose lakes, this mutant form comprises as much as 10 percent of the population (Paetz and Nelson 1970:113).

**Distribution:** The northern pike has a Holarctic distribution, being found throughout the northern portions of Europe, Asia and North America. In Canada it is common almost everywhere in the interior, being absent only from the Pacific drainage of British Columbia, the Arctic Archipelago, the Arctic coast, the Gaspé Peninsula, the Maritime provinces, Anticosti Island and the island of Newfoundland (Crossman 1978:17). In Alberta, northern pike occupy every drainage (Paetz and Nelson 1970:117). They are absent from the mountains except in the Athabasca and Waterton River drainages.

**Refugia/Postglacial Dispersal:** McPhail and Lindsey (1970:208) believed that northern pike survived glaciation in two refugia, Beringia and a refugium in the Mississippi basin, but that the upper Mackenzie system was invaded only by fish from the latter. Crossman and McAllister (1986:85) cited fossil evidence for survival in two refugia, and evidently accepted the Beringian Refugium as well as the Mississippian as a possible source for northern pike of the Hudson Bay basin. If so, the Beringian stock would have had to enter the Athabasca drainage. Seeb et al. (1987:556) provided evidence from geographic variation of allozymes that northern pike survived in two separate refugia within the Mississippi basin, one in the Missouri drainage and another in the Mississippi proper. They proposed that northern pike invaded western Canada from the Missouri drainage. Although they included one population from the Athabasca drainage in their study (Chip Lake, Pembina River drainage), their data set was sparse and derived only from the central part of the continent. It did not include populations from areas further west or north than Chip Lake, where pike of Beringian origin would be more likely to occur. On the basis of present evidence, however, northern pike in the Jasper area were most likely derived from the Missourian Refugium of Seeb et al. (1987).

**Jasper Stocks:** Records of northern pike in and near the waters of Jasper National Park date from the summer of 1863, when Cheadle (1931:164) recorded in his journal that he fished for pike in the outlet of Talbot Lake. Other later records report pike in Talbot Lake and in the Athabasca River within or very near the park as well (Saint Cyr 1909:150, 1910:195, 198; Hawkins 1910:458, 459; Herriot 1913:98). Bajkov (1927:26) reported that pike are found in the Athabasca River, Miette River, Mildred Lake and Lac Beauvert, but probably does not ascend any higher than the latter location. Rawson (1940a) caught the species in Talbot, Mildred and Beauvert lakes when he surveyed them in 1939. Notes on file (JNP Warden Service lakes files) record that Edna Lake and the lower Snake Indian River hold pike. There are creel census records of anglers capturing pike in the Athabasca, Miette and Snaring rivers, and in Edna and Talbot lakes (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954). Ward (1974:23-4; see also his distribution maps 8 and 9) stated that the species penetrates into the park as far as the Jasper townsite in the Athabasca River, and that it is occasionally caught in river backwaters downstream to the park boundary.

**Habitat:** Critical habitat for northern pike has not been documented in Jasper National Park. Bajkov (1927:26) states that from the Athabasca River it “enters the Miette River and Beauvert and Mildred Lakes, where it spawns in spring.” It apparently is resident in Talbot Lake, which is springfed but shallow and margined with abundant aquatic plants, and may be resident in other lakes, ponds and backwaters associated with the Athabasca River.

In a major study of the effects of environmental factors on this species, Casselman (1978:126) concluded that northern pike can tolerate a wide range of environmental conditions. They grow best at water temperatures of 19 to 21 °C, but still grow well at temperatures from 10 to 23 °C. They are most productive in temperate mesotrophic to eutrophic environments with high transparency, abundant vegetative cover and extensively developed zones of contact between vegetation beds and open water (edge effect).

Northern pike are able to survive extraordinarily low dissolved oxygen concentrations in winter. They have been captured alive in concentrations as low as 0.04 mg per litre, although below concentrations of 0.7 mg per litre fish were extremely inactive. In very low oxygen conditions under winter ice they are able to detect areas of slightly elevated dissolved oxygen concentrations and congregate there (Casselman 1978:114).

Crossman (1978:16) characterized the general habitat of pike as small lakes, the shallow vegetated areas of large lakes, marshes, backwater sloughs and, to a much lesser extent, rivers. Flooded grassy shores or shallow, weedy protected bays seem to be required for successful spawning and early rearing. Pike in some populations use tributary streams or adjacent ponds for spawning where suitable habitat is particularly abundant. Older juveniles and adults inhabit weedy areas in shallow water usually less than 5 m deep (Scott and Crossman 1973:360).

**Biology and Life History:** Almost nothing has been reported about the biology or life history of this species in Jasper National Park. Ward (1974:23) stated that pike as large as 11 kg have been caught. Most records are for much smaller fish, usually not exceeding 2.5 kg or about 70 cm in length (Rawson 1940a:20, 22, 64; National Parks Service 1948, 1950?; Cuerrier and Ward 1952:18, 1953:13; data for Talbot, Mildred and Beauvert lakes, JNP Warden Service lakes files).

In general, pike spawn in early spring just after the ice has left the lakes, usually in late April or early May in Alberta. The eggs are scattered at random through the submerged vegetation, often in very shallow water — it is common to see spawning fish with their backs protruding. The adhesive eggs stick to the plants, hatching in approximately two weeks at the cold temperatures common at spring breakup (i.e., less than 10 °C). The young hatchlings remain attached for six to 10 days to the vegetation by an adhesive glands on their heads. Growth is rapid thereafter, the young reaching 4 cm at the end of a month, and 15 cm by the end of the first summer (Scott and Crossman 1973:358-359). Some may reach 28 cm by the end of the first season of growth (Paetz and Nelson 1970:115).

The young take zooplankton and other small aquatic invertebrates at first, but consume mostly small fish by the time they are 5 cm long. Adult females are usually larger than males of the same age, at least in southern populations. Adults are said to eat “virtually any living vertebrate available to them within the size range they can engulf” (Scott and Crossman 1973:360). And occasionally some they cannot: I once found a pike that died with a sucker half its own length protruding from its jaws, and other similar occurrences have been recorded in the literature (e.g., Prince et al. 1912:15). Predation on waterfowl can be significant in some lakes.

**Ecological Significance:** Data are not available on the role of northern pike in the ecology of Jasper National Park. As adults pike are top aquatic predators, although they are a common prey of man and conceivably could be taken by other mammalian predators and large predaceous birds. Presence of pike may have been the factor preventing several small fish species (e.g., pearl dace, northern redbelly dace, finescale dace, fathead minnow, brook stickleback) from colonizing some park waters that otherwise would be suitable for them (Robinson and Tonn 1989).

**Fishing:** It is reasonable to assume that natives took pike from park waters for hundreds or even thousands of years before the coming of the fur traders to the area in the early 1800s. They are large, inhabit shallow water, tend to remain still and would make relatively easy targets for spearfishers such as the Shuswaps and others that used the area (see Aboriginal Fish Use, Section II of this report).

The earliest record of pike fishing in Jasper National Park is that of Cheadle (1931:164), who tried (and failed) to catch pike in the outlet of Talbot Lake on the afternoon of 1 July 1863. The nineteenth century net fishery operated by the Hudson's Bay Company on Talbot Lake to supply Jasper House undoubtedly took pike as well as the whitefish mentioned by early travellers (De Smet 1847, Cheadle 1931). Saint Cyr (1910:198) also referred to pike fishing in lakes and streams of the park in connection with his surveys in the area in 1909.

Thereafter, no mention appears to be made of pike fishing until Rawson (1940a:64) recommended that the pike of Talbot Lake "should be used by those tourists who wish trolling of this kind", since the lake was "of no use for the production of the better kinds of game fish." A winter net fishery was again operated on the lake as recently as 1950. A request from local petitioners to resume the operation in 1962-63 was turned down (B.I.M. Strong to JNP Superintendent 9 November 1962, J.296-1-34). Winter sport fishing has been conducted on this lake since 1964 (file data, JNP Warden Service lakes files). Creel census data from five years in the period 1948-53 (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954) indicate that northern pike formed a small but significant proportion of the total sport fishery in the park in those years. Talbot Lake and the Athabasca River were the principal producers.

**Conservation Status (general):** Northern pike appear on no lists of threatened or endangered fishes (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Johnson 1987, Williams et al. 1989, Campbell 1991). The species shows remarkably little variation throughout its Holarctic range, and appears to be a single well-defined, uniform species that is both widespread and abundant (Crossman 1978, Seeb et al. 1987). The only indications of geographically separate stock development are the differences in vertebral counts thought to be characteristic of fish from Beringian and

Mississippian glacial refugia (McPhail and Lindsey 1970), and some limited differences in allozyme alleles among some North American and Eurasian populations (summarized by Seeb et al. 1987). There is as yet no satisfying explanation for the apparent uniformity of this species over such an enormous geographic range.

**Conservation Status (Jasper):** In Jasper National Park the status of northern pike is presently unknown. It is apparent from the life history and habitat information outlined above that the species occupies very marginal habitat in the swift, cold, heavily-silted Athabasca River (if in fact it uses the mainstem itself), or lives in small insular populations isolated by highly unfavourable conditions in the mainstem. Scudder (1989) has argued that populations in ecologically marginal habitats are especially important in contributing to and maintaining genetic diversity in the species as a whole.

The northern pike appears to have been extirpated by poisoning from Lac Beauvert (Ward 1968a, JNP fish stocking records). Although another of its former haunts, Edna Lake, was poisoned with rotenone in 1956 and 1965, pike have been caught there in recent years (D. Donald, personal communication).

**Required Action:**

1. A survey of the distribution, abundance, life history and critical habitat of northern pike in Jasper National Park should be conducted. The survey should be used to develop a comprehensive conservation and management plan for the species in Jasper waters.

## *Lake whitefish* — *SALMONIDAE*

*Coregonus clupeaformis* (Mitchill)

Coregoninae
Whitefishes

**SPECIAL CONCERN**

**Summary:** Lake whitefish were native to at least three lakes closely associated with the Athabasca River in Jasper National Park: Beauvert, Edna and Talbot. The species has been reported to occupy the Athabasca River and several backwater ponds associated with it, but I have found no actual records of the species being caught there.

There is evidence that Lac Beauvert may have held a distinctive and highly unusual stock resembling, but different from, the broad whitefish. Lake whitefish in Lac Beauvert and the native stock in Edna Lake were extirpated by poisoning in the 1950s and 1960s.

The Talbot Lake population is the only native stock of lake whitefish known certainly still to exist in the park. The population is genetically unique and zoogeographically informative, based on extensive, recently published isozyme analyses. Additional genetic screening comparing the Talbot Lake stock to other local and regional populations in the Fraser, Peace, Athabasca and North Saskatchewan drainages is needed to confirm its status as a unique stock.

In view of our present lack of critical information on the remaining stocks, the evidence of unusual and possibly unique stocks (one now perhaps extirpated) in at least two lakes, and the possibility of toxic contamination of a population presumed to exist in the Athabasca River, the conservation status of lake whitefish in Jasper National Park is of **special concern**. Surveys are required to determine the distribution and abundance of lake whitefish in Jasper National Park, to identify stocks, and to delineate the life history and critical habitat used by the most important stocks. If a population of the species exists in the Athabasca River, the possibility that it is transporting toxins into the park ecosystem from outside the park boundaries needs urgent investigation. A comprehensive management plan for the remaining native stocks should be developed based on the results of the above studies.

**Nomenclature:** There have been no recent changes in nomenclature. Elsewhere, most fishes referred to simply as “whitefish” probably are this species. In Jasper National Park, however, it is likely that historical use of the term also included mountain whitefish. Older literature used the name “common whitefish.”

**Description:** The lake whitefish is a flat-sided, silvery-grey fish with an adipose fin and forked caudal fin, very small mouth, apparently toothless, and with the tip of the blunt snout projecting beyond the lower jaw. This fish can be distinguished from mountain whitefish by its deeper, laterally flattened body form (round body cross section in mountain whitefish), blunt, squarish snout (pinched or bottle-nosed in mountain whitefish), smaller adipose fin (unusually large in mountain whitefish), and double nasal flaps (single in mountain whitefish). See Schultz (1955) for other features useful for distinguishing the two species in the field.

**Distribution:** Lake whitefish are native to almost the whole of continental Canada, being absent only from most of the Arctic Archipelago and some Pacific and Atlantic coastal drainages including the island of Newfoundland (Scott and Crossman 1973:271, Lee et al. 1980:80). Lake whitefish populations previously thought to have been introduced in waters of the southern Canadian prairies (Lee et al. 1980:80) may be native there (Prince et al. 1912:4 re Pelletier Lake, Nelson and Paetz 1976:3 re Red Deer and South Saskatchewan rivers, Bodaly et al. 1992:776 re Lake Diefenbaker reservoir). In Alberta the species is native to all major drainages with the possible exception of the Bow (Paetz and Nelson 1970:72, Nelson and Paetz 1976).

**Refugia/Postglacial Dispersal:** The stock of lake whitefish inhabiting Talbot Lake was included in a major zoogeographic study by Franzin and Clayton (1977). These workers examined the geographic distribution and frequencies of five alleles in two enzyme systems. In their interpretation they argued that most of western Canada was invaded by lake whitefish from a Mississippian refugium with some input from a Beringian stock. At an early stage in the mixing of the two stocks, the headwaters of several major drainages were invaded, including those in the Athabasca and Fraser systems. The second wave of invasion did not penetrate into some headwater lakes. In their view, Talbot Lake was colonized only by whitefish from the first wave.

This interpretation has been substantially altered by a recent zoogeographic study based on many more genetic data. Foote et al. (1992) published strong genetic evidence for a distinctive refugial stock of lake whitefish that survived one or more Pleistocene glaciations in the northern end of the Ice-free Corridor region. Termed the Nahanni race, these lake whitefish are believed to have survived in a refuge in or near Nahanni National Park on the South Nahanni River, North West Territories. Nahanni-race lake whitefish now occupy waters in the immediate area of the refugium, as well as regions southward in the Liard, Peace, Fraser and Athabasca river headwaters, the latter represented by the population in Talbot Lake. Lake whitefish of Beringian and Mississippian origin occupy the vast regions to the northwest and east, respectively, of this narrow zone.

Foote et al. (1992:765) suggested two possible ways that this distribution could have arisen. Nahanni stock whitefish may have dispersed southward during deglaciation by taking advantage of known glacial lakes and drainage shifts that would have given the fish direct access via the Liard drainage (below Liard Canyon) to the headwaters of the Peace drainage (above Peace Canyon) and thence to the Fraser system. Alternatively, they suggested that the Nahanni race may have dispersed southward along the Ice-free Corridor during the Wisconsinan, or early in deglaciation, accounting for the presence of Nahanni-race whitefish in Talbot Lake. As discussed below, the Talbot Lake stock has a unique allele, suggesting that its history differs somewhat from the Nahanni race as a whole. One possible explanation is that it survived part of the Wisconsinan locally, isolated from the main body of the Nahanni race. The closest known possible ice-free area that might have sufficed as a refugium is the Ice-free Corridor.

**Jasper Stocks:** Lake whitefish occur in Jasper, Talbot and Edna lakes, and in lakes 508, 509 and 510, all part of or closely associated with the Athabasca River mainstem below Jasper townsite (Ward 1974 distribution maps 8 and 9). Undoubtedly they use the river also, but I was unable to find any record of a specimen captured there. They were found in former years in Lac Beauvert, but have been extirpated and have not recolonized that lake (see below). They have not been collected from Moab Lake (Rawson 1940a, Donald and De Henau 1981, JNP file data), suggesting that they never ascended as far as the Moab Lake outlet to the Whirlpool River. There is no record of lake whitefish being stocked in Jasper Park waters (JNP fish stocking records, Ward 1974).

Bajkov (1927:18) described in detail a single specimen of a 627 mm long, 9.5 pound (4.3 kg) whitefish from Lac Beauvert which he identified as *Coregonus nasus* (Pallas), the broad whitefish. His two photographs of this specimen are reproduced in Figure 8. Bajkov deposited the specimen in the museum at the University of Manitoba (No. 2610), but evidently it has been lost (Lindsey 1962:708). A new subspecies, *C. nasus canadensis*, was proposed by L. S. Berg in 1932 on the strength of Bajkov's description of this specimen (Lindsey 1962:708). In North America, the broad whitefish currently is considered to occur only in parts of Alaska, Yukon, the western Arctic mainland coast and the lower Mackenzie River (McPhail and Lindsey 1970:88, Lee et al. 1980:85).

Rawson (1940a:22) stated that the measurements of Bajkov's fish were within the normal range of variation for lake whitefish, so he assumed it was that species. Paetz and Nelson (1970:73) suggested the fish may have been a lake whitefish, "but it is more likely that [Bajkov's] report is completely erroneous." McPhail and Lindsey (1970:88) cited Lindsey (1962) to support their contention that the specimen "was probably an aberrant *C. clupeaformis*."

In his definitive study on the systematics of the broad whitefish, Lindsey (1962:708) considered the Lac Beauvert record at length. He stated that published data on another whitefish specimen from Lac Beauvert (Dymond 1943) unequivocally show it to be a "humpback" lake whitefish. Lindsey (1962:708) studied Bajkov's (1927) data and photographs of his whitefish in detail, finding the specimen to conform to the "humpback" form of lake whitefish in some diagnostic characters, but was clearly a broad whitefish in others (Figure 8). *C. nasus* characters noted by Lindsey (1962:708) are maxilla length (as a proportion of standard length, head length or interorbital width), caudal peduncle depth as a proportion of standard length, and the acute shape of the preopercular margin. Lake whitefish characters (the so-called "humpback" form) are Bajkov's published counts of gill rakers (26, 27) and lateral line scale counts (81, 83), and the apparently small adipose fin. Lindsey noted that both the gill raker counts and the scale counts lie just outside the limits for the broad whitefish in his data.

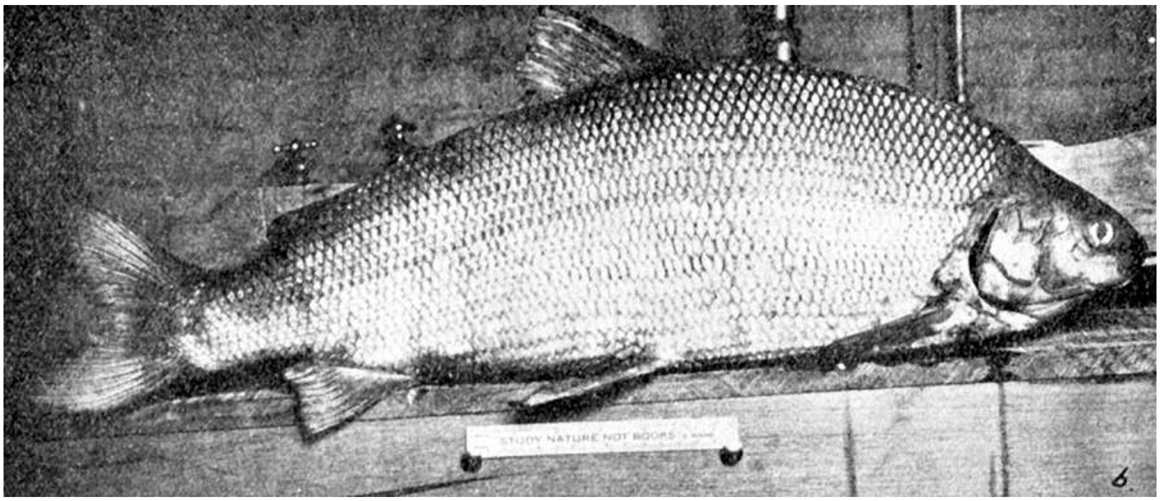
However, taking note of the size of this specimen, its general similarity to four very large aquarium-raised museum specimens known without doubt to be of lake whitefish ancestry, the highly disjunct occurrence, the mountain environment, and suggesting that the specimen might conceivably have originated from a hatchery, Lindsey (1962:709) rejected *C. n. canadensis* as an invalid subspecies, implying that it was an aberrant lake whitefish.

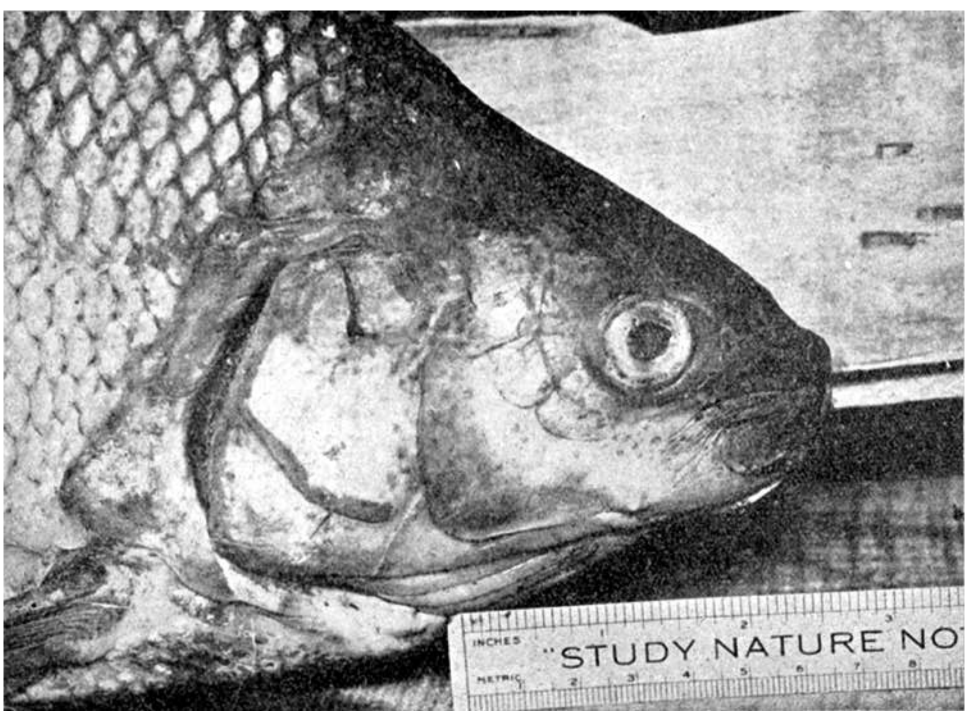
Lindsey (1962) was correct to reject Bajkov's identification and any new taxonomic distinction for this fish on the available evidence. His analysis and Bajkov's photographs (Figure 8), however, clearly show the fish to differ from typical lake whitefish. His explanation that Bajkov's specimen was an aberrant lake whitefish is plausible given the specimen's aberrantly large size, and the morphological effects of allometric growth noted elsewhere in his paper (Lindsey 1962:697-698). But given also that we have practically no morphological information on other lake whitefish from the Jasper area, apart from Dymond's (1943) single specimen noted above, and given evidence of the genetic distinctiveness of the nearby Talbot Lake stock (discussed below), another possible explanation should be considered. Bajkov's specimen may have represented a distinctive stock confined to Lac Beauvert, or one found in the Athabasca River to which Lac Beauvert drains. If the former, it now no longer exists: Lac Beauvert was poisoned in 1964 (Jasper National Park stocking records, Ward 1968a), and subsequent reports indicate that it is absent (Ward 1974:22; Yamamoto 1974b:34, 1978:33; Anderson and Donald 1978b:51).

The lake whitefish of Edna Lake are thought to have been eliminated by poisoning with rotenone in 1956 and 1965 (Jasper National Park fish stocking records). The species is said to have reinvaded from the Athabasca River (Ward 1974:22), although it was not captured in gillnetting conducted in 1973 (Yamamoto 1974b:34).

Franzin and Clayton (1977:625) found the G-3-PDH$b^{1}$ allele to be absent in the Talbot Lake stock, resembling stocks in the Yukon, British Columbia and a few other headwater lakes in this respect. Talbot Lake whitefish clearly differed from the Lake Athabasca whitefish they examined, which carried this allele at a relatively high frequency, and thus are not part of that stock. Inspection of their allelic frequency data for both enzyme systems studied by Franzin and Clayton (1977:619, 625) suggests that the Talbot Lake stock is quite different in the frequencies of these alleles from all 37 other populations included in the study, resembling only that of Summit Lake, Fraser River drainage near Prince George. On their own, frequency differences of this sort do not prove great genetic isolation and divergence among stocks (Allendorf and Phelps 1981), but they are sufficiently suggestive that a more comprehensive genetic screening using many more loci is warranted.

**Figure 8.** Bajkov's photographs of an unusual whitefish from Lac Beauvert (Bajkov 1927), identified by him as *Coregonus nasus*, presently known as the broad whitefish (Robins et al. 1991:28). **a**: Bajkov's Plate IIb, captioned "*Coregonus nasus* (Pallas)." **b**: Bajkov's Plate III, captioned "Head of *Coregonus nasus*." *C. nasus*. characters of this specimen noted by Lindsey (1962:708) are maxilla length (as a proportion of standard length, head length or interorbital width), caudal peduncle depth as a proportion of standard length, and the acute shape of the preopercular margin. Lake whitefish characters (the so-called "humpback" form) are Bajkov's published counts of gill rakers (26, 27) and lateral line scale counts (81, 83), and the apparently small adipose fin. Both gill raker counts and scale counts lie just outside Lindsey's limits for the broad whitefish.



Foote et al. (1992) and Bodaly et al. (1992) recently published such studies. Inspection of their data (Foote et al. 1992:763, 768; Bodaly et al. 1992:771-774) suggests that the Talbot Lake whitefish most closely resembles certain populations in headwaters of the Peace and Fraser drainages. The Talbot Lake stock, however, has a unique allele, *LDH–A–2*b*, present at a frequency of 0.10. This allele is absent from all 23 other populations examined for it, including those in the Nahanni putative source area, and in the Mississippian and Beringian stocks, the alternative possible sources Foote et al. (1992) considered for Talbot Lake whitefish. These observations show that the stock of lake whitefish represented by the Talbot Lake population has diverged in isolation from the Nahanni refugial race that otherwise it most resembles.

Unfortunately, Foote et al. (1992:768) did not publish *LDH–A–2** frequency data for most of the populations nearest Talbot Lake, including populations in the Fraser, most of the upper Peace, the upper Athabasca and upper North Saskatchewan drainages. It is therefore unclear whether the Talbot Lake stock is truly unique, or represents a somewhat more widespread local variant. Data were provided for only one of these populations: the McLeod Lake population of the upper Peace, which lacked the *LDH–A–2*b* allele.

**Habitat:** The lake whitefish frequently is thought of as a lentic species that occasionally occurs in rivers (McPhail and Lindsey 1970:83, Paetz and Nelson 1970:72), but large rivers may be more important to some stocks than previously suspected. Jones et al. (1978) found two major spawning areas for this species in the Athabasca River above Fort McMurray, one below Mountain Rapids and one below Cascade Rapids. The adults migrate approximately 300 river kilometres from Lake Athabasca to these areas, and the young must rear in the river between the spawning areas and the lake. The rapids block further movement upstream. Some spawning and rearing also occurs in the Clearwater River above Fort McMurray, far from any lake (Tripp and McCart 1979:99, Tripp and Tsui 1980:187).

In Jasper National Park, Lake whitefish must use (or once must have used) the Athabasca River from the east boundary upstream approximately to Jasper townsite at least as an access route to a few small lakes, but details of the habitat used by lake whitefish while in the river are not known. Of the six small lakes reportedly inhabited by lake whitefish, Talbot and Edna are shallow at less than 3 metres maximum depth (Moberly and Cameron 1929:97, Anderson 1974c:Table 6, JNP file data). There are no reported data for lakes 508, 509 and 510. Only Lac Beauvert is known to be relatively deep (maximum depth 25 m, Anderson and Donald 1978b:45). Anderson and Donald (1978b) provide more detailed data on Lac Beauvert. Rawson (1940a) provides some information on the limnology of Talbot Lake.

Nothing has been reported or is on file regarding migration routes and critical habitat used by the various life history stages of lake whitefish in any of the waters it inhabits in Jasper National Park.

**Biology and Life History:** Very little information is available on the life history of lake whitefish in park waters. Lake whitefish are known to be resident in Talbot Lake, and once were resident as the most abundant fish in Lac Beauvert (Rawson 1940a, JNP file data). In Lac Beauvert in the 1950s, "many hundreds" of lake whitefish were said to spawn near shore every fall (W. C. Cable to JNP Superintendent, 21 Dec 54 J.296-13). In the late 1940s and early 1950s, Lac Beauvert lake whitefish commonly reached 1.4 kg, the maximum being 1.9 kg (JNP file data), much smaller than the specimen described by Bajkov (1927).

Henry John Moberly described the Talbot Lake whitefish of the 1850s as small, ranging from 0.45 to 0.68 kg (Moberly and Cameron 1929:98), which suggests that he was referring to mountain whitefish. Both species occur in the lake (Rawson 1940a:64). Talbot Lake lake whitefish examined by Rawson (1940a:64) and D. Alger (and D. Donald? — circa 1984, file data in Warden Service lakes files) were much larger, several exceeding 2 kg. Many of the 1980s fish exceeded 15 years in age (maximum age 19+ using sectioned otoliths, JNP file data).

Length, weight and catch rate data are available for lake whitefish in Beauvert and Talbot lakes for various times, but age data from earlier periods that were based on scales cannot be relied upon. No life history data are available for lake whitefish in any other park waters.

In lakes elsewhere, lake whitefish spawn in fall in depths generally less than 8 m over rocky reefs or other hard, stony bottom, but sometimes over sand. The eggs hatch in late winter to early spring. Optimal temperature for incubation is approximately 2 °C, a temperature of 10 °C producing 99 percent mortality. Larval fish aggregate along steep shorelines in some lakes, but leave the shallows for deeper water by early summer. Growth rate and age at maturity vary widely from lake to lake, with maximum ages exceeding 50 years in some northern populations (Power 1978).

Distinct sympatric stocks, often referred to as "dwarf" and "normal" forms, are known from several localities (e.g., Scott and Crossman 1973:270, Bodaly et al. 1992, and references therein). Many stocks of lake whitefish are benthic feeders, but a number of plankton-feeding stocks are known. The differences in mode of feeding are reflected in gill raker numbers and morphology. Young lake whitefish may use plankton initially, later consuming more benthic organisms. Small fish form part of the diet in some lakes.

Jones et al. (1978) provided data on a partly riverine stock spawning in the Athabasca River above Fort McMurray. This stock, numbering in the tens of thousands, migrates over 300 km from Lake Athabasca to spawn mostly in the 32 km of mainstem between Fort McMurray and Mountain Rapids. Significant spawning also occurs above

Mountain Rapids to Cascade Rapids, but little or none above that point. These are major rapids, both rated Class IV for boating purposes (Alberta Transportation 1978), i.e., they have obstructed passages; rocks; high, powerful and irregular waves; and boiling eddies. Spawning takes place in October at 3-6 °C in fast water over broken rock, rubble and coarse gravel substrates. No eggs were found in pure sand or mud substrate. Mature lake whitefish preyed heavily on whitefish eggs. The spawners moved back downstream toward Lake Athabasca at least as far as the Embarras River immediately after spawning, and have been found in and near the Chenal des Quatre Fourches, Peace-Athabasca Delta, in December (Jones et al. 1978:21). The species is common in the Athabasca River throughout the open-water season. Young-of-the-year initially must rear in the river, considering the great distance between the spawning sites and the lake, but no data are available on these fish.

**Ecological Significance:** The ecological role of lake whitefish in Jasper National Park has not been documented. Even the existence of what may be the largest and most important stock, that of the Athabasca River, is as yet unconfirmed. If this postulated stock exists, and if it undertakes long migrations similar to the major river-spawning stock of the lower Athabasca River described under Biology and Life History, above, it may be an important transporter of toxic pulpmill contaminants into the park. Although data on lake whitefish were not included, recently released data (Alberta Government press release 153, 27 July 1990) show that all of five species of fish tested from downstream of the pulpmill at Hinton were contaminated with dioxin (2,3,7,8 T4CDD) and furan (2,3,7,8 T4CDF). Concentrations were considered high enough for the government to issue guidelines for the quantities of upper Athabasca fish that might be safely consumed by the public.

The small lake stocks, such as that in Talbot Lake, are probably an important prey species for northern pike and perhaps other vertebrate predators. For example in Talbot Lake, lake whitefish presumably were an important prey of river otter, now rare in the park but formerly abundant at Talbot Lake in 1939 (lake survey report, D. S. Rawson per W. C. Cable, JNP Warden Service lakes files — see Study Area). Lake whitefish probably are significant predators of zooplankton, benthic invertebrates or even small fish in these lakes, but data on the food of this species in park waters have not been reported.

**Fishing:** Aboriginal people probably captured lake whitefish from park waters in prehistoric times (see Section II). Whitefish in general formed a significant part of the food supply for Jasper House. De Smet (1847:197) estimated that 50 per day were taken over a 26-day period in 1846. There was a company fishery for whitefish on Talbot Lake about that time, and natives fished the lake as well (Cheadle 1931:164). Hector (1863:128) reported that the person in charge of Jasper House always returned to that post before the frost set in to secure a supply of fish from the mountain lakes, which he said abounded in whitefish and trout. Earlier, Drummond (1830:196) had subsisted on small whitefish (mountain whitefish?) from a lake in this area. These historical references are discussed in greater detail in Section II.

The nineteenth century net fishery on Talbot Lake might explain why Moberly (Moberly and Cameron 1929:198) mentioned only small whitefish there: the larger fish would have been selectively removed early on.

A commercial winter net fishery for lake whitefish was operated on Talbot Lake as recently as 1950. A request from local petitioners to resume the operation in 1962-63 was turned down (B.I.M. Strong to JNP Superintendent 9 November 1962, J.296-1-34). Winter sport fishing has been conducted on this lake since 1964 (file data, JNP Warden Service lakes files).

**Conservation Status (general):** Lake whitefish have not been listed as threatened or endangered as a species (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Campbell 1991, Williams et al. 1989), but the status of some subspecies and stocks is of concern. Illinois, on the periphery of the lake whitefish range, gives the species legislated protection (Johnson 1987:4). An undescribed subspecies in Lake Simcoe, Ontario formerly listed as of special concern (Johnson 1987:5) now is listed as threatened (Williams et al. 1989:4, Campbell 1991:152). Two undescribed species formerly treated as *C. clupeaformis*, the Squanga whitefish presently known only from only two localities in the Yukon, and the Opeongo whitefish in the lake of that name, Algonquin Provincial Park, Ontario, are both listed. The former is considered threatened, the latter endangered by some authorities (McAllister et al. 1985, Williams et al. 1989:4). COSEWIC presently lists the Squanga whitefish as vulnerable, and is considering listing the Opeongo whitefish as threatened (Campbell 1991:152,154). The Province of Ontario currently lists the Opeongo whitefish as of special concern (Johnson 1987:5). COSEWIC lists the possible status of lake whitefish in lakes Erie and Ontario as endangered, and that of a related undescribed species, the Mira whitefish, as vulnerable (Campbell 1991:155).

There are many forms of lake whitefish differing in morphological, ecological and genetic traits (McPhail and Lindsey 1970, Scott and Crossman 1973, Franzin and Clayton 1977, Foote et al. 1992, Bodaly et al. 1992). This species, with its numerous genetically, structurally and ecologically distinctive stocks, some of them sympatric, well illustrates why it is critical to manage at the level of individual stocks.

**Conservation Status (Jasper):** The status of lake whitefish in Jasper National Park is almost completely unknown. The existence of lake whitefish in the Athabasca River and associated lakes and backwaters has long been assumed, but there are no catch data reported or on file. If an Athabasca River stock exists, there is reason to think it would be highly migratory and therefore vulnerable to contamination by effluents from a pulpmill outside the park.

Lake whitefish are known to exist still in Talbot Lake, but their current status there is undocumented. Lake whitefish were extirpated from Lac Beauvert by poisoning in 1964. The original stock in Edna Lake was extirpated in 1956 and 1965 by poisoning. Although Edna Lake purportedly was repopulated by lake whitefish from the Athabasca River, it is conceivable that these were descended from survivors of the poisoning operations. There are no recent records of lake whitefish from Edna Lake.

In view of our present lack of critical information on the remaining stocks, the evidence of unusual and possibly unique stocks (one now perhaps extirpated) in at least two lakes, and the possibility of toxic contamination of a population presumed to exist in the Athabasca River, the conservation status of lake whitefish in Jasper National Park is of **special concern**.

**Required Action:**

1. The distribution and abundance of lake whitefish in park waters needs to be determined, and the life history of the most significant stocks worked out in detail. The Talbot Lake and presumed Athabasca River populations are the most important in this respect. The study should include an assessment of past, present and possible future impacts on this species in park waters.

   It is not known for certain that a lake whitefish population even exists in the Athabasca River within the park. If it does, it would be significant: strictly riverine populations of lake whitefish are uncommon. Developments both within and outside the park make it critical to determine the presumptive Athabasca River population's size and life history, especially its migratory patterns and the location of critical habitat. Of particular concern are reports of fish contaminated by pulpmill effluent from outside the park. If an Athabasca River lake whitefish population exists, it may be a significant transporter of chemical contaminants into the park.

2. A study of the systematics and genetics of lake whitefish in Jasper National Park is required to identify stocks and determine if the populations are significant taxonomically or zoogeographically. This study should use standard taxonomic and biochemical genetic techniques to identify taxa and examine geographic variation represented by the Jasper populations. The apparent genetic distinctiveness of the Talbot Lake stock needs to be examined using more loci, and compared to others in the general region, especially those in the headwaters of the Fraser and Peace rivers.

3. A detailed management plan for the the remaining stocks of lake whitefish in Jasper National Park should be developed based on the results of the above studies.

## *Pygmy whitefish* — **SALMONIDAE**

*Prosopium coulteri* (Eigenmann and Eigenmann)

Coregoninae
Whitefishes

**RARE** (provisional)

**Summary:** The pygmy whitefish is a peculiarly distributed little fish having many widely separated and morphologically distinct populations. Its variability makes it a highly informative species zoogeographically as a marker of possible fish refugia and postglacial dispersal routes, so it is of significant scientific interest. It was not discovered in Jasper National Park until 1980 (in the lower Snake Indian River), and is now known from just three locations in Alberta. The only available evidence suggests that it is rare both in the park and in the province as a whole, but it is possible that future collecting with the aid of more suitable equipment in appropriate habitat may change this evaluation.

Data are available from only one adult specimen (and are questionable for that reason) suggesting that the Jasper stock may differ in morphology from all other stocks so far described, including that in Yellowhead and Moose lakes, the closest known neighbouring populations to Jasper. This, and the ability of pygmy whitefish to tolerate cold, silty, periglacial conditions, hint that the Jasper population could represent a stock that survived in a local refugium such as the Ice-free Corridor. Much more data are required on this and several other populations that are known from only a small number of specimens to test this hypothesis.

A detailed survey is needed to discover the distribution and abundance of this species, to describe its life history and critical habitat requirements, to resolve its taxonomic status and to identify stocks. A comprehensive conservation plan to protect the species should be developed based on the results of the survey. Damage to braided channel and side channel habitat of the Athabasca River and its left bank tributaries (detailed in the species account for mountain whitefish) might have detrimentally affected this species.

**Nomenclature:** The pygmy whitefish originally was named *Coregonus coulteri.* It has been referred to occasionally as Coulter's whitefish in older literature.

**Description:** A small, silvery, brown-backed, large-scaled, round-bodied whitefish, with large eyes, small mouth and blunt, rounded, slightly overhanging snout. Juveniles and adults less than about 13 cm long have 7-14 small, oval parr marks along the lateral line. Pygmy whitefish seldom exceed 15 cm in length, but reach almost 28 cm in a few populations (McPhail and Lindsey 1970:119). Because of the parr marks they may easily be mistaken for underyearling and young juvenile mountain whitefish, especially in large collections of the latter, but the blunt, rounded, slightly overhanging snout and large eyes are distinctive.

Meristic data are available for a single 86-mm fork length adult male at the end of its second season of growth from the Snake Indian River in Jasper National Park. This fish had 19 caudal peduncle scales, 4+9=13 gill rakers on the first arch, 60±1 lateral line scales, 10 dorsal fin rays, 11 anal fin rays, and 14 pectoral fin rays (D. Mayhood, unpublished data).

**Distribution:** This species exists in several widely-separated areas of North America: the Bristol Bay-Alaska Peninsula region of Alaska, in a broad band extending from south-central Yukon through central and eastern British Columbia to Columbia River headwaters in western Montana (Weisel et al. 1973), in Lake Superior, and in eastern Lake Athabasca (D. B. Tripp, personal communication 22 October 1990). In Alberta the species is known only from Waterton Lake (Lindsey and Franzin 1972), and from two locations in the Athabasca River system (Mayhood 1980:143, W. E. Roberts, personal communication 21 March 1985).

**Refugia/Postglacial Dispersal:** The presently known distribution of the pygmy whitefish suggests that it survived Wisconsinan glaciation in at least three refugia: Beringia, Cascadia and a Mississippian refugium. In reality its origins and postglacial dispersal may be considerably more complicated, as the following discussion suggests.

In a preliminary survey of geographic variation in the species, McCart (1970:93) distinguished at least two forms based on a combination of numbers of gill rakers, caudal peduncle scales and dorsal fin rays (Figure 9). He proposed that a low-rakered form survived glaciation in a western refugium south of the ice sheet (Cascadia), a high-rakered form survived in a Yukon-Bering Sea refugium (Beringia), and the Lake Superior form survived in a Mississippian refugium (Figure 1). The high-raker form he believed was able to disperse as far north as Alaska postglacially, where it encountered the low-rakered form and existed sympatrically with it in at least two lakes without hybridizing.

Lindsey and Franzin (1972) reported two new populations that did not fit the pattern described by McCart (1970). One of these, in the most northerly locality known for the species (Elliot Lake, Yukon), resembled the low-rakered form that McCart (1970) proposed had survived south of the Pleistocene ice in Cascadia. The southern Waterton Lake population, on the other hand, resembled most closely the high-rakered form that had survived north of the ice in Beringia, according to McCart's scheme (Figure 9).

The hypothesis that morphological variation has arisen during isolation in multiple refugia is not necessarily negated by the disruption to the geographic pattern identified by McCart (1970), Lindsey and Franzin (1972:1774) argued, provided it can be shown that the atypical populations might have been derived from refugia other that the Columbia (i.e., Cascadian) and Bristol Bay (i.e., Beringian) regions. They observed that both of their new populations lie close to separate unglaciated areas in which pygmy whitefish could have survived the Wisconsinan, and suggested that the species survived and diverged in several different refugia (Figure 10). The various Wisconsinan refugia they suggested were (a) Columbia River basin; (b) near Bristol Bay (which might have harboured two forms, one possibly derived from a preWisconsinan invasion from the south); (c) the upper Yukon River basin (which may or may not have been isolated from Bristol Bay watersheds); (d) the Peel River area (which is now tributary to the Mackenzie River but which during maximum glaciation was tributary to the Yukon River via the Porcupine — see also Bodaly and Lindsey 1977); (e) the Missouri River headwaters close to Waterton Lakes; and (f) the upper Mississippi River region which gave rise to the Lake Superior population. In concluding, Lindsey and Franzin (1972:1775) remarked that "with all these possibilities for allopatric divergence, it is not remarkable that the present mosaic of characters is complex."

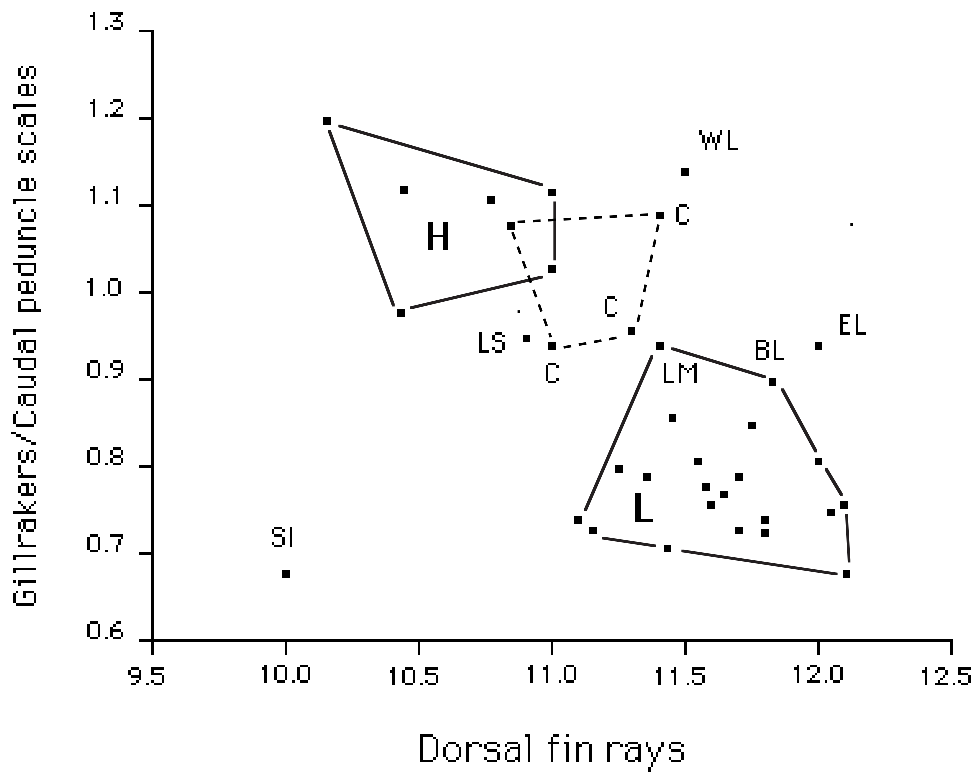



**Figure 9.** Plots of population means for gillrakers, caudal peduncle scales and dorsal fin rays of pygmy whitefish from various localities, showing refugial stocks proposed in the literature as compared to a single specimen from the Snake Indian River. The original boundaries of the low-rakered (Cascadian) and high-rakered (Beringian) forms proposed by McCart (1970) are shown in solid lines for all populations represented in his data by 5 specimens or more. The boundaries shown in dashed lines include the populations derived from a proposed Yukon River refugium (Lindsey and Franzin 1972:1775, Bird and Roberson 1979:470). **H** - high-rakered form, assumed Beringian Refugium; **L** - low-rakered form, assumed Cascadian refugium; C - Copper River drainage, Alaska (Bird and Roberson 1979); WL - Waterton Lake, Alberta, EL - Elliot Lake, Yukon (Lindsey and Franzin 1972); LS - Lake Superior, BL - Bull Lake, Montana, LM - Lake McDonald, Montana (Eschmeyer and Bailey 1955); SI - Snake Indian River, Jasper National Park (D. Mayhood, unpublished data). C, WL, EL and SI are all represented by fewer than 5 specimens.

Weisel et al. (1973:590) concluded that the relatively high gill raker counts on pygmy whitefish in lakes Flathead, Bull and McDonald in the Columbia drainage of Montana did not support McCart's (1970) view that the low-rakered form survived in or near the Columbia Basin during the Pleistocene. They based their conclusion only on gill raker counts, whereas McCart (1970:94) actually separated his high- and low-rakered forms on the basis of population means for gillrakers/caudal peduncle scale counts plotted against dorsal fin rays. Weisel et al. (1973) did not report counts of caudal peduncle scales or dorsal fin rays for their populations, so their data neither support nor refute McCart's (1970) thesis.

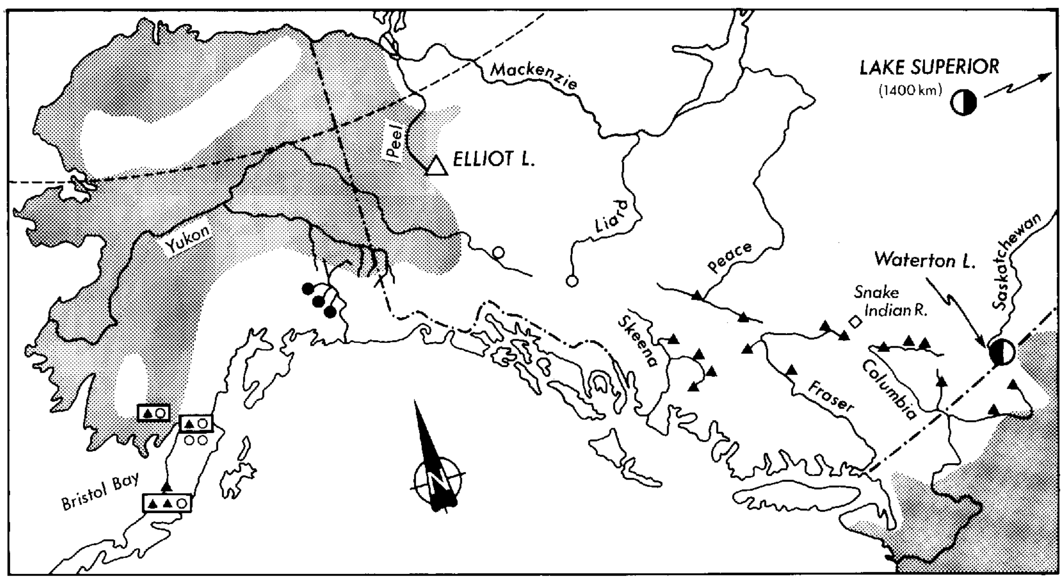



**Figure 10.** Distribution of refugial stocks of pygmy whitefish in northwestern North America, as proposed by various authors in the recent literature. Racial distinctions are based on gillrakers/caudal peduncle scales plotted against dorsal fin rays (McCart 1970). Major known unglaciated regions are shaded. Solid triangles, low-rakered (Cascadian) form; open circles, high-rakered (Beringian) form; closed circles, Copper drainage form; other refugial stocks as labelled. Populations enclosed by rectangles are sympatric. Alternatively, populations in the Copper, upper Yukon and upper Liard may have been derived from a common Yukon River refugial stock (Figure 9; see text). Data from Eschmeyer and Bailey (1955), McCart (1970), Lindsey and Franzin (1972), Bird and Roberson (1979), and Mayhood (1980, and unpublished data). Map adapted from Lindsey and Franzin (1972).

McCart (1970:94-5) had included two of the three populations discussed by Weisel et al. (1973) — Bull and McDonald lakes, Montana — in his analysis, including their caudal peduncle scales and dorsal ray counts (Figure 9). They are part of the cluster defining his nominal low-rakered form, even though their gill raker counts alone were high, and are consistent with his view that a low-rakered form survived in a Cascadian Refugium.

Bird and Roberson (1979) described pygmy whitefish from three headwater lakes in the Copper River drainage, a short coastal system entering the Gulf of Alaska, but sharing a divide with the Yukon River. In Figure 9, these three populations fall between the low-rakered and high-rakered forms defined by McCart (1970:94) on the basis of numbers of gillrakers, caudal peduncle scales and dorsal fin rays. (The H and L labels for high- and low-rakered clusters are transposed in their Figure 2).

Bird and Roberson (1979:469) recognized that the Copper drainage fish were meristically different from the Yukon River pygmy whitefish [apparently they were referring to those populations described by McCart (1970:84-85)], but not extremely so. They suggested an origin in a Yukon River refugium for these populations based on geological and geographic considerations. This refugium might correspond to the upper Yukon refugium postulated by Lindsey and Franzin (1972:1775), and probably gave rise to pygmy whitefish populations in the upper Liard also (Lindsey and McPhail 1986:661). If this postulated origin is accepted, we must include McCart's (1970) Yukon and upper Liard populations in a newly defined Yukon refugial group (Figures 9 and 10).

Meristic data are available for only a single specimen representing the population in Jasper National Park (see Description, above). This specimen is a distant outlier, distinct from all other populations (Figure 9). The within-population ranges for the individual diagnostic meristic characters of pygmy whitefish (Eschmeyer and Bailey 1955:169-71, McCart 1970:84-5, Lindsey and Franzin 1972:1773, Bird and Roberston 1979:469) are just barely wide enough to include individual specimens with the characteristics of the single Jasper specimen in the low-rakered group, but not in the high-rakered group or in the other isolated populations. More specifically, the extremes in 20 specimens from Maclure Lake, Skeena drainage, and 11 specimens from Yellowhead Lake, Fraser drainage (both in the low-rakered group) were identical (McCart 1970:84-5): 13 gillrakers (minimum), 20 caudal peduncle scales (maximum) and 10 dorsal fin rays (minimum). Individual fish with these counts would plot slightly beyond the Snake Indian River specimen, including it in the low-rakered group. It is not known, however, whether all the extreme counts were found in any one fish in the Mclure Lake and Yellowhead Lake populations.

It should be emphasized that much of the apparent geographic variation in meristic characters reported since McCart's (1970) publication may be spurious, an artifact of the small number of specimens that investigators have been able to obtain. McCart's analysis is relatively robust because of the large number of specimens used (always more than five specimens, but usually 20 or more). In contrast, the Waterton Lake and Elliot Lake populations are represented by only two fish each (Lindsey and Franzin 1972:1773). The three Copper River drainage populations are represented effectively by four fish each, although dorsal rays were counted on up to 20 fish (Bird and Roberson 1979:469). Ranges for the three meristic characters used in the analysis are wide in many populations, and by choosing the extreme values it is possible to show that some individuals from the high- or low-rakered forms may plot very close to the "unusual" populations.

Another possibility is that all of the observed morphological variation represents recent adaptation unrelated to glacial history. Lindsey and Franzin (1972:1775) countered this alternative explanation by pointing to the consistent morphological differences between the southeastern (low-rakered Cascadian) and northwestern (high-rakered Beringian) populations as they were known at the time. The populations described subsequently for the Copper River drainage by Bird and Roberson (1979) and the refugial group of which they may be a part, however, are intermediate both geographically and morphologically between the northwestern and southeastern forms (Figures 9 and 10). This pattern suggests a cline related to an ecological gradient, climate being the most obvious factor possibly responsible. If so, the cline in dorsal ray number (and perhaps in caudal peduncle scale count) is in the direction of higher counts in the south than in the north, opposite to that expected according to "Jordan's Rule" (Lindsey 1975). Furthermore the Lake Superior, Waterton Lakes and Elliot Lake populations clearly do not follow the clinal pattern, and the only available data suggests the Snake Indian population is morphologically remote from all others, even though it is geographically very close to the southeastern group.

Further study of all populations, preferably by means of biochemical genetic techniques, obviously is required. As the matter stands now, the Snake Indian population of Jasper National Park conceivably represents a distinctive stock that survived in a separate refugium such as Crossman and McAllister's (1986) proposed Banff-Jasper Refugium, perhaps in the nearby Ice-free Corridor. Weisel et al. (1973:596) pointed out that the known range of the species is restricted to recently glaciated areas, and suggested that its small size and early spawning age were adaptations for survival in cold and nutrient-poor waters. Certainly it lives under near-glacial conditions today in many parts of its range (e.g., Moose Lake, Blaeberry and Kicking Horse rivers, BC; Tazlina, Klutina and Tonsina lakes, Alaska, Snake Indian River). It would seem to be capable of surviving the rigourous periglacial conditions that would have existed in the Ice-free Corridor during the Wisconsinan.

**Jasper Stocks:** Pygmy whitefish in Jasper National Park are known only from two specimens caught in the Snake Indian River approximately 4 km from the mouth on 4 October 1980 (Mayhood 1980:143). One, an 86-mm fork length male at the end of its second season of growth (scale age), was ripe and freely running milt when captured. Its meristic data are presented under Description, above. The second specimen was a 55-mm fork length juvenile at the end of its first season of growth. It is likely that the species is not restricted to the lower Snake Indian River, but probably is widespread in the Athabasca drainage within the park, and simply has gone undetected.

**Habitat:** Both Jasper specimens were taken close together in a small side channel 10 cm deep in gentle current over a bottom comprised of small gravel. This habitat is apparently both spawning and rearing habitat, since one specimen was a ripe adult and the other was a young juvenile. The Snake Indian River itself at this point is a large braided stream in a clean medium to coarse gravel and cobble bed. The species appears to occupy similar habitat to that of the type locality, the Kicking Horse River at Field, in Yoho National Park, BC. There the river also is highly braided in a bed of gravel.

The pygmy whitefish is known from many lakes as well (Eschmeyer and Bailey 1955, McCart 1970, Lindsey and Franzin 1972, Weisel et al. 1973, Bird and Roberson 1979), including Yellowhead Lake and Moose Lake in the upper Fraser drainage immediately adjacent to Jasper National Park on the west (McCart 1970:84-5). In Bull Lake, Montana, spawning is thought to occur only in streams associated with the lake; in nearby Flathead Lake spawning is believed to occur in two major inlets (Weisel et al. 1973:595). Spawning in the shallows of lakes is believed to occur elsewhere (Scott and Crossman 1973:283). Details of critical habitat have not been published for any population.

**Biology and Life History:** In the Snake Indian River, at least some pygmy whitefish males reach sexual maturity by the end of their second season of growth, as evidenced by the single ripe male captured there with two seasons of growth showing on its scales. Spawning may occur in early October, although males might be ripe for some time before spawning. Some fish in this population reach 55 mm by the end of their first season of growth and 86 mm by the end of their second season, but a wide variation in individual growth rates is to be expected.

The apparent growth rate in the Snake Indian River is within the bounds of rates observed in other populations. It is higher than growth rates for pygmy whitefish in Brooks, Tazlina and Klutina lakes, Alaska, and in Lake Superior; similar to those of Tonsina Lake, Alaska, Lake McDonald, Montana, and Mclure Lake, BC; but much lower than those of the fish in Flathead and Bull lakes, Montana, or Wood Lake, Alaska (Weisel et al. 1973:Figure 2, Bird and Roberson 1979:469).

Age at maturity in male pygmy whitefish in the Snake Indian River is similar to that reported for other populations. Weisel et al. (1973:593) found that 50 percent of the male pygmy whitefish of Bull Lake, Montana, attained sexual maturity in their second season of growth, and that 74.5 percent of the males of the Flathead Lake population were mature in their second season of growth (ibid. p. 594). Pygmy whitefish in three lakes of the Copper River drainage, Alaska, reached sexual maturity in their second year (Bird and Roberson 1979:468).

The apparent spawning period in the Snake Indian population is earlier than that in the Montana lake populations studied by Weisel et al. (1973). Bull Lake fish spawn from mid-December into January in inlet streams to the lake; Flathead Lake pygmy whitefish apparently spawn in late November and December in major inlets to the lake (ibid. p. 595). In three lakes of the Copper River drainage, Alaska, spawning occurs “sometime after September” (Bird and Roberson 1979:468). In British Columbia lakes, indirect evidence suggested that pygmy whitefish spawn in October or November (McCart 1965, cited by Scott and Crossman 1973:283), roughly similar to that posited for the population in the Snake Indian River. Presumably the eggs incubate within the gravel over winter and hatch in the spring, but really nothing at all is known about this phase of the life history.

Pygmy whitefish probably consume mainly benthic invertebrates in streams, although this evidently has not been studied. In lakes they also prey upon benthic invertebrates, but at least in some lakes they eat substantial amounts of zooplankton as well (McCart 1970:93, Scott and Crossman 1973:285, Weisel et al. 1973:593). In some lakes (e.g., Chignik Lake, Alaska) certain stocks may consume only zooplankton, while others consume only benthic invertebrates (McCart 1970:93).

Stock development is pronounced in this species, both geographically (discussed above) and in some cases even within populations. McCart (1970) described three separate stocks in Chignik Lake, and two in each of Aleknagik and Naknek lakes, Alaska, each of which occupied separate habitats within the lake and had a distinctive external morphology, meristic characteristics, ecology and life history.

**Ecological Significance:** It is not possible even to speculate on the function of pygmy whitefish in the ecology of Jasper National Park, considering how little is known about its distribution, abundance and life history here.

**Fishing:** Unless the stock in Jasper National Park is one of the rare ones in which individuals may reach 28 cm in length (McPhail and Lindsey 1970:119), it is unlikely that pygmy whitefish ever have been exploited in the park. They are usually far too small to take a hook or to be caught in all but the smallest-mesh gillnets.

**Conservation Status (general):** Pygmy whitefish are not listed as endangered, threatened or rare on most international or national lists (McAllister et al. 1985, Williams et al. 1989, Campbell 1991), although they are listed as a species of special concern by the states of Washington and Wisconsin (Johnson 1987:5). Of possible concern also are two Canadian populations of “giant” pygmy whitefish (McAllister et al. 1985:169), and populations in Alberta, where the species is known in the province from few specimens collected in only a few localities (Nelson and Paetz 1982:53). A status report on the species for the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has been in preparation or under review since 1987 (Campbell 1988:83, 1991:154).

In Alberta pygmy whitefish appear to be rare in the only two locations for which information is available. Only two specimens have been collected from Waterton Lake (Lindsey and Franzin 1972:1773) and two from the Snake Indian River (see below). It also has been collected from “a tributary of the Athabasca River” (W. E. Roberts, personal communication 21 March 1985). This is a species that is likely to be overlooked, and may well be more abundant and widespread than it appears to be from present records. We cannot be sure of this, however. For conservation purposes it is safest to consider it rare in Alberta until contradictory data are forthcoming.

**Conservation Status (Jasper):** The only available evidence suggests that the pygmy whitefish is **rare** in the park. In October 1980, three of us captured only two specimens in a total of over 90 hauls of a minnow seine (mean area swept approximately 27 $m^2$ per haul) in Moosehorn Creek and Snake Indian, Snaring and Miette rivers, as well as various smaller tributary creeks and springbrooks (Mayhood 1980). In comparison, we caught 38 underyearling mountain whitefish in the same stretch of the Snake Indian River in which we captured the two pygmy whitefish specimens, and caught at least 420 underyearling mountain whitefish in total in all the sites we seined. We were sampling during the spawning period for the species, a time when adult pygmy whitefish could be expected to concentrate in a few suitable areas. It is possible that we just failed to find many specimens for that reason, but until more are found, the species must be considered rare in the park. The pygmy whitefish conceivably has a distribution in the Athabasca drainage similar to that of the mountain whitefish (Map 2).

The damage to rearing habitat discussed in connection with mountain whitefish undoubtedly has affected this species in the Snake Indian River, and quite likely in other locations in the Athabasca drainage as well.

**Required Action:**

1. A survey is required to delineate the distribution and abundance of pygmy whitefish in Jasper National Park. Depending on the numbers revealed by the survey, the taxonomic status, life history, critical habitat requirements and stock composition need to be determined for this species in the park.

2. Should the work in (1) confirm that the pygmy whitefish is rare in the park, a conservation and management plan to protect the species should be drawn up based on the findings. In particular, if the work in (1) provides grounds to suspect that lost or damaged habitat has contributed to the rarity, a habitat restoration plan should be developed and implemented.

## *Mountain whitefish*

*Prosopium williamsoni* (Girard)

## *SALMONIDAE*

Coregoninae
Whitefishes

**SPECIAL CONCERN**

**Summary:** The mountain whitefish is one of the most abundant and widespread fishes of the East Slopes in Alberta, where it is characteristic of rivers and a few of the larger accessible mountain lakes. It is widely-distributed and common in Jasper National Park in both rivers and some lakes in the Athabasca and Brazeau river drainages. To this extent the park protects representative populations of this typical fish of the Rocky Mountain East Slopes region. The species also is one of the most likely native fishes to have survived late Wisconsinan glaciation in local refugia, perhaps in the Ice-free Corridor. If it did so, we should expect to find genetically distinctive stocks of mountain whitefish in the region, and some of these may be protected within the boundaries of the park.

Mountain whitefish probably play at least a locally important role in the ecology of Jasper Park, judging only from their apparent abundance. They are also a mainstay of the present-day sport fishery for native fish, as they must have been for earlier domestic fisheries during the fur trade era of the 1800s, and the subsistence fisheries of aboriginal peoples dating back possibly for thousands of years.

There is significant damage to mountain whitefish rearing habitat, especially along the left bank of the Athabasca and its major left bank tributaries, from roads and railways. There is a strong possibility that mountain whitefish in the upper Athabasca system are contaminated with pulpmill contaminants from outside the park. The species is of special concern because of the damage to its critical habitat and because of the possible contamination, which would pose a threat to public health and the park ecosystem, as well as to the mountain whitefish stocks themselves.

**Nomenclature:** There have been no recent changes in the scientific name. The names *Coregonus williamsoni* and *Prosopium oregonium* have been used in older literature. Rocky Mountain whitefish and grayling are the most frequently-used common name synonyms in Jasper National Park and vicinity.

**Description:** The mountain whitefish is a round-bodied whitefish with prominent silvery scales, light to dark olive green or brown on the back, dusky dorsal and caudal fins, whitish or yellowish paired fins, very small mouth, pinched or bottle-nosed snout, distinctly forked caudal fin, and a noticeably large and prominent adipose fin. Bajkov (1927:18-19) described and provided measurements of several specimens from the "Fraser River, B.C.", but not for specimens from the park. Mountain whitefish may be distinguished from lake whitefish by characters discussed for that species.

**Distribution:** Mountain whitefish are found in extreme northern California, Nevada and Utah (a few isolated populations), and are widespread northward through Oregon, Idaho, Washington, Montana (both sides of the Continental Divide), throughout mainland British Columbia north to the 60th parallel, western Alberta, and the central Mackenzie River. In Alberta, mountain whitefish are widespread and abundant throughout small to large rivers and some of the larger accessible lakes of the eastern slopes, penetrating deep into the prairie region in the mainstems of the Oldman, Bow, Red Deer and North Saskatchewan rivers. In the Athabasca River system mountain whitefish extend downstream at least as far as Fort McMurray (Jones et al. 1978:Figures 4,5; Tripp and McCart 1979:99; Tripp and Tsui 1980:188).

**Refugia/Postglacial Dispersal:** The present distribution of mountain whitefish includes unglaciated areas in Cascadia and the headwaters of the Missouri in Montana, as well as the Wisconsinan Ice-free Corridor of western Alberta. One current interpretation proposes that the species survived the Wisconsinan in Cascadia, dispersing northward and eastward postglacially, crossing the Continental Divide from the west to enter Alberta (Paetz and Nelson 1970:5, Nelson 1977:131, Lindsey and McPhail 1986:669). McPhail and Lindsey (1970:116) recognized that mountain whitefish may have survived on both sides of the Continental Divide south of the ice sheets, and may have crossed the Divide in either direction more than once. Crossman and McAllister (1986:86-7) extended this explanation, suggesting that mountain whitefish also may have survived glaciation in their proposed refugium in southwestern Alberta.

Like bull trout with which they are often associated in Alberta, mountain whitefish are tolerant of periglacial conditions. They are found in many of the frigid, heavily silted glacial rivers and lakes throughout the Alberta Rocky Mountains almost as close to present-day active glaciers as barriers to upstream movement permit (e.g., McHugh 1940:134, 1941:339; Ward 1974:20-21, his distribution maps 7-9 and 25-26). Waters of this type would have been characteristic of the Ice-free Corridor. Given the current interpretation of the age and extent of the Ice-free Corridor in Alberta (Fulton et al. 1984, Rutter 1984; see Section I), it is likely that mountain whitefish survived in place here since at least the mid-Wisconsinan, and perhaps longer in the south.

**Jasper Stocks:** Mountain whitefish occur in the mainstem Athabasca River from the park boundary upstream to Athabasca Falls. The species is found downstream from migration barriers in the major Athabasca tributaries within this reach, including the Whirlpool, Astoria, Miette, Snaring, Snake Indian, Fiddle, Rocky and Maligne rivers. Hardisty Creek and probably the lower portions of other small creeks tributary to the Athabasca also hold mountain whitefish (Ward 1974:21; National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954).

Waterfalls restrict mountain whitefish to the lower reaches of the Maligne and Astoria rivers. They have been reported only in the lower 2 km of the Fiddle River (Donald et al. 1977:15). How far mountain whitefish have penetrated upstream in the remaining tributaries has not been fully documented. The species was not collected in Dolly Lake in the upper Snake Indian River drainage, nor in Miette Lake at the head of the Miette River when these waters were surveyed recently, even though bull trout are native to both lakes (Donald et al. 1985). There is a credible anecdotal report of mountain whitefish from the Willow Creek area of the upper Snake Indian drainage (M. Sullivan, personal communication). This location lies above Snake Indian Falls, but downstream from two sets of falls below the confluence of the Dolly Lake outlet with the Snake Indian River (Map 2). In the Miette River, mountain whitefish extend upstream at least to just above the Derr Creek confluence (Mayhood 1980:154). The species is common in Rock Lake (Miller and Paetz 1953:101, Bradford 1990:206), so presumably enters the park in Rock Creek.

Mountain whitefish also are said to occur in Moab, Pyramid, Beauvert, Edna and Talbot lakes (Ward 1974:21). There are no records of mountain whitefish captured in Moab Lake, and the most recent survey failed to capture the species there (Donald and De Henau 1981:161).

In the Brazeau drainage mountain whitefish have been found in Southesk Lake (Yamamoto 1979:15, Baraniuk 1989). The species undoubtedly occurs throughout the Southesk River from the lake to the park boundary, including at least part of the Cairn River. How far it extends upstream in the Brazeau River is not documented. Rawson (1940a:83) captured no mountain whitefish in Brazeau Lake in limited gillnetting conducted in mid-September 1939, and Yamamoto (1979:15) did not catch any there in gillnetting operations conducted in mid-June 1979. Donald and Alger (1986b:1734) did not record the species from Brazeau Lake either.

Mountain whitefish may not enter the park in the Smoky River drainage. Mountain whitefish have not been captured in Twintree Lake or in some other lakes in the Smoky system during recent gillnetting (Yamamoto 1979:15, Donald et al. 1985).

The possible distribution of mountain whitefish in Jasper National Park is illustrated in Map 2 (map pocket). Upstream limits in many drainages are speculative because of the uncertainties noted above.

**Habitat:** Details of critical habitat used by mountain whitefish in Jasper National Park are largely undocumented. Young-of-the-year mountain whitefish rear in the lower 2 km of the Fiddle River (Donald et al. 1977:21). They also use shallow side channels, braided channels and other shallow water and gentle currents in the lower Snake Indian, Snaring, and middle and upper Miette rivers (Mayhood 1980). Underyearling and juvenile mountain whitefish rear in at least one springbrook tributary to the Athabasca River (Mayhood 1980:149).

In the Sheep River (Bow drainage), Alberta, Thompson and Davies (1976:211) found mountain whitefish spawning in two very different habitat types. In the mainstem headwaters spawning was observed in shallow (approximately 40-50 cm), fast (approximately 90-100 cm/s) white water over large gravel, cobble and boulder substrate. In the lower mainstem, a group of approximately 700 adult fish "in all stages of gonad activity" were believed to be spawning in a pool 40 m long and more than 2 m deep. The daily range in water temperature over the spawning period was 0-8 °C. Data summarized by Bovee (1978:72) suggest that mountain whitefish are most likely to spawn at a water temperature of approximately 4 °C in water over 30 cm deep, flowing at 50 cm/s over gravel to cobble substrate. According to Nelson (1965:736), the presence of ripe and spawned-out females along the shore of Barrier Reservoir (Kananaskis River) in his study suggested that mountain whitefish spawn in the lake near shore.

Davies and Thompson (1976:2396) reported that newly hatched fry in the Sheep River could not swim against a current of more than a few centimetres per second, and collected in shallow (5-20 cm deep) backwaters in the central and lower river mainstem. Braided reaches provided particularly abundant fry habitat (Davies and Thompson 1976:2398). Young mountain whitefish used areas of slow water over gravel, sand and mud until they reached a fork length of 55-60 cm, thereafter occupying the fringes and tails of pools in noticeably faster water over rock and rubble. Similarly in Kelly Creek, Idaho, Pettit and Wallace (1975:75) found mountain whitefish fry (15-20 mm long) to use protected side pools, moving into deeper water after about two months' growth. Whitefish fry are most likely to use water 60 cm deep flowing at less than 15 cm/s over silt and sand, according to data summarized by Bovee (1978:75). The same source indicates that juvenile mountain whitefish are most likely to use water 40-80 cm deep, flowing at 40 cm/s over cobble bottom (ibid. p. 74). Nelson (1965:733-5) noted that schools of underyearling mountain whitefish "tended to occupy small bays of the [Kananaskis] river with mud bottoms."

Apparently adults in the Sheep River use small tributaries for feeding in spring and early summer when turbidity in the mainstem is high, feeding in the mainstem headwaters in mid-summer. Later, they spend much of their time in deep (greater than 2 m) mainstem pools with the approach of the spawning season. Some fish were seen to overwinter in shallow (less than 30 cm) backwaters in the lower mainstem, but most overwintering habitat is believed to be even further downstream in the Bow, the larger river to which the Sheep is tributary via the Highwood River (Davies and Thompson 1976:2398). Mature mountain whitefish in the North Fork Clearwater River, Idaho, used the upper reaches of the system for summer feeding and spawning, overwintering in deep pools in the lower reaches of the mainstem (Pettit and Wallace 1975:68). Nelson (1965:735) reported that 95 percent of mountain whitefish moved down the Kananaskis River into the Barrier Reservoir by the age of 20 months. Bovee (1978:73) summarized data suggesting that adult mountain whitefish are most likely to use water more than 80 cm deep, flowing at 40-60 cm/s over mostly cobble substrate.

**Biology and Life History:** There is little information on this species in Jasper National

Park. Bajkov (1927:4) stated that mountain whitefish, "*Coregonus (williamsoni?)*", come upstream in the Athabasca River in Jasper National Park when the water clears in the fall, which started about September 10 in 1926. In Pyramid Lake Rawson and Elsey (1950) found that mountain whitefish grew to 39 cm and 737 g at an age, as determined from scales, of 10 years. The principal food organisms consumed were aquatic insects, Cladocera and amphipods. Because of the high proportion of Cladocera in the mountain whitefish diet, Rawson and Elsey believed that they competed for food with the young of all species in Pyramid Lake.

Yamamoto (1979:69-72) presented data on over 100 mountain whitefish captured in Southesk Lake. One of them reached age 24 (41 cm length, 705 g weight), with a large number of individuals exceeding age 15 (he did not indicate whether these are scale or otolith ages). Sex and maturity data were presented for part of the sample. All but one fish identified as immature were age 4; the one exception was age 5. All age 4 fish identified as to sex were males. The youngest fish identified as a female was age 5, but there was only one of these. There were, however, several age 6 females identified. These data suggest that many males are mature by age 4, but most females do not mature before age 6 in this population.

Data and observations on populations elsewhere provide an outline of what the biology and life history of the species might be in Jasper National Park.

Davies and Thompson (1976) offered the following interpretation of mountain whitefish life history in the Sheep River (Bow drainage), Alberta. Most of the population is highly migratory, undergoing complex, rapid long-distance movements that may extend over 80 km from downstream overwintering areas to headwater summering areas. In the spring, adults and subadults apparently move upstream from overwintering areas in the lower mainstem. Many enter clear tributary streams draining the foothills and front ranges to feed at a time (May and June) that the mainstem is in freshet, running high and murky. They move downstream as discharge in the tributaries decreases sharply in mid- to late June, returning to the mainstem to feed where the freshet has abated and the water then is clear. Some adults and subadults move far upstream in mid-July to feed in the headwaters for the remainder of the summer. In mid-September, many adult and subadult fish move out of the headwaters to congregate in a few deep pools further downstream, perhaps prompted by a sudden drop in water temperature. These aggregations then moved further downstream at the end of September, spawning in the middle to lower reaches of the river in the first two weeks of October. The fish continued to move downstream after spawning to overwinter in the lower Sheep, Highwood and Bow rivers.

A small number of fish are resident in the headwaters of the Sheep River, remaining there throughout the year. All parts of the life cycle presumably are completed there by this group.

A somewhat different life history pattern was described by Pettit and Wallace

(1975:68) for mountain whitefish in the North Fork Clearwater River, Idaho. There, adults moved upstream from deep overwintering pools in the lower river to feed in the upper river in late spring and early summer. They remained in the upper river to spawn in November, returning downstream 88 km to the overwintering pools. Underyearling mountain whitefish spent their first summer rearing in the upper river, moved downstream to the lower river in their first September, and reared to maturity in the lower river. Evidence of significant homing to spawning streams was found in this population.

Thompson and Davies (1976:215) estimated the egg incubation period as 180-210 days at 0 °C, which in the Sheep River would mean that hatching would take place in the first two weeks of April. Fry at this time are approximately 12 mm total length; however none were found of this size in the Sheep River. The earliest any young-of-the-year were collected was May 17, when they were nearly 20 mm total length. It may be that fry remain in the interstices of the stream bottom for a long period before emerging into the open water, a common feature of salmonid life history.

Mountain whitefish did not exceed a scale age of 8 in the Sheep River (Thompson and Davies 1976:214), but they are long-lived in many populations. McHugh (1941) reported a scale age of 17-18 for fish 375 mm standard length in Bow Lake, Banff National Park, a scale age of 15 for fish 390 mm standard length in Waterton Lake, and a scale age of 10 for fish 320 mm standard length in Lac des Arcs (Bow River near Canmore). Pettit and Wallace (1975:71) found a maximum scale age of 14 in mountain whitefish of an Idaho river. In Kinuseo Creek (Peace drainage, BC) northwest of Jasper Park, mountain whitefish may attain an age of 19 or more and often exceed age 11 as determined from otoliths (D. W. Mayhood and P. J. McCart, unpublished data). I am not aware of any data showing greater ages for mountain whitefish than those reported by Yamamoto (1979:69-72) for Southesk Lake (see above).

Long-lived fish often require several years to achieve sexual maturity. In the short-lived mountain whitefish of the Sheep River most males were mature by a scale age of 3, and most females by age 4 (Thompson and Davies 1976:211). In the long-lived mountain whitefish of Kinuseo Creek and Flatbed River (Peace drainage, BC), only 50 percent of the males were mature by age 4 (all mature at age 5). Only 20 percent of females in these populations were mature by age 4; 75 percent were mature by age 5, but 14 percent did not mature until age 8 (D. W. Mayhood and P. J. McCart, unpublished data). These latter ages at maturity are similar to those for mountain whitefish in Southesk Lake suggested by the data of Yamamoto (1979:69-72, see above).

The food of mountain whitefish in most streams is primarily benthic invertebrates (McHugh 1940:134, Thompson and Davies 1976:216, D. W. Mayhood and P. J. McCart unpublished data). Mountain whitefish in Sheep River fed mostly on drift, not by picking organisms off the bottom, and adults consumed substantial quantities of terrestrial insects in addition to benthic ones (Thompson and Davies 1976:217).

Mountain whitefish consume fish eggs at times (Rawson and Elsey 1950, D. W. Mayhood and P. J. McCart unpublished data), but do not do so at others, even when they are available (Thompson and Davies 1976:218). In lakes the species feeds on zooplankton in addition to benthic invertebrates (McHugh 1940, Rawson and Elsey 1950).

**Ecological Significance:** The function of mountain whitefish in the ecology of Jasper National Park has not been documented, but the species appears to be abundant, and therefore must play a significant role. In unproductive waters where populations are large, predation by mountain whitefish must have an influence on the structure and function of zooplankton (lakes only) and benthic invertebrate communities. Whether they are important competitors of other fishes, birds or other vertebrate species for these resources depends on whether the resources are limiting.

Mountain whitefish in turn may be a significant prey species for other vertebrate predators such as bull trout, burbot, northern pike and the larger piscivorous birds and mammals. For example, they likely were important prey for river otters when that species was abundant at Talbot Lake in the late 1930s (lake survey report dated 1939, D. S. Rawson per W. C. Cable, JNP Warden Service lakes files — see Study Area).

Data recently released by the Alberta Government show that mountain whitefish taken from the Athabasca River below the pulpmill at Hinton are contaminated with dioxin (2,3,7,8 T4CDD) and furan (T4CDF) (Alberta Government press release 153, 27 July 1990). Mountain whitefish, which are highly migratory in many river systems, may transport these extremely toxic compounds into Jasper National Park where they could contaminate the larger park ecosystem.

**Fishing:** Natives probably caught and ate mountain whitefish from the waters of Jasper Park perhaps for thousands of years. There are no records of this use other than a reference to Shuswaps spearing fish by torchlight in Talbot Lake in 1863 (Cheadle 1931:164, 166). Talbot Lake has a native population of mountain whitefish, among other species.

Alexander Ross (1855:202-3) described a meal of “titameg, or white fish” he had at Henry House in 1825 that could have been mountain whitefish. Mountain whitefish may have been the small whitefish that Drummond (1830:196) subsisted on for a time while encamped on a small lake about halfway between Brûlé Lake and the Whirlpool River-Athabasca River confluence in 1826. De Smet (1847:197) recorded that 50 whitefish per day were supplied to the users of Jasper House during a 26-day period in 1846. It is likely that some of these were mountain whitefish. Henry John Moberly mentioned “delicious” small whitefish entering Talbot Lake from the Athabasca River in the 1850s (Moberly and Cameron 1929:97-98) that very likely were this species. Hector (1863:128) observed that the whitefish that abounded in the mountain lakes in the vicinity of Jasper House in the 1850s routinely were used to provision Jasper House at that time. A company fishery for Jasper House was in operation on Talbot Lake in 1863, and must have captured mountain whitefish along with the other species that inhabit the lake (Cheadle 1931:164). These records are discussed at length in Section II.

Data from a voluntary creel census document angling catches of mountain whitefish in Pyramid Lake and numerous streams for five years in the period 1947-53 (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954). Total reported catches ranged from approximately 300 to 700 mountain whitefish annually in the park, with Snaring River providing most of the fish in most years. Other important mountain whitefish angling waters were the Athabasca, lower Maligne and Rocky rivers and Pyramid Lake, with Hardisty Creek and the Snake Indian River occasionally providing significant catches. The Athabasca River (possibly near its confluence with the Snaring River) also provided the Alberta record mountain whitefish from 1976 to 1989, a 2.4-kg specimen (C. Hunt, personal communication).

**Conservation Status (general):** Mountain whitefish do not appear on any lists of endangered or threatened species (Nelson 1982, Ono et al. 1983, McAllister et al. 1985, Campbell 1991, Williams et al. 1989). There are no jurisdictions recognizing the species as of special concern, or requiring legislated protection (Johnson 1987:5). In Alberta they are common to abundant (Paetz and Nelson 1970:76-77).

Although Holt (1960) failed to find evidence of morphological differences among several populations in this species, some aspects of mountain whitefish origins, life history and biology discussed above suggest that separate stock development may be common. Mountain whitefish may have survived Wisconsinan glaciation in as many as three separate refugia, two of them small and isolated, conditions promoting evolutionary divergence. Where these stocks encountered each other postglacially, mountain whitefish populations may be comprised of more than one stock. The observation of Pettit and Wallace (1985:75) that adults in one tributary homed to the same tributary the next year suggests that the mountain whitefish population in their study drainage may have consisted of separate stocks, each using a different spawning area. Certainly homing behaviour would promote separate stock development, but it has not been examined in other populations. Davies and Thompson (1976:2399) believed that there were both resident and migratory fish in the Sheep River, and suggested that this arrangement had selective advantages for the species in this system, promoting a gene pool with greater genetic diversity. McPhail and Lindsey (1970:117) reported that Kootenay Lake BC may hold two or more races of mountain whitefish that may differ morphologically, and may spawn at different times and in different places.

If separate stocks go unrecognized, the smaller, less productive ones easily can be overexploited (Larkin 1977). The integrity and diversity of the species or its populations is not assured unless the stock structure is maintained intact. Until we have delineated the stock structure of mountain whitefish or its individual populations, we should not assume that all is well.

**Conservation Status (Jasper):** The status of most populations in Jasper National Park is not known.

The original stock of mountain whitefish in Lac Beauvert was poisoned in 1964 (Ward 1968a, JNP fish stocking records). Mountain whitefish now are rare in that lake (Yamamoto 1974b:34, 1978:33; Anderson and Donald 1978:51). They were present in much higher numbers in earlier years, although test netting catches sometimes varied widely from one year to the next (e.g., Rawson 1940a, data in numerous file reports by W. C. Cable in Warden Service lakes files).

In Pyramid Lake it appears that there has been a substantial increase in mountain whitefish as a proportion of the total number of fish, but there has not necessarily been an increase in the absolute numbers of the species. Mountain whitefish comprised 22 percent of the gillnet catches in Pyramid Lake during the period 1939-45 (Rawson and Elsey 1950:17). In 1973 and 1977 the species averaged 44 percent of the gillnet catch (Yamamoto 1974b:34, 1978:33). In 1980, mountain whitefish comprised 55 percent of the test gillnet catch (Donald 1987:551). Units of effort were not reported for the netting done in the 1940s and 1970s, so it is not clear whether the species abundance has increased or decreased in Pyramid Lake.

As described above, underyearling mountain whitefish favour shallow side channels, backwaters and shallow braided reaches for rearing. A substantial amount of this type of habitat in left bank tributaries of the Athabasca River, and along the river bank itself, has been destroyed or rendered inaccessible to mountain whitefish (Mayhood 1980). Some examples are listed below.

1. Moosehorn Creek for at least 600 m above the Canadian National Railway right of way had been completely destroyed as fish habitat, and the entire stream rendered inaccessible to fish from the Athabasca, by diversion works when examined 4 October 1980 (ibid. p. 140). This situation reportedly has been improved (Wes Bradford, personal communication 9 May 1990), but whether mountain whitefish now use the area is not known.

2. Numerous small creeks and springbrooks that formerly were accessible to mountain whitefish and other species now are blocked by culverts, roadbeds, and railbeds.

3. Side channels of the Athabasca River are cut off by railbeds (ibid. pp. 141–142).

4. Several side channels of the Snake Indian River near the mouth (as much as 25

percent of the total side channel area) are blocked off or obliterated by a 1.6-km long dike that protects the railbed (ibid. p. 142).

5. Many side channels of the Snaring River near the mouth are blocked and dewatered by extensive dikes, diversion works, rail- and roadbeds (ibid. p.146).

The Snaring River, even in its present degraded condition near the mouth, is a significant mountain whitefish stream, both for rearing (Mayhood 1980:146) and for use by larger juveniles and adults (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954). The damage to rearing habitat at this site alone must be considered potentially serious. When the total damage along the left bank and tributaries to all potential habitat for mountain whitefish and other fishes is considered, there is reason to suspect that there has been significant damage to Athabasca River stocks as a whole in Jasper National Park.

The Alberta Government has released data showing upper Athabasca River mountain whitefish to be contaminated with dioxins and furans (Alberta Government press release 153, 27 July 1990). Concentrations were high enough to prompt the government to issue a public warning suggesting limits on consuming mountain whitefish from the upper Athabasca drainage. The contaminants are probably toxic to the fish as well. In view of (a) the potential toxicity of these compounds to both the fish and to the public, (b) the possibility that they are being introduced into the park ecosystem in part via migratory mountain whitefish, and (c) the evidence of extensive damage to rearing habitat in the Athabasca valley, the status of this species provisionally is of **special concern** in Jasper National Park.

**Required Action:**

1. A contaminant survey of mountain whitefish and other species in the Athabasca River system within the park is required immediately to document concentrations in fishes of contaminants associated with pulpmill effluent, especially dioxins and furans. The appropriate agency of Environment Canada should be approached for advice.

2. A major survey of mountain whitefish in the upper Athabasca River system is required. The emphasis in this work should be placed on identifying critical habitat (spawning, rearing, overwintering), on documenting movements, and describing the distribution, size and structure of the population, including its stock structure and its age, sex and size composition. The work should be undertaken jointly with Alberta Fish and Wildlife.

3. The findings of the population status and life history study (2) should be used to guide habitat restoration and protection, and to develop a comprehensive management plan for the species.

***Rainbow trout*** (native Athabasca stocks)
*Oncorhynchus mykiss* (Walbaum)

***SALMONIDAE***
Salmoninae
Salmon, Trout & Charr

**ENDANGERED,** possibly **EXTIRPATED**
in Jasper National Park (Provisional Status)

**Summary:** Rainbow trout are native to the Athabasca headwaters, including Jasper National Park, one of only three locations where the species occurs naturally on the eastern slopes of the North American Cordillera. A unique subspecies of rainbow trout was described from the park many years ago, but its taxonomic status and present existence requires confirmation. Unpublished data demonstrate that a representative native Athabasca stock from just outside the park is highly distinctive genetically, and may have survived Wisconsinan glaciation in a local refugium. The Athabasca rainbow trout should be considered provisionally as one of a large number of black-spotted North American trouts (genus *Oncorhynchus*), including many distinctive and valuable stocks of rainbow trout, which are of special concern, threatened, endangered, or extinct as a result of introgression with introduced stocks, habitat destruction and overharvesting.

The present status of native Athabasca rainbow trout stocks in Jasper National Park is unknown, but there is considerable reason for concern that massive introductions of non-native strains have destroyed many of them through introgression. Park stocks provisionally should be considered as **endangered**, possibly **extirpated**, for management purposes. A comprehensive taxonomic and genetic survey of rainbow trout in Jasper National Park is needed to identify native, non-native and hybrid populations, and to establish the taxonomic identity of any native populations found. A detailed recovery and management plan for native stocks of rainbow trout should be developed based on the results.

**Nomenclature:** This species is referred to as *Salmo gairdneri* in most recent literature up to, and including, 1989. Smith and Stearley (1989) documented the need for the name change, which has been adopted by the American Fisheries Society and the major scientific journals. Early records of this fish often used the name *Salmo irideus* (e.g., Prince et al. 1912, Bajkov 1927, Neave and Bajkov 1929).

**Description:** Bajkov (1927) described two types of rainbow trout in Jasper Park waters. He identified the “typical” form as *Salmo irideus* Gibbons, describing it as being dark, with large spots and firmly set scales of even ellipsoid shape numbering 120-140 along the lateral line, and head length “4 in the body” (Bajkov 1927:387). The most visible characteristics of this fish were its overall dark colour and heavy black spotting, including on the operculum three large black spots as large as the pupil with many smaller black spots on the head, snout, operculum, back, sides and all fins, including the upper surfaces of the pectoral and pelvic fins. The sides were said to covered with “large undefined bluish-gray spots”, presumably parr marks. The belly was “darkly pigmented, with a golden shade”, and the sides had a “dark red rainbow stripe with golden reflection.” The flesh was pink or white. In contrast to the second type (described below), the scales “show and even ellipsoid outline” (Bajkov 1927:387,388). Later he applied the name *Salmo irideus* morpha *typica* to this fish (Neave and Bajkov 1929:199).

The second type of rainbow trout Bajkov (1927:387) described as a new form of the species, *Salmo irideus* morpha *argentatus*. He described this fish as silvery, “with small spots, or almost without spots, with loosely set scales”, 75-100 lateral line scales, head length 5-5.5 “in the body” (his p. 387). The spots were X- or C-shaped, not round. The gill cover was “bright pink and rainbow coloured”, and the side of the body showed only a weak rainbow stripe with pink and silver reflection. The dorsal fin was tipped with yellow or pink; the pectoral fins were gray, brown or, in old fish, dark red with white tips; and the anal fin was immaculate dark crimson with a white tip. The flesh was bright red. The scales of *argentatus* differed from those of the *typica* morph in having “a wide base, beyond which the outline is more irregular than the typical form” (Bajkov 1927:387,388). Bajkov (1927:389) described rainbow trout from Minaga Creek as being very similar to the *argentatus* form, but with 8 to 12 bright red spots along the sides, with a green reflection, and with white flesh.

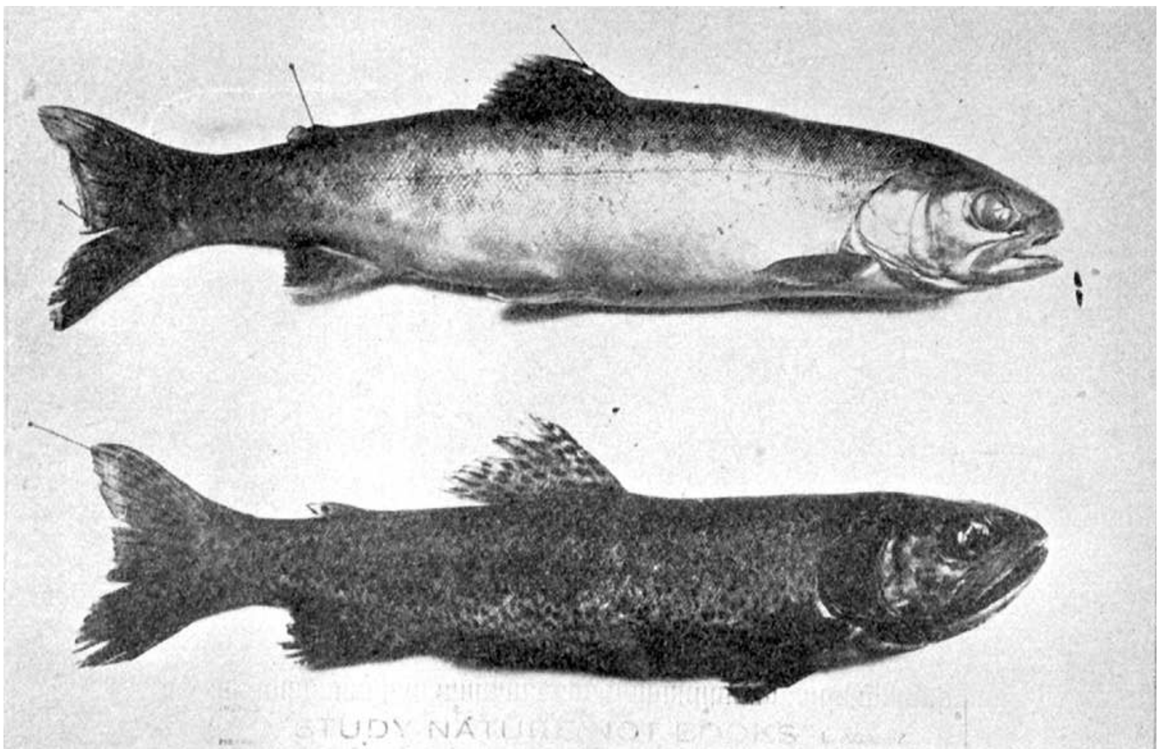
Bajkov’s photographs of the two forms are reproduced in Figure 11.

Bajkov (1927:391-392) provided detailed morphometric and meristic data for numerous specimens from “Buffalo Prairie” and Caledonia lakes, and from Minaga Creek, but did not indicate which specimens are typical *irideus*, and which are the *argentatus* form. The lateral line scale counts for most specimens are within the range he indicated were diagnostic of the typical form, but several (11 out of a total of 46) had lateral line scale counts of 111-119 inclusive, intermediate between the two ostensibly distinctive forms.

Bajkov (1927:390) stated that the lighter-coloured rainbow trout from the Fraser River near Lucerne (on Yellowhead Lake) were distinguishable from the rainbows of the Mackenzie River system by their smaller scales (130 to 150 — lateral line scales, presumably), and were indistinguishable from the rainbow trout of the upper Sacramento River basin, *Salmo irideus shasta*. The latter subspecies is absent from Jasper National Park, he wrote. The scale counts in fact obviously overlap widely those of his Jasper stocks of *Salmo irideus*, and clearly could not be used to distinguish between these groups.

**Distribution:** Rainbow trout are very widely distributed in Pacific and Bering Sea drainages of western North America, from Rio Del Presidio on the Tropic of Cancer in Mexico to the Kuskokwim drainage of Alaska (MacCrimmon 1971:664), and in Kamchatka of northeastern Asia also (Smith and Stearley 1989). In North America, rainbow trout occur as native fish east of the continental divide only in the upper Peace and upper Athabasca systems in Canada, and in the Rio de Casas Grandes, an internal drainage in Mexico (MacCrimmon 1971:664). The range of the species has been extended almost worldwide by extensive introductions of a very widespread hatchery stock formed from a combination of coarse-scaled anadromous steelhead and fine-scaled resident rainbows of the McCloud River, California (Needham and Behnke 1962, MacCrimmon 1971).

**Figure 11.** Bajkov's photographs of two rainbow trout morphs found in Jasper National Park (Bajkov 1927:Plate Ia). **Top:** "*Salmo irideus* m. *argentatus*, [female]. Age 3 years." **Bottom:** "*Salmo irideus* Gibb. Typical form. [Female]. Age 3 years."




Van Tighem (1988a) was the first to draw attention to a nineteenth century traveller's diary entry, the earliest evidence yet found that a form of rainbow trout is indigenous to the East Slopes in the upper Athabasca drainage. In his journal entry for 14 June 1863, Walter Cheadle described the trout he caught in a small brownwater creek somewhere between the Pembina and McLeod rivers on the trail from Fort Edmonton to Jasper House.

*"...soon captured a small trout of some 2 oz. but could not get another run; the fish was very like an English burn trout, but instead of the red spots, it had a red line along each side about 1/8 inch broad; the black spots similar to English variety;..."* (Cheadle 1931:150).

The black spots identify this fish as a true trout (*Oncorhynchus*), not a char (*Salvelinus*), and the red line on the side defines it as one of the rainbow group. Trout certainly would not have been introduced from elsewhere at that time, almost fifty years before the railway, and before widespread settlement provided any motivation for it.

Supporting evidence that rainbow trout are indigenous to the upper Athabasca drainage comes from the work of the Alberta and Saskatchewan Fisheries Commission of 1910-11. It is Cheadle's trout that Sisley (1911:114) seems to refer to as "another valuable species of trout of which full particulars cannot be given at present", occurring in the Athabasca River tributary, the McLeod River, and its tributary, the Embarras River. The Fisheries Commission, of which Sisley was a member, later called the trout in these rivers "*Salmo irideus Athabasca*" (Prince et al. 1912:43). The Commission's field work was done in 1910 and 1911. By spring of the latter year, the Grand Trunk Pacific Railway had reached the upper Athabasca River tributaries as far as Prairie Creek, 294 km west of Edmonton, from the east (Douglas 1912a:17). The closest, perhaps at that time the only, source of rainbow trout for stocking was the Fraser River drainage to the west of the Continental Divide, an area still far from the railway, so it is unlikely that the upper Athabasca rainbow trout mentioned by the Commission were introduced from elsewhere.

Paetz and Nelson (1970:5) cite personal communications from two early fishermen, R. Krause and C. Picarello, in support of their statement that rainbow trout were present in the upper Athabasca drainage many years before introductions were possible. These areas included streams on the east and south slopes of the Swan Hills, and throughout most of the upper parts of the Athabasca system. Elsewhere (ibid. p. 101) they stated that "employees of the Grand Trunk Pacific railway report them being abundant in areas near Hinton and Jasper in 1910 and 1911"; i.e., at the time the first railway arrived in that region.

**Refugia/Postglacial Dispersal:** The present-day native distribution of rainbow trout includes parts of known permanently ice-free areas in Beringia and Cascadia, and the Wisconsinan Ice-free Corridor in the upper Athabasca drainage, Alberta. The most complete zoogeographical interpretation for this species in our area proposed that rainbow trout survived glaciation in Cascadia, dispersed northward postglacially by an interior route and crossed the Continental Divide into the Athabasca system (McPhail and Lindsey 1970:17,161). Behnke (1972:652) largely concurred, suggesting however that "Kamloops trout" of the upper Fraser, which would have been the source stock for the upper Athabasca rainbow populations under his proposal, are a fish of the "golden trout complex" from an interior glacial refuge that has been introgressed by migratory coastal rainbow stocks. Other recent interpretations suggest that rainbow trout crossed the Continental Divide from the Fraser to the Athabasca, but do not specify a refugium (Paetz and Nelson 1970:5, Lindsey and McPhail 1986:669). Crossman and McAllister (1986:86) and Sterling (1989:1) suggested that a unique form of rainbow trout may have survived Wisconsinan glaciation in or near Jasper National Park. This latter possibility, if true, would have major consequences for fish management in Jasper National Park and will be examined in detail.

The population of rainbow trout in Wampus Creek, a tributary of McLeod River immediately east of Jasper Park, is believed to be a genetically-pure indigenous stock of Athabasca rainbow trout, based on an unpublished genetic screening of this population (Sterling 1989, L. Carl, personal communication 8 February 1990). (The issue of the genetic purity of this stock is discussed in detail under Conservation Status.) Certain meristic characters of the Wampus Creek stock are identical to those of rainbows described by Bajkov (1927) in Jasper National Park (L. Carl, personal communication). Wampus Creek fish are superficially similar in their spotting patterns and general colouration to Bajkov's (1927) "typical" form of the species in the park (cf. Van Tighem 1989a). The Wampus Creek rainbows therefore will be considered as representative of at least one native Jasper Park stock for the purposes of the following discussion.

Regional Fisheries Biologist Carl Hunt of the Alberta Fish and Wildlife Division, and Dr. Leon Carl, former Salmonid Coordinator with that agency, kindly have allowed me to refer to some of the unpublished results of protein electrophoresis done on the Wampus Creek population in 1984 (Table 5). The electrophoretic analysis, comparative data (unless otherwise noted) and some interpretive comments were provided to Alberta Fish and Wildlife under contract by James Seeb and Lisa Wishard of Pacific Fisheries Research of Seattle, Washington. Some of the key features of these data are discussed below.

The Wampus Creek population has allelic frequencies distinctly different from those in Salmon River, Idaho; the middle and lower Columbia and the Willamette rivers, Washington; Dworshak hatchery, Washington; and an Idaho hatchery stock. The latter is said by J. Seeb and L. Wishard to be representative of the McCloud River coastal stock, the source of most hatchery stocks throughout the world (Needham and Behnke 1962, MacCrimmon 1971). Wampus Creek rainbows show no strong affinities to any of the populations examined, which include four groups of populations within the refugium (Cascadia) from which Wampus Creek was populated postglacially, according to the interpretation of McPhail and Lindsey (1970:161).

The presence of unique alleles, especially at high frequency, or absence of common ones, may be strong evidence in helping to establish stock origins (e.g., Foote et al. 1992). Next in value for this purpose are large differences in the frequencies of alleles. In these respects the most striking aspects of the data are the following.

**Table 5.** Allele frequencies for certain polymorphic loci in Wampus Creek rainbow trout compared to selected other stocks. Unpublished 1984 data, Alberta Fish and Wildlife Division, reproduced with permission. From a report prepared under contract to AFWD by J. E. Seeb and L. N. Wishard, Pacific Fisheries Research, Seattle, WA. Enzyme and allele designations as in the original.

| Location | | ---LDH------- | | | AGP1 | AGP2 | -------MDH3------ | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| (Source) | N | 100 | 76 | 120 | 100 | 100 | 100 | 81 | 120 | 76 |
| Wampus Creek | 127 | 0.91 | 0.00 | 0.09 | 1.00 | 1.00 | 1.00 | 0.00 | 0.00 | 0.00 |
| Dworshak Hatchery | 482 | 0.31 | 0.69 | 0.00 | 1.00 | 0.97 | 0.99 | 0.01 | 0.00 | 0.00 |
| Salmon River | 97 | 0.24 | 0.73 | 0.03 | 1.00 | 1.00 | 0.98 | 0.00 | 0.01 | 0.01 |
| middle Columbia | 388 | 0.38 | 0.62 | 0.00 | 0.97 | 1.00 | 0.97 | 0.01 | 0.02 | 0.00 |
| lower Columbia | 200 | 0.80 | 0.20 | 0.00 | 0.82 | 1.00 | 0.87 | 0.12 | 0.01 | 0.01 |
| Willamette River | 200 | 0.90 | 0.10 | 0.00 | 0.90 | 1.00 | 0.78 | 0.22 | 0.00 | 0.00 |
| Idaho hatchery | 50 | 0.99 | 0.01 | 0.00 | 0.89 | 1.00 | 0.90 | 0.10 | 0.00 | 0.00 |

| Location | | ------GL-1------- | | | | -----IDH-3,4----- | | | | PGM |
|---|---|---|---|---|---|---|---|---|---|---|
| (Source) | N | 100 | 111 | 94 | 116 | 100 | 38 | 67 | 171 | 100 |
| Wampus Creek | 127 | 0.00 | 0.76 | 0.00 | 0.24 | 0.66 | 0.15 | 0.19 | 0.00 | 1.00 |
| Dworshak Hatchery | 482 | 0.47 | 0.53 | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 | 0.00 | 0.99 |
| Salmon River | 97 | 0.95 | 0.04 | 0.01 | 0.00 | 0.67 | 0.15 | 0.18 | 0.01 | 1.00 |
| middle Columbia | 388 | 0.91 | 0.09 | 0.00 | 0.00 | 0.62 | 0.24 | 0.14 | 0.00 | 1.00 |
| lower Columbia | 200 | 0.95 | 0.02 | 0.04 | 0.00 | 0.67 | 0.16 | 0.16 | 0.00 | 1.00 |
| Willamette River | 200 | 0.99 | 0.01 | 0.00 | 0.00 | 0.66 | 0.18 | 0.12 | 0.02 | 1.00 |
| Idaho hatchery | 50 | | | | | | | | | 0.72 |

| Location | | PMI | ----SOD----- | | | GPI1 | GPI3 | PGK | EST | ME |
|---|---|---|---|---|---|---|---|---|---|---|
| (Source) | N | 100 | 100 | 152 | 48 | 147 | 100 | 100 | 100 | 100 |
| Wampus Creek | 127 | 0.71 | 1.00 | 0.00 | 0.00 | 0.00 | 1.00 | 0.89 | 0.98 | 0.71 |
| Dworshak Hatchery | 482 | 1.00 | 1.00 | 0.00 | 0.00 | | 1.00 | | | |
| Salmon River | 97 | 0.98 | 0.96 | 0.01 | 0.03 | 0.01 | 0.99 | | | |
| middle Columbia | 388 | 1.00 | 0.96 | 0.06 | 0.02 | | 0.97 | | | |
| lower Columbia | 200 | 1.00 | 0.78 | 0.22 | 0.00 | | 0.96 | | | |
| Willamette River | 200 | 1.00 | 0.71 | 0.29 | 0.00 | | 0.98 | | | |
| Idaho hatchery | 50 | 1.00 | 0.67 | 0.33 | 0.00 | 0.00 | 1.00 | | | |

LDH: lactate dehydrogenase, Enzyme Commission Number (ECN) 1.1.1.27
AGP: glycerol-3-phosphate, ECN 1.1.1.8
MDH: malate dehydrogenase, ECN 1.1.1.37
GL: peptidase resolved using glycyl leucine, ECN 3.4.11
IDH: isocitrate dehydrogenase, ECN 1.1.1.42
PGM: phosphoglucomutase, ECN 2.7.5.1
PMI: mannose phosphate isomerase, ECN 5.3.1.8
SOD: superoxide dismutase, ECN 1.15.1.1
GPI: glucose phosphate isomerase, ECN 5.3.1.9
PGK: phosphoglycerate kinase, ECN 2.7.2.3
EST: esterase, ECN 3.1.1.1
ME: malic enzyme, ECN 1.1.1.40

1. The LDH-4(76) and GL-1(100) alleles are completely absent in the Wampus Creek population. The former is present and often frequent in all the comparative populations except the Idaho hatchery, where it is rare. The latter is frequent (usually very frequent) in all the comparative populations except possibly the Idaho hatchery stock, for which no data for the GL-1 locus were reported.

2. The GL-1(116) allele was present at a frequency of 24% in the Wampus Creek population, but was entirely absent from all the comparative populations, except possibly the Idaho hatchery population, for which no data on this locus were reported.

3. The LDH-4(120) allele, which Seeb and Wishard described as having "been rarely seen previously", was present with a frequency of 9% in the Wampus Creek fish and at 3% in the Salmon River rainbows, but did not occur in any of the other populations.

4. The SOD(152) allele was absent from the Wampus Creek population, but it was common in the lower Columbia, Willamette and Idaho hatchery populations. It was present, though infrequent, in two others, and absent only from the Dworshak hatchery fish.

The Salmon and middle Columbia rivers lie in or near that part of Cascadia from which rainbow trout may have invaded Canada by interior routes during deglaciation, according to the current views of postglacial dispersal noted above. The Willamette and lower Columbia rivers may have contributed fish via dispersal upstream from the Pacific Coast. Both routes would have required headwater transfer. If the upper Athabasca were populated by rainbows derived from interior stocks of rainbows in Cascadia, we could expect them to carry at least the common alleles found in the Salmon and middle Columbia populations; if they were derived from coastal stocks they should carry the common alleles of the Willamette and lower Columbia populations.

The LDH-4(76) and GL-1(100) alleles do not occur in the Wampus stock, but are present at high frequencies in all of the Columbia stocks. The LDH-4(76) allele is present but at low frequencies (approximately 5-6%) in wild stocks in the Chehalis region (Reisenbichler and Phelps 1989:70), considered an autonomous refugium by McPhail and Lindsey (1986:630). These alleles apparently never reached the headwaters of the Athabasca. On the other hand, the GL-1(116) allele is entirely unique to Wampus Creek (in these data), and evidently was not derived from Cascadia rainbows. [There is an allele identified as GL-1(120) present at a mean frequency of 0.0525, range 0.0-0.714, in some California populations (Berg and Gall 1988:127) that conceivably is the same GL-1 allele found in Wampus Creek rainbows.] Although other less likely explanations are possible, involving recent mutations in the putative donor stock or loss through selection or genetic drift in the Wampus Creek population (see below), these data are strong evidence that Wampus Creek rainbows did not come from Cascadia.

At least three distinct major stocks of *Oncorhynchus mykiss* are distinguishable in the Pacific drainages of the northwestern US and southwestern Canada on the basis of frequencies of the most common allele at the LDH-4 and SOD loci (Campton and Johnston 1985:789, Parkinson 1984:1419). These allele frequencies show little variation within stocks, and evidently are independent of whether populations are anadromous or nonanadromous. They depend solely on geographic origin. Several authors have related the distribution pattern of these two stocks to differing patterns of postglacial dispersal (see Campton and Johnston 1985:789).

One form has a relatively high frequency of the LDH-4(100) allele and a relatively low frequency of the SOD(100) allele. This form, termed coastal rainbow trout, is characteristic of rivers west of the Cascade Mountains in Washington, including the lower Columbia River and tributaries; and British Columbia coastal drainages south of the Skeena, including the Fraser drainage below Hell's Gate. A second stock, termed interior rainbow trout, has in contrast a relatively low frequency of the LDH-4(100) allele, and a relatively high frequency of the SOD(100) allele. Interior rainbow trout are found in the Columbia drainage east of the Cascade Mountains, and in the Fraser drainage from Hell's Gate an unknown distance upstream. A third stock is evident in Parkinson's (1984) data, in which both common alleles are present at high frequencies. Parkinson found this combination of allele frequencies only in the Skeena system. The relationships of the stocks to each other with respect to LDH and SOD allelic frequencies are illustrated in Figure 12.

Again the Wampus Creek rainbow trout are clearly distinct from both the coastal and inland stocks in their LDH and SOD allelic frequencies. Instead they closely resemble several populations in the Skeena system in these respects. Unfortunately, Parkinson (1984) did not publish data on any of the alleles diagnostic for the Wampus Creek rainbows [LDH-4(76), GL-1(100), GL-1(116), LDH-4(120) and SOD(152)]; however unpublished data exist showing that the LDH-4(76) allele, absent from the Wampus rainbows, is present in the Skeena population (L. Carl, personal communication). If so, the Skeena and Wampus stocks probably are not closely related. Parkinson's (1984) data for the most common alleles at the MDH, IDH and AGP loci individually show little variation and no geographic patterns among all populations, and their mean frequencies are virtually identical to their frequencies in the Wampus population. Parkinson's cluster analysis of several allelic frequencies showed the Skeena populations to be quite different from interior and all but two coastal populations.

Wampus Creek rainbow trout thus probably were not derived postglacially from Cascadian rainbows, but may have survived in either of two other possible refugia — Beringia or the Ice-free Corridor. Both hypotheses have serious problems. Wampus Creek lies near (perhaps in) the Ice-free Corridor, and that is the most obvious alternative refugium for this stock. If rainbow trout survived glaciation in the corridor, there is no apparent reason why they would not have moved north or south along the east slopes, yet they are not found in the immediately adjacent Smoky River or North Saskatchewan River drainages. Alternatively, the pattern of their very restricted distribution in Alberta suggests that rainbow trout “spilled” over the divide from British Columbia (MacCrimmon 1971:Figure 1), favouring a Beringian source. The pattern of rainbow trout distribution in Alaska, however, suggests that Beringian rainbows dispersed only a short distance (McPhail and Lindsey 1970:161, MacCrimmon 1971:Figure 1). Some other unknown refugium may be involved, such as that postulated to exist “somewhere between Prince George and the Nahanni” by Lindsey and McPhail (1986:668). More study of geographic variation in this species, particularly comparisons among Athabasca, Peace, upper Fraser, Skeena and more northerly populations, is required to settle the question.

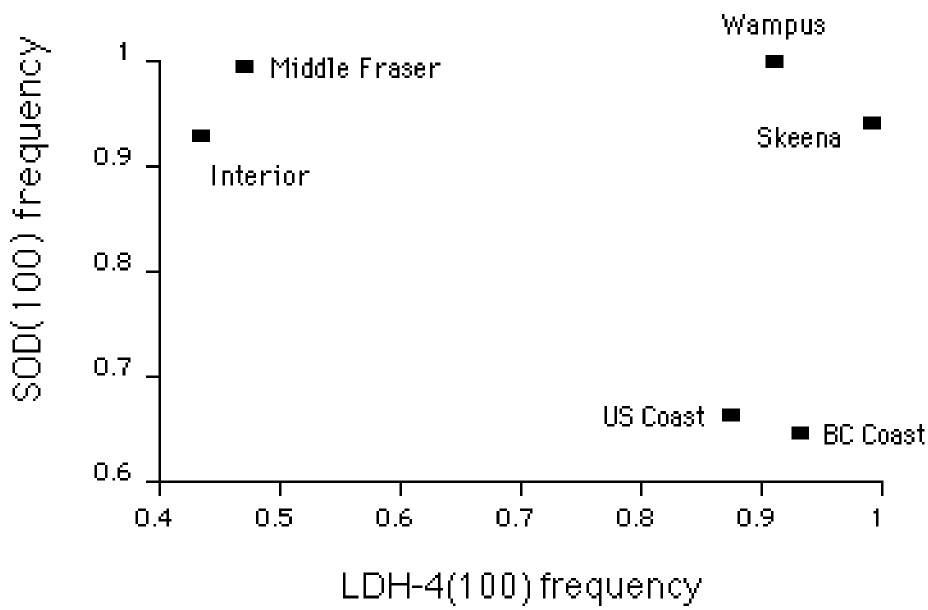



**Figure 12.** Geographic variation in frequencies of the most common alleles of SOD and LDH4 in selected stocks of rainbow trout. Data sources: Wampus Creek, Alberta Fish and Wildlife 1984 unpublished data; all others, Parkinson (1984).

In the foregoing analysis I have interpreted the genetic differences between Wampus Creek rainbows and other geographic stocks as evidence of relatively long isolation of the former. Alternatively, it might be argued that the unique or unusual alleles and divergent allele frequencies in the Wampus population are unrelated to glacial history. Conceivably they arose rapidly since the end of the Wisconsinan.

An important difficulty with this hypothesis, but not the only one, lies in understanding how at least three now-common alleles in the putative source rainbow populations of Cascadia [LDH-4(76), GL-1(100), and SOD(152)] came to be absent from the Wampus stock over a short time, in evolutionary terms. It is unlikely that common alleles will be lost due to small numbers of founders, because most founders are likely to carry common alleles. Furthermore, the Wampus stock is genetically diverse, not depauperate as would be expected if the founder effect was the cause. There is good evidence that natural selection causes differences in enzyme allele frequencies at individual loci in certain instances, but there is also evidence that most enzyme alleles are selectively neutral or near-neutral (e.g., Allendorf and Ferguson 1990:53-54). It is therefore possible, but unlikely, that all three absent alleles have been completely eliminated (i.e., their frequencies reduced to zero) by strong selection pressure against them. Although some other mechanisms for how these three common alleles came to be absent from the Wampus stock postglacially could be advanced, all are weakened because they require invoking several additional assumptions. Again, more study of geographic variation in this species, particularly more detailed genetic comparisons among Athabasca, Columbia, Peace, Fraser (especially upper Fraser), Skeena and more northerly populations, would help in testing the validity of the two hypotheses. At present neither can be rejected on the available evidence. The lack of some common Cascadian alleles from the Wampus stock favours the hypothesis of relatively long isolation in a separate refugium for Wampus rainbows, in my view.

**Jasper Stocks:** Some nineteenth century records exist of several kinds of trout in waters of what is now Jasper National Park (see Section II of this report), but identifiable species were seldom described. The earliest records of fish specifically identified as rainbow trout within the park are for 1911 in the Athabasca River (Herriot 1913:98, Section II), and in a government annual report covering the 1913 season (Rogers 1915:97, Section II).

Although the earliest recorded fish introductions in Jasper National Park were made in 1917 (Park fish stocking records), by 1911 the means (railway — Douglas 1912b:23-24), motivation (railway workers, tourism), and accessible source (McLeod River, Yellowhead Lake, hatcheries in British Columbia and Ontario) were in place to make rainbow trout introductions feasible into these and many other park lakes. There is thus no conclusive proof that rainbow trout are indigenous to Jasper Park.

Several pieces of evidence suggest that this species actually is a Jasper native, however.

1. Rawson (1940a:91) reported that “J. Hargreaves, Jasper, claims to have assisted in transferring native rainbow to Cabin Lake in 1914.”

2. No barrier exists on the Athabasca River between the park and native rainbow stocks downstream in the drainage that would block known indigenous Athabasca stock from moving into the park.

3. There is no evidence that non-native rainbows really were stocked into park waters prior to 1919, when the first *recorded* introductions of the species in park waters were made (into lakes from which they were unlikely to escape, Hibernia and Patricia, Ward 1974:C1-C3), yet they seem to have been widespread in the park before then. As noted above, Herriot (1913:98) reported them to occur in the Athabasca River in 1911. Rainbow trout contributed to "excellent catches" in park waters in 1913 (Rogers 1915:97), and apparently were abundant in "smaller streams and shallow lakes" in 1916 (Driscoll 1918:66).

4. Rainbow trout reportedly were stocked *once* in at least one, and perhaps two waters from which Bajkov (1927) described *two* distinctive kinds of rainbow trout that had been caught no later than 1926. (In 1921, 25,000 rainbows were stocked in Caledonia; in 1925, 16,000 rainbows were stocked in one of the Wabasso lakes — according to Rawson 1940a:91, these were eyed eggs only.) One kind (Bajkov's morpha *typica*) also was found in other park waters, the other (his morpha *argentatus*) he reported only from the two stocked lakes and the Athabasca River. One possible interpretation is that Bajkov's *typica* morph was native, while his *argentatus* was introduced. Furthermore, if the Wabasso Lake he sampled in 1925 or 1926 was the one that had been stocked in 1925, the fish he sampled appear to be too large (183-323 mm, mean 247 mm) to be in their first or second summer of growth, judging from the age data of Neave and Bajkov (1929:200,204-206). Those authors believed that fish 152-310 mm in length in "Buffalo Prairie" (Wabasso) Lake were in their third summer or older, probably based on scale annuli (cf. Bajkov 1927:388), although they do not describe their aging method. If Neave and Bajkov's ages are correct, their specimens must have been native rainbows or the result of an unrecorded earlier stocking.

Rainbow trout were recorded from Minaga Creek, Miette River, Caledonia Lake, "Buffalo Prairie" (Wabasso) lakes and creek, beaver ponds at Old Fort Point, Maligne River (near mouth), the Athabasca River, and unspecified small tributaries to the Athabasca within the park, but were absent from Rocky River and lakes Beauvert, Mildred, Trefoil, Annette, Edith and Jacques when the Jasper Park Lakes Investigations were conducted in 1925-26 (Bajkov 1927). Bajkov reported the "typical" form, *Salmo irideus*, from "Buffalo Prairie" Lake, "Buffalo Prairie" Creek, Caledonia Lake, Caledonia Creek, and the beaver ponds near Old Fort Point. He described a new form, *Salmo irideus* morpha *argentatus*, from "Buffalo Prairie" Lake, Caledonia Lake and the Athabasca River. Paleolimnological evidence indicates that fish were native to Caledonia Lake, but which species were native is not determinable from the available data (S. Lamontagne, personal communication).

It is of interest to note that Miller and Paetz (1953:96-104) did *not* capture rainbow trout in Rock Lake in gillnetting and seining conducted in August 1952, nor did they mention whether the species was collected by W. H. MacDonald a few years earlier, although they refer to MacDonald's lake trout data. There are no confirmed reports of the species in the lake from more recent surveys (cited by Bradford 1990:206). Rainbow trout thus might not be native to Rock Creek within the park even though the species is native to other parts of the Wildhay drainage.

With few exceptions, native rainbow stocks in all park waters have been exposed to non-native stocks of rainbow trout with which they may introgressively hybridize. Rainbow trout mostly of unknown origin have been stocked in the Athabasca and the following river and creek drainages tributary to it: Snake Indian, Vine, Snaring, Miette, Astoria, Whirlpool, Fryatt, Sunwapta and its tributary Poboktan Creek, Maligne, Rocky and Fiddle (Ward 1974:C1-C3, JNP fish stocking records). Rainbow trout are widespread above a major falls on the Snake Indian River (Donald et al. 1985:104), but the species is known to have been stocked in one lake (Topaz) and one stream (Blue Creek) in this area (Ward 1974:C1-C3, JNP fish stocking records). Cabin Lake reportedly was stocked with "native" rainbow trout in 1914 (J. Hargreaves of Jasper, cited by Rawson 1940a:91), and received one planting of rainbows or rainbow-cutthroat hybrids, in 1929 (JNP fish stocking records).

In addition, native rainbow stocks have been exposed to introgression from introduced cutthroat trout, a species not native to Jasper National Park. Cutthroats have been stocked in the following river and creek drainages tributary to the Athabasca: Astoria, Beauvert, Miette (several West Block lakes with intermittent or small permanent outlets), Snake Indian (above and below Snake Indian Falls, but apparently not above unnamed falls between Blue Creek and Deer Creek), Sunwapta, Pyramid, ponds at Moberly Flats, upper Fiddle and Wabasso (Ward 1974:C1-C3, JNP fish stocking records).

There is no record of rainbow trout stocking in Minaga Creek, nor of any stocking in beaver ponds near Old Fort Point, and there is a single stocking record for only one of the four Wabasso lakes. Minaga Creek has a 3-m waterfall approximately 800 m above its confluence with the Miette River (Bajkov 1927:381), and this may have protected native rainbows above it. Cutthroat trout were stocked in 1934 in a lake in the upper Minaga Creek drainage (439, JNP fish stocking records:122A), but the outlet to Minaga Creek is shown only as intermittent on some maps. If these fish survived and were able to escape downstream, they might have contaminated upper Minaga native rainbows. It is conceivable that rainbow trout in Caledonia Creek upstream from Caledonia Lake have been protected by the many beaver dams along the stream. Rainbow trout exist in the middle reaches of Moosehorn Creek (J. Strachan, personal communication September 1980) where they may be isolated, but there is no record of them being stocked there. There is no record of rainbow trout being stocked in Moat Lake in the Meadow Creek drainage, nor in Meadow Creek itself, yet the creek near its confluence with the Miette River is very steep and apparently impassable to fish. Anderson and Donald (1978a:59) interpreted the existence of rainbow trout in Moat Lake as an unrecorded introduction.

The possible distribution of native rainbow trout in Jasper National Park is illustrated in Map 3 (map pocket). Limits are entirely speculative because of the uncertainties discussed above.

**Habitat:** Bajkov's "typical" *Salmo irideus* "lives in shallow places under the shade of trees or among water plants" (Bajkov 1927:12). His *argentatus* morph "lives in deep places" (Bajkov 1927:13). Details of critical habitat, including spawning, rearing and overwintering habitat, for native rainbow trout have not been reported for any waters in Jasper National Park.

Bajkov (1927:5) stated that Minaga Creek is very rapid, with clear, well-oxygenated cold water, and seemed to indicate that rainbows ascended above 3-m high falls to spawn. He believed that the falls presented no difficulties to ascending rainbow trout, but a 3-m vertical drop certainly would be a barrier to any size of trout in a small creek. The creek is steep, bouldery and torrential with numerous waterfalls for at least several hundred metres upstream and downstream of the railway crossing (Mayhood 1980:152; notes by J. E. Martin, quoted in JNP Warden Service lakes files for Miette River). If fish spawn above this area, they are most likely resident. Unnamed small tributaries of the Athabasca are believed to be spawning areas for rainbow trout (Bajkov 1927:6).

Only two of the lakes originally occupied by rainbow trout that might possibly have been native stocks have been described. "Buffalo Prairie" (Wabasso) Lake is a circular beaver pond approximately 400 m in diameter, 4 m deep, with both surface inlet and outlet and clear water (Bajkov 1929:14). Caledonia Lake is a 13-ha body of water, 11 m deep, thermally stratified in mid-summer, with a permanent surface outlet (Anderson and Donald 1980:209).

In the Tri-Creek Watershed study area (Wampus, Eunice and Deerlick creeks) in the McLeod drainage immediately east of the park, native Athabasca rainbow trout spawned in pool-riffle transition areas where mean current was 32.3 cm/s and mean depth 14.5 cm. Geometric mean particle diameter at the spawning sites was approximately 8 mm, fines (diameter less than 0.841 mm) were usually less than 12 percent, and 75 percent of the particles in the spawning substrate were less than 25.4 mm in diameter. In other words, native rainbows in these streams spawn in gentle current at the heads or tails of riffles in water about 15 cm deep over clean small gravel. Egg development, hatching and fry escapement were directly related to water temperature. High discharges during the incubation period for a year class apparently reduced yearling abundances (Sterling 1986). Rainbow trout from this slow-growing small stream stock grew much faster in more productive environments (a eutrophic pond and a reclaimed gravel pit), indicating that the small-stream habitat, not some genetic factor, was limiting growth of rainbows in this stock (Sterling 1989).

**Biology and Life History:** Bajkov (1927:381) believed that rainbow trout spawned in Minaga Creek, and reared there until their third year when they moved downstream to the Athabasca and Miette rivers. They are highly opportunistic feeders, consuming a wide variety of benthic, terrestrial and planktonic invertebrates (Neave and Bajkov 1929). Other aspects of the biology of rainbow trout in Jasper National Park have been presented in the reports and publications of D. B. Donald, R. S. Anderson and coworkers, especially Donald and Anderson (1982), Donald et al. (1985:111) and Donald and Alger (1986b). These concern non-native stocks.

Native rainbows in the Tri-Creek Watershed of the McLeod drainage immediately east of the park are mostly resident fish, only small numbers migrating into the tributaries from the McLeod River to spawn. Within the tributaries, resident fish moved only short distances, primarily during the spawning season (Sterling 1980). The fish spawn after spring break-up when the maximum daily water temperature reached 6 °C, usually in the first 10 days of June. The length of the incubation period depends on temperature, but the young fry emerged from the gravel in late July to early August. Survival from spawning to emergence averaged 33 percent, and was weakly correlated with dissolved oxygen in the interstitial water but not with substrate quality. Of the fry that successfully emerged, survival to the second summer of growth was only 8 percent and was density dependent, lower fry densities in August being associated with higher first-year survival (Sterling 1986).

**Ecological Significance:** The role of native rainbow trout in the ecology of Jasper National Park is not known. It reasonably may be speculated that they are important predators of invertebrates in the lakes and streams they inhabit; therefore they are likely to strongly influence the structure of benthic and planktonic communities. They in turn may be important locally as prey of bull trout, burbot, garter snakes, mink, otter, kingfisher, dipper, mergansers and many other piscivorous vertebrates.

**Fishing:** Native rainbow trout probably were fished by fur traders beginning in the early 1800s, and may have been used by aboriginal fishermen for hundreds or even thousands of years prior to that. Accounts dating from the mid-1800s mention trout (species unnamed) in connection with the food supplies for Jasper House. De Smet (1847:197) indicated that trout were a staple of the diet at Jasper House. His wording is ambiguous, but it appears that twenty trout per day were consumed by the denizens of the post over a 26-day period in 1846. Henry John Moberly, a factor at Jasper House in the 1850s, described the rivers and streams as being stocked with “mountain, silver, and speckled trout”; a lake 16 km north of the post “swarmed with trout. One had only to drop a hook when dozens would jump for it. They weighed three-quarters to a pound and a half” (Moberly and Cameron 1929:54). Writing of the practices of factors up until a few years prior to 1859 at Jasper House, the Palliser Expedition’s James Hector (1863:128) observed: “He always returned in time to secure a stock of fish before the frost set in and closed the mountain lakes, which abound in ‘white fish’ and trout.”

More recent records of exploitation in Jasper Park of trout which may have been native rainbows date from approximately 1912 (Douglas 1912b:26), who wrote that trout (species not named) were caught in large numbers in many of the lakes scattered throughout the park. Caledonia Lake, which may have held native rainbows, was said to be "an excellent fishing point" in 1913 (Rogers 1915:96), and that some excellent catches of rainbow trout had been made (Rogers 1915:97). Driscoll (1918:66), writing of the 1916 season, stated that "the smaller streams and shallow lakes did well in the way of providing a good supply of that gamey little fighter, the rainbow trout."

Native rainbow trout thus appear to have provided good fishing in the early days of the park. Creel census data are available for the period 1947-53 for rainbow trout fisheries in many waters in which native stocks may have occurred (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954). By that time non-native stocks had been disseminated widely in the park, so the figures may not represent catches of native rainbows.

**Conservation Status (general):** As a species rainbow trout are absent from most "endangered or threatened" lists (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Williams et al. 1989, Campbell 1991). Indeed, the species is far more widespread and abundant now than originally (MacCrimmon 1971).

Taken in isolation, these observations obscure a very serious situation for rainbow trout and other western black-spotted trouts. Fish management agencies and some individuals throughout western North America have introduced hatchery stocks of rainbow trout into the ranges of other stocks of western black-spotted trouts, including those of distinctive wild stocks of rainbow trout, over a period of well over a century. These introductions have destroyed innumerable native stocks of nearly all species of western black-spotted trouts through introgressive hybridization.

A large number of jurisdictions recognize numerous blackspotted trouts, including certain stocks and subspecies of rainbow trout, as of special concern or grant them legislated protection (Johnson 1987:5). Of 21 species and subspecies of western North American black-spotted trouts (genus *Oncorhynchus*) recently listed as endangered, threatened or of special concern, 17 are included in part because of hybridization (Williams et al. 1989). Two more valuable subspecies of cutthroat trout have been declared extinct largely as a result of introgression with introduced rainbows (Miller et al. 1989:24). Of the 21 black-spotted trouts still listed, one is endangered, six are threatened and fourteen are of special concern. One is a still-undescribed Mexican species, two are described full species, eleven are described subspecies, and six are as yet undescribed subspecies. Eight subspecies of rainbow trout are listed, four of them as yet undescribed.

The listing above covers only stocks deemed to deserve at least subspecific rank, but the value of conserving distinct stocks at the level of populations or subpopulations is widely recognized (e.g, Behnke 1972; many papers in Berst and Simon 1981, Ryman and Utter 1987, and Allendorf 1988; Meffe 1987; Ferguson 1990). At this level, many

Canadian black-spotted trout stocks have been extirpated or are in danger of extirpation largely because they have been introgressed by non-native rainbow genes. For example, it is likely that pure native stocks of westslope cutthroat trout are gone from virtually all of their original habitats in southern Alberta (Mayhood 1989). At present there is actual genetic evidence of just six still in existence in what might possibly be their native habitats [Elk, Fish (2), Mystic, lower Twin lakes, Picklejar — McAllister et al. 1981, Carl and Stelfox 1989], some of them quite likely contaminated with genes of introduced westslope cutthroats stocked on top of them. Perhaps another half-dozen or so pure westslope cutthroat stocks exist in mountain lakes [e.g., upper Block, Fish (1), Marvel, Job — McAllister et al. 1981, Carl and Stelfox 1989] where they have been introduced perhaps from local native waters, and where in some cases they may pose a threat to any remaining but as yet unrecognized separate native stocks downstream. Native rainbow stocks in Alberta are threatened for similar reasons, though possibly not to the same degree as yet.

The rainbow trout is not merely a "Typhoid Mary", corrupting native stocks wherever it comes in contact with them: it is as much a victim of introgression as the stocks with which it has introgressed. Two prominent trout geneticists have warned (Allendorf and Leary 1988:181):

"*The eventual outcome of widespread introgression and continued introduction of hatchery rainbow trout is the homogenization of western North American trout into a single taxon (*Salmo ubiquiti*?). Thus, we would exchange all of the diversity within and between many separate lineages, produced by millions of years of evolution, consisting of taxa capable of existing from the Arctic to the desert, for a single, new mongrel species*."

**Conservation Status (Jasper):** The status of native rainbow trout in Jasper National Park is unknown. Most if not all native stocks in the park have been exposed to introduced non-native rainbows and cutthroat trout with which they may have introgressed. Even massive exposure to non-native trout does not ensure that introgression has occurred, however. Where hatchery stocks of trout are introduced into waters (especially streams) with a well-established resident population of the same species, growth and survival of the hatchery stock often is very poor (Miller 1952, 1954, 1958). Marnell et al. (1987) found 12 natural populations of native westslope cutthroat trout in Glacier National Park, Montana, that showed no evidence of introgression despite a 60-year history of non-native trout introductions in park waters, including millions of rainbow trout and Yellowstone cutthroats.

Some idea of the potential for finding non-introgressed native rainbow trout in Jasper National Park might be gained from examining the genetics of the Wampus Creek population of Athabasca rainbows, the only native Athabasca stock for which there are adequate data.

A subhatchery run by the federal Department of Fisheries was operated in Jasper beginning in the early 1930s (Lothian 1981:20). Trout, especially rainbow trout fry, were reared here and distributed widely, especially outside of the park in the earliest years. Between 1932 and 1936, at least 660,000 rainbow trout fry were stocked throughout the McLeod River drainage from the Jasper hatchery, 147,000 of them in creeks or lakes near Wampus Creek (i.e., upstream from the Gregg River and including that drainage) (federal Department of Fisheries annual reports published in 1933, 1934, 1935, 1936, 1937). The sources of most of these fish were commercial and government hatcheries in Montana, Idaho, and perhaps elsewhere in the US. Mary Gregg Lake, in the Mary Gregg Creek watershed immediately adjacent to Wampus Creek, was stocked with rainbow trout in 1952, 1953, 1956, and most years since 1974 to the present (C. Hunt, personal communication 14 April 1991). There is no record that Wampus Creek itself was stocked in those years, but there are no barriers to dispersal to Wampus Creek from the nearby stocked areas, and some rainbows are known to move into Wampus Creek from the McLeod River to spawn (Sterling 1980). Wampus Creek rainbows thus must have been exposed to potential introgression from non-native stocks.

The likelihood of introgression may be judged qualitatively by looking for the presence in the supposed introgressed population of diagnostic alleles that occur at a high frequency in the suspected donor populations. If the supposed hybrid population lacks any of these high-frequency alleles, the prospective recipient stock could not have been extensively introgressed by the suspected donor stocks. In such a case, the higher the frequency in the donor stocks, the less likely it is that the subject stock lacking the allele has been introgressed, or the less extensive has been any introgression.

The gene frequencies in the Idaho hatchery stock were described by J. Seeb and L. Wishard as “typical of most rainbow trout populations which originated from the McCloud River, California”, the origin of most hatchery stocks of rainbows, especially in the US (Needham and Behnke 1962, MacCrimmon 1971). They are generally similar to those in the Wampus Creek population, with one exception: the SOD(152) allele, absent from Wampus Creek trout, was present at a frequency of 33% in the Idaho hatchery population. The absence of this gene in the Wampus rainbows shows that the Idaho hatchery (presumptive McCloud River) stock is very unlikely to have contributed genetically to this population.

Another hatchery stock, Dworshak, carries two alleles that are absent from the Wampus Creek stock: LDH-4(76) at 76% and GL-1(100) at 47%. The absence in the Wampus Creek stock of two alleles that are frequent in the Dworshak hatchery stock suggests that there has been no introgression from that source. The same may be said for the wild Columbia, Salmon and Willamette river stocks, all of which carried one and sometimes two alleles at high frequency that are missing from the Wampus Creek fish.

There is thus no evidence that the Wampus Creek stock is an extensively introgressed one; at least it has not been heavily introgressed by the genes of at least one stock to which it almost certainly was exposed, nor has it been introgressed by the genes of common and widespread interior or coastal stocks. But introgression from other unknown stocks cannot be ruled out. As shown above, the Wampus Creek population closely resembles several populations in the Skeena drainage with respect to the frequencies of two common alleles deemed to identify major geographic stocks. Also, it has not yet been compared to native populations in the upper Fraser River drainage (above Prince George) and the upper Peace drainage, or to hatchery stocks derived from them.

One published study appears to contradict much of the genetic analysis in this account. Using mitochondrial DNA analysis, Wilson et al. (1985) were unable to detect any difference between Wampus Creek stock and stocks of rainbow from Pennask Lake, B.C., or steelhead from Coquihalla River, B.C., both in the Fraser drainage. They showed that these three populations did differ genetically from McCloud River rainbow stock, lower Fraser River steelhead, as well as several other British Columbia rainbow and steelhead stocks, and from Fraser River coastal cutthroat trout.

Parkinson's (1984) electrophoretic study tends to support Wilson et al.'s (1985) mtDNA findings to some extent. Coquihalla steelhead have relatively high frequencies of the most common LDH and SOD alleles, (0.784 and 0.844, respectively), and would plot close to Skeena and Wampus rainbows in Figure 12. Coquihalla steelhead were one of only two coastal populations (Parkinson's R1) that were similar to, but distinguishable from, the Skeena populations in a cluster analysis of the frequencies of several alleles (Parkinson 1984:1417).

Coquihalla River steelhead have been exposed to potential introgression by longterm extensive stocking throughout the Fraser system. The rainbow in Pennask Lake are the Kamloops variety, and are not native to the lake. I have been unable to determine the source of the Pennask stock. According to stocking records in federal Department of Fisheries Annual Reports, Kamloops trout from Paul Lake (where they were introduced from Granite Creek, Shuswap Lake hatchery) were present in the Jasper hatchery in the 1930s when the McLeod River basin was stocked. While no Kamloops introductions into that basin are recorded, hatchery stocks were often mixed purposely or inadvertently. Kamloops fry are not likely to be visibly distinguishable from other rainbow trout fry. It is entirely possible that Kamloops trout were stocked into the McLeod system.

A comparison of other studies employing protein electrophoresis does show differences among Coquihalla, Pennask and Wampus stocks not detected by Wilson et al. (1985). Electrophoresis data published by Huzyk and Tsuyuki (1974:107) show different allelic frequencies for LDH-4 between Coquihalla steelhead and Pennask Lake rainbows. Although sample sizes were small, their LDH-B'4 allele was obviously more frequent in Coquihalla steelhead than in Pennask rainbows, where the alternate B" form predominated. Assuming that their more common B' allele and somewhat less common B" allele of LDH-4 are the LDH-4(100) and LDH-4(76) of more recent authors[1], the Wampus Creek rainbows are different genetically from either of these BC populations. The LDH-4(76) allele is missing entirely from the Wampus Creek population, being replaced by the seldom-found LDH-4(120) allele, which in turn apparently does not occur in the Pennask and Coquihalla populations. If the Pennask population is typical of Kamloops rainbows, it appears that the Wampus stock has not been extensively introgressed by Kamloops trout to which they may have been exposed.

The mtDNA analytical technique used by Wilson et al. (1985) has the least power to resolve differences between stocks of four mtDNA techniques available (Gyllensten and Wilson 1987:303). Other enzymatic cutters and other ways of detecting DNA fragments, had they been used, might have shown differences among the populations (A. Beckenbach, personal communication 20 September 1990). Wilson et al. (1985) were able to distinguish two sympatric intraspecies stocks with their technique, but the method was inadequate to detect known genetic differences among Coquihalla, Pennask and Wampus populations. A genetic study of the Wampus Creek stock based on more recent data is now being prepared for publication by C. Hunt and L. M. Carl, and should help to resolve some of the issues discussed here.

Although the above considerations suggest that Athabasca rainbow trout may have resisted introgression by introduced strains, this remains to be confirmed. Other populations may not have fared as well as that in Wampus Creek. In particular, depleted stocks are likely to be far more susceptible to introgression than are healthy stocks. For this reason and the fact that we are presently totally ignorant of the present location and status of native populations in the park, the conservation status of Athabasca rainbow trout in Jasper National Park must be considered provisionally as **endangered**, possibly **extirpated** for management purposes.

**Required Action:**

1. A comprehensive taxonomic and genetic survey of rainbow trout in Jasper National Park and its connecting waters is needed to identify native, non-native and hybrid populations, and to establish the taxonomic identity of any native populations found.

2. A detailed recovery, conservation and management plan for native stocks of rainbow trout should be developed based on the results of the taxonomic and genetic survey. The plan probably will require that detailed life history and population surveys be conducted for major stocks, but these will depend on the outcome of the taxonomic and genetic survey.

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1 measurements of liver LDH bands illustrated by Northcote et al. (1970) and Williscroft and Tsuyuki (1970) support this interpretation

## *Bull trout*

*Salvelinus confluentus* (Suckley)

## SALMONIDAE

Salmoninae

Salmon, Trout and Charr

**VULNERABLE**

**Summary:** The bull trout is probably Jasper's most widespread native fish and for that reason is perhaps its most characteristic. It is arguably its most spectacular in terms of the large adult size it achieves in pristine populations, and in the brilliant spawning colours typically exhibited by populations in mountain lakes. It is one of the species most capable of surviving the Wisconsinan in local refugia, so is one of the most likely to have developed distinctive locally-adapted stocks.

Bull trout also may be the most sensitive fish species in the park. Almost everything about its biology and life history leaves it vulnerable to extirpation from human activity (especially overfishing), including its large adult size, ease of capture, restrictive spawning and rearing habitat requirements, strong homing tendency to the natal stream, apparent preference for cold water, slow growth and late sexual maturity. The species has been designated as a "Species of Special Concern" throughout its range, including Alberta (where most accessible stocks have been decimated) and British Columbia.

In Jasper National Park there is reason to believe that abundances of some stocks may be well below pristine levels. Some Jasper populations are apparently in marginal habitats (Dolly and Miette lakes), where they show evidence of frequent yearclass failures. Marginal populations such as these are believed to be a major source of genetic diversity, have great adaptive significance for the species as a whole, and are especially important to preserve. At least one population (Osprey Lake) may be below its minimum viable population size and risks imminent extirpation. Potentially serious threats to Jasper stocks include unrecognized overfishing, hybridization with introduced brook trout, and contamination with pulpmill waste products from outside the park.

The problem of pulpmill contamination, because of its immediate implications for human health, requires that a contaminant survey be conducted without delay to determine the extent and degree of contamination of this and other species in the park. A detailed survey to identify stocks, examine taxonomic and hybrid status, delineate life histories and movements, describe and map critical habitat, and document present population structure and abundance also should be initiated as soon as possible. A comprehensive management and recovery plan for bull trout should be developed, based on the results of these surveys.

**Nomenclature:** This species was not distinguished from Dolly Varden, *Salvelinus malma*, until quite recently (Cavender 1978, 1980). Cavender (1978:143) examined 10 specimens from Jacques Lake in his taxonomic revision, identifying them as bull trout. All records of Dolly Varden or *Salvelinus malma* in Jasper National Park are undoubtedly bull trout (Cavender 1978:141,143). Bajkov (1927), and Neave and Bajkov (1929) referred to this species as *Salvelinus alpinus malma*, a subspecies of Arctic charr. Genetic studies have confirmed that bull trout are distinct from all other North American charrs, but are most similar to Arctic charr (Leary 1985), in particular

*S. a. stagnalis* of the eastern Arctic (Grewe et al. 1990).

Members of the genus *Salvelinus* are more properly called charr, not trout, and the common name "bull charr" is sometimes used in recent literature.

**Description:** Bajkov (1927:8) described non-spawning bull trout from the Jacques Lake-Rocky River population, providing detailed morphometric and meristic data for 19 Jacques Lake specimens (see cover drawings) and one Athabasca River specimen.

*"The color of this fish is quite variable according to the conditions under which it lives. Color in life: back — dark-olivaceous, sides brownish gray with golden shade. On the sides of the body are many small, red, sometimes bright orange, round spots, not so large as the pupil, in number about 40-60 on each side. No dark spots on head or body. On the back the spots are not so large and bright as on the sides of the body and are sometimes grayish. Belly white. Dorsal and caudal fins dark dove colored. Pectoral, ventral and anal fins are not so dark colored and have a bright white anterior border… "*

Bull trout from other Jasper Park populations have not been described. Bajkov (1927:8) described the colouration of Jacques Lake spawners.

*"During the breeding season all the colors are very bright and the beautiful red spots on the sides of the body are very marked. At this period only the red spots become a little larger than the pupil. Very small pale spots are present on the caudal, dorsal and adipose fins. (If held against the light these spots show up very clearly). On the caudal and dorsal fins is a narrow sub-terminal dark stripe. Pectoral and ventral fins are very dark, almost black, with bright white anterior borders. Anal brown, with posterior portion orange, border white. The belly is a brilliant orange or red."*

Carl et al. (1989:239) described the brilliant colouration of spawners in another Alberta mountain lake, Pinto, as looking more like an Arctic charr than a bull trout (Carl et al. 1989:239). Marnell (1985:34) described bull trout with "distinctive pumpkin coloured fins which grade to brilliant crimson during the spawning season" from two high lakes in Glacier National Park, Montana. These observations probably explain Whitcher's (1887:88) remark that "there is reason to think" Arctic charr inhabited "some mountain tarns in the Rockies."

The following is a more general description of bull trout based on that of Paetz and Nelson (1970:83) and my own observations unless otherwise noted.

Except at spawning time, bull trout in Alberta streams usually are rather drab fish, often grey-green, grey-blue or olive brown with a silvery sheen on the sides, depending on the stock. Small light-coloured spots, mostly yellowish with a smaller number of orange, pink or red, are widely distributed over the body. The paired fins and the anal fin have light-coloured leading edges without a following black line, the dorsal fin is unspotted (Alberta Fish and Wildlife 1990:8), and the caudal fin is somewhat forked. The belly and sides are sometimes orange to red in spawning males.

Bull trout may distinguished from Dolly Varden and Arctic charr by their distinctive heads, which are very broad and flat on top, low and sharply conical when viewed from the side, with the eye near the dorsal margin of the head and the maxilla obviously decurved (Cavender 1978:148, 1980:299 ff.). Bull trout lack the wormlike light-coloured dorsal markings, the distinct black line behind the white leading edges of the paired and anal fins, and the heavy black dorsal fin markings of brook trout. Their orange, pink or red body spots in live or fresh unpreserved specimens, and the less dense pattern of smaller body spots, distinguish them from lake trout. They lack the black body spots of the western true trouts (*Oncorhynchus*) and brown trout (*Salmo trutta*).

Bull trout may randomly mate and hybridize with brook trout where the latter has been introduced into waters occupied by the former (Leary et al. 1983). The hybrids are not meristically intermediate between the parental species, but tend to resemble one or the other of the parents with the higher count for a character, or have mean counts higher than those of either parent. Hybrids can be detected unambiguously by electrophoresis, because bull trout and brook trout have different alleles at several diagnostic loci. Hybrids are invariably males, and probably are sterile.

Cavender (1978:165-6) described and illustrated two specimens he identified as hybrids of bull trout and brook trout from a creek in the Klamath drainage of Oregon, and compared them to pure-strain bull trout from the same creek. The hybrids had much darker pigmentation over the head, body and fins than typical bull trout, the dorsal fins were mottled and the lower fins were “tricolored.” The maxillary bones were long and straight like those of the brook trout, the vertebral counts were intermediate between those of the parental species, but the branchiostegal ray count was high, resembling the bull trout. Behnke (1980:467) also reported hybrids of bull trout and brook trout in the Klamath drainage.

Bull trout-brook trout hybrids are suspected to occur in headwaters of the North Saskatchewan drainage (Paetz and Nelson 1970:84, 88; Tebby 1974:31-2). Tebby (1974:31-2) described three mature specimens of both sexes that he suspected of being hybrids. The fish resembled bull trout in general body shape but were more intensely coloured than that species, had faint bars on the dorsal fin, and vermiculations and spots on the dorsal surface. All three had rudimentary or abnormal-looking gonads during the spawning period.

**Distribution:** Bull trout are known only from western North America, from the Yukon to northern California, mostly but not exclusively in interior drainages (Cavender 1978:141, Lee et al. 1980:113, Haas and McPhail 1991:2202-2204). In Canada, bull trout are found from the southern Yukon, southeastern Northwest Territories and northeastern British Columbia to the US border on both sides of the Rocky Mountains. In Alberta bull trout occupy the headwaters of the Peace, Athabasca, North Saskatchewan, Red Deer, Bow and Oldman drainages (Paetz and Nelson 1970:84). In the lower Athabasca drainage individual bull trout have been found in several locations as far downstream as the Muskeg River (Bond and Machniak 1979), which enters at Fort MacKay. There are records of the species from far out into the prairie reaches of the North Saskatchewan (Edmonton, Paetz and Nelson 1970:84), Red Deer (Morrin, Cavender 1978:143) and Bow rivers (apparently near Bassano, Cavender 1978:141).

**Refugia/Postglacial Dispersal:** Until recently the only certain refugium now occupied by charr positively identified as bull trout was Cascadia, including the small isolated Chehalis Refugium (Cavender 1978:141, Lee et al. 1980:113). On this basis, Paetz and Nelson (1970:5) and Nelson (1977:131) suggested that bull trout may have entered Alberta by headwater transfer over mountain passes such as the Kickinghorse, between the Kickinghorse River (Columbia drainage) and Bow River watersheds. Alternatively, Nelson (1977:131) proposed a route from the Missouri headwaters via a Milk River-South Saskatchewan interconnection. Crossman and McAllister (1986:83) acknowledged Nelson's (1977) suggestion of a northward dispersal from the Missouri, but apparently did not accept it. Speaking of Cascadia, they (ibid., p. 86) stated that bull trout in the Hudson Bay drainage “would appear to have come from this refugium only”, but observed that “a refugium in southwest Alberta could easily have been involved also” (ibid., p. 87; also their Table 3.2). Lindsey and McPhail (1986:669) treated bull trout and Dolly Varden as the same species, *Salvelinus malma.* To explain the distribution along the Rocky Mountain east slopes, they suggested that *S. malma* may have crossed from the Pacific drainage via Glacial Lake Miette, which they assumed once straddled the Continental Divide at the Yellowhead Pass. Current geological interpretations reject the notion of Glacial Lake Miette; however the Yellowhead Pass was still a possible route for fish movement between the Fraser and Athabasca drainages, as discussed elsewhere in this report (Section I).

A recent comprehensive study of bull trout taxonomy and distribution reported that specimens of this species from the upper Missouri system were not found (Haas and McPhail 1991:2204); hence Nelson's (1977:131) proposed dispersal of bull trout northward from that drainage is unlikely. Dispersal of bull trout over mountain passes from the Columbia to the Saskatchewan headwaters is possible, but hardly seems able to account for the ubiquitous existence of this species along the entire East Slopes of Alberta unless there were many such crossing points. The existence of at least one population within the northern portion of the Ice-free Corridor (Haas and McPhail 1991:2203,2210 — their collection number 308; cf. Prest 1984:Map 1584A) suggests that bull trout could have dispersed from a refugium in the South Nahanni area as recently proposed for lake whitefish (Foote et al. 1992). A Nahanni source for Alberta bull trout seems unlikely simply because the species is apparently far more widespread and abundant in Alberta East Slopes streams than in the north (Haas and McPhail

1991:2203).

Of the possible refugia for Alberta bull trout, the Ice-free Corridor of western Alberta is the closest and most readily accessible. The greatest concentration of populations of the species appears to be in western Alberta as well. Writing in The Atlas of North American Freshwater Fishes (Lee et al. 1980:113), T. M. Cavender characterized bull trout as inhabiting "large, cold rivers and lakes draining high mountainous areas, especially where snowfields and glaciers [are] present." Bull trout are native to many glacial waters in Alberta, including many close to present-day glaciers (Paetz and Nelson 1970:85, Ward 1974, Map 4 of this study). Although the species has been found in moderately warm habitats (there are several records from far out in the plains reaches of large rivers), young bull trout in particular are associated with cold water (Allen 1980; Pratt 1984, 1985; Fraley and Shepard 1989:138). Bull trout probably were capable of surviving under the periglacial conditions of the late Wisconsinan Ice-free Corridor. Jasper stocks are more likely to have been derived from populations that survived at least the latter part of the Wisconsinan in the Ice-free Corridor of western Alberta and its associated waters than from those in refugia in Cascadia or the Nahanni.

**Jasper Stocks:** In Jasper National Park bull trout are reported to inhabit many lakes, including Brazeau, Kerkeslin, Long, Southesk, Jacques, Maligne Range Pond (382), Beauvert, Miette, Jasper (Ward 1974:Appendix D), Moab (Ward 1974:distribution map no. 7), Osprey, Mile 54 J.B., 230 (Ward 1974: distribution map no. 8), Dolly lakes 685 and 686, and 496 (Ward 1974: distribution map no. 9). There is an additional report in a voluntary creel census summary of catches from Hardisty Lake (National Parks Service 1948), and this lake is mentioned in an angling guide (National Parks Service 1949?) as holding bull trout. Hardisty Lake is apparently the former name of present-day Kerkeslin Lake (D. Donald, personal communication). Despite the indication by Ward (1974:Appendix D) of bull trout in Brazeau Lake, there are no actual catch records of this or any other native fish species there (Rawson 1940a, Yamamoto 1979:72-74, JNP file data).

Bull trout been reported from the following rivers and streams: Athabasca, Miette, Hardisty, Portal, Rocky (Bajkov 1927:6-7), Rocky River especially downstream from confluence with Jacques Lake outlet (JNP file notes), creeks connected to Jacques Lake (Neave and Bajkov 1929:15), Fiddle River, Sulphur Creek (Donald et al. 1977:15), Athabasca above Athabasca Falls (at Long Lake — Donald and De Henau 1981:216), native "to the upper Snake Indian River" (Donald et al. 1985:105), lower 3 km of Astoria (i.e., below falls), lower Snake Indian, Snaring, Sunwapta (whether above or below Sunwapta Falls not stated), Whirlpool (JNP file notes). There are additional records of bull trout from voluntary creel census in the following rivers and streams (only the first recorded occurrence is cited): Maligne below the canyon, Meadow, Tekarra, Deer (National Parks Service 1948), Caledonia, Cottonwood, Ranger, "Hy. Beaver Dams" (National Parks Service 1950?), Chaba, Sunwapta (above or below falls not stated — Cuerrier and Ward 1952:18), Blue (Woody? 1963). The species undoubtedly uses accessible tributaries to these streams also. Bull trout have been taken from Rock Lake just outside the park (Bradford 1990:206), so undoubtedly enter the park in the Rock Creek drainage. I have found no documentary evidence thus far of bull trout in the Smoky River drainage within the park (Donald et al. 1985; JNP files, including lakes files), but it is known from tributaries further downstream (Paetz and Nelson 1970:86), so may be excluded by falls from the park.

JNP fish stocking records show that 28 adult bull trout were introduced into Maligne Range Pond (382) 1 May 1959. Donald and De Henau (1981:179) reported that the Kerkeslin Lake population was the result of an unrecorded introduction made circa 1930. These are the only recorded introductions of bull trout in the park. It appears that all of the remaining bull trout populations referred to above are native stocks.

Donald and De Henau (1981:139, 216) did not collect any bull trout from Long Lake when they sampled it 25 June 1979, but stated that it may be colonized by bull trout from the Athabasca River during some years. In contrast to Ward (1974: Appendix D), they found only non-native brook trout and no bull trout in Mile 54 Pond (their Hostel Pond; officially 32) when they sampled it 12 June 1979 (ibid. p. 111). Chalet Pond (no number — near the Columbia Icefields Chalet), a very small and shallow widening of a Sunwapta River tributary, held only non-native brook trout when sampled 12 June 1979 (ibid. pp. 34, 211). Both of these sites are in the Sunwapta drainage above Sunwapta Falls. D. B. Donald (personal communication) believes that there are no native fishes above Sunwapta Falls in the Sunwapta drainage, and his 1979 collection data, discussed above, support this view. I have been unable to find any unequivocal record of bull trout captured above Sunwapta Falls in the JNP fisheries files.

The possible distribution of native stocks of bull trout in Jasper National Park is illustrated in Map 4 (map pocket).

**Habitat:** There have been as yet no formal surveys of critical habitat for any species of fish in Jasper Park streams. Only a few incidental observations are available.

Bajkov (1927:9) stated that young fish of the Jacques Lake population used the creeks associated with the lake, occupying shallow areas less than 1 m deep, over gravelly or sandy bottom. The main inlet stream to Jacques Lake, which enters at the south end, was said to have "a good volume of water flowing over gravelly bottom; holes from two to four feet [0.6 to 1.2 m] deep occur intermittently" when examined on 5 October 1950 (Cable 1950). The same investigator described the outlet stream as flowing over gravel bottom and mud, with holes up to 1.8 m (six feet) deep occurring along the course, piles of heavy debris blocking the channel in places. Cable (1950) found bull trout 20 to 25 cm long using the holes and the deeper water among the debris. Jacques Lake itself is a small water body of 27 ha with a maximum depth of 4.5 m (Rawson 1940a). Bajkov (1927:7) described it as having a "marsh" at the south end.

The physical limnology of five other lakes in Jasper Park that now or once harboured native populations of bull trout was described by Rawson (1940a), Anderson and Donald (1978b), Donald and De Henau (1981) and Donald et al. (1985). They range from as shallow as Miette Lake (mean depth 1.0 m) to as deep as Moab Lake (mean depth 8.6 m) and Lac Beauvert (maximum depth 25 m); they are silty (Osprey Lake, Secchi depth 1 m) or clear (Lac Beauvert, Secchi depth 19 m); cold in summer (Osprey Lake, almost uniformly 6 °C) or moderately warm (Long Lake, mean temperature about 15 °C); with a substantial surface outlet (most) or with very little surface outflow (Osprey, Long?). Just south of Jasper National Park bull trout inhabit Pinto Lake, a 30-m deep water body with a mean depth of 14.2 m and low midsummer oxygen (approximately 3 mg/l) below the thermocline (Carl et al. 1989:240-241). Data available on other Alberta bull trout lakes [e.g., Bow and Waterton lakes, Rawson (1942)] show that much larger and much deeper mountain lakes, and even heavily-silted glacier-fed lakes, also are used by native bull trout in this province.

In the Clearwater River stock (North Saskatchewan drainage, Alberta), Allan (1980) reported that adult bull trout overwinter in deep pools in the lower mainstem and spawn in small springfed tributaries in the headwaters. Fry spend approximately 60 days in the gravel, then rear in slow currents in the same headwaters. Allan (1980:20) observed yearlings “behaving almost like sculpins”, spending most of their time hiding under large rocks in areas where the current was low. Juvenile bull trout in the Kananaskis system also hide under rocks (Nelson 1965:736).

Adult bull trout in adfluvial stocks of the Flathead system overwinter in Flathead Lake, spawning in headwater tributaries at low-gradient sites characterized by gravel substrates with low compaction, groundwater inflow and nearby cover (Fraley and Shepard 1989:137). Leggett (1980:732), in a study of what is probably an adfluvial population of bull trout[1], reported that the fish selected (and apparently required) coarse gravel for spawning. These narrow requirements apparently restrict spawning to only a small proportion of the available stream habitat in the Flathead system (Fraley and Shepard 1989). The gravel at the spawning sites serves as the habitat for eggs and alevins. Young-of-the-year occupy side channels and tributary stream margins. Densities of juvenile bull trout are greatest in pools, and lower but generally similar in runs, riffles and pocket water (Fraley and Shepard 1989:138). By definition for these adfluvial stocks, final rearing to sexual maturity was completed in Flathead Lake. A few stocks in this system are stream resident, however, completing their life history entirely within single tributaries. In resident stocks, all critical habitat is found within these small tributaries.

Pratt (1984, 1985) found juvenile bull trout in tributaries of the Flathead system to be strongly bottom-oriented, using instream cover along the stream bottom, especially the interstices of unconsolidated or unembedded cobbles or submerged wood. They seek

1 Confirmed as bull trout, not Dolly Varden, by Haas and McPhail (1991:2203,2209, their sample site 202).

slow water associated with submerged cover. Highest population densities of bull trout juveniles were found in stream habitat with the coarsest, least embedded substrate materials (Shepard et al. 1984a:151). Pratt (1984:30) also noted that juvenile bull trout were present in an area of stream influenced by a cold spring that was not used by cutthroat trout, whereas the two occurred together outside this area in the same stream (Pratt 1984:30). Citing several studies, she drew attention to the fact that bull trout seem to be distributed mostly in areas with temperatures less than 12 °C, often associated with perennial springs (Pratt 1984:77, 1985:17). Fraley and Shepard (1989:138) mentioned that juvenile bull trout in the Flathead system rarely used streams in which summer maximum temperatures exceeded 15 °C.

Incubating bull trout eggs, embryos, alevins and subgravel fry are highly sensitive to siltation. In one study, percent survival of embryos through emergence decreased by about 25 percentage points for every increase of 5 percentage points of fines less than 6.4 mm diameter as a proportion of total substrate material (Shepard et al. 1984a:151). Likewise, bull trout free-swimming fry and juveniles are considered to be especially sensitive to streambed changes because of their close association with the substrate and bottom cover noted above (Fraley and Shepard 1989:141).

**Biology and Life History:** Bajkov (1927:8-9) commented on some aspects of the life history of bull trout using Jacques Lake, but did not describe the evidence upon which he based his comments. Bull trout of the Jacques Lake population were said to move into the inlet creek or down the outlet to the Rocky River beginning in late August and September, in preparation for spawning in late September to the beginning of November. The young fish, he believed, usually stay in the rivers and creeks in shallow areas less than 1 m deep, over gravelly or sandy bottom. Neave and Bajkov (1929:15) believed that the two-year-old bull trout of the above waters reared in the creeks and fed upon benthic invertebrates, whereas the older fish used the lake feeding mostly upon amphipods and *Siphlonurus* mayflies until they moved into the creek in fall to spawn. They found little evidence that bull trout in this population ate significant numbers of fish. The young bull trout were said to grow rapidly, reaching 6-7 cm in length by the end of August of their first summer, and maturing in their third or fourth year (Bajkov 1927:9), ages corresponding to 28-40 cm in length (Neave and Bajkov 1929:15).

Cable (1950) examined Sirdar Creek, the main inlet and the near-shore area of Jacques Lake for spawners but found no adult bull trout, redds or eggs on 5-7 October 1950. He received an angler report that the fish spawn in the first week of September. He was unable to find any spawning bull trout or their redds in the inlet, outlet or near shore in late August to early September 1951 (Cable 1951). He found one 33-cm ripe female; many others of this size and larger were immature. Angler reports had indicated there were near-ripe females in the lake in early August. Noting that some fish up to 44 cm in length were further from spawning condition than other much shorter fish, he concluded that Jacques Lake bull trout may take two years to develop their eggs. He suggested that the population may spawn in the first two weeks of August, that they spawn outside of the lake in an undetermined location, and that they leave the lake well in advance of spawning. Cable (1953) found no bull trout in spawning condition in Jacques Lake in mid-July 1952. On 25 August of the same year he collected only one fish near spawning condition, out of 26 in total captured. He found no spawning fish in the inlet or outlet streams, or in the near-shore area of the lake. In early October 1952 a 25-cm female from Jacques Lake held in the hatchery was observed to be gravid, and its eggs were stripped and fertilized. Cable had difficulty obtaining enough milt from males to fertilize the eggs, and only 8.7% hatched.

Cable (1950) found “50 or 60” bull trout 20 to 25 cm long in some of the holes and deeper water of the outlet stream, and described these as immature. The next year he trapped and released alive 60 bull trout 23 to 28 cm long in the outlet stream (Cable 1951), again calling them immature. He reported seeing “only small fish” in the outlet stream in late August 1952 (Cable 1953). Evidently juveniles rear in the outlet of Jacques Lake; however the size of the female stripped in the hatchery suggests also that at least some of these fish were spawning age. Cable (1950, 1951, 1953) reported only two adults (including one female near spawning condition) and a single small (5 cm long) bull trout in the inlet stream. If Bajkov’s (1927:9) estimate for first-summer growth is true, this suggests that some spawning does occur in the inlet to Jacques Lake, though apparently very little.

More recent data tend to confirm some of Cable's observations. Baraniuk (1989) reported finding no spawning bull trout or redds in Jacques Lake, the inlet or the outlet streams when he examined them in early September 1988.

The simplest explanation of Cable’s observations taken together is that the Jacques Lake bull trout population is being maintained by a very small number of spawners. This could be a natural condition, but is also characteristic of overfished stocks. It is quite possible, however, that some of the fish Cable believed to be immature in fact were mature and spawned in the outlet. Finally, Jacques Lake may be primarily a rearing area separate from the habitat used by larger adults, a characteristic feature of free-ranging populations of bull trout (McCart 1985; see also life history descriptions below).

Observations on the biology and life history of other Jasper Park populations of bull trout are limited. Bajkov (1927:6, 9) believed that bull trout from the Athabasca River entered the Rocky River, Hardisty Creek, Portal Creek and other unnamed tributaries to spawn. Donald et al. (1977:22) found bull trout from age 1 to 9 occupying the Fiddle River. These fish were judged to have a growth rate close to that typical of streams at moderate to high altitudes.

In an appendix to a survey of pathogens in wild populations of fish, Yamamoto (1979:69) presented unanalyzed length, weight, age and sex data for 14 bull trout from Southesk Lake. Both scales and otoliths were collected, but only otoliths were used for age determinations (D. Donald, personal communication). The bull trout were found to be disease-free, and ranged in length from 16 cm to 72 cm, in weight from 50 g to 4404 g, and in age from 3 to 14 years. Two were females, 11 were males, and only one (16 cm, 50 g, age 3) was judged immature and unidentifiable as to sex. Others as young as age 4 and age 5 were identifiable as males, but it is not known whether these were mature. Baraniuk (1989) captured eleven female and five male bull trout from Southesk Lake in 1989, ranging in age from 4 to 12 years (determined from otoliths), and in weight from 80 to 1532 g.

Donald and De Henau (1981) and Donald et al. (1985) provide otolith age, length, weight and stomach contents data for four lake populations. A study of lake populations of bull trout in the Rocky Mountains, including several Jasper Park populations, is in preparation by D. B. Donald.

Bajkov (1927:4-5) actually described two forms of bull trout from the Athabasca River, "one of them a permanent freshwater fish, the other a migrant from the sea." He described the sea-going form as a larger, brighter, silvery fish reaching a weight of 12 pounds [5.4 kg], but it is not clear whether he was describing fish he had actually seen in the Athabasca, or was providing a more general account.

Bajkov's view that the Athabasca held an anadromous stock of bull trout is not credible considering the enormous distance to the Arctic Ocean (over 4000 km, including several major rapids), and the absence of any records of the species from the Mackenzie and Slave river mainstems (see Distribution, above). Two separate life history forms or distinctive stocks, however, one of which is migratory, is entirely plausible. Allan (1980) found the Clearwater River (North Saskatchewan, Alberta, drainage) population of bull trout to consist of juvenile and first-year adult stream residents, and older adult migratory fish. Two distinct life history forms of bull trout are well-documented to occur together in other river systems. For example, the North Fork Flathead River of Montana and British Columbia holds two forms of bull trout: stream-resident and adfluvial (Shepard et al. 1984b, Fraley and Shepard 1989:135). Stream-resident fish live their entire lives in the natal stream, while adfluvial fish (as described below) rear in the natal streams, then migrate downstream to Flathead Lake to feed and grow to adulthood. Adfluvial adults are much larger than stream-resident adults. Ross (1909:132-133) reported "a large species of trout" to occur in the Athabasca and McLeod rivers in 1907, perhaps Bajkov's "sea-run" bull trout.

Life histories of bull trout in several drainages outside Jasper National Park have been worked out, some in considerable detail. Immediately east of Jasper Park, bull trout spawners move into the streams of the Tri-Creek study area in early August and are found spent in the McLeod River in mid-September. Immatures move into the tributaries after wintering in the McLeod River. Juveniles are believed to move into the McLeod from the tributaries at age 3+ to 5+ (Sterling 1980).

Allan (1980) found adult bull trout in the Clearwater system (North Saskatchewan drainage, Alberta) to be highly migratory. They winter in the lower mainstem river, moving gradually upstream during the spring and summer and entering groundwater-fed tributaries in August. The bull trout spawn in September in these tributaries, moving downstream in late fall to overwinter. In this system bull trout home strongly to the natal streams, spawning annually over several years. The eggs incubate through the fall and early winter, hatching in mid-winter and emerge from the substrate in early spring. Fry move downstream to areas of low current speeds, remaining in their natal streams for up to six years. Males are mature at age 4 or 5, females at age 5 or 6. Newly matured adults spawn together with older migratory adults, then move downstream with them to overwinter.

In Pinto Lake, a small (124.5 ha) subalpine lake 14 km south of Jasper National Park, adult bull trout move into the outlet stream shortly before spawning there, which occurs in late September to early October (Carl et al. 1989). The eggs incubate over winter in the outlet, emerging in the spring. Most young spend at least one summer in the stream; many juveniles use it at least in summer and autumn for two to four years thereafter, judging from catch, length, age and maturity data (Carl et al. 1989:241-243). Data are sparse, but it appears that sexual maturity is not reached until age 7 or 8 in this population.

Fraley and Shepard (1989) have summarized the results of numerous investigations on the adfluvial stocks of bull trout the Flathead drainage, Montana-British Columbia. In this population, most fish reach sexual maturity at age 6 in Flathead Lake. Spawners begin migrating slowly upstream from the lake in April, travelling as much as 250 km to headwater tributaries. Many in this population apparently do not spawn annually, only 38 to 69 percent leaving the lake each spring and summer for the purpose. The spawners pair up near the mouths of the tributaries, moving into the spawning streams by pairs at night from July through September. There they hold for up to a month in deep holes or near log or debris cover until they reach spawning condition. The fish spawn in the tributaries in September and early October when temperatures drop below 9-10 °C. The spent adults move out of the tributaries after spawning, migrating downstream to overwinter and (in many cases) spend another full year or perhaps more in Flathead Lake. Eggs incubate within the spawning gravels for several months, hatching in January. The alevins remain in the gravel resorbing the yolk sac, and emerge about mid-April. Juvenile bull trout move upstream to rear in many stream reaches not used by the adults. They consume mostly invertebrate prey, including small trout and sculpins in the diet after reaching a length of 110 mm. Most juveniles remain in the tributaries for one to three years, but a few remain for four years before emigrating to the river system. Emigrating juveniles leave the tributaries from June through August, most moving downstream rapidly to find their way to Flathead Lake, where they complete their rearing to adulthood.

Much additional information on the biology and life history of Flathead Basin bull trout stocks is provided by Shepard et al. (1984b), Fraley and Shepard (1989), and references therein. Carl (1985) provided a good summary of bull trout biology and life history in Alberta in support of his proposed management plan for the species. These documents should be consulted for further details on all aspects of bull trout biology.

**Ecological Significance:** The ecological role of this species in Jasper National Park is not documented.

Bull trout are voracious predators of other fish where this source of food is available; otherwise they are predaceous on invertebrates. In either case they are likely to influence strongly the structure of fish, benthic and planktonic communities. Particularly as young fish they might be a significant source of food for other fish-eating vertebrate predators, including burbot, snakes, mink, otter, and numerous species of piscivorous birds. As a headwater area, Jasper Park conceivably holds spawning and rearing streams that are important for maintaining adult stocks of this highly migratory species outside the park.

Recently released data (Alberta Government press release 153, 27 July 1990) show that bull trout in the Athabasca River taken below the Weldwood pulpmill at Hinton carry a dangerous burden of dioxin (2,3,7,8 T4CDD) and furan (2,3,7,8 T4CDF). Concentrations in whole fish were high enough to cause the provincial government to warn fishermen to discard “organ parts”, and consume only muscle from bull trout caught in the Athabasca River upstream from Whitecourt. As highly migratory fish, bull trout may be carrying these poorly-understood toxins into park ecosystems.

Even if they do not themselves migrate out of the park and become contaminated, Jasper Park bull trout may still acquire dioxins and furans through the food web. Bull trout probably consume other migratory species such as mountain whitefish or longnose suckers. Both of these species in the upper Athabasca River are known to be contaminated with at least one type each of dioxin and furan (Alberta Government press release 153, 27 July 1990). As a predator high on the aquatic food chain, bull trout may concentrate these chemicals to levels much higher than those found in the prey species.

**Fishing:** Bull trout must have been one of the trout fished in Jasper National Park by the fur traders supplying Jasper House in the 1800s, and very likely by the natives before that. The Jacques Lake bull trout may have been the fish caught by Macaulay in 1863 (Cheadle 1931:166, see Section II). Jacques Lake provided a popular sport fishery for the species since the earliest days of the park (Prince et al. 1912:11; Rogers 1915:96, 97; Sparks 1916:65; Driscoll 1918:66).

Tables 6 to 9 summarize the limited information available on the angler catch of bull trout from lakes and streams in Jasper National Park. These data were reported voluntarily by anglers, and represent only a portion of the total catch. The proportion of the total catch that was reported is not known. Even with major promotion efforts voluntary reporting typically is light, so the following data probably are very minimal estimates of the annual total catch of bull trout in the park.

**Table 6.** Numbers of bull trout caught by angling in streams of Jasper National Park 1947-53, according to a self-reporting creel census (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954).

| **Stream** | **1947** | **1950** | **1951** | **1952** | **1953** | **Totals** |
|---|---|---|---|---|---|---|
| Astoria | | 2 | 9 | | | 11 |
| Athabasca | 60 | 66 | 113 | 134 | 92 | 465 |
| Beaver Dams | | 3 | | | | 3 |
| Caledonia | | 10 | | | | 10 |
| Cottonwood | | 1 | 3 | | | 4 |
| Chaba | | | 7 | | | 7 |
| Deer | 2 | 10 | | | | 12 |
| Fiddle | | | 12 | 4 | 10 | 26 |
| Hardisty | 98 | 133 | 45 | 23 | 79 | 378 |
| Maligne | 37 | 44 | 68 | 46 | 36 | 231 |
| Miette | 14 | 37 | 60 | 4 | 10 | 125 |
| Meadow | 1 | | | | | 1 |
| Portal | 44 | | | | | 44 |
| Ranger | | 7 | | 8 | | 15 |
| Rocky | 4 | 2 | 1 | 3 | 16 | 26 |
| Snake Indian | | 9 | | 3 | 1 | 13 |
| Snaring | 18 | 11 | 12 | 9 | 3 | 53 |
| Sunwapta | | | 2 | | | 2 |
| Tekarra | 5 | 22 | 62 | 12 | | 101 |
| Whirlpool | 8 | | 8 | 38 | | 54 |
| **Totals** | **291** | **357** | **402** | **284** | **247** | **1581** |

**Table 7.** Bull trout caught per angler-hour in streams of Jasper National Park 1947-53, according to a self-reporting creel census (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954). Means are weighted for numbers of fish caught.

| **Stream** | **1947** | **1950** | **1951** | **1952** | **1953** | **Means** |
|---|---|---|---|---|---|---|
| Astoria | | 0.25 | 0.42 | | | 0.39 |
| Athabasca | 0.94 | 0.26 | 0.29 | 0.33 | 0.17 | 0.36 |
| Beaver Dams | | 0.30 | | | | 0.30 |
| Caledonia | | 0.71 | | | | 0.71 |
| Cottonwood | | 0.01 | 0.01 | | | 0.01 |
| Chaba | | | 0.32 | | | 0.32 |
| Deer | 8.00 | 10.00 | | | | 9.67 |
| Fiddle | | | 0.07 | 0.05 | 0.17 | 0.11 |
| Hardisty | 1.87 | 1.28 | 0.96 | 0.20 | 1.44 | 1.36 |
| Maligne | 0.73 | 0.19 | 0.17 | 0.18 | 0.15 | 0.26 |
| Miette | 0.82 | 0.22 | 0.31 | 0.07 | 0.11 | 0.32 |
| Meadow | 1.00 | | | | | 0.13 |
| Portal | 2.59 | | | | | 2.59 |
| Ranger | | 0.45 | | 0.43 | | 0.43 |
| Rocky | 0.40 | 0.09 | 0.03 | 0.06 | 0.32 | 0.27 |
| Snake Indian | | 1.07 | | 0.46 | 0.07 | 0.85 |
| Snaring | 1.47 | 0.07 | 0.03 | 0.03 | 0.05 | 0.53 |
| Sunwapta | | | 0.22 | | | 0.22 |
| Tekarra | 1.25 | 0.74 | 0.55 | 0.11 | | 0.57 |
| Whirlpool | 0.89 | | 0.22 | 1.06 | | 0.91 |
| **Means** | **1.55** | **0.95** | **0.37** | **0.37** | **0.58** | **0.75** |

**Table 8.** Bull trout catch data, Jacques Lake 1943-77. The 1977 data were obtained in angler interviews, the remainder are extracted from a self-administered creel census (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954; JNP Warden Service lakes files and creel census files). Some hours were back-calculated from fish per hour and catch figures.

| Year | Number Caught | Hours | Efforts | Fish/ effort | Fish/ hour | Length range cm | Median length |
|---|---|---|---|---|---|---|---|
| 1942 | 103 | 37.00 | 9 | 11.44 | 2.78 | 25-51+ | 38.00 |
| 1943 | 22 | 3.74 | 3 | 7.33 | 5.88 | 36-51 | 43.50 |
| 1944 | 42 | 16.80 | | | 2.50 | 30-53 | 41.50 |
| 1945 | 20 | 11.98 | | | 1.67 | 0.9-1.4* | |
| 1946 | 63 | 47.73 | 8 | 7.88 | 1.32 | 23-51 | 37.00 |
| 1947 | 76 | 50.25 | 16 | 4.75 | 1.51 | 25-76 | 50.50 |
| 1949 | 66 | 26.40 | 9 | 7.33 | 2.50 | 30-69 | 49.50 |
| 1950 | 275 | 137.50 | 24 | 11.46 | 2.00 | 30-66 | 48.00 |
| 1951 | 140 | 30.75 | 12 | 11.67 | 4.55 | 30-46 | 38.00 |
| 1952 | 128 | 128.00 | 32 | 4.00 | 1.00 | 23-53 | 38.00 |
| 1953 | 150 | 75.00 | 19 | 7.89 | 2.00 | 25-66 | 45.50 |
| **Means** | **98.64** | **51.38** | **14.67** | **6.73** | **1.92** | **28-58** | **42.95** |
| 1962 | 7 | 84.00 | 8 | 0.88 | 0.08 | 25-64 | 44.50 |
| 1977 | 15 | 18.00 | 2 | 7.50 | 0.83 | | |

**Table 9.** Bull trout catch data, various lakes in Jasper National Park 1941-62, as reported by anglers in a self-administered creel census (National Parks Service 1948, 1950?; Cuerrier and Ward 1952, 1953, 1954; data in lakes files and creel census files, JNP warden office).

| Lake | Year | Number Caught | No. Hours | No. Efforts | Fish/ Effort | Fish/ Hour | Length (cm) |
|---|---|---|---|---|---|---|---|
| Beauvert | 1951 | 3 | | 3 | 1.00 | | 20-38 |
| | 1952 | 4 | | 8 | 3.50 | 1.30 | 25-41 |
| Dolly | 1947 | 10 | 3 | 1 | 10.00 | 3.33 | |
| | 1949 | 10 | | 2 | 5.00 | 10.00 | |
| | 1951 | 10 | 3 | 3 | 3.30 | 3.30 | 30-56 |
| | 1954 | | 4 | 1 | 4.00 | 0.19 | 51-58 |
| | 1962 | 24 | | 8 | 3.00 | | 1.1-2.3* |
| Hardisty | 1941 | 14 | | | | 7.14 | 30 |
| | 1947 | 100 | 16 | 8 | 12.50 | 6.25 | mean 30 |
| | 1949 | 23 | | 3 | 7.70 | 1.25 | 25-38 |
| Long | 1953 | 5 | | 6 | 2.70 | 1.60 | 20-71 |

* - kg

For five years in the period 1947-53, an average of 316 bull trout (range 247-402) were reported captured from 20 park streams by fishermen. Anglers reported catching an average 99 bull trout annually (range 20-275) from Jacques Lake alone for 11 years in the period 1942-53. The only other lakes for which bull trout catches were reported were Beauvert, Dolly, Hardisty and Long lakes, from which fewer than 25 fish were reported caught in any one year. The lone exception to this statement was Hardisty Lake in 1947, when 100 bull trout were reported caught.

Even if we allow for a possible large difference in the rate of creel census returns from streams in comparison to lakes, it appears that a high proportion of the bull trout caught in Jasper Park came from a single rather remote lake. Only in 1947, in the years of record, did another lake (Hardisty, 100 bull trout) make a substantial contribution.

The annual mean catch rate for the period 1942-53 averaged 1.92 bull trout per angler-hour in Jacques Lake. The catch rate in Jacques Lake was quite high, remaining above 1.00 bull trout per angler-hour during the 11-year period of record. Catch rates in the other lakes likewise were high, ranging from 1.25 to 10.00 bull trout per angler-hour except for 1954 in Dolly Lake, when a single fisherman recorded a 0.19 bull trout per angler-hour rate.

In contrast, the annual mean catch rate in the 20 streams tended to be lower, averaging 0.75 bull trout per angler-hour during 1947-53 and exceeding 1.00 bull trout per angler-hour only rarely. On average, catch rates for bull trout in Jacques Lake were approached in streams only in Deer Creek, Portal Creek and Hardisty Creek. These are small (second order) streams in which fish would be especially vulnerable to angling.

The catch rate for bull trout in Jacques Lake appears to have declined in later years. In 1962 only 0.08 bull trout per angler-hour was reported, and two anglers in 1977 recorded 0.83 bull trout per angler-hour.

It is important to recognize that the bull trout catch rates reported for the period of record, although they are often quite high by today’s angling standards, are undoubtedly far below those experienced by the earliest visitors to Jasper National Park. Up to four men in a hunting party provisioning Jasper House in 1863 reportedly caught 42 large trout in two hours (5.25-21 trout per angler-hour) in a lake that may have been Jacques Lake (Cheadle 1931:166). In a stream tributary to the McLeod River along the trail from Fort Edmonton to Jasper, one man claimed he and his partner caught 100 trout (some as large as 4.6 kg and therefore probably bull trout in part) in the space of two hours in 1871 (Grant 1873:211-212), a catch rate of 25 trout per angler-hour. Even if one allows for a substantial amount of exaggeration, these catch rates are remarkably high. Both of these records are critically examined in Section II of this report.

**Conservation Status (general):** The bull trout in general is widespread in western

North America and apparently still occupies most of its former range. This, however, is misleading. It is listed internationally as a species of special concern in Alberta, British Columbia, Montana, Idaho, Washington, Oregon, Nevada and California (Johnson 1987, Williams et al. 1989:4). In California, the species is protected by legislation (Johnson 1987:5,27). A taxon is assigned “special concern” status if (Williams et al. 1989:3)

1. it may become threatened or endangered by relatively minor disturbances to its habitat; or

2. additional information is required to determine its status.

The bull trout is assigned “special concern” status under the first criterion, so would more appropriately be termed “vulnerable.” The species is listed because of “present or threatened destruction, modification, or curtailment of its habitat or range”, and because of “other natural or manmade factors affecting its continued existence (hybridization, introduction of exotic or transplanted species, predation, competition)” (Williams et al. 1989:3-4).

Accentuating the positive, Haas and McPhail (1991:2302) state that “local extinction does not yet appear to be a problem in Canada *except in developed regions*” (emphasis mine), cautioning that “their [bull trout] gradual disappearance in the south indicates that they are environmentally sensitive and that care should be taken in their management.” Alberta’s East Slope is one of these developed regions: Nelson and Paetz (1982) and Carl et al. (1989:239) pointed out that many Alberta populations have declined markedly. Bull trout have been extirpated from much of the Alberta range because of susceptibility to angling, angling pressure, slow growth and late maturity, according to Carl (1985). The Alberta Government recognized these declines and their causes, proposing to increase all naturally reproducing populations and to reintroduce the species into previously occupied habitat (Alberta Fish and Wildlife 1984:35), as well as introducing new restrictive angling regulations to protect remaining populations. One authority considers the species to be endangered or threatened in Alberta mostly due to overharvesting (Roberts 1987:129,131; 1991:196); another suggests that it may be rare and vulnerable in the province (Campbell 1988:84, 1991:154). A COSEWIC status report is in preparation (Campbell 1991:154).

The reasons for the bull trout’s “special concern” status are numerous: almost everything about the biology of the fish (as outlined under Biology and Life History, above) make its populations vulnerable to extirpation. Because bull trout mature late, they are relatively large and vulnerable to fishing mortality well before the age of first spawning. They seem to favour spawning sites with substantial groundwater discharge, and may require them for successful incubation of their eggs. Such sites often have a limited distribution in a drainage system. Incubating bull trout eggs, embryos, alevins and early fry are highly sensitive to silting and other bottom disturbances, in part because they remain in the gravel of the spawning site for an unusually long time.

Because bull trout home strongly to their natal streams, stocks that are destroyed will not soon be replaced. Bull trout juveniles rear in headwater areas, which are characteristically cold, unproductive and subject to severe variations in flow. The juveniles use large spaces among stones and debris on the streambed for cover, and these spaces quickly fill in when a stream becomes silted, as generally happens when roads and other developments are built within a drainage basin. Bull trout are notoriously easy to catch by angling. Adults reach very large sizes, attracting the attention and interest of anglers, especially when they are exposed in small tributaries during spawning. They congregate in deep pools, sometimes in large numbers. Deep pools tend to be relatively rare and located in more accessible downstream areas in each drainage.

For all of these reasons bull trout stocks often are severely reduced or extirpated wherever they are exposed to fishing pressure (Allan 1980, Carl 1985, Roberts 1987, Van Tighem 1988b). Only in locations with unusually productive adult habitat do they seem to be able to withstand exposure to significant amounts of angling (e.g., Flathead drainage, Montana, Shepard et al. 1984b). The single attribute that may ensure their survival in at least low numbers is their strong migratory tendency, which might work to keep some part of the population remote from danger at all times. This feature of the life history arguably exposes individual fish to more dangers, however.

**Conservation Status (Jasper):** The present status of bull trout in streams of Jasper National Park is not documented. What few relevant data there are (1947-53 self-administered angler interviews) show generally low catch rates (i.e., no more than 0.50 bull trout per angler-hour). Moderate to high mean rates (1.36 to 9.67 bull trout per angler-hour) are known only from small headwater streams in which bull trout may concentrate as rearing or spawning fish. What impact there has been of angling on these stocks is not known. The abundance of trout in the vicinity of Jasper National Park mentioned in historical documents was not in evidence in the bull trout catch statistics of 1947-53 for park streams.

One lake population, that in Lac Beauvert, was extirpated by poisoning in 1964 (Ward 1968a, JNP fish stocking records). Neither Bajkov (1927) nor Rawson (1940a:22) reported bull trout from the lake in their studies. Although Anderson and Donald (1978b:51) did not find bull trout in their sampling on 14 September 1976, Yamamoto (1978:33) captured six specimens on 6 October 1977. It may be that the native bull trout of this lake were transient fish, part of the Athabasca River population.

The former Long Lake population has been largely supplanted by brook trout, a non-native species, if indeed it ever permanently existed in the lake. Now it is probably sustained only by occasional invasions from the Athabasca River during high water (Donald and De Henau 1981:216).

The present Osprey Lake population is very small, on the order of 46 individuals longer than 20 cm in 1980, and is at risk for that reason (Donald et al. 1985:110). In principle, even light fishing pressure sustained for as few as three or four consecutive years could prevent recruitment and eliminate the population. A population of such small size also is vulnerable to extirpation by chance events, as well as to the effects of inbreeding. Lethal or semilethal conditions may be expressed more frequently (Carson 1983:195), or perhaps more often the fish may be generally less vigourous and fertile (Gall 1987:80).

Small population size is of greatest concern if the population is isolated, but the bull trout in Osprey Lake may be a part of a larger one in Ranger Creek. Bull trout use Ranger Creek: several were caught in 1950 and 1952 (Table 6). Osprey Lake lies on a small perennial brook that is the principal tributary of Ranger Creek. W. C. Cable found only a small population of introduced rainbow trout, not bull trout, in two gill net sets in the lake when it was first investigated on 18 August 1941 (JNP Warden Service lakes files). The species may have invaded the lake quite recently, perhaps under unusually high water conditions.

Bull trout in Miette Lake are small and very slow-growing; at age 12 they are still less than 30 cm fork length (Donald et al. 1985:65). Age-frequency data hint at frequent year-class failures. Age 6 and 8 bull trout were the most common age classes in 1984, but there were few age 7 and no age 9 or 10 fish (ibid.). These facts suggest that the population is living in ecologically marginal conditions. Miette Lake is mostly shallow (mean depth 1 m), but a small portion of the lake exceeds 3 m in depth, and might be important overwintering habitat for bull trout in the upper Miette River, of which the lake is near the source.

In Dolly Lake bull trout grow more quickly and to a larger size than the same species in Miette Lake or Osprey Lake (Donald et al. 1985, cf. Donald and De Henau 1981). The age-frequency data suggest that in this lake year-class failures or near-failures are the rule rather than the exception. The age 5 year class alone comprised over 60 percent of the catch; no other year classes of the remaining nine comprised more than 8 percent of the population (Donald et al. 1985:47).

Kerkeslin Lake (formerly Hardisty Lake) has an introduced population of bull trout that is slow growing (Donald and De Henau 1981:117). Donald et al. (1985:108) emphasized that bull trout populations that are the dominant species in lakes are rare and therefore a natural resource worth protecting. They included the introduced Kerkeslin Lake population in this group.

The present status of the Jacques Lake population is not documented. Baraniuk (1989) caught 17 bull trout from the lake in 1988 ranging in weight from 148 to 942 g. He found no spawners in the lake or the inlet or outlet creeks when he visited the lake September 7 to 9, 1988. No attempt has yet been made to evaluate the impact of fishing pressure on Jacques Lake bull trout. Creel census data collected in various years from 1942-77 suggest that there has been a decline in angling success, and historical data hint that the stock may have been dramatically reduced from its natural levels of abundance.

Bull trout × brook trout hybrids evidently have not been reported from waters of Jasper National Park, but probably occur there and simply have gone unnoticed. Brook trout have been stocked very widely in the park, and unquestionably the two species have come into contact. The infertility of the hybrids prevents the danger of introgression; nevertheless hybridization with brook trout poses a serious threat to small or depleted bull trout populations. Under these conditions the bull trout may be swamped by much more numerous brook trout. Because the species may mate randomly with each other (Leary et al. 1983:372) bull trout of a depleted population will mate more frequently with brook trout than with members of their own species, few or no young will be produced and the stock will be extirpated. This course of events appears to have eliminated at least one Montana stock of bull trout within a decade of contacting a larger brook trout population (F. W. Allendorf, personal communication July 1988).

Dioxins and furans from wastes of pulpmills on the Athabasca River may pose a threat to the health of bull trout in Jasper National Park (see discussion of Ecological Significance, above). As a predator near the top of the food chain, bull trout might be expected to concentrate the contaminants and therefore could be especially vulnerable to damage from them.

In short, the present conservation status of bull trout stocks in Jasper National Park is largely unknown. What few data exist suggest that some populations are below historical levels of abundance, that some populations probably are at risk from contact with introduced populations of brook trout, and that several populations exist in habitats that are ecologically marginal for the species. Such ecologically marginal populations are thought to be adaptively significant, playing an important role in maintaining the genetic diversity of a species as a whole (Scudder 1989). Jasper National Park has an obligation to preserve both the marginal habitats and access to them by stocks of this fish. Finally, there is reason to think that Jasper bull trout have been exposed to pulpmill contaminants from outside the park. If so, they and the people that consume them may be at risk.

**Required Action:**

1. A contaminant survey of bull trout and other species in the Athabasca River system within the park is required immediately to document concentrations in fishes of contaminants associated with pulpmill effluent. The appropriate agency of Environment Canada should be approached for detailed advice.

2. A major survey of bull trout populations in Jasper National Park is required to identify stocks, examine taxonomic and hybrid status, delineate life histories and movements, describe and map critical habitat, and document present population

structure and abundance. The purpose of this work is to provide the information needed to support fish management, habitat protection, benchmark ecosystem designation and interpretive programs.

The bull trout is the most widespread and probably one of the most wide-ranging fish species in the park, and therefore is one of Jasper's most characteristic fish. It is also potentially one of the park's most spectacular species in terms of the large size achieved by adults in some pristine, unexploited populations, and in the brilliant spawning colours of some lake stocks. As one of the species most sensitive to damage from exploitation and environmental degradation, bull trout need to be well understood so that stocks can be restored and protected adequately inside and outside of the park.

3. A comprehensive conservation and management plan for bull trout should be developed, based on the results of the above surveys.

## *Lake trout*

*Salvelinus namaycush* (Walbaum)

## *SALMONIDAE*

Salmoninae

Salmon, Trout and Charrs

**EXTIRPATED** (Moab Lake; status provisional for Pyramid Lake)

**Summary:** At least two populations of lake trout probably were native to Jasper National Park, one in Pyramid Lake and one in Moab Lake. These stocks were two of perhaps only ten or so native to the Canadian Rocky Mountain region. Populations presently occupying the Sassenach lakes and Kidney Lake are believed on the basis of anecdotal reports to be introduced stocks, but should be considered as indigenous for conservation and management purposes pending further investigation.

Lake trout are among the most biologically capable of having survived the Wisconsinan in a local refugium such as the Ice-free Corridor. Whether or not they did so, the indigenous Rocky Mountain stocks, including those in Jasper, may have been especially distinctive and well adapted to local conditions. The Pyramid Lake stock, if it still exists in any form, is almost certainly extensively introgressed by the genes of non-native lake trout, which were heavily introduced after the original Pyramid stock was depleted. The Moab Lake stock was extirpated by poisoning with toxaphene in 1958.

A genetic and taxonomic survey of lake trout populations in the Canadian Rocky Mountains is needed to identify and characterize the remaining native stocks and the introduced stocks. The results of the study should be used to develop a restoration and management plan for lake trout in Jasper National Park.

**Nomenclature:** This species often has been referred to as *Cristivomer namaycush* in the past. Older literature may use the common names salmon trout or grey trout. It is a charr, not a true trout. Some recent authors have used “lake charr” as the common name, favouring the double r ending in solidarity with their beleaguered colleague W. M. Morton (Balon 1980:2, Morton 1980:4).

**Description:** Lake trout show a wide range of variation in colour. In general, they are densely covered with light spots (never black, pink or red) on a dark or silvery background, including the head, dorsal, adipose and caudal fins; pink, orange or red sometimes present on pectoral, pelvic, anal and caudal fin; caudal fin distinctly forked. The species is distinguished from true trout by the lack of black spots on the body; from bull trout by dense light-coloured spotting and lack of pink or reddish spots on the body; from brook trout by the lack of light-coloured vermiculations on the back and the lack of pink or red body spots, and by the forked tail.

**Distribution:** The lake trout is found as a native fish only in northern North America, from Alaska throughout much of Canada south of the Arctic coast. Though widespread in Canada, native lake trout are absent from most of the Arctic Archipelago, the Hudson Bay Lowlands, insular Newfoundland and drainages to the Gulf of St. Lawrence, the southern prairies, the Columbia River system, and several Pacific coastal drainages (Lindsey 1964:978,993-994; Scott and Crossman 1973:222; Lee et al. 1980:117-8). In Alberta it is widespread in the north, but restricted to a few suitable lakes. It is absent from the prairie and parkland lakes south of the North Saskatchewan. [Lake trout said to exist in Lake Diefenbaker (D. Donald, personal communication), a reservoir on the South Saskatchewan, most likely are the result of introductions.] Lake trout are believed to be native to several lakes and two rivers in the Rocky Mountains and foothills, including lakes Yellowhead, Moose (Carl et al. 1959:59), Waterton, Minnewanka, Clearwater, Glacier, Pyramid, Moab (Ward 1974:11), Rock (Miller and Paetz 1953:101), Swan (Paetz and Nelson 1970:80) and Outram (Tebby 1974:17 — Howse River valley, no record of stocking; T. Hurd, personal communication), and the upper North Saskatchewan and Alexandra rivers (Ward 1974:11).

**Refugia/Postglacial Dispersal:** Lake trout survived the Wisconsinan in southern and northern refugia, but all Canadian populations except those in or near the Beringian Refugium are a Mississippian morphotype, including those in our area (Crossman and McAllister 1986:60). The “Mississippian” morphotype might better be referred to as a southern morphotype because its distribution shows it to be present in possible Atlantic and Missourian refugial areas also. The species simply may have persisted in meltwater impoundments along the ice front (Martin and Olver 1980:210). If so, the Ice-free Corridor in Alberta may have served as a refugium for lake trout.

Lindsey (1964:980) proposed a refugium for lake trout in Montana that may have extended some distance into Alberta in the Ice-free Corridor, from which the species could have moved northward following the retreating ice. Khan and Qadri (1971:474) adopted this hypothesis to explain the existence of morphologically distinctive lake trout in the Peace River basin. If so, the lake trout from this refugium would have colonized suitable Jasper Park waters.

Lindsey (1964:981) believed that lake trout probably gained access to the upper Fraser system via Glacial Lake Miette, which was supposed to have connected the upper Fraser drainage as far downstream as Moose Lake to the upper Athabasca drainage, flowing toward Glacial Lake Edmonton at that time (Taylor 1960:169). Current geological interpretations of landforms and deglaciation in the Jasper area (Mountjoy 1974, cited by Weir 1987:208; Roed 1975; Levson and Rutter 1989) abandon the notion of a Glacial Lake Miette. Fish still may have moved over the Continental Divide at the Yellowhead Pass even in the absence of a glacial lake there, as discussed in Section I.

**Jasper Stocks:** Prince et al. (1912:43) alluded to lake trout in Pyramid Lake based on work done in 1910, and reported fish to be spawning in the lake on 23 September (ibid., p. 9). Referring to the 1913 season, Rogers (1915:97) mentioned ambiguously that "tourists visiting Jasper have had some enjoyable outings at Pyramid and Caledonia lakes, and excellent catches of large lake trout, *Salvelinus Namaycush* [sic], and rainbow trout have been made." Caledonia, a shallow lake with a mean depth of just 4.7 m, little water less than 10 °C in midsummer, and low dissolved oxygen in summer in the hypolimnion (Rawson 1940a:31, Anderson and Donald 1980:33), is unlikely habitat for lake trout, primarily a cold- and deepwater species. There is no other record of lake trout in Caledonia Lake.

The first recorded stocking of lake trout into waters of Jasper National Park was in 1917 in Pyramid Lake (Ward 1974:C3), but many fish introductions in the park have gone unrecorded. The first of two railways nearly had reached the east boundary of Jasper Park by the end of 1910, and was completed through the park in 1911. It is unlikely, but conceivable, that Pyramid Lake was stocked with lake trout from an eastern Canadian source by 1910. Lake trout are thought to be native to nearby Yellowhead and Moose lakes in the Fraser drainage (Carl et al. 1959:59), and a railway tote road undoubtedly was present to at least the former by 1910. Capturing wild lake trout alive at remote locations and transporting them in significant numbers by overland means takes special knowledge and equipment. Again, it is unlikely, but possible, that lake trout were transplanted into Pyramid Lake from a western source by 1910. Several comments in early JNP file documents seem to imply that Pyramid Lake was not stocked prior to 1917. See Section II, where the issue of early stocking is discussed further.

Non-native lake trout have been stocked on top of the Pyramid Lake native population 51 times with a total of 431,481 fish beginning with the 1917 planting (JNP fish stocking records). All of the sources of the introduced fish are not known, although some were eastern Canadian (JNP file data, Donald et al. 1985:105).

Cuerrier (1954:9) stated that native lake trout were found in Moab Lake, but did not mention any supporting evidence. Rawson and Elsey (1950:18) and Ward (1974:11) pointed out that lake trout were present in Moab Lake in the early days before stocking began. It is true that the earliest recorded stocking of lake trout in Moab was in 1950, and Rawson (1940a:58) found lake trout there in 1939, but this ignores the possibility of unrecorded introduction in the period prior to 1939. In the 1910s and 1920s, the Whirlpool River valley within which Moab Lake lies was logged by railway workers to supply lumber for constructing railway facilities and for ties (Woodrow 1987a:484). Records of early trail and road construction near and in the Whirlpool valley date from 1914 (Sparks 1916:66, Driscoll 1918:65, Rogers 1922:55, Harkin 1925:23). Moab Lake apparently was readily accessible at a time when lake trout are known to have been used to stock other waters in the park (JNP fish stocking records — Pyramid Lake stocked with lake trout 1917, 1919, 1920, 1923; Donald et al. 1985:105 — anecdotal report of unrecorded lake trout stocking in Kidney and Sassenach Lakes 1920s). Perhaps the strongest argument that lake trout were native to Moab Lake is only the fact that historically lake trout have been able to sustain a population there, and the species likely had early natural access to the lake via the Athabasca River from proglacial lakes east of the mountain front.

From 1950 to 1955, 1642 yearling lake trout were stocked on top of the original Moab Lake population. The population was destroyed with toxaphene in July 1958, and from 1964 to 1972, 30,000 non-native fingerlings and 2000 non-native yearlings were stocked.

No other native lake trout populations are known within the park. Lake trout stocks in Kidney Lake and the Sassenach Lakes are thought to be the result of unrecorded introductions (anecdotal reports cited by Donald et al. 1985:105, and Donald and Alger 1986a:608). Nearby Rock Lake, within 4 km of the park boundary, is thought to have had a native lake trout population [J. S. Nelson personal communication to Lindsey 1964:994; "Rock Lake lake trout had been there as long as he (Billy McGee, a longtime local resident) could remember, and he had never heard of them being introduced" (C. Hunt, personal communication 14 April 1991)]. If so, these fish would have had access to Rock Creek within the park, but there is no record of them in that creek. For management purposes, however, it is safest to treat all of these populations as native pending further investigation.

**Habitat:** The two Jasper lakes formerly occupied by native lake trout are said to have spawning grounds of poor quality (Ward 1974:11). Pyramid Lake is 19 m at the deepest point, the mean depth being 8.7 m (Anderson and Donald 1978b:83). About half the volume of the lake remained below 10 °C in summer 1972 (Anderson and Donald 1978b:87), but in 1939 temperatures well above 10 °C penetrated below 10 m, and minimum observed dissolved oxygen in the hypolimnion was 4.9 cc/l (Rawson 1940a:43). There is an extensive limnological and fisheries literature on this lake (listed by Anderson and Donald 1977; see also Anderson and Donald 1978b and Herzig et al. 1980).

Moab Lake has a maximum depth of 18 m and a mean depth of 8.6 m (Donald and De Henau 1981:153). There was no thermal stratification down to 11.5 metres on 21 September 1939, and dissolved oxygen was high (5.4 cc/l) at 11.5 m on that date (Rawson 1940a:58).

Behnke (1980:471) has emphasized that, even though the lake trout is a taxonomically stable species showing little (structural) variability throughout its range, genetic differentiation expressed as variability in ecological, physiological and life history attributes has arisen in various populations. For this reason, the summary of habitat requirements below should be generalized with caution to lake trout stocks in Jasper Park.

Martin and Olver (1980) have published an exhaustive review of lake trout biology, including observations on lake trout habitat throughout the range of the species.

Habitats used vary widely depending on the stock in question, but a few generalizations are possible. Most stocks are lake-dwelling, but many populations are riverine for at least part of the year, including at least one in the Alberta Rocky Mountains (upper North Saskatchewan and Alexandra rivers, Banff National Park, Ward 1974:11). The species is found in standing waters ranging from small tundra ponds through small Shield lakes to the largest and deepest North American great lakes. Temperature has a strong effect on the distribution of lake trout in many lakes, most fish tending to remain at depths where temperatures do not exceed 10 to 12 °C (Martin and Olver 1980:228). These observations suggest that a preference for water no warmer than about 10 °C is probably the reason that most southern populations inhabit relatively deep lakes.

Most stocks spawn in lakes over rocky substrate ranging in size from gravel to boulder. Some stocks are known that spawn over small gravel to boulder-sized rock in the outlet of lakes, in rivers (sometimes requiring the ascent of steep rapids), and even in a small stream in at least one case. Spawning sites in lakes may be shallow (0.2- 1.2 m) to very deep (30.4- 45.7 m). Some stocks spawn when surface water temperatures are 5-8 °C, while many others spawn when surface temperatures are near 10 °C, and one stock that spawns in very deep water reportedly does so when surface temperatures are still as high as 14 to 17 °C. In many stocks spawning occurs when water temperatures fall to about 10 °C. Most spawning sites in lakes are in places kept clean by wave action, often along exposed shorelines, points, islands or mid-lake shoals facing the prevailing winds. In fact, wind seems to trigger spawning in some lake stocks. Darkness, or at least lack of bright light, might be required for spawning.

**Biology and Life History:** There is very little biological information on the native lake trout stocks in the park. Some evidence suggests lake trout originally were abundant in Pyramid Lake. In an undated list of early records of fish in Jasper Park held in the JNP warden office lakes files, the following citation is found.

"*This lake* [Pyramid] *is back in the Mountains of Jasper Park. Sometime ago there was a very plentiful supply of trout and graylings which afforded good sport and which were never abused in those days. The fish were not of large size and by proper supervision by the Park authorities they can be preserved ...20-10-1915... 718-11-1/2. p.89*"

Rogers (1915:97), quoted in Section II of this report, also referred to "excellent catches" of lake trout from Pyramid Lake in the 1913 season.

The field work for the Jasper Park Lakes Investigations (Bajkov 1927, Neave and Bajkov 1929) was carried out in 1925 and 1926, nine, seven, six and three years after non-native lake trout were stocked in Pyramid Lake (JNP fish stocking records). To judge from the numbers stocked, all but the first introduction of 350 fish involved eggs, fry or fingerlings, which would be expected to mature in not less than four years, but probably longer (Martin and Olver 1980:211). It is quite possible that Neave and Bajkov's (1929) data on lake trout in Pyramid Lake are for the native stock.

Bajkov (1927:18) stated that the species was known to grow to 7.7 kg in Pyramid Lake. Neave and Bajkov (1929:18) collected 10 young-of-the-year (32 to 45 mm long) "in the small inlet creek at Pyramid Lake." In other stocks, fry of this size are still in the mid- to late alevin (yolk sac) stage (Balon 1980b:532); nevertheless, these authors found "Diptera, chiefly Chironomidae and miscellaneous small adults from the surface" in the alimentary canals. A creek is unusual habitat for such young lake trout fry (Martin and Olver 1980:218, 226), and the presence of small fry there seems to suggest that spawning took place in the creek upstream of the sampling point. Again, lake trout only rarely spawn in running water (Martin and Olver 1980:218). The collection might have been made at the mouth of the creek, in which case the locale would be more accessible to fry hatched in the lake.

Prince et al. (1912:9) reported "fish in Pyramid lake spawning on 23 September" when they visited the park in 1910, but they were not necessarily lake trout: another native fall spawner, mountain whitefish, is known from the lake. In 1941 and 1942, after non-native lake trout had been stocked frequently and in high numbers into Pyramid Lake, hatchery superintendent W. C. Cable observed lake trout spawning between October 3 and 22 on rocky bottom in water 2.1 to 7.6 m deep at 10.8 °C (Rawson and Elsey 1950:19). Cable also found mountain whitefish and lake trout to be eating lake trout eggs.

The two lake trout caught 22 September 1939 by Rawson (1940a:58) in Moab Lake may have been native. Although at 37 and 46 cm in length and 0.7 and 1.5 kg in weight they were small for sexually mature adults of this species (Martin and Olver 1980:212), they were said to be "approaching the spawning season", and had empty stomachs.

There appears to be no other reported life history data on native stocks of lake trout in Jasper. The biology of lake trout and bull trout in Rocky Mountain lakes is presently under study by D. B. Donald.

A brief summary of lake trout biology and life history can be compiled from the detailed review of this species by Martin and Olver (1980). As Behnke (1980:471) has emphasized, there are many variations depending on the particular stock, so generalizations to the native stocks in Jasper should be made while keeping this caveat in mind.

Lake trout move onto the spawning sites in fall, often September and October, in many large lake populations homing with a high degree of fidelity from long distances. Spawning usually takes place after dark. No redd is dug; the eggs are simply broadcast over the spawning site of coarse rock, and fall down among the interstices. Ova often are consumed by other species, especially whitefish. The eggs incubate over the winter, for about four months in most southern populations. The alevins remain for a short time in the substrate, resorbing the yolk sac. Their lives for the first year are poorly known, but in deep-spawning stocks they must migrate substantial distances to the surface to fill their air bladders shortly after resorbing the yolk sac. In some stocks fry have been observed in shallow water near shore, but in many others it is believed that they move into deep water to rear.

In some large lake stocks, lake trout often move long distances (on the order of hundreds of kilometres), often in a short time (one Lake Superior trout travelled 306 km in 19 days). Other large lake stocks (e.g., Great Bear Lake) remain within their natal bays, and stocks as little as 13 km apart appear not to mix. It seems to be general among lake trout populations in lakes to enter shallow waters in the spring and fall, remaining in deep water in summer, in all locations staying close to the bottom. Lake trout consume invertebrates initially, but become more and more piscivorous as they become larger.

**Ecological Significance:** The ecological role of indigenous lake trout in the ecology of Jasper National Park lakes has not been investigated, but it undoubtedly functioned as top predator in the lakes in which it occurred. Its most important prey as an adult in Pyramid and Moab lakes likely would have been mountain whitefish. Mountain whitefish in turn may have been important predators of lake trout eggs (Rawson and Elsey 1950:19).

**Fishing:** Some evidence suggests lake trout originally were abundant in Pyramid Lake, and provided good fishing. The citation dated "20-10-1915" referring to "a very plentiful supply of trout and graylings which afforded good sport" and quoted in the Biology and Life History heading above is one example. Rogers (1915:97), quoted in Section II of this report, also referred to "excellent catches" of lake trout from Pyramid Lake in the 1913 season. Soon, however, the stock evidently was depleted by angling. Again a quote from the JNP warden office lakes files:

"*Suggestion by Supt. of Jasper Park that the lake be restocked and improved. Contains some lake trout which are mostly caught by trolling... The Dept. replies that it hears the Fishery Regulations are violated in the Park and for this reason as well as for the shortage of trout fry the Dept. could not stock at present... 4-5-1916 ...718-11-1/3. p.11.*"

Bajkov (1927:18) noted that "some years ago lake trout were more plentiful in Pyramid Lake", but he indicated that by 1925-26 they were scarce there, despite several introductions of non-native lake trout.

**Conservation Status (general):** As a species lake trout are widespread and abundant, in no danger of extinction. Lake trout do not appear on lists of endangered fishes for

North America (Ono et al. 1983, Williams et al. 1989), Canada (McAllister et al. 1985, Campbell 1991), or Alberta (Paetz and Nelson 1982). Apparently not a single North American jurisdiction considers its stocks to be of special concern or in need of legislative protection (Johnson 1987).

It would be misleading to consider the status of lake trout as safe, however. Numerous stocks have been severely depleted (e.g., the Great Lakes), some have been extirpated and many remaining stocks undoubtedly are under some threat. Given the numerous biological differences among distinct stocks noted above, these losses must be considered serious. Martin and Olver (1980:269) point to the vulnerability of lake trout to overfishing, in part due to the species' inherent slow growth and late maturity. These in turn are partly owing to the lakes in which they live, which are typically nutrient-poor, cold and have short growing seasons. They consider lake trout to be "extremely sensitive to exogenous, man-induced perturbations", and warn, "It is essential that pristine conditions be maintained for the well-being of this species" (Martin and Olver 1980:268).

**Conservation Status (Jasper):** It is highly unlikely that the native Pyramid Lake stock of lake trout exists, at least in its pure form. The frequent and large introductions of non-native stocks on top of the depleted native population would have flooded the native gene pool unless the two forms segregated completely during spawning. Neave and Bajkov's (1929) observation of lake trout fry in an inlet to Pyramid Lake offer only a faint hope that the native stock used a highly unusual spawning habitat differing markedly from that used by non-native trout (cf. Rawson and Elsey 1950:19). Somewhat more likely is the possibility that part of the native gene pool still exists, albeit introgressed with that of the non-native stocks. Unfortunately, exploited native stocks of lake trout are likely to be displaced by non-native introductions within just a few generations, even where there is no introgression of native and non-native stocks (Evans and Willox 1991).

The poisoning of Moab Lake with toxaphene in 1958 left the lake toxic for three years, and certainly would have eliminated all fishes from the lake. There is no record of native lake trout from the Whirlpool River that might have been able to recolonize the lake. Even if this had occurred, introgression with introduced stocks is highly likely.

The lake trout in Kidney and Sassenach lakes are presumably introduced. Despite anecdotal reports that these lakes were stocked with lake trout, it is at least conceivable that the population in Kidney Lake is native, given that lake trout are thought to be native to nearby Rock Lake. For conservation and management purposes, it is safest to consider all of these populations as indigenous pending a genetic screening.

**Required Action:**

1. For the time being, all stocks of lake trout in Jasper National Park should be considered as indigenous and managed accordingly, except for that in Moab Lake, which is known to be a recently introduced stock.

2. Certain immediate, preliminary investigations are needed to form the foundation of a management and recovery plan for native lake trout in Jasper National Park. In cooperation with Alberta and British Columbia authorities, available data on the lake trout populations in Rock, Yellowhead and Moose lakes should be reviewed to determine if one or more of these populations might be suitable as a source for fish to be reintroduced into Pyramid and Moab lakes, should the need arise. Most importantly, we need to know if these populations still exist intact, if they have been depleted, or if their lakes have been stocked with non-native lake trout. [Rock Lake is known to have been stocked in 1983, 1986 and 1987 with wild stock from Cornwall Lake, to supplement an apparently depleted native population (C. Hunt, personal communication 14 April 1991). It is nevertheless just possible that the native stock still exists.] If the Rock, Moose and Yellowhead native populations are intact, it is critical that the Alberta and BC authorities know of our strong interest in them as a possible source of transplant stock for reintroducing regionally native lake trout into two JNP lakes. They should be asked to refrain from stocking these lakes and if necessary to take special precautions to safeguard their lake trout.

   The lake trout native to Rock, Yellowhead and Moose lakes, like those indigenous to Pyramid and Moab lakes, may have had a common source. For example, they may have been part of a population that inhabited glacial lakes east of the mountain front. If so, the Rock, Moose and Yellowhead stocks are likely to resemble the Jasper native stocks much more closely than those introduced from elsewhere; therefore would be preferred for reintroduction into Jasper lakes.

3. A genetic and taxonomic survey of lake trout populations in Pyramid, Moab, Kidney and the Sassenach lakes in Jasper National Park, Yellowhead and Moose lakes in Mount Robson Provincial Park, and Rock Lake, Alberta, should be conducted to document their present genetic and taxonomic status, and if possible to determine whether or not they are native stocks. Ideally, this would be carried out as part of a broader survey of geographic variation in the genetics and morphology of all known Rocky Mountain lake trout stocks in Alberta and BC.

4. A comprehensive restoration, conservation and management plan for all lake trout stocks in Jasper National Park should be developed, based on the results of the above work.

## *Arctic grayling*

*Thymallus arcticus* (Pallas)

## *SALMONIDAE*

Thymallinae

Graylings

**EXTIRPATED?**

**Summary:** Arctic grayling are native to the upper Athabasca River drainage outside Jasper National Park. They are known from within the park only from ambiguous or questionable accounts in three historical references, and from two questionable published scientific reports. All recent records of Arctic grayling in Jasper Park are traceable to introductions. Habitat apparently suitable for Arctic grayling exists within the park, although it is not common. The species is unusually sensitive to overfishing, so it is conceivable that netting conducted to supply fish for the fur trade eliminated the few Jasper populations in the 1800s. More historical research is necessary to test this hypothesis.

**Nomenclature:** This species was sometimes referred to as *Thymallus signifer*, *Thymallus tricolor* or *Thymallus montanus* in early literature (e.g., Sisley 1911, Prince et al. 1912, Bajkov 1927). Mountain whitefish, *Prosopium williamsoni*, are commonly called "grayling" in western Alberta and southwestern British Columbia, and should not be confused with this species, a true grayling (also see below).

**Description:** No specimens have been described from Jasper National Park.

The Arctic grayling is a distinctive trout-like fish with a very large, ovoid dorsal fin, especially in mature males. Typical specimens are dark steel-blue on the back, silvery-grey on the sides with a few small irregular black speckles scattered mostly on the forward half, with an adipose fin and a forked caudal fin. Pelvic fins are dark, boldly striped with orange or pink, and the dorsal fin is striped and spotted orange or pink. Colours are most pronounced in males.

**Distribution:** This species has a Holarctic distribution extending from the Kara and Ob rivers in northern Eurasia eastward to Hudson Bay. In North America it is indigenous to all of mainland Alaska and northern Canada from the Arctic coast south to northern British Columbia, Alberta, Saskatchewan and Manitoba, and eastward to the west coast of Hudson Bay (McPhail and Lindsey 1970:126, Scott and Crossman 1973:301-2, Lee et al. 1980:120).

In Alberta grayling are indigenous to, and widely distributed in, the Athabasca, Peace and Hay river drainages (Sisley 1911, Prince et al. 1912, McPhail and Lindsey 1970:124, Paetz and Nelson 1970:63, Scott and Crossman 1973:302). Grayling are known from streams close to Jasper Park in or near the Athabasca River mainstem at least as far upstream as the Berland River confluence (Lee et al. 1980:120), from the Berland and Wildhay rivers, and from the McLeod River upstream at least as far as McPherson Creek (Paetz and Nelson 1970:63; C. Hunt, personal communication 14 April 1991). They are also found close to the park in the headwaters of the Smoky and Little Smoky rivers (Paetz and Nelson 1970:63).

**Refugia/Postglacial Dispersal:** Arctic grayling are known to have survived in at least two refugia: Beringia and the upper Missouri (McPhail and Lindsey 1970). Arctic grayling scales found with dated material from a cave in southwestern Alberta (Crossman and McAllister 1986:88) are evidence that this species occupied the Ice-free Corridor near the beginning of the late Wisconsinan advance. Conceivably grayling persisted in the region throughout the late Wisconsinan, becoming locally extinct in the south since then. This possibility is discussed in more detail in Section I. It is possible that stocks in the Jasper region were derived from any combination of these refugia, but if the Ice-free Corridor acted as a refugium for grayling, that is their most likely source of Jasper stocks.

**Jasper Stocks:** Alexander Ross (1855:202) reported being served a meal of "titimeg, or white fish" in 1825, apparently at what was Henry House. "Tittimeg" is listed as a common name synonym only for Arctic grayling by Scott and Crossman (1973:305). See the discussion of this point in Section II.

George Ross (1909:132), writing generally of his survey of the 14th base line between the fifth and sixth meridians, stated that the Athabasca River contained great numbers of "graylings", as distinct from whitefish. The sixth meridian passes through the site of Jasper House at the outlet of Jasper Lake, so he was describing the river mostly below Jasper Park. The record is anecdotal, and it is not clear whether it is based on his own catches or local scuttlebutt. This record is discussed further in Section II of this report.

The following citation is found in an undated list of early records of fish in Jasper Park held in the JNP warden office lakes files.

"*This lake* [Pyramid] *is back in the Mountains of Jasper Park. Sometime ago there was a very plentiful supply of trout and graylings which afforded good sport and which were never abused in those days. The fish were not of large size and by proper supervision by the Park authorities they can be preserved ...20-10-1915... 718-11-1/2. p.89*"

This record cannot be accepted on its own as a record of Arctic grayling in Pyramid Lake because the name "grayling" was widely used for mountain whitefish in the Jasper area, and mountain whitefish were historically common to abundant in Pyramid Lake.

Bajkov (1927) reported grayling from Jasper National Park in the Athabasca, Miette and "Snake" (probably Snake Indian) rivers, and in Pyramid Lake, to which he believed they gained access via the outlet, Pyramid Creek. Nelson and Paetz (1976) state that Bajkov's records of the species in the park are probably erroneous, but do not say why they think so. Ward (1974:19), however, notes that "the species presently found there [Pyramid Lake] and commonly mistaken for grayling is the mountain whitefish."

It hardly seems likely that an ichthyologist with specimens in hand would mistake mountain whitefish for Arctic grayling. Bajkov worked at the University of Manitoba, and it is conceivable, even probable, that he would not be aware of the local Rocky Mountain idiosyncrasy of calling the mountain whitefish "grayling." Indeed, he noted that "*Coregonus williamsoni* Girard", which he called Rocky Mountain whitefish, was incorrectly known as mountain herring, but did not mention the much more serious source of confusion (Bajkov 1927:394). Bajkov (1927:396) admitted "we have no adult grayling from Pyramid Lake", and Neave and Bajkov (1929:214) state in connection with lake trout in Pyramid Lake that "*according to information supplied by local fishermen*, the adults subsist to a large extent on grayling (*Thymallus signifer*)" (emphasis added). Neave and Bajkov (1929:214) did describe the stomach contents of two specimens they called *Thymallus signifer* from Pyramid Lake, but these fish were very small (just 54 mm and 36 mm long). It is possible that they received only the stomachs or stomach contents for analysis, or even misidentified such small fish. Bajkov did not describe any grayling specimens from any of the Jasper localities. While Bajkov's record cannot be disproven on the available evidence, it cannot be accepted without verification.

There is thus no incontrovertible evidence that Arctic grayling are native to any waters in Jasper National Park, despite the indigenous populations in the Athabasca mainstem and in the Berland, Wildhay and McLeod river drainages immediately east of the park (G. Ross 1909, Sisley 1911, Prince et al. 1912, Paetz and Nelson 1970:63). There are no barrier rapids or waterfalls to prevent migration between the downstream populations in the mainstem and the park.

Other early records of fish caught in what are presently park waters mention only whitefish, rainbow trout, lake trout, bull trout (as Dolly Varden), trout in general or pike (Hector 1863, Moberly and Cameron 1929, Cheadle 1931, Douglas 1912b, Rogers 1914, Driscoll 1918), even though the grayling is an easily caught, readily identifiable fish. All confirmed records of grayling within the park can be traced to hatchery introductions (Ward 1974:19). Park stocking records show that grayling have been stocked in Lac Beauvert (1969), Buck Lake (1954, 1957), Edna Lake (1957, 1958), Iris Lake (1957), Katrine Lake (1963), Miette River (1963), Moab Lake (1969), Osprey Lake (1954), and Palisade Lake (1963). There are no recent records of Arctic grayling being caught in any of these locations, or elsewhere in the park.

**Habitat:** Hubert et al. (1985) reviewed and summarized published habitat requirements of this species throughout its range. There are numerous conflicting observations regarding habitats used or required, suggesting that different stocks have different requirements, or at least behave differently.

In general, Arctic grayling use mostly pool habitat in clearwater rivers, streams, bog-fed and brownwater streams, and lakes. They are said to avoid turbid parts of the Mackenzie River, but do enter milky glacial streams (Scott and Crossman 1973:303). Overwintering is in large rivers, lakes, deep pools of smaller streams, or in the open water of springfed creeks.

Spawning has generally been reported to occur over gravel, but some stocks apparently use substrates incorporating substantial amounts of sand (Eriksen 1975:2449,2455; Beauchamp 1990:196), and others seem to show no substrate selection. Some observers have reported grayling to spawn above riffles, others at the lower end of riffles above a pool, still others in shallow backwaters. While some grayling have been observed to spawn over mud-bottomed pools with vegetation, in other cases pure mud, silt or clay are not used. A critical feature of spawning habitat for Arctic grayling may be a current stable and slow enough that the exposed, semibuoyant, sticky eggs and weak-swimming alevins are not washed away, but swift enough to prevent them from being buried by silt (Feldmeth and Eriksen 1978:2042, Beauchamp 1990:206). If so, low-gradient springbrooks, muskeg creeks and other wetland discharge areas would appear to be ideal spawning habitat for the species.

Rearing habitat changes as the fish grow. Fry use quiet backwaters and protected areas along the streambank away from strong currents. “Interstitial spaces and shadows of boulders” are said to be critical habitat for age 0 grayling (Hubert et al. 1985:5), although such instream hiding places may not be essential for stocks not in contact with predator or competitor fishes (Eriksen 1975:2455). Fry tolerate high temperatures (24.5 °C) and low dissolved oxygen concentrations (less than 2 mg/l when acclimated at 13 °C). Juveniles are less tolerant of high temperatures, surviving at 22.5 °C but succumbing at 24.5 °C. They use pool and slough habitat, using logs, boulders and turbulence for instream cover, but may feed in riffles.

Adult grayling tolerate temperatures higher than 20 °C, but avoid them. They have a critical oxygen minimum of approximately 2 mg/l, depending on acclimation temperature. They have been seen to avoid turbid water, but can survive in it. Differential abilities to tolerate warm water and possibly low oxygen appears responsible for segregating rearing fry and adults in some southern lake populations (Eriksen 1975). Adults occupy the cooler open water of small mountain lakes in Montana in midsummer, while fry remain in the warmer, heavily vegetated nearshore zone.

The habitat used in Jasper National Park by this species, if any, is not known. Suitable low-gradient clearwater or brownwater stream habitat with stable, moderate current is not common in the park, but does exist. Possible locations include parts of the Miette valley and small Athabasca tributaries from Athabasca Falls downstream to the east boundary.

**Biology and Life History:** Since the present or past existence of Arctic grayling in Jasper National Park has not been confirmed, nothing is known of the biology and life history of the species in park waters. Hubert et al. (1985) have reviewed and summarized published life history data on stream stocks of Arctic grayling elsewhere. Grayling range in life span from seven years in southern populations to 22 years in some Arctic populations. Sexual maturity varies with latitude and crowding, ranging from age 2 to 3 under favourable southern (i.e., Wyoming and Montana) conditions, to age 9 to 11 in many Arctic populations. They are sight feeders, consuming mostly insects.

Spawning occurs in small streams in spring at water temperatures of 2 to 10 °C, with most activity near the upper end of the range. Males establish territories, but no redd is built. Instead, the small adhesive eggs become coated with sand and gravel, and settle to the bottom. Eggs hatch in 8 to 27 days at water temperatures of approximately 2 to 16 °C. Alevins spend three or four days in the gravel (if present) resorbing the yolk sac before emerging into the spawning stream, where they rear through the summer.

Migration patterns for many stocks are complex. Craig and Poulin (1975:695) cite several other workers in support of their statement that “a) some grayling return annually to a particular stream to spawn, and b) some tributaries serve as spawning streams and rearing areas for fry, whereas other tributaries, mainstreams, or lakes are used by immatures and adults as summer feeding areas.” Adults in different populations may move upstream, downstream, into lakes or into other streams for summer feeding. Spring spawning migrations in flowing water stocks may extend over 150 km, or may be as short as 10 km, while some lake stocks spawn in inlets within a few hundred metres of the lake. Grayling move downstream in late fall to overwintering areas.

Subtle but crucial differences in behaviour between stocks have been found. Lacustrine and fluvial Montana grayling stocks studied by Kaya (1991), for example, were genetically different. Kaya found that fry of both stocks had strong downstream responses during the first 10 days after hatching. The fluvial stock, however, had a strong tendency to hold position thereafter, while the lacustrine stock did not. The response of the fluvial fry appears to be an adaptation permitting permanent stream residence. Kaya (1991) suggested that to have any hope of retaining stream resident populations of Montana grayling, an officially-listed “Species of Special Concern”, it was necessary to conserve this last remaining stream resident stock.

**Ecological Significance:** Until the present or past existence of Arctic grayling in the park can be confirmed, it is not possible even to speculate on its ecological significance here.

**Fishing:** Fisheries that are known to have exploited this species as yet are undocumented in Jasper Park. Net fisheries were operated over many years in the 1800s on Talbot Lake and probably others nearby to supply Jasper House. These would have captured grayling had they been present.

Where they are readily accessible, Arctic grayling are highly susceptible to overexploitation (e.g., Falk and Gillman 1974 and references therein; Tripp and Tsui 1980:126; L. Carl, personal communication). The slow-growing, late-maturing stocks typical of cold unproductive habitats like those found in Jasper Park are especially vulnerable.

**Conservation Status (general):** Arctic grayling as a species does not appear on current threatened and endangered lists for North America (Ono et al. 1983, Williams et al. 1989), Canada (McAllister et al. 1985, Campbell 1991), or Alberta (Nelson and Paetz 1982). The subspecies *T. a. montanus* (Milner) is a Species of Special Concern in Montana (also listed federally) as a result of extensive habitat loss there (Johnson 1987:5, Williams et al. 1989:4). The subspecies *T. a. tricolor* (Cope) native to Michigan is now extinct (Scott and Crossman 1973:301). Many local populations of the species have been extirpated. Owing to the susceptibility of this species to overfishing, the Arctic grayling must be considered vulnerable wherever it is exposed to significant fishing pressure. It is abundant and widespread elsewhere throughout its range where conditions are still nearly pristine.

**Conservation Status (Jasper):** As noted under the heading Jasper Stocks, above, Arctic grayling may not be native to Jasper Park. If it was native, the species is now very rare at best (Ward 1974:18-19) and probably has been extirpated.

**Required Action:**

1. Further historical research should be undertaken to determine if Arctic grayling are native to any park waters. Hudson's Bay Company records for Jasper House, files held by the National Archives, and other historical documents should be searched for records of this species in the park.

2. The reason why Arctic grayling now are absent from Jasper National Park needs to be established. There is no physical barrier to their movement into the park from known populations downstream in the Athabasca mainstem and tributaries. The

species coexists elsewhere with all species known to be native to Jasper Park. Suitable habitat would appear to be present in accessible park waters along the Athabasca Valley. There are three ambiguous or questionable historic references to Arctic grayling in the park, and two questionable records in the scientific literature. These observations suggest that Arctic grayling once may have occurred in Jasper Park but have disappeared, perhaps before the park was formed. Nineteenth century netting operations conducted for a period of several decades by the provisioners for Jasper House might have eliminated them. Rail- and roadbeds on both sides of the Athabasca river dating from the early 1900s might have blocked access to spawning streams.

Self-sustaining populations of nonnative grayling stocks often have proven difficult to establish in new localities, even those formerly supporting grayling (Scott and Crossman 1973:301-2, Ward 1974:18-19, R. D. Jones, personal communication). As discussed above, different grayling stocks have different, highly specific habitat preferences and may home to natal streams. They have complex migrations that may show broad similarities among stocks within a region, but clearly are specific to the particular habitat occupied. It may be that any native stocks, once eliminated, were not replaced by natural invasion because of such stock-specific traits.

3. Should strong evidence be found that Arctic grayling are native to the park, or if some human-induced factor is found to be causing the present absence of grayling in Jasper Park, then a plan to restore this fish to park waters should be carefully considered.

## *Trout-perch* — PERCOPSIDAE

*Percopsis omiscomaycus* (Walbaum) — Trout-perches

**Summary:** The trout-perch is a widespread and often abundant species in lakes and streams of northern North America. It is common throughout nearly all of Alberta. It has been found in Jasper National Park only once, at the outlet of Lac Beauvert, most likely because little sampling has been done in suitable habitat using appropriate techniques. It probably occupies the Athabasca River downstream from Athabasca Falls, and perhaps the accessible parts of some of the major Athabasca tributaries.

Stock development has not been examined seriously in trout-perch. The possibility that trout-perch survived Wisconsinan glaciation in at least two different refugia, and apparent differences in habitat preference among populations from different geographic areas, hint that distinct geographic stocks exist. If separate stocks exist, it is not evident which of these are represented by the trout-perch of Jasper Park.

Trout-perch are a notable forage species. In Jasper waters they conceivably are prey for burbot, pike, bull trout, several species of fish-eating birds and other predaceous vertebrates.

A survey is required to determine the distribution, abundance, life history and critical habitat of trout-perch in Jasper National Park. To discover what geographic and local stocks of trout-perch Jasper Park is responsible for conserving, the Canadian Parks Service should encourage, and contribute some support to, a study of geographic variation in this species.

**Nomenclature:** There have been no changes in nomenclature in this century (Scott and Crossman 1973:682). I know of no other common names in use for trout-perch in Alberta. Subspecies are not recognized at present.

**Description:** The trout-perch is a big-headed, translucent silvery, dark-spotted small fish. In profile it tends to have a Roman-nosed look because of its arched snout. It has a small mouth narrowly attached to the snout by a frenum, and located clearly on the lower half of the head. The dorsal fin is large; the caudal forked. Trout-perch have an adipose fin, but can be easily distinguished from salmonids by the placement of the pelvic fins, which are so far forward that the large pectorals overlap the pelvic bases by about half the pectoral length.

This is a distinctive little fish, and once seen is not likely to be mistaken for any other species within its natural range. The combination of adipose fin plus pelvic fins overlapped by pectoral fins is diagnostic.

**Distribution:** Trout-perch are found in the Yukon River from the mouth to the Alaska-Yukon border, the Porcupine River, the Mackenzie Delta southward east of the

Mackenzie and Rocky mountains to the Oldman drainage, eastward to tributaries of Great Bear and Great Slave lakes, Hudson Bay and James Bay, southern Quebec, the Gaspé Peninsula; in the US from the lower (but not the upper) Missouri River to southern Illinois, Kentucky, Ohio, Maryland and New England (Lee et al. 1980:485). In Alberta the species has been recorded from every major river system except the Petitot (Liard drainage — it is present in the British Columbia portion of the Liard) and the Milk (upper Missouri drainage).

**Refugia/Postglacial Dispersal:** Although the present distribution of the trout-perch includes unglaciated areas in Alaska, the upper Mississippi drainage (but not the upper Missouri) and the Atlantic seaboard, it is widespread only in the upper Mississippi. McPhail and Lindsey (1970:292) felt that the lack of any consistent pattern of geographic variation in this species, in particular the lack of morphological differences between Yukon and Mackenzie populations or those further south, indicated that all populations in their area (including the Athabasca drainage) were derived from a single source, probably the upper Mississippi. The present restricted distribution of trout-perch in the Yukon system suggested that it was a recent arrival there, in their view (see also Lindsey and McPhail 1986:660).

Crossman and McAllister (1986:85) believed that it was necessary to suggest also a Beringian and a possible Missourian refugium as the origin of trout-perch populations in the Hudson Bay basin. They did not elaborate on the Beringian possibility, and did not deal with McPhail and Lindsey's arguments against it. Their argument in support of a Missourian origin seems to be based on the idea that "isolation in the Qu'Appelle and headwaters of the Red River suggest two refugia or all the intervening territory [is] no longer suitable" (Crossman and McAllister 1986:80, footnote 12). The argument they used for spottail shiner; i.e., that records of the species from southwestern Alberta north to the Mackenzie suggested a Missourian origin for these populations (Scott and Crossman 1986:80, footnote 9) might also apply to trout-perch.

A refugium in the upper Mississippi River is the most obvious source of trout-perch colonizing western Canada. If trout-perch survived in Beringia and spread postglacially to the Hudson Bay basin, they would have had to enter the Athabasca drainage. The Beringian source seems unlikely for reasons discussed by McPhail and Lindsey (1970:292) and Lindsey and McPhail (1986:660), but cannot be ruled out. If trout-perch survived in, and dispersed postglacially from the upper Missouri River to the Hudson Bay basin, they could have invaded the Athabasca from that source as well. This possibility requires an explanation of why trout-perch no longer occupy the upper Missouri drainage, but there is no obvious explanation, and none has been forthcoming from fish biogeographers. As it stands, there is no agreed-upon source for the trout-perch that colonized Jasper Park waters.

**Jasper Stocks:** The only record of this fish in Jasper National Park is a collection of 37 specimens in the Canadian Museum of Nature, catalogue number NMC 69-0256, collected by J. C. Ward circa July 1969 from the outlet of Lac Beauvert (B. W. Coad, personal communication 26 September 1990). Trout-perch have not been reported from Lac Beauvert itself (Bajkov 1927, Rawson 1940a, Ward 1974, Anderson and Donald 1978b, JNP Warden Service lakes files). The lake was poisoned in 1964 (JNP fish stocking records). The population probably occupies the Athabasca River downstream from Athabasca Falls, and perhaps the accessible parts some of its major tributaries.

**Habitat:** The outlet of Lac Beauvert is a shallow perennial creek that is passable to fish (Rawson 1940a:20). The lake itself was described by Rawson (1940a:20) and Anderson and Donald (1978b:45). The Athabasca River at the outlet of Lac Beauvert is braided, with numerous islands dividing it into many side channels. Several of the islands immediately above the outlet are vegetated and persistent, of approximately constant size and shape, appearing in the same locations on 1:190,080 topographic maps printed in 1934, 1936 and 1956 (Department of Mines and Resources 1939a, 1939b; Canada Mines and Technical Surveys 1956) and in a recently published air photo stereo pair (Levson and Rutter 1989:1327). The river is cold and remains glacially turbid from spring to fall.

Paetz and Nelson (1970:211) characterized trout-perch as a fish of deep lakes and slow rivers. McPhail and Lindsey (1970:292) noted that it is typically found in quiet backwaters of large, muddy rivers, and along shallow sandy beaches in lakes. Scott and Crossman (1973:681) described it as primarily a lake species in the east, occurring also in shallow, sometimes turbid streams in the west and northwest portion of the range. Tripp and Tsui (1980:39) found trout-perch to be the most frequent species taken in minnow seine collections in slow-flowing, sandy bottomed reaches of the Hangingstone River, a major tributary of the Athabasca River near Fort McMurray.

Scott and Crossman (1973:680) summarized observations on spawning habitat. In their opinion most eastern Canadian populations spawn in streams, returning to lakes after spawning; however they drew attention to records of nearshore spawning in lakes. Spawning streams were described as shallow and rocky (in northern Manitoba); lake spawning was said to occur over sand and gravel bottom in 0-1.2 m of water. Paetz and Nelson (1970:211) stated that spawning occurs in small streams and along beaches in lakes. McPhail and Lindsey (1970:293) characterized spawning habitat as slow streams or along lake beaches. Citing a Minnesota study, they described the behaviour of trout-perch spawning in a creek within 10-13 cm of the surface near the edges of a stream. From the same study, they drew attention to the fact that juveniles in the lake mostly remained in deep water in summer, whereas the adults concentrated in the shallows for spawning.

Apart from information on stream spawning habitat just mentioned, I have found no data on use of critical habitat by river populations of trout-perch.

**Biology and Life History:** According to Scott and Crossman (1973:680), trout-perch usually spawn in early spring, most often in May, but in lake-spawning populations it is prolonged over several months. In Lake Erie, for example, spawning has been observed from May to August; in Red Lake, Minnesota, from early June to late August with a peak from 25 June to 4 July; in Lake Michigan, from late June or early July to late September (House and Wells 1973:1225). McPhail and Lindsey (1970:293) reported that ripe fish had been taken in the Muskwa River (Liard drainage near Fort Nelson, B.C.) from 5 June to 21 July; and at Circle, Alaska, (Yukon system) on 28 June. No nest is built, the adhesive eggs are simply released and stick to whatever they touch, hatching in approximately one to three weeks (McPhail and Lindsey 1970:293, Scott and Crossman 1973:680), probably depending on temperature.

There seems to be little biological information on river populations, most of what is known being derived from studies on lake stocks. Trout-perch are sexually mature as early as age 1 in some populations, but not until age 2 in others. Age 4 apparently is the maximum age in many populations, (Paetz and Nelson 1970:211), but fish in some others reach age 7 or age 8, based on scale annuli, and a maximum size of about 15 cm (House and Wells 1973:1222). Females may or may not grow faster than males, depending on the population.

Several authors have drawn attention to a marked propensity of trout-perch to move inshore at night, at least in lakes, Scott and Crossman (1973:681) pointing out that it is seldom caught in lake surveys unless otter trawls or night seining are employed. Direct observations by Emery (1973:763-4) indicated that trout-perch in Georgian Bay schooled very near the bottom in deep water close to the thermocline during the day, but moved into shallow water (2-15 m in his study site) at night, not schooling but forming a patchy distribution swimming close to the bottom.

Trout-perch feed upon aquatic insects (especially chironomids and mayflies), crustaceans (especially amphipods), molluscs and even small fish (Paetz and Nelson 1970:211, McPhail and Lindsey 1970:293, Scott and Crossman 1973:681, Crowder et al. 1981:664-5).

**Ecological Significance:** Trout-perch are said to be an important forage fish, used by northern pike, burbot and lake trout, among others (Paetz and Nelson 1970:211, McPhail and Lindsey 1970:293, Scott and Crossman 1973:681). In Jasper Park waters, they are likely to be prey of the former two species plus bull trout, several species of fish-eating birds, and possibly several other vertebrate predators. McPhail and Lindsey (1970:293) suggested that they may serve as nutrient transporters in stratified lakes because of their habit of feeding in the shallows at night, then moving into the depths by day, there to be consumed by lake trout.

**Fishing:** There is no fishery for trout-perch in Jasper Park.

**Conservation Status (general):** The trout-perch is widespread and often abundant in Canada. It is absent from most lists of rare, threatened or endangered fishes (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Williams et al. 1989, Campbell 1991). It is listed as a species of special concern by the states of Montana and Kentucky, and is given legislated protection by South Dakota (Johnson 1987:11). All three of these jurisdictions lie at the extreme southern margin of the trout-perch range (Lee et al. 1980:485).

**Conservation Status (Jasper):** Other than that it existed in the park in 1969, the status of this species here is not known.

**Required Action:**

1. A survey of park waters, especially the major river drainages, is required to determine the distribution, abundance, life history, critical habitat requirements and general biology of this species in the park. As part of this survey, the only known location in the park used by this species, the Lac Beauvert outlet, should be examined to determine if the species still uses it, and if so, what it uses it for.

2. We need to know what geographic and local stocks of trout-perch are under the care of Jasper National Park. Unfortunately, geographic variation in this fish appears not to have been studied seriously, so it is impossible to evaluate the significance and relative importance of our stocks even at the level of a first estimate.

   An examination of geographic variation in trout-perch is required. The study should examine specimens from populations throughout the range of the species using both conventional morphological characters and biochemical genetic techniques. It is not reasonable that Jasper Park be responsible for the work on its own, but the park could encourage such a project by qualified authorities, and cooperate by contributing specimens and a modest proportion of the funding.

## ***Burbot*** — ***GADIDAE***

*Lota lota* (Linnaeus) — Codfishes

**Summary:** The burbot, the only wholly freshwater representative of the codfish family, is found in lakes and streams throughout northern Eurasia and northern North America. It is common in rivers and lakes throughout Alberta. In Jasper National Park the species is thought to occupy the Athabasca River below Athabasca Falls, as well as tributaries and lakes accessible from that part of the river. A population in Celestine Lake is not native there.

On this continent two morphologically distinct, geographically limited stocks and an intermediate form are known, each apparently derived from burbot that survived the Wisconsinan in separate refugia. Which stocks are represented in Jasper Park is not known. Any combination of Cascadia, the upper Mississippi, the upper Missouri, or conceivably a more local refugium associated with the Ice-free Corridor could have contributed burbot to Jasper waters. A Beringian stock probably reached the park, if at all, only as a hybrid of the Beringian and Mississippian forms.

In the larger size classes, burbot are highly predaceous on other fish. This, plus their perceived ugliness, induces in some a profound but unwarranted revulsion toward a species which otherwise has many intriguing biological attributes. In its educational and interpretive role, Jasper National Park has an opportunity to counter the prejudice and develop a public appreciation for this misunderstood animal.

The burbot should be included in a public education program designed to change the current negative views of it and several other fish species native to Jasper waters. A survey is needed to define the distribution, abundance, life history and critical habitat of burbot in Jasper National Park. The refugial and local stocks to which Jasper Park burbot belong need to be identified.

**Nomenclature:** According to Scott and Crossman (1973:645), twentieth century references to this species have employed the scientific name currently in use plus subspecific designations *maculosa* or *lacustris*, or have elevated *maculosa* to full species status. The subspecies name *leptura* has been applied to Alaska specimens (McPhail and Lindsey 1970:298). Subspecies are no longer recognized because of apparent clinal variation in the characters proposed to distinguish them, but that is not to say subspecies-level variation does not exist in this very widespread fish.

Several alternative common names are current for this remarkable fish, which even fish biologists have called “very ugly”, “repulsive” and “disgusting” (Prince et al. 1912:21). Ling, maria and lawyer are often used in Alberta. Paetz and Nelson (1970:207) mentioned that burbot are sometimes called catfish in this province. Many other common names are listed by Prince et al. (1912:21), McPhail and Lindsey (1970:299) and Scott and Crossman (1973:645).

**Description:** The burbot is a long, mottled olive brown and yellowish, apparently scaleless fish with a broad flat head, and with a laterally compressed body posterior to the anus. It has two dorsal fins, the first small and short, the second very elongate (almost half the length of the body). The anal fin is also very long (nearly as long as the dorsal), the caudal fin is small and rounded, the pectoral fins are broad, round and attached high behind the operculum, the pelvic fins small and narrow with a threadlike projection, and are set ahead of and lower than the pectoral fins. A single thin, wormlike barbel is attached to the centre edge of the lower jaw; a shorter barbel emerges from each nostril. The skin only appears to be scaleless, but does bear minute scales embedded in it.

**Distribution:** This species is found throughout northern Eurasia and northern North America. On this continent it occurs from Alaska to northeastern Quebec, and south from the Arctic coast to the upper Columbia, Missouri, upper Mississippi and Great Lakes drainages and northern New England. It is absent from the lower portions of Pacific coastal rivers, including the lower and middle Columbia River and lower Fraser River; from the Arctic Archipelago and the extreme northern Canadian Arctic mainland, from the Labrador coast and from the Gulf of St. Lawrence coast, including Nova Scotia and Newfoundland (Lee et al. 1980:487). In British Columbia the distribution includes the Fraser River headwaters in Mount Robson Provincial Park, adjacent to Jasper Park on the west (Scott and Crossman 1973:642); BC Fish and Wildlife file data, fall 1980). In Alberta burbot have been found in every major river system (Paetz and Nelson 1970:208).

**Refugia/Postglacial Dispersal:** The present distribution of burbot includes parts of the Beringian and Mississippi-Missouri basin unglaciated areas. McPhail and Lindsey (1986:620) indicated burbot as occurring in the middle Columbia (part of the Cascadian Refugium), but later stated that burbot are "virtually confined" to the glaciated part of the Columbia basin (ibid., p. 628). Lindsey and McPhail (1986:668) likewise stated that burbot occur "solely within the glaciated portion" of the Columbia River drainage, in agreement with Lee et al. (1980:487), who showed no locality records for burbot in the unglaciated part of the Columbia system. McPhail and Lindsey (1986:628-629) argued that survival of burbot in the Cascadian Refugium was implied by the presence in the Columbia drainage of a form that is morphologically distinctive, and that the present restricted distribution in that drainage is probably due to temperature limitation.

McPhail and Lindsey (1970:21) described burbot as having quite distinct Beringian and Mississippian forms, with an intermediate form occupying the Cascadian refugial area. They suggested that each successive glaciation during the Pleistocene fragmented the range of this fish, allowing differentiation in the isolated refugia. During each interglacial period the continuous range was reestablished, a zone of intergradation developing in the area of contact. They believed the Mackenzie system to be the present-day zone of contact and intergradation. They interpreted the present-day intermediate populations in the area of the Cascadian Refugium as intermediate populations forced to the southwest by advancing ice, and suggested that similar intergrades may have survived glaciation in the upper Missouri region as well. They admitted the possibility that present clines in morphological characters may be the result in part of climatic gradients in addition to hybridization and mixing of stocks (McPhail and Lindsey 1970:298). These workers stated that the Beringian form of burbot advanced no further south postglacially than the Liard drainage; intergrades between the Beringian and Mississippian forms occurring throughout the Mackenzie system (ibid., p. 22). Lindsey and McPhail (1986:668) stated that the upper Peace could have been colonized by burbot originating from either side of the Continental Divide; i.e., from Cascadia or from Mississippi basin stock.

Crossman and McAllister (1986:79,85) distinguished between the Mississippian and Missourian refugia, indicating that burbot populations in the Hudson Bay basin were derived from both as well as from Beringia. They did not list Cascadia as a likely source for burbot stocks in their study area.

The views summarized above suggest several possibilities for the source of Jasper Park burbot stocks. Hybrids of the Beringian and Mississippian burbot stocks are said to occupy the entire Mackenzie drainage, and these could be the stock in the park. It has been suggested that a similar hybrid stock survived in the upper Missouri and moved northward postglacially into the Hudson Bay basin. If so, this presumably would have been the source of western populations in the basin, and there is no obvious reason why this stock would not have colonized the waters in Jasper Park also. Finally, it would appear that Cascadian burbot moved northward postglacially through the BC interior perhaps as far as the upper Peace River, and therefore would have colonized the upper Fraser on the way. From there they might have moved into Jasper Park via Yellowhead Pass.

To further complicate things, the burbot is a coldwater species that would appear from the present distribution to be quite capable of surviving the periglacial conditions that presumably would have existed in the Ice-free Corridor at the height of the late Wisconsinan glaciation. The only form that evidently could not have colonized the park is the pure Beringian form, which McPhail and Lindsey (1970:22) state did not advance south of the Liard drainage.

**Jasper Stocks:** Bajkov (1927:4) did not collect burbot in his investigations of 1925-26, but predicted that they would be found in the Athabasca River near Jasper on the basis of earlier studies far downstream. Rawson (1940a:58) captured one specimen in Moab Lake in September 1939. Paetz and Nelson (1970:208) gave locality records for burbot in the Miette and Whirlpool rivers. Ward (1974:30) described burbot as being common in Jasper National Park in the Athabasca drainage as far upstream as Athabasca Falls, mentioning that it had been taken from lakes Beauvert, Edna and Talbot, from the

Maligne River below the canyon and from the Miette River as far upstream as the marshy area west of Giekie station. He suggested that it may penetrate into the park in the Smoky River, and probably frequents all of the major streams entering the Athabasca below the falls, although he noted that burbot were not found during rotenone sampling of the Whirlpool River in the vicinity of Moab Lake. Ward (1974:distribution maps 11 and 12) showed burbot as occupying numerous lakes and ponds connected with the Athabasca River between Jasper townsite and the east park boundary. Recent additional records of the species include lakes Beauvert and Patricia (Anderson and Donald 1978b:80) and Celestine (Donald et al. 1985:41), but not Moab Lake (Donald and De Henau 1981:161). The population in Celestine Lake must have been introduced (Donald et al. 1985:105-6): paleolimnological evidence shows that Celestine Lake held no fish until recently (S. Lamontagne, personal communication). Burbot apparently are native to Rock Lake just outside the park boundary (Miller and Paetz 1953:101), so probably are native to at least the lower part of Rock Creek within the park boundary. There is no record of burbot in the Brazeau drainage inside the park, the nearest locality record for this drainage being far downstream in the North Saskatchewan River, a short distance above the Brazeau confluence (Paetz and Nelson 1970:208).

**Habitat:** All of the Jasper lakes said to hold burbot have surface outlets except two: Patricia and Celestine. The lakes range from very shallow (Edna, Talbot both less than 3 m) to rather deep (Patricia 42 m) (Rawson 1940a, Anderson 1974c). The streams inhabited by burbot in the park are cold, fast, rocky and, with the partial exception of Miette River, glacially turbid in summer. Details of critical habitat required by burbot in Jasper National Park have not been reported.

McPhail and Lindsey (1970:299) observed that burbot occur in large rivers, small streams, elevated lakes and low-lying ponds, but especially in the south it often lives in deep water. They cite another observer as stating that it “commonly lives under stones and in holes”, locations in which I have found it in East Slopes streams. In lakes burbot are generally restricted to the hypolimnion throughout the summer, being taken at depths as great as 213 m (Scott and Crossman 1973:643). Scott and Crossman also report the optimum temperature for the species as approximately 16-18 °C; the upper temperature limit for burbot they believed to be about 23 °C.

McPhail and Lindsey (1970:299) described the burbot as spawning in streams or lake shallows under ice, in 0.3 to 1.3 m of water. Scott and Crossman (1973:643) stated that burbot spawn in 0.3 to 1.3 m of water over sand or gravel bottom in shallow bays, or on gravel shoals 1.5 to 3.0 m deep, but they also mentioned that there is circumstantial evidence of spawning in deep water in some areas.

They may spawn in rivers also. Tripp and McCart (1979:109) found young-of-the-year burbot to be abundant in June in shallow, weedy side channels in the upper Clearwater River, a tributary of the Athabasca at Fort McMurray. They interpreted this as indicating that burbot had spawned in these areas, which are also believed to be a major spawning area, and certainly a major rearing area, for northern pike. There is no lake above this reach. Tripp and McCart (1979:35) characterized this reach of the river as having many islands and quiet, shallow side channels. "The side channels range from 1 or 2 m to more than 10 m in width and from less than 0.15 m to more than 1 m in depth. The substrate is largely composed of heavy silt and organic debris with a dense cover of aquatic macrophytes. In June, the latter was formed primarily of Mare's-tail (*Hippuris vulgaris*) with pickerel weed (*Potamogeton richardsoni*) and other pond weeds (*P. pectinatus, Myriophyllum exalbescens*) also present. A dense growth of partly submerged *Equisetum* sp. and occasionally *Scirpus* sp. often dominated the bank vegetation. Current speed was usually negligible."

Sac fry may be pelagic for a time, as in Waskesiu Lake, Saskatchewan, where burbot sac fry were common within about one metre of the surface in the open lake in late May and early June (Saunders 1972). In Lake Opeongo the larvae are pelagic through a size of approximately 20 mm, move to shallow littoral waters until they reach 20-25 cm, then take to the bottom of the lake (L. Carl, personal communication 14 March 1991). The young are sometimes abundant in small streams and the shallows of lakes (McPhail and Lindsey 1970:299). Summer habitat in the north is said to be "often in the river channels of lakes" (Scott and Crossman 1973:643). According to these writers, young-of-the-year and yearling burbot frequently are found along rocky shores, and sometimes in weedy areas of tributary streams.

**Biology and Life History:** Burbot spawn in winter, probably anywhere from January to March in Canada (Scott and Crossman 1973:643). Spawning occurs at night, and is said to involve "a writhing ball about 2 feet in diameter" of intertwined males and females moving over the bottom, releasing eggs and milt. Water temperatures at spawning are in the range 0.5 to 2.0 °C. After spawning, burbot may move into tributary rivers during late winter to early spring. Females produce immense numbers of tiny eggs, numbering in the hundreds of thousands. They hatch within 30 days or so, depending on the temperature, usually in early spring. By late spring the young are rearing: Tripp and McCart (1979:109) captured numerous young-of-the-year burbot by minnow seining in the upper Clearwater River (Fort McMurray area) between 13 and 24 June 1978.

Growth undoubtedly varies from population to population depending on the habitat and food supply. Sixteen young-of-the-year burbot caught in Gregoire Lake (Athabasca drainage south of Fort McMurray) from 16 to 23 August 1978 ranged from 65 to 88 mm (Tripp and Tsui 1980:194). Athabasca and Clearwater River fish (Fort McMurray area) of 464 to 664 mm ranged in age from 6 to 12 years (Jones et al. 1978:65). There is said to be differential growth of males and females, the latter growing more rapidly than the former beginning at age 4 (Scott and Crossman 1973:643). These authors give the usual age at maturity as the third or fourth year at lengths of 280 to 480 mm, but males often mature at a smaller size.

Burbot are nocturnal feeders, consuming mostly aquatic invertebrates as small fish, but adopting a diet of other fishes, sometimes in enormous quantities, at larger sizes. Eggs of whitefish and ciscoes are also eaten in season — again, in large quantities (McPhail and Lindsey 1970:299, Paetz and Nelson 1970:207, Scott and Crossman 1973:644).

**Ecological Significance:** Because of its supposed voracious appetite the burbot has often been considered both a competitor of, and predator on, more desirable fishes, supposedly causing their populations serious damage. This may well be true in some cases, but undoubtedly the effect is variable, and rarely has it been satisfactorily demonstrated. For example, Day (1983, cited by Carl 1991) found that burbot abundance increased with a decline in lake trout abundance in Lake Athapapuskow, Manitoba. In Lake Opeongo, however, Carl (1991) found that burbot growth, length-weight relationship and population size did not change in response to a substantial decline in abundance of lake trout.

Nevertheless, the view of burbot as a devastating predator and/or competitor has been used by some fishermen and fish biologists alike to justify an unreasonable hatred of the species, rating it almost literally on a par with night-stalking child killers. As one rather staid trio of professionals and informed laymen put it, "this fish has no redeeming qualities.…it is a glutton, feeding at night, and with its capacious mouth gulps down many small fry when they are gathered together for the night resting on the bottom. Its destruction should be encouraged whenever and wherever found" (Prince et al. 1912:21). McPhail and Lindsey (1970:299) quote the, as they put it, "trifle subjective" remarks of Seeley (1886) for a similar example from a slightly earlier year:

*"Its insticnts… are those of robber and pirate. It waylays the female and young brood, especially of the perch, and is a terror to all small fishes."*

While the colourful anthropomorphisms seem to have disappeared from the recent literature, the lethal attitudes toward burbot have remained among some fishery workers and fishermen, in my experience.

In the context of a national park, native burbot are neither good nor bad, they simply *are*. Their ecological significance is seldom known. Certainly in Jasper Park we do not know what role they play, because they have never been investigated here. Presumably here, as elsewhere, they are predators on benthic invertebrates and other fish as juveniles and adults; presumably they compete with other fishes for resources, when these are limiting; as small fish they may be eaten themselves by other predators (e.g., Carl 1991).

**Fishing:** There is no known fishery for burbot in Jasper National Park. It probably is taken on occasion by fishermen angling for other species. Although it is not commonly considered a sport fish, recreational fisheries for the species are said to be well established in some areas of British Columbia and Wyoming (Scott and Crossman 1973:645), and burbot have been promoted as "a great eating fish" in Alberta (C. Hunt, personal communication 14 April 1991).

**Conservation Status (general):** Burbot do not appear on most lists of rare, endangered or threatened species (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Williams et al. 1989, Campbell 1991), but local populations are of some concern over a wide area. The species is listed as of special concern on the southern margin of their range in Idaho, Kansas, Kentucky, and Missouri, and is given legislated protection in Iowa and Ohio (Johnson 1987:11).

Scott and Crossman (1973:644) drew attention to evidence of the considerable former abundance of the species in the Great Lakes, noting that it no longer occurs there in numbers because conditions have changed drastically. As they point out, few agencies keep records of burbot catches, which means that its current status really is undocumented. The passing of this fish would be mourned by few, making it vulnerable at least to local decimation or extirpation that easily might go unrecognized.

**Conservation Status (Jasper):** The status of burbot in Jasper National Park is undocumented. The population in Moab Lake was destroyed with toxaphene in July 1958 (JNP fish stocking records) and apparently has not been replaced by burbot from the Whirlpool River (Donald and De Henau 1981:161). Burbot appear to have survived rotenone poisoning operations conducted in Patricia Lake in September 1966 (Anderson and Donald 1978b:155). The population in Celestine Lake is not native to the lake, but was introduced sometime after rotenone poisoning in September 1967 (Donald et al. 1985:105-6). There are no estimates of the actual or relative abundance of burbot anywhere in the park.

**Required Action:**

1. A survey of the distribution, abundance, life history and critical habitat of burbot in Jasper National Park is required.

2. An attempt should be made to identify the refugial stock or stocks to which Jasper Park burbot belong so that we know just what it is we are protecting, and what is its likely significance. There is abundant morphological evidence for distinctive stocks in this very widespread species, and the wide differences in its biology and life history throughout the range suggest possible differences among geographic and local stocks. Because morphological distinctions are reportedly confused by gradients or clines in many characters (McPhail and Lindsey 1970:298), biochemical genetic techniques would have to be used to compare samples from presumptive refugial areas to those from Jasper Park.

3. This species should be included in a public education program designed to counter the current unreasonably negative views of it and several other fish species native to Jasper waters. It needs to be interpreted as an integral part of aquatic ecosystems in Jasper National Park.

## *Spoonhead sculpin* — *COTTIDAE*

*Cottus ricei* (Nelson) — Sculpins

**Summary:** The spoonhead sculpin is distributed almost wholly within Canada. It is apparently scarce throughout much of its range, many populations being known from only from one or two specimens, but it is common in the larger rivers of Alberta's East Slopes. It has been collected in small numbers in the Athabasca River in Jasper National Park. It is likely that sampling has been inadequate to properly detect the species in most park rivers.

The origin of all spoonhead sculpin populations is problematic, because the present range of the species does not include any areas known unequivocally to have remained unglaciated. It is argued here that postglacial dispersal from refugia in the Ice-free Corridor best explains the northern and western distribution of spoonhead sculpin, including its presence in Jasper. Observations in the literature hint that these northern and western stocks differ from those in the south and east in their life history and habitat preferences.

Like most other freshwater sculpins, the spoonhead sculpin requires clean water and clean substrate in order to prosper, leaving it especially sensitive to habitat degradation. Although it is relatively common along the East Slopes, there is reason to believe that dams and progressive habitat damage could severely reduce its numbers, leaving parks increasingly important as refuges for the remaining stocks.

A survey is needed to work out the distribution, abundance, life history and critical habitat of spoonhead sculpin in Jasper National Park. Research is needed on geographic variation in the species to determine what distinct geographic stocks there are, and which are protected in Jasper.

**Nomenclature:** There apparently have been no changes to the name of this species in this century (Scott and Crossman 1973:842). The names muddler, miller's thumb and bullhead are occasionally used for sculpins.

**Description:** Freshwater sculpins are front-heavy little fish with flat, broad heads and large fan-like pectoral fins. There are two dorsal fins, the first short and spiny-rayed, the second very long-based and soft-rayed. The anal fin likewise is soft-rayed and long, and the caudal fin is triangular to somewhat rounded (convex on the trailing edge). The pelvic fins are set far forward beneath the pectorals.

The several species found in northwestern North America are frequently misidentified, but spoonhead sculpins are relatively distinctive because of the combination of an unusually wide, flat head (even for a sculpin), long upcurved spines on the preopercula, single median pore on the midline of the jaw, and on small to medium-sized specimens the dense prickles over much of the body (much reduced in larger specimens) (McPhail and Lindsey 1970:337, Roberts 1988a:122). The colour varies throughout the range.

Alberta specimens are light brown to greenish-brown on the back, with darker markings (Paetz and Nelson 1970:247).

**Distribution:** The spoonhead sculpin occurs from the Peace River below Peace Canyon, below the Grand Canyon of the Liard, the Mackenzie Delta, Great Slave Lake and the Back River drainage southeastward to the South Saskatchewan River in central Saskatchewan, Lake Winnipeg, the Great Lakes and southern Quebec, thence northward again to Lac Mistassini. In Alberta it is known from the Slave, Peace, Athabasca, North Saskatchewan, Red Deer, Bow and Oldman drainages, but has not been recorded in the Petitot (Liard drainage), Hay (present at the mouth, Great Slave Lake), Beaver (Churchill drainage) or Battle (N. Saskatchewan tributary) (McPhail and Lindsey 1970:336, Paetz and Nelson 1970:249, Scott and Crossman 1973:840, Lee et al. 1980:823, Roberts 1988a:122, Houston 1990:17). The species is known from the Milk River (Missouri drainage) only as a single young-of-the-year specimen (Roberts 1988a:121). Roberts was unable to verify the existence of a spoonhead sculpin population in the Milk River despite heavy collecting, and suggested this specimen probably had entered via a diversion canal from the St. Mary River (Oldman drainage) in Montana, where it is more abundant.

Spoonhead sculpins were quite common in the Red Deer River under unregulated flows prior to 1982 (Roberts 1988b:1-2). The many locality records for the province, especially along the East Slopes (Roberts 1988a:122), suggest that it is common throughout the region.

McPhail and Lindsey (1970:338-339) described the distribution of this species as unique, being quite wide but “curiously bounded.” Scott and Crossman (1973:840) interpreted its distribution as comprising a continuous band from the lower Mackenzie River in the northwest to the Great Lakes and St. Lawrence River in the southeast, with a constriction in the middle at the Churchill drainage of Saskatchewan and Manitoba. Scott and Crossman (1973:840-841) warned that many locality records for spoonhead sculpin are based on only one or two specimens, many of those from the stomachs of lake trout or burbot, or from individual dead specimens washed up on shores. They suggested that this species may be more widespread than present records indicate. Houston (1990) concurred, emphasizing the possible inadequacy of collecting methods. His compilation of records filled in the apparent gap in the Churchill River portion of the range, and extended the range slightly northward in the Northwest Territories, and northeastward in Quebec (Houston 1990:17).

**Refugia/Postglacial Dispersal:** The present range of spoonhead sculpin does not include any areas that unquestionably were unglaciated. McPhail and Lindsey (1970:338) believed that it survived glaciation in the upper Mississippi basin, moved northward with the retreating ice, and became extinct in the southern part of its Wisconsinan range. The same authors later described the fish as one of “only three species that invaded the Liard solely from a southern refugium" (Lindsey and McPhail 1986:660).

D. E. McAllister and B. Parker, in their entry for spoonhead sculpin in the atlas of Lee et al. (1980:823), hinted of some evidence suggesting an additional refugium for the species in the upper Missouri. Crossman and McAllister (1986:79) indicated that populations in the Hudson Bay basin originated in a Mississippian refugium, but also showed Missourian and Banff-Jasper refugia as possibilities. The reason for their view is not fully developed, but evidently they would argue that spoonhead sculpin do not occur in Minnesota (the upper Mississippi River basin) and are absent today in the Red River drainage of Manitoba, North Dakota and Minnesota (ibid., p. 82), which implies that western populations were not derived from eastern ones via the usual postglacial lake dispersal routes. They cited the spoonhead sculpin's apparently greater abundance in the Oldman River than downstream in the South Saskatchewan River as a possible indication of a refugium in southwestern Alberta, but acknowledged that the availability of deep, coldwater habitat rather than a refugium may account for its distribution there (ibid., pp. 88-9).

Spoonhead sculpins are distributed along the whole length of the zone of contact between Cordilleran and Laurentide ice in western Alberta (where they are widespread and sometimes abundant), northeastern BC and east of the Mackenzie Mountains, either in or closely associated with rivers in nearly every case. They may have survived the Wisconsinan glaciation in one or more refugia within the Ice-free Corridor in this area, which could be taken to include both the postulated Banff-Jasper Refugium and the Bow-Oldman Refugium in southwestern Alberta proposed by Crossman and McAllister (1986:86-88). From there they could have invaded regions to the east by using rivers draining to the proglacial lakes along the retreating ice front. Their apparent rarity in southern Saskatchewan probably reflects habitat limitation in the warm rivers of this region.

D. E. McAllister and B. Parker (in Lee et al. 1980:823) indicated that there is a tendency toward lower counts in several meristic characters toward the northwest of the distribution. A detailed analysis by morphological and biochemical genetic means of populations throughout the range probably will be required to solve problems of stock origins in spoonhead sculpin.

**Jasper Stocks:** Ward (1974:32) reported that spoonhead sculpins have been found in the Athabasca River near Jasper townsite, and in the Whirlpool River. Specimens from Jasper Park waters collected by J. C. Ward on 9 September 1969 and identified by A. Peden are held in the collection of the Canadian Museum of Nature (B. Coad, personal communication 26 September 1990). Two were taken from a backwater of the Athabasca River 22.6 km below Jasper townsite (catalogue number NMC 71-0205), and four were taken in the Athabasca River at the Lac Beauvert outlet (catalogue number NMC 71-0206). Roberts (1988a:121) noted that they have been recorded in

Rock Lake just outside the park (see also Bradford 1990:206); therefore they probably are present in Rock Creek and conceivably the upper Snake Indian River drainage within the park boundaries. The same writer mapped a record of spoonhead sculpin in the headwaters of the Smoky River just outside the park boundary, so the species may exist within the park in that drainage. There are no records for the Brazeau drainage inside or outside the park.

I did not collect any sculpins by electrofishing and extensive seining in the Miette, Snake Indian and Snaring rivers and several small creeks near the CNR right-of-way in fall 1980 (Mayhood 1980). Sculpins are easily missed by such sampling techniques because they hide under large rocks during the day (Roberts 1988b:2). Night seining, live trapping, turning over rocks and direct observation at night with lights may prove to be effective in locating sculpins in the park.

**Habitat**: In Jasper National Park spoonhead sculpins have been found in two glacially turbid rivers. The only two precise locations mentioned for the park have been in the Athabasca River at the outlets of lakes or ponds. Nothing is known of the critical habitat required by spoonhead sculpins in the park.

McPhail and Lindsey (1970:338) drew attention to an apparent difference between northern and southern populations in the habitat they occupy. In the north, they said, most records are from the shallows of large, muddy rivers, a few are from lakes and, in James Bay, from tide pools. They noted in contrast that spoonhead sculpins in the south are not found in tributary streams, although they have been taken from the St. Lawrence River, and frequently occupy deep water (to at least 200 m) in the Great Lakes. How deep was disputed by Scott and Crossman (1973:841), who suggested 137 m as the maximum depth. McAllister and Parker (in Lee et al. 1986:823) concurred, suggesting a usual depth of 20 to 50 m in the Great Lakes, and only 15 to 20 m in the lakes of eastern Ontario and western Quebec.

In the upper North Saskatchewan River, spoonhead sculpin were restricted to the mainstem, its side channels, and the lower reaches of the larger tributaries (Tebby 1974:27). Roberts (1988a:121,127; 1988b:1) described this fish in Alberta as inhabiting "streams and rivers of the major east slope drainages", but is "usually not found in lakes within Alberta", and "reaches its greatest abundance in clean-bottomed, free-stone streams such as the upper Red Deer River", or in "clean but productive rivers such as the Red Deer and Tay." It also is known from at least two recently-formed Alberta reservoirs, Glennifer (Red Deer River) and Abraham (North Saskatchewan River) (Tebby 1974:66, Roberts 1988a:121), and from clear "salty" rivers near Fort Smith (Paetz and Nelson 1970:248). Possibly it is significant for the habitat used by spoonhead sculpins that in most of the large northern lakes where it has been reported (e.g., Athabasca, Great Slave, Dubawnt, Nueltin), the records usually are mapped at the outlets or at the mouths of major tributary rivers (McPhail and Lindsey 1970:336, Lee et al. 1980:823). McPhail and Lindsey speculated that they may be common in the depths of big turbid rivers, where there has been little sampling. Houston (1990:16) suggested that the apparent habitat differences beween eastern and western populations could be a sampling artifact. He felt that rivers seldom were sampled in the east, while the lakes of the west are few and rarely are sampled by appropriate means.

Roberts (1988a, 1988b) recently has provided almost the only significant observations available on critical habitat used by spoonhead sculpins. They spawn on the undersides of rocks along rocky shorelines, creek bottoms and the margins of rivers. Newly-hatched larvae do not have a subgravel stage, but drift with the current and begin rearing near the surface in shallows and quiet water near shore. Later in their first summer they take cover in the spaces among the rocks on the bottom. Tebby (1974:27) found young-of-the-year in desiccated side channels of the North Saskatchewan River. Clean, coarse rocky bottom seems to be essential for survival of larvae, juveniles and possibly adults. All life history stages have virtually disappeared from formerly well-occupied locations in the Red Deer River where heavy growths of diatoms now coat the rocks since the closure of the Dickson Dam upstream. Nearly all of the daylight lives of juveniles and adults is spent under large rocks or in the spaces among them, thus such habitat is critical for rearing and protection. Data from eastern populations suggest that low water temperatures (typically 4 to 8 °C, no more than 18 °C) are an important habitat characteristic (Dadswell 1972, cited in Lee et al. 1980:823).

**Biology and Life History:** Roberts (1988a, 1988b) recently relieved an almost complete void of knowledge about the life history of this species by publishing brief summaries of his 13 years of observations, mostly on the substantial Red Deer River population. The following account is extracted from his descriptions except where noted otherwise.

Spoonhead sculpins spawn from mid-April to early May after the water has warmed to 6 °C. (In sharp contrast, the few data for eastern populations summarized by Scott and Crossman (1973:841) suggest a much later spawning date: late summer or early fall.) The male selects a suitable rock and defends it from other males and other species of small fish. Females are courted, inducing them to lay an adhesive mass of 280 to 1200 eggs on the underside of the rock. The male fertilizes them and drives the female away, but may spawn with two or three females. The male guards the eggs until they hatch, fanning them with his large pectoral fins. The eggs hatch in three weeks at 8 °C, but temperatures in the river can drop to 4 or 5 °C at night (or perhaps lower during cold weather) and rise to more than 10 °C during the incubation period, so hatching times may vary rather widely.

The sac fry are 6.7 to 7.0 mm long at hatching. They swim away from the nest upward toward the light, unmolested by the male. This behaviour causes them to be distributed in the quiet shallow water near the bank where they are active by day. By the time they are 10 mm long they resemble miniature adults. Late in their first summer they begin to seek shelter among the rocks during the day, foraging actively only at night, a behaviour that continues throughout the rest of their lives.

By the end of their first summer in the Red Deer River spoonhead sculpins are 40 to 47 mm long, by the end of the second summer they are 63 to 74 mm, and by the end of the third summer they may be 85 mm and more; however there is a great deal of overlap in sizes of fish two or more years old. Size-frequency data published by Tebby (1974:67) for the North Saskatchewan River population above Nordegg suggest that fish there grew more slowly. They were approximately 24 to 29 mm long at the end of their first summer (1973 data), typically 25 to 35 mm long in their second summer, 55 to 70 mm in their third summer, and perhaps 85 to 95 mm in their fourth summer (second to fourth summer sizes estimated from 1972 data). Fish larger than 110 mm are uncommon, but one individual of 135 mm is known from the Clearwater River (North Saskatchewan drainage). Some males and females are sexually mature at 23 months of age in the Red Deer River, spawning first at the beginning of their third summer.

Larvae feed during the day in shallow, still waters near the bank, consuming microinvertebrates such as crustaceans and insect larvae. Larger juvenile and adult spoonhead sculpins are active at night, in the Red Deer River feeding upon invertebrates, often including the large perlid stonefly *Hesperoperla*, the largest invertebrate available. Planktonic crustaceans and aquatic insect larvae are assumed to be the food of this species in lakes and inshore regions, respectively (Scott and Crossman 1973:841).

**Ecological Significance:** Spoonhead sculpins frequently are consumed by a variety of trout and charr, including bull trout (Tebby 1974:27), other predaceous fishes such as northern pike, burbot, and perhaps even by mountain whitefish and goldeye. Roberts (1988a:127) suggested predators that forage among rocks in the shallows of rivers and in creeks, such as dippers (*Cinclus mexicanus*) and water shrews (*Sorex palustris*), may eat them. In the Great Lakes they were eaten by lake trout and burbot before the populations of those species were devastated.

**Fishing:** There is no fishery for spoonhead sculpins in Jasper National Park. Roberts (1988a:127) noted that they "provide an occasional surprise for anglers especially when fishing with small baited hooks and much less frequently on artificial flies. They are very 'watchable' fishes as they may be viewed by carefully turning over rocks in the shallows of clear streams. They may also be seen by night-lighting, when they have left their daytime cover to forage at night."

**Conservation Status (general):** The spoonhead sculpin has been evaluated by COSEWIC (Houston 1990), and has been judged as not requiring special designation (Campbell 1991:152). It is not listed as of special concern, rare, threatened or endangered in most other jurisdictions (Nelson and Paetz 1982, Ono et al. 1983, McAllister et al. 1985, Williams et al. 1989). It is protected by legislation in the state of New York, and Montana classifies it as a species of special concern (Johnson 1987), doubtless due to its very limited distribution in both states.

There are a number of reasons to monitor carefully the status of spoonhead sculpins. Some evidence summarized here suggests there are two or more distinct geographic stocks of this species differing in habitat requirements and life history characteristics. To maintain the full diversity of the species it is necessary to maintain the integrity of all such stocks. As noted above, many populations are known by only a few specimens. They do appear to be quite common in some of Alberta’s East Slopes streams, but the observations of Roberts (1988b) strongly suggest that one of the healthiest populations has been decimated by the effects of a dam on the Red Deer River. Existing and proposed dams on several other major rivers inhabited by this species may have already, or may in the future, destroy significant spoonhead sculpin populations, as may progressive habitat damage in general have that effect. As Roberts (1988a, 1988b) has emphasized, sculpins are sensitive indicators of stream and substrate quality; they require clean water and clean substrate in order to prosper. As damage to Alberta’s East Slopes rivers continues, we should expect further losses of this species.

**Conservation Status (Jasper):** The status of the spoonhead sculpin in Jasper National Park is not known.

**Required Action:**

1. A survey is required to determine the distribution, abundance, life history and critical habitat used by spoonhead sculpin in park waters.

2. A detailed comprehensive study of geographic variation in this fish throughout its range is required to determine if the species exists as two or more distinct geographic stocks, and if so, which stocks are present in Jasper National Park. This work should employ biochemical genetic techniques together with morphological methods. Jasper National Park should encourage such a study, and participate in funding it.

## *Records from Adjacent Areas*

For the most part, the waters of the park and those immediately surrounding it have not been sampled comprehensively enough to determine the complete species composition of their fish communities. The species briefly discussed below have been recorded from waters bordering Jasper National Park. They might be found within the park in appropriate habitat. The purpose of this section is to draw attention to these species and their potential significance to minimize the possibility that they will be overlooked in future collecting work.

Whether these fishes actually do occupy park waters depends on several factors, including the following.

Movement of fishes into the park from the Smoky, Brazeau and Fraser rivers presently is impeded or completely blocked by physical barriers to fish movement. It is possible that these features were not always an impediment, and that fishes were able to surmount them in the past.

Two waterfalls on the Smoky River mainstem are marked approximately 4 km and 6 km (river distance) below the park boundary on the current 1:200,000 topographic map for Jasper Park (Surveys and Mapping Branch 1985; see Maps 1-4, map pocket). They are presumably substantial falls if they are marked on a map of that scale, but I do not know whether they completely block upstream movements of fish. Only one fish survey has included waters in the Smoky drainage within the park, and that sampled only three lakes in this remote region: Adolphus, Beatrix and Twintree (Donald et al. 1985). There are as yet no records of native fishes in the Smoky drainage within Jasper Park.

Fish movements into the Brazeau River now are blocked by the Brazeau Dam near the confluence with the North Saskatchewan River. Numerous natural rapids or small waterfalls are found on the Brazeau River below and within the park which might impede upstream movements of fish, but whether they are sufficient to completely block fish now I do not know. Bull trout and mountain whitefish occupy Southesk Lake well upstream of these rapids and several others on the Southesk River (Maps 2 and 4, map pocket), so it is possible that other native species have entered Jasper Park in this drainage.

On the west, the Continental Divide commonly is thought to prevent fish movements into Jasper National Park from the Fraser River system. In fact the divide itself may be less of a barrier than Rearguard Falls and Overlander Falls, on the Fraser River just outside of and inside of the western boundary of Mount Robson Provincial Park, respectively. Both are sufficiently high and steep to exclude small fishes, and even the largest chinook salmon are unable to negotiate 10-m high Overlander Falls. Any fishes that might have reached Robson Park waters from the west after the Cordilleran ice receded but before these obstacles formed might have found their way into the Athabasca headwaters in Jasper Park by way of Yellowhead Pass. The Continental Divide here is low, very flat and wet, making it quite conceivable that small fishes could have passed over it during wet periods in the past — or even recently. In fact the pass is even more likely to have been a point where fishes were able to enter the Fraser drainage from the east. There are no significant barriers to upstream movement of fishes in the Miette River, so species in the Athabasca drainage could move into the waters of Yellowhead Pass and perhaps slip over the divide by means of the "Summit Lake" connection (Rogers 1915:100, see the discussion of this matter in Section I).

In the following discussion, species are organized in taxonomic order by family, and alphabetically within families by scientific name (Robins et al. 1991).

## *Acipenseridae* — *Sturgeons*

**Lake sturgeon**
*Acipenser fulvescens* Rafinesque

There is a record of this species from the lower Brazeau River at (below?) the Brazeau Dam (Paetz and Nelson 1970:54). There is a remote possibility that it enters the extreme southeast corner of the park if a remnant population was trapped in the Brazeau Reservoir.

McAllister et al. (1985) did not mention lake sturgeon in their major survey of rare, endangered and extinct fishes in Canada. COSEWIC judged it to be not in jeopardy in Canada as of 1987 (Campbell 1988:82), but its present status is under review (Campbell 1991:154). The American Fisheries Society's Endangered Species Committee has listed lake sturgeon as threatened throughout its considerable range, including Alberta, due to "present or threatened destruction, modification, or curtailment of its habitat or range" (Williams et al. 1989:3). Ono et al. (1983:29-32) described the biology, history and destruction of this once abundant fish in the Great Lakes, a poignant case study.

In Alberta, lake sturgeon have been reported from the Brazeau, North and South Saskatchewan, Clearwater, Red Deer, Bow and possibly St. Mary's rivers [Whitehouse 1919, as *A. transmontanus*; Paetz and Nelson 1970:52-4, Nelson and Paetz 1976, Alberta Fish and Wildlife 1990:9). None of the latter three references mentions a recent occurrence in the Bow River, so it may no longer exist there. Until recently it was found in the North Saskatchewan very infrequently (Nelson and Paetz 1976). "Its numbers in the North Saskatchewan River in Alberta have decreased markedly since the turn of the century, and its present status is uncertain" (Nelson and Paetz 1982:53). Sullivan (1991:26), in contrast, noted that "lake sturgeon are being angled in rapidly increasing numbers in the Edmonton area." The species also is thought to be on the increase in the South Saskatchewan, based on increases in angler-reported catches (F.

Bishop, personal communication). Whether this trend of increasing catches marks an increase in absolute abundance is debatable. The former and current status of this fish in Alberta has been briefly summarized elsewhere (Mayhood 1991:5-12).

This spectacular fish matures at 12 to 33 years, spawns only every 4 to 9 years, may live 154 years, may reach a length of more than 2.4 metres, a weight of 140 kg and may travel 400 kilometres on spawning migration (Scott and Crossman 1973:84-6). It is Alberta's freshwater equivalent of the African elephant or blue whale. Still, repeated warnings of its decline in this province have engendered no detectable public concern.

The lake sturgeon is vulnerable to extinction because of the very traits that make it so impressive. All populations need to be meticulously monitored, damaged habitat needs to be restored, and populations need to be reintroduced where they have been extirpated. If this species ultimately is found in Jasper Park, it will require careful protection.

## *Cyprinidae* *Minnows*

**Brassy minnow**
*Hybognathus hankinsoni* Hubbs

This minnow is known from the Athabasca drainage in the Fort McMurray area, including the Athabasca mainstem both above and below a series of major barrier rapids (Tripp and McCart 1979:109), and from the upper Smoky River drainage south of Grande Prairie (Bishop 1975, cited by Nelson and Paetz 1976; Lee et al. 1980:175). One view of its postglacial dispersal (McPhail and Lindsey 1970:268-9) suggests that it could occur in Jasper National Park, and it may yet be found once extensive collecting is undertaken using methods appropriate for capturing small fishes.

All Alberta records of the brassy minnow are of great importance for understanding the zoogeography of this and possibly many other fishes in the northern BC Interior and western Alberta. Known British Columbia and northern Alberta populations of brassy minnow are widely separated from the rest of the range in southern Alberta, southern Manitoba, Missouri River drainage, upper Mississippi drainage, Great Lakes, upper St. Lawrence and upper Hudson river drainages (Lee et al. 1980:175). New records would help to sort out how they got there. McPhail and Lindsey (1970:268-9) have suggested that they moved northward postglacially from the Missouri, Mississippi, or both, but were unable to find populations in western Alberta that would be expected if the Missouri were the refugium. Populations in the South Saskatchewan, lower Athabasca and Smoky drainages subsequently have been found, but there are evidently no records of brassy minnows in the North Saskatchewan or Churchill drainages as would be expected if the upper Mississippi were the refugium. Lindsey and McPhail (1986:668) have pointed to another problem with their hypothesis, notably that this little fish, which seems to favour near-lentic vegetated habitat, must have beaten several larger and better-swimming Mississippian species to the upper Peace River drainage.

If intervening populations are not found, explaining the disjunct populations becomes a difficult zoogeographic problem. The intervening populations may have become extinct postglacially, but there is no obvious reason why that should have happened. The present BC-northern Alberta distribution suggests a refugium in or near the Peace River headwaters, an area long considered to have been glaciated during the Wisconsinan. No evidence from geographic variation is available, and the taxonomic identity of the species may be in question. The genus is said to hold four to six recognized species, and needs revision (B. M. Burr, in Lee et al. 1980:175). Taxonomic revision within the genus would not solve the zoogeographic problems, however: the only other member of the genus in western Canada barely enters Alberta in the extreme south, from the southeast.

If the brassy minnow occurs in Jasper National Park, it most likely will be found in such habitats as overflow ponds adjacent to rivers, slow streams, boggy lakes and shallow bays. Some of these habitats are common along the Athabasca River from Jasper townsite to the east boundary of the park, at various locations along the Miette River, and in the Prairie de la Vache area.

**Peamouth**

*Mylocheilus caurinus* (Richardson)

The record of this species in the Athabasca River at Athabasca, Alberta, mentioned by R. L. Wallace (in Lee et al. 1980:208) appears to be the same one reported by McPhail and Lindsey (1970:232,234) and Scott and Crossman (1973:426). Paetz and Nelson (1970:253) disputed it, J. Nelson (personal communication) emphasizing that the record is almost certainly erroneous. There appear to be no other indisputable records of peamouth in this province.

Peamouth occupy the Fraser drainage at least as far upstream as the Prince George area, and some standard references (Carl et al. 1959:112, Scott and Crossman 1973:425) indicate by shading that it may occur as far upstream as the Continental Divide. There are no actual records of it in Mount Robson Provincial Park. It is possible that the species has been excluded from the area by Rearguard and Overlander falls. If it does exist above the latter falls, it could have gained access to the Athabasca headwaters via the Yellowhead Pass (Section I).

If the peamouth occurs in Jasper National Park, it most likely would be found in weedy shallows of lakes and rivers of the Athabasca drainage. Habitat of this type exists in the Miette River near Yellowhead Pass, and along the Athabasca River from Jasper townsite to the east park boundary.

**Emerald shiner**
*Notropis atherinoides* Rafinesque

Emerald shiners are fish of large rivers and lakes, where they are sometimes very abundant. The locality records in the Athabasca mainstem are for points far below Jasper Park, but the species is recorded from the upper Pembina and/or McLeod drainages near the park (Lee et al. 1980:232). If they do occur in the park, they most likely will be found in the Athabasca River, despite the lack of close records in the mainstem downstream.

**Northern redbelly dace**
*Phoxinus eos* (Cope)
**Finescale dace**
*Phoxinus neogaeus* Cope
**Fathead minnow**
*Pimephales promelas* Rafinesque

These three species are known from the Athabasca drainage east of Jasper National Park (Paetz and Nelson 1970, Lee et al. 1980). The finescale dace is recorded from as near to the park as Rock Lake (Bradford 1990), so should be expected in suitable habitat within the park portion of the Rock Creek drainage. These fishes, together with pearl dace and brook stickleback, use similar habitat, share a requirement for absence of pike and yellow perch, and frequently are found together in various combinations in this area (Robinson and Tonn 1989). Pearl dace have been reported in Jasper Park, so it is reasonable to believe that these species may occur as well. Favoured habitat is shallow muskeg lakes, beaver ponds and slow-moving streams, often in association with submerged macrophytes. In Jasper National Park this type of habitat probably is rare. Appropriate pike-free habitat perhaps occurs in a few isolated beaverdammed creeks in the Athabasca valley downstream from the town of Jasper to the park boundary, the Miette River valley, the West Block lakes area, some Prairie de la Vache streams, and possibly the Snake Indian valley between Deer Creek and Rock Creek.

**Northern squawfish**
*Ptychocheilus oregonensis* (Richardson)

To date northern squawfish have been found only in the Pacific drainage except in the upper Peace River system, where they are found in small numbers in Alberta in the Peace mainstem (Paetz and Nelson 1970:144, Nelson and Paetz 1976, Lee et al. 1980:349). There is a record of this species in the central part of the Smoky River drainage (Scott and Crossman 1973:488). A locality record mapped apparently in the upper North Saskatchewan drainage in one standard reference (Lee et al. 1980:349) contradicts a statement in the discussion of the distribution of the species in the same species account and is almost certainly in error. Carl et al. (1959:112) mapped the range of northern squawfish as not extending above the approximate location of Rearguard Falls in the Fraser drainage, but Scott and Crossman (1973:488) indicate by shading on their distribution map that they may occupy the Fraser River as far upstream as the Continental Divide. The nearest actual records are for the Prince George area.

Unless northern squawfish occupy the Fraser drainage above Overlander Falls, There is little chance that they will be found in Jasper National Park. As of 1980 the BC Fish and Wildlife Branch had no record of this species in Mount Robson Park, although their records were based on limited sampling. If they do occur above Overlander Falls there is little to prevent them from moving into Jasper Park, because the Continental Divide at the Yellowhead Pass is very low, flat and wet (Section I). If they exist in the upper Smoky drainage in Alberta they may be excluded from the park by falls a short distance below the park boundary.

**Longnose dace**

*Rhinichthys cataractae* (Valenciennes)

Paetz and Nelson (1970:131) interpreted Bajkov's (1927) Jasper records of *Agosia nubila* as longnose dace. This is unlikely for reasons discussed in the species account for lake chub. As yet there are no indisputable records of longnose dace in Jasper National Park.

There are numerous records of this widespread and sometimes abundant species in drainages north and south of Jasper Park, but surprisingly few in the Athabasca drainage near the park (Paetz and Nelson 1970:132). Nevertheless it is likely to be found here, probably in riffles of stony streams or possibly in lakes associated with the Athabasca River. It is known from the upper Brazeau and central Smoky drainages, so might be found in those drainages within the park boundaries.

**Leopard dace**

*Rhinichthys falcatus* (Eigenmann and Eigenmann)

Paetz and Nelson (1970:254) listed leopard dace as a species in an area adjacent to Alberta, so presumably it might be found here. It is known from the Columbia and Fraser drainages in British Columbia, but so far has not been reported above the Prince George area in the Fraser (Lee et al. 1980:355, Peden 1991:182-183). If it occupies the Fraser drainage in Mount Robson Provincial Park, it could have moved into the Athabasca River headwaters in Jasper National Park via the low, wet, flat Yellowhead Pass (Section I). It is not known from any other similar extreme headwaters in this drainage, however, so this possibility seems unlikely.

**Redside shiner**
*Richardsonius balteatus* (Richardson)

In Alberta redside shiners have been found only in the Peace River system, in which they evidently approach Jasper National Park in the headwaters of the Smoky River (McPhail and Lindsey 1970:220, Scott and Crossman 1973:504). Carl et al. (1959:106) and Scott and Crossman 1973:504) map their distribution as including the Fraser River as far upstream as the Continental Divide, but the nearest actual records to Jasper Park are from the Prince George area on the Fraser (Scott and Crossman 1973:504, Lee et al. 1980:358). As of 1980 the BC Fish and Wildlife Branch had no record of this species from waters in Mount Robson Provincial Park (BC Fish and Wildlife file data). If redside shiners exist above Overlander Falls they are very likely to be found in Jasper National Park.

## *Catostomidae* — *Suckers*

**Bridgelip sucker**
*Catostomus columbianus* (Eigenmann and Eigenmann)

The bridgelip sucker occurs in the Fraser River drainage at least as far upstream as the Prince George area. It appears that there has been little collecting above that point, so it is possible that it occupies waters further upstream in the drainage. If it exists above Overlander Falls, it is entirely possible that it has crossed the Continental Divide into the Athabasca headwaters of Jasper National Park via Yellowhead Pass (Section I). The bridgelip sucker would most likely be confused with juvenile longnose or mountain suckers. It can be distinguished from the former by its incompletely cleft lower lip, and from the latter by its lack of large notches at the corners of the mouth (Carl et al. 1959:93).

**Largescale sucker**
*Catostomus macrocheilus* Girard

The largescale sucker has been found in Alberta only in the Peace River drainage, where it is widespread in the Smoky River and its tributaries, and in the Peace mainstem. Carl et al. (1959:87) and Scott and Crossman (1973:545) map its distribution to include the Fraser River headwaters as far upstream as the Continental Divide, but the closest actual records to Jasper National Park in the Fraser are in the Prince George area. As of 1980 it was not known to occur in the Fraser headwaters in Mount Robson Provincial Park (BC Fish and Wildlife file data). If it does exist above Overlander Falls in that park, it may well have entered the Athabasca headwaters via Yellowhead Pass (Section I). Falls just outside the park boundary on the Smoky River may prevent its entry into Jasper Park in that drainage. It is most likely to be confused with the white sucker, but largescale suckers have a clearly longer dorsal fin base and a distinctly narrower caudal peduncle.

**Mountain sucker**
*Catostomus platyrhynchus* (Cope)

Mountain suckers have been recorded from as close to Jasper National Park as the Brazeau River at the Brazeau dam, and are widespread in the North and South Saskatchewan drainages and the Milk River in Alberta. They are to be expected the Brazeau drainage within the park. They should be watched for in the Athabasca drainage also, as it is quite possible that they have crossed the low present-day drainage divide at some point. They resemble juvenile longnose suckers closely enough in general body form that it is conceivable they simply have been overlooked in the upper Athabasca system. They are readily distinguished from all other species that might possibly occur in this region by the incompletely divided lower lip, large notches separating the upper from the lower lip, and the lack of papillae on the leading margin of the lip (Carl et al. 1959:95).

## *Gasterosteidae* *Sticklebacks*

**Brook stickleback**
*Culaea inconstans* (Kirtland)

Brook sticklebacks are widespread and often abundant in every major drainage in Alberta except for Petitot River in the Liard drainage, for which there is no published record as yet (Paetz and Nelson 1970:216, Lee et al. 1980:562). There are records of the species from the extreme headwaters of the Smoky River, and from the Athabasca drainage just outside Jasper National Park (Scott and Crossman 1973:662, Lee et al. 1980:562). They are likely to be found within the park boundaries in the habitat and locations mentioned in connection with finescale dace, northern redbelly dace and fathead minnow, above.

**Ninespine stickleback**
*Pungitius pungitius* (Linnaeus)

There are records of ninespine sticklebacks in the upper Athabasca River system near the Jasper National Park boundary (McPhail and Lindsey 1970:306, Lee et al. 1980:566). The species may be found within the park in suitable habitat such as shallow bays and slow streams. They are at the extreme western edge of their North American range in this area.

**Prickly sculpin**
*Cottus asper* Richardson

The prickly sculpin only recently has been reported in Alberta waters, in the Peace River near the British Columbia boundary (Roberts 1990:24). Carl et al. (1959:159) mapped its distribution in BC as extending nearly to the Continental Divide in the Fraser River, but the nearest actual records to Jasper National Park are the Prince George area in the Fraser drainage (Lee et al. 1980:802). If it occurs in Mount Robson Provincial Park (i.e., above Overlander Falls), there is a good chance that it reached Jasper's Athabasca head waters via Yellowhead Pass (Section I).

**Slimy sculpin**
*Cottus cognatus* Richardson

In Alberta the slimy sculpin most closely approaches Jasper National Park in the headwaters of the Smoky River, where it appears to be common (Lee et al. 1980:808, Roberts 1988a:122). In the Athabasca drainage it is known only from reaches far downstream from the park in the Fort McMurray area. In the Fraser drainage it exists at least as far upstream as the Prince George area, and there appears to be a mapped locality record for the extreme headwaters near the Continental Divide (Lee et al. 1980:808). If slimy sculpins occupy the Fraser above Overlander Falls, there is a good chance that they have penetrated the headwaters of the Athabasca in Jasper Park, crossing the Continental Divide at Yellowhead Pass (Section I).

**"Speckled Rocky Mountain bullhead"**
"*Cottus punctulatus* (Gill)"

Bajkov (1927:23,26) described a single specimen of a sculpin with palatine teeth that he identified as this species from the "Athabasca River System", noting that it occurred on "both slopes of the Rocky Mountain region, Athabasca River, Maligne River near Jasper." Paetz and Nelson (1970:242) drew attention to this record, noting that *C. punctulatus* now is considered to be a subspecies of the mottled sculpin (*C. bairdi*), and Bajkov's record would constitute a significant range extension. They also observed that mottled sculpins had been confused with slimy sculpins in the past.

Unfortunately it is not possible to identify the species from Bajkov's description. The mottled sculpin is one of two or three very similar species the precise taxonomic limits of which presently are in question (Peden et al. 1989). Slimy sculpins only rarely have palatine teeth, and then only a few (Roberts 1988a:122). Bajkov's (1927:26) published measurements for length of the anal fin base (30 mm) and snout to dorsal fin distance (31 mm) likewise suggest that this specimen was not a slimy sculpin, which has relatively a much greater snout to dorsal length (Roberts 1988a:124). Additional collecting with suitable gear in appropriate habitats within Jasper National Park is needed to determine the probable identity of Bajkov's sculpin.

## *Percidae* *Perches*

**Iowa darter**
*Etheostoma exile* (Girard)

There are records of the Iowa darter in the Athabasca drainage just east of Jasper National Park (McPhail and Lindsey 1970:350, Paetz and Nelson 1970:224). It might occur within the park in suitable habitat; i.e., clear standing waters or slow-flowing streams with rooted vegetation and sand, peat or organic debris on the bottom (Scott and Crossman 1973:785).

Iowa darters are at the extreme western limit of their distribution in this area. McPhail and Lindsey (1970:352) noted that eastern and western specimens differ morphologically. They suggested that the northwesternmost populations may represent a discrete stock derived from a glacial refugium in the upper Missouri, while eastern populations had an upper Mississippi River source. If so, Jasper-area darters would most likely be of the Missouri refugial stock.

**Yellow perch**
*Perca flavescens* (Mitchill)

Yellow perch have been reported from the Athabasca River just below Jasper National Park (McPhail and Lindsey 1970:342, Scott and Crossman 1973:757, Lee et al. 1980:714), and might occur within the park on occasion. The species is able to use a wide variety of habitats, but high turbidity and low macrophyte density might inhibit them from entering park waters via the Athabasca River.

**Walleye**
*Stizostedion vitreum* (Mitchill)

Walleye have been reported from the Athabasca drainage just east of Jasper National Park (McPhail and Lindsey 1970:346, Lee et al. 1980:748). It is possible that they enter the park in the Athabasca River. A fish biologist has reported briefly sighting what appeared to be walleye (identified by the distinctive white caudal spot) in slow, clear shallow side channels at the mouth of the Snake Indian River (Sullivan, personal communication). Unlike yellow perch, walleye are tolerant of and adapted to turbid conditions, reaching their greatest abundance in shallow, turbid lakes (Scott and Crossman 1973:772).

# GENERAL DISCUSSION

The goal of this study was to discover what is significant about the native fish stocks of Jasper National Park, and to outline how to proceed in protecting them as required by the National Parks Act and Canadian Parks Service policies. The five specific objectives set for the work were to identify the native stocks and describe their original condition, to determine whether there is anything unusual or especially valuable about them, to assess their present condition, to outline what is known about their biology and life history, and to describe what action should be taken next to protect them adequately. In this section, I summarize my conclusions on these questions.

## Which fish stocks where native, and what was their original condition?

Sixteen species or subspecies are native to the park, and an additional three might be added on the basis of disputable records (Table 1). It should be kept in mind that this listing was made without benefit of a complete fisheries survey of park waters. Twenty-two more species are known to occupy adjacent drainages, and might yet be found, with various degrees of likelihood, in Jasper Park.

Nearly all of the sixteen confirmable native fishes originally were confined to appropriate habitat in the Athabasca River and its associated lakes and tributaries below major barriers to dispersal (Athabasca and Snake Indian falls, Maligne Canyon, and numerous other unnamed barriers). In other words, most were found only in the Athabasca valley from near the town of Jasper to the east park boundary (i.e., the lower Athabasca valley for present purposes). Exceptionally, bull trout appear to have been more widespread (Map 4), occupying the upper Athabasca drainage even above major barriers such as the Snake Indian and Athabasca falls, and much of the Brazeau drainage. Like bull trout, mountain whitefish were native in the Brazeau drainage as far upstream as Southesk Lake, but otherwise conform to the general pattern so far as has been reported. Lake chub are known from certain waters above Athabasca Falls, but there is some doubt whether they are native there.

Several historical records from the early 1800s to early this century, all anecdotal, allude to large numbers of whitefish, trout and northern pike in waters of the lower Athabasca valley, giving the distinct impression that these fish originally were at least locally abundant. This conclusion is consistent with other historical accounts suggesting that these and other fishes were, if anything, even more numerous in drainages just outside the present park boundary, such as the Wildhay, McLeod, Brazeau and mainstem Athabasca. Talbot Lake, for example, was able to sustain a significant seasonal domestic fishery in the mid-1800s, supplying the fur traders and other travellers using Jasper House with whitefish as a dietary staple.

Species of whitefish and trout were not identifiable in the historic record until after the park was formed in 1907. Early records from shortly after this refer to good to excellent fishing for rainbow, bull and lake trout, and “grayling” in several identifiable park waters, or more generally. Again, the clear impression is left that these species were abundant in the waters in which they were found. What the stocks of the remaining native fishes originally were like is not known because there are no early records of them.

Whatever their historic abundance may have been, the original condition of some native fish stocks must have reflected the effects of exploitation by man. Human beings were part of the Athabasca valley ecosystem for thousands of years before the first Europeans fished its waters in the early nineteenth century. Many of the aboriginal groups that used the valley, but especially the Shuswaps, are known to have been proficient fishermen, and presumably would have exercised their skills in the streams and lakes of the area.

## *What is significant about the native fishes of Jasper National Park?*

To an angler, the answer to this question is obvious: many species native to the park are important sport fish. Among the most valuable are rainbow trout, lake trout and bull trout, but northern pike, mountain whitefish and even lake whitefish sustain significant sport fisheries. As discussed in other volumes of this series (Parts 1 and 4), the very “nativeness” of these stocks is in itself highly valued by a substantial portion of the angling public.

At least equally important, but often overlooked, is the role these and the other species play in the ecology of the park. While it has been possible only to speculate in this report on the ecological significance of the native stocks, in general terms it is obvious that various native fishes are a critical food supply for piscivorous species such as pike and bull trout, as well as certain mammals (e.g., otter) and especially fish-eating birds (e.g., mergansers and several other ducks, loons, kingfishers, terns, dippers, osprey, bald eagles, herons and others). Furthermore, it may be that benthic- and plankton-feeding fishes compete with many species of waterfowl for food where these organisms are a limiting resource.

Several of Jasper’s native fishes are (or originally were) common throughout the eastern slopes of the Rocky Mountains in Canada. To this extent they are valuable as representative stocks of fishes that are (were) characteristic of the region. Bull trout, mountain whitefish, longnose sucker, burbot and spoonhead sculpin fall into this category. Of these, the bull trout has become scarce throughout the region wherever its populations have been made readily accessible to man. Jasper National Park has an obligation to protect its stocks of these fishes in part to fulfill its overall purpose to "protect a representative cross-section of the eastern system of the Canadian Cordillera-Rocky Mountain natural region" (Canadian Parks Service 1988:5).

In contrast, many other native fish stocks in Jasper Park are significant because they are atypical.

1. Although rainbow trout are indigenous to Pacific drainages throughout western North America, the species is native to the *eastern* slopes of the North American Cordillera in only three small areas. One of these is the upper Athabasca drainage, including part of Jasper National Park. The native Athabasca rainbow trout is genetically distinct, clearly differing from all others for which sufficient comparable data are available. The existence of such a distinctive stock here poses a difficult but important zoogeographic puzzle. As a native stock, it also is likely to be better adapted to local conditions than non-native or hatchery stocks. The Athabasca rainbow therefore has both substantial scientific and fishery management value.

2. The native lake trout populations, one now certainly extirpated, the other almost certainly so, were two of only about ten thought to have been native to the Canadian Rocky Mountains. It is reasonable to expect that such isolated, remote stocks in unusual mountain habitat would have diverged substantially from those elsewhere, and may have been particularly well adapted to local conditions.

3. The stock of lake whitefish in Talbot Lake is genetically unique in the data set presently available (published electrophoresis results for 22 loci in nine enzyme systems in several dozen populations throughout North America). It is a zoogeographically informative stock of considerable scientific interest. In addition, published photographic evidence suggests that Lac Beauvert once may have held a remarkable stock of lake whitefish resembling, but different from, the broad whitefish of the Arctic.

4. The pygmy whitefish is apparently rare both in the park and in Alberta as a whole, judging from the limited data available. It is known only from the Snake Indian River, upper Waterton Lake, and another location in the Athabasca River drainage outside Jasper Park. A single Jasper specimen (the only data available from the park stock) differs enough in a combination of certain meristic characters from all other known populations to suggest that the Jasper stock is distinct from them. Whether or not this stock ultimately is shown to be distinguishable from that which it most closely resembles (Fraser drainage), its presence here is an important zoogeographic marker.

5. A new subspecies of pearl dace was described from one location in the park in 1927. The published description is inadequate to identify it with complete

confidence, and the subspecies has been considered invalid, even though specimens from the type locality have not been examined since the original collection was made. The data for lateral line scale counts are clearly below those expected for pearl dace in our region.

6. A new subspecies of longnose sucker was described from Jasper Park in 1927. Long dismissed as invalid, the Jasper longnose sucker recently has been redefined according to gill raker count, based on a re-examination of longnose suckers from the type locality. Photographs published with the original description also show the fish to differ from the widespread typical form in ways considered to be taxonomically important. The proposed subspecies is endemic to Jasper National Park, where it is now known only from Pyramid Lake.

For the most part, the significance of these apparently unusual stocks does not lie in the actual differences in scale counts, enzyme-coding alleles, and other arcane physical characters that we can observe. These are simply tags that make separate stocks recognizable. What is of value is the genetic diversity that the different stocks represent. Unique or unusual electrophoretic patterns, for example, show that a stock differs genetically from others, and if it differs genetically, it very likely differs in other biological properties as well. This diversity not only has adaptive value for the species as a whole (allowing it to take advantage of a wide variety of available habitats, for example), but enables it ultimately to evolve and form new species. This is the goal of conservation, and the goal of park managers as conservationists. To conserve a species, its genetic diversity must be conserved. To conserve genetic diversity of a species, the integrity of its individual stocks must be maintained.

In addition to the direct evidence referred to above, there are other reasons to suspect that unusual stocks of fish exist in Jasper Park. Although the Mississippi-Missouri Refugium likely contributed the greatest number of our fish stocks (Table 3), the park lies in an area that probably received fishes from Cascadia and Beringia as well. The increasing evidence that the Ice-free Corridor in western Alberta remained open for much longer than previously believed offers the possibility that many of our fishes survived glaciation close by, in one or more refuges remote from those in the major unglaciated areas south and north of the ice sheets. Certainly many of our native species are quite capable of tolerating the near-glacial conditions that must have prevailed in the Corridor region during the late Wisconsinan maximum. Though inconclusive, evidence was reviewed in this report supporting the idea that the Corridor was a refuge for some aquatic organisms including fishes.

Not only did different species survive in separate refugia, but some species survived in more than one refugium. In isolation these would be expected to diverge, producing separate stocks with differing ecological or behavioural attributes. Fishes surviving locally in the Ice-free Corridor might be particularly well adapted to local habitats because they would have evolved with them for a relatively long time.

Native stocks in a third category are significant neither because they are typical nor atypical, but because they evidently exist in ecologically marginal conditions in Jasper National Park. It recently has been argued (Scudder 1989) that ecologically marginal populations contribute a disproportionately large amount of genetic diversity to the species as a whole, and for that reason have adaptive value. Examples in this category within Jasper park might be northern pike and white sucker in the Athabasca River and associated waters below various migration barriers, and bull trout populations in Dolly and Miette lakes.

## *What is the present status of the native fish stocks in the park?*

The simplest answer to this question is that the present status of all native stocks is unknown, except for several that were extirpated by poisoning. I have assigned status categories to several stocks based primarily on the nature and apparent seriousness of the known threats to them.

One of the two stocks of native lake trout was certainly extirpated by poisoning with toxaphene (Moab Lake), and the other almost certainly has been extirpated by fishing depletion and possible introgression from introduced stocks (Pyramid Lake). Likewise, two native stocks of lake whitefish (Beauvert and Edna lakes) were extirpated by poisoning. The native Athabasca rainbow trout is provisionally considered endangered, possibly extirpated, in park waters because it has been exposed to introgressive hybridization by non-native stocks introduced into the Athabasca system on a massive scale over many decades. The Jasper longnose sucker is listed as threatened on the evidence of catches in the 1970s and 1980s that were consistently far below those recorded in the 1940s. Bull trout are here considered vulnerable because of numerous biological attributes that render the species highly sensitive to overfishing, some indications that catch rates had declined by the 1950s, the probability in depleted stocks of destructive hybridization with introduced brook trout, and the possibility of toxic contamination from a pulpmill outside the park. The same potential for toxic contamination in Athabasca River stocks accounts for mountain whitefish, lake whitefish, and longnose suckers being listed as of special concern. The Jasper pearl dace is of special concern because if confirmed as a distinct subspecies it would be of scientific importance as a Jasper Park endemic, it is known at present from only a single location within the park near the townsite, and it has not been reported since it was first described in 1927.

Apart from lake chub, which is widespread and sometimes abundant in the park, the remaining stocks are too poorly known to even hazard a guess as to their present status.

## What is known about the biology and life history of the native stocks?

There is no information available on the biology, life history or critical habitat of the great majority of native fish stocks in the park. The little that is known comes mostly from two small published studies carried out in 1925 and 1926 (Bajkov 1927, Neave and Bajkov 1929), a published account of a sucker reduction program operated on one lake in the 1940s (Rawson and Elsey 1950), a superficial examination of stream fishes along the CNR right-of-way (Mayhood 1980), rare observations made during limnological surveys conducted mostly on lakes holding introduced stocks (e.g., Donald 1987; Donald and De Henau 1981; Donald et al. 1977, 1985), a few collection records held by the Canadian Museum of Nature, and some incidental observations in brief project reports held in Warden Service lakes files. One study presently being prepared for publication by D. B. Donald will provide some new data on certain bull trout stocks in Jasper.

The compilations of biology, life history and habitat data in this report have come almost entirely from published summaries of data on stocks from throughout the range of each species. In most cases, wide variations have been reported in biological attributes, life histories and critical habitat among separate stocks, demonstrating that generalizations from the literature will have limited usefulness for conserving and managing native fishes in Jasper Park.

## What action is required now?

Details of all proposed work, including timing and cost estimates, are presented in the management plan. Only required work concerning native stocks alone is discussed in this section.

Most of the required work identified in the individual accounts for each species can be combined and considered as part of a single major project, a comprehensive survey of the native fishes of Jasper National Park. The survey should consist of the following elements.

1. Intensive fish survey of the mainstem Athabasca River (lower Athabasca valley) and accessible major tributaries, including the Miette River

   A four-season intensive survey should be conducted on these waters to identify the species using them, estimate their abundances, determine their life histories, and locate and describe critical habitat. Major migratory species should be sampled throughout the year and analyzed for pulpmill and other contaminants. Other specimens of all species should be used in a taxonomic analysis of local stocks. Where feasible, biochemical genetic techniques should be used to identify stocks and to serve as a benchmark against which possible future changes in stock structure can be measured.

The level of life history and critical habitat analysis initially needed would be comparable to that achieved on the lower Athabasca River in the Alberta Oil Sands Environmental Research Program (AOSERP). Although other designs should be considered, the project could involve trapping and marking at one fixed location at least, combined with extensive sampling and habitat description surveys elsewhere in the drainage inside and outside of the park. The project therefore should be conducted in cooperation with the Alberta Fish and Wildlife Division. This study should have top priority because of changes occurring within the Athabasca watershed outside the park. The lower Athabasca valley also probably has the highest concentration of indigenous stocks and productive habitat.

2. Extensive fish survey of the remote drainages

   Surveys of the fish stocks occupying the drainages outside of the lower Athabasca valley should be conducted during the open-water season. The purpose of these surveys is to identify the fish stocks using the drainages, outline their life histories, estimate their abundances, and locate and describe their critical habitat. Specimens from these surveys should be included in the taxonomic analysis of local stocks mentioned under (1). These surveys could be conducted over a period of years, but the upper Athabasca valley should take priority because it carries a major highway and is most the heavily-used by visitors of the “remote” drainages.

In addition to the surveys, special studies are required for several stocks in the park already identified as unusual, and have been mentioned in the appropriate species accounts. The most urgent include the following.

3. Taxonomic and genetic work on the Jasper longnose sucker must be completed, and an intensive search for other populations of this rare Jasper endemic needs to be made.

4. A comprehensive search is also needed to locate any remaining stocks of indigenous Athabasca rainbow trout. Both traditional taxonomic methods and a variety of newer biochemical genetic techniques should be used to confirm their identity.

5. A search for the “Jasper pearl dace”, a possible rare endemic, should be made in the type locality, and its taxonomic status either confirmed or rejected.

Some of the necessary searches could be conducted in connection with the major surveys described in (1) and (2), but should not wait on them if they are delayed. The surveys and special studies will provide the essential information needed to prepare stock-specific plans to conserve, manage, and where appropriate to restore the native fish and their habitats in Jasper National Park.

6. Finally, an effective interpretive effort is needed to counter sometimes strong hostility among a part of the angling public toward such native fishes as suckers, burbot and others. This might most usefully be incorporated into programs dealing with the overall ecology of the park, presenting all native fishes as integral parts of a functioning whole.

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# PERSONAL COMMUNICATIONS

As required by the Terms of Reference for this project, I interviewed many individuals with firsthand local knowledge of Jasper National Park and its fishes. Only those whose information I specifically cited in the text are listed here. I have also spoken to, or corresponded with, several people with specialized knowledge bearing on this project over a period of 15 years or more, and have cited some of their views where it was relevant to do so. I am grateful to all for their information, patience and many other kindnesses.

Many communications cited refer to inquiries I made specifically for this project, or to written comments made by reviewers on a previous draft. A few were interviews done for other projects, some of them made several years ago. Most communications were by telephone, although some were by written correspondence or conversations conducted in person. I kept notes on most telephone calls. Because personal communications are inherently subject to misinterpretation, all references to them require confirmation. The year is given for communications prior to this project. Addresses were those current at the time of the communication.

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