Canadian Manuscript Report of

Fisheries and Aquatic Sciences 2397

1997



# A REVIEW OF BURBOT (*Lota lota*) LIFE HISTORY AND HABITAT USE IN RELATION TO COMPENSATION AND IMPROVEMENT OPPORTUNITIES

by

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Cat. No. Fs 97-4/2397E ISSN 0706-6473

Correct citation for this publication:

McPhail, J.D. 1997. A review of burbot (*Lota lota*) life-history and habitat use in relation to compensation and improvement opportunities. Can. Manuscr. Rep. Fish. Aquat. Sci. 2397: viii+37 p.

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## ABSTRACT

The burbot (*Lota lota*) is a true cod found in freshwater lakes and rivers throughout the Holarctic region. Its spawning time (mid-winter), enormous fecundity, and pelagic larvae are unique amongst British Columbia freshwater fishes. There is a growing interest in burbot as a recreational species, especially as the object of winter fisheries, but the species is proving difficult to manage, and burbot fisheries have a history of collapse. In British Columbia, there is no detailed study of life-history, but studies elsewhere in North America suggest a life-history that is especially vulnerable to recruitment over-fishing. In lakes, the larvae appear shortly after ice-out and remain in the pelagic zone for about a month. The mortality in the larval stage is high but at about 30 mm the larvae transform, leave the water column, and take up a demersal life. This habitat shift is accompanied by a transition from crepuscular to nocturnal activity, and a change in diet. Juvenile burbot remain inshore in relatively shallow water and feed and grow throughout the winter. As they grow, their diet gradually shifts to fish, and adult burbot are primarily piscivores. With increased size they progressively move to deeper water and recruit to the adult population at about the time of sexual maturity. The age at first maturity varies latitudinally and males usually reach sexual maturity a year or two before females. The adults are temperature sensitive and usually avoid temperatures above 12°C. Spawning occurs in lakes (over shallows) and in rivers (side channels behind deposition bars) at temperatures ranging from 0° to 4°C.

There are suggestions in the European literature of genetically different ecotypes (e.g., lake and river forms). In British Columbia lacustrine, adfluvial, and fluvial populations occur in the same river system. Presumably, the selection regimes associated with these different life-history types also differ (especially in the larval and juvenile stages). Since information on population dynamics and life histories are major components of any management strategy, an obvious place to start in British Columbia is with a study of burbot biology (particularly recruitment and mortality rates). Because the province was colonized from at least two, and probably three, ice-free areas, such an investigation should include both Columbia and Mackenzie populations.

# RÉSUMÉ

La lotte (*Lota lota*) est un gadidé qui se retrouve dans les lacs et les rivières d'eau douce de toute la région holarctique. Sa période de fraie (le milieu de l'hiver), son extraordinaire fécondité et la nature pélagique de ses larves en fait une espèce tout à fait à part parmi les poissons d'eau douce de Colombie-Britannique. On observe un intérêt croissant pour la lotte comme poisson de pêche sportive, spécialement pendant les pêches d'hiver, mais cette espèce semble difficile à gérer, et sa pêche s'est souvent effondrée. En Colombie-Britannique, il n'existe pas d'études détaillées sur son cycle biologique, mais des travaux effectués ailleurs en Amérique du Nord permettent de penser qu'elle est particulièrement vulnérable à la surpêche du potentiel reproducteur. Dans les lacs, les larves apparaissent peu de temps après la fonte de la glace, et elles restent dans la zone pélagique pendant un mois environ. La mortalité est élevée au stade larvaire mais, à environ 30 mm, les larves se transforment, descendent dans la colonne d'eau et adoptent un mode de vie démersal. Ce changement d'habitat s'accompagne d'une transition de l'activité crépusculaire à l'activité nocturne, et à une modification du régime alimentaire. Les juvéniles restent sur le littoral, dans les eaux relativement peu profondes, et se nourrissent et grandissent tout au long de l'hiver. À mesure qu'ils se développent, leur régime alimentaire s'oriente graduellement vers les poissons, et les lottes adultes sont essentiellement piscivores. À mesure que leur taille augmente, elles se déplacent vers les eaux plus profondes, et recrutent dans la population adulte vers la période de la maturité sexuelle. L'âge à la première maturité varie largement, et les mâles l'atteignent généralement un an ou deux avant les femelles. Les adultes sont sensibles à la température, et évitent généralement des températures de plus de 12°C. La ponte a lieu dans les lacs (sur les hauts-fonds) et dans les cours d'eau (dans les bras, derrière les bancs de sédiment) à des températures situées entre 0 et 4°C.

Les études européennes permettent de penser qu'il existe des écotypes génétiquement différents (p. ex. des formes lacustres et lotiques). En Colombie-Britannique, on retrouve dans le même réseau fluvial des populations lacustres, adfluviales et fluviales. Les régimes de sélection associés à ces différents types de cycle biologique diffèrent aussi probablement (particulièrement dans les stades larvaire et juvénile). Étant donné que les renseignements sur la dynamique des populations et les cycles biologiques sont des éléments fondamentaux de toute stratégie de gestion, il apparaît à l'évidence que les travaux doivent commencer en Colombie-Britannique par une étude de la biologie de la lotte (particulièrement les taux de recrutement et de mortalité). Étant donné que la province a été colonisée à partir d'au moins deux, et probablement trois régions libres de glaces, une telle étude devrait porter sur les populations du Columbia et du Mackenzie.

## DISCLAIMER

The views expressed herein are those of the author, and do not necessarily represent those of the Department of Fisheries and Oceans.

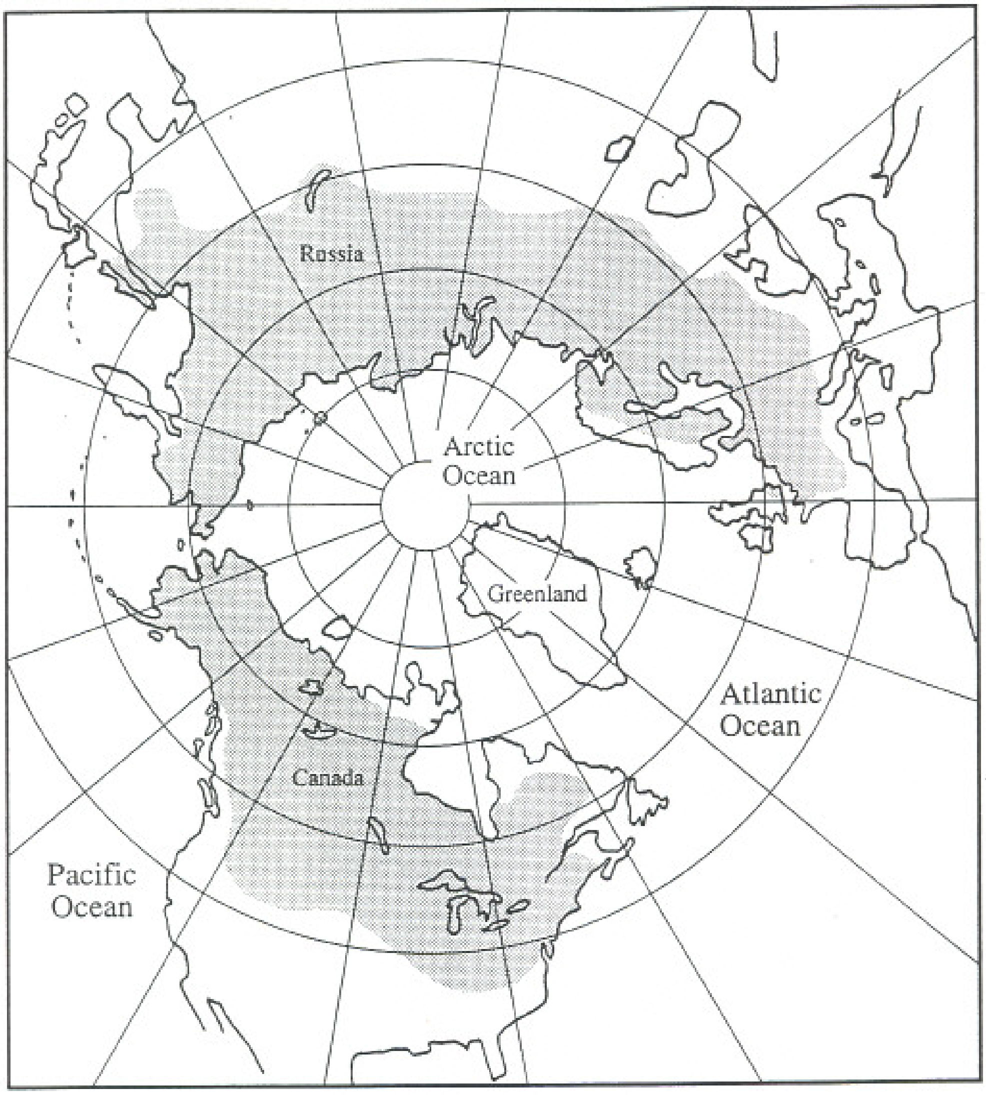
## 1.0 INTRODUCTION

The burbot, or ling, (*Lota lota*) is an unusual fish in two ways: it is the only true freshwater representative of an otherwise marine family (the cods, Gadidae), and it has a remarkably wide, Holarctic distribution (Figure 1). One other cod, the Atlantic tomcod (*Microgadus tomcod*), often spawns in brackish, or even fresh, water but spends most of its adult life in the sea. In Newfoundland and eastern Quebec, however, a few tomcod populations are landlocked and complete their entire life cycle in fresh water (Legendre and Lagueux 1948; Scott and Crossman 1973). In contrast to the tomcod, the burbot normally completes its life cycle in fresh water and only rarely enters the sea, but in some areas (e.g., the Gulf of Bothnia in Finland and Sweden; the Mackenzie Delta in northern Canada) it occurs in estuaries and brackish lagoons (Preble 1908; Percy 1975; Pulliainen et al. 1992). Residence in these areas is transitory and, apparently, under brackish conditions, a high proportion of adult burbot are either sterile or fail to mature (Pulliainen and Korhonen 1990). These observations suggest that although burbot can tolerate brackish water, estuaries are marginal environments, and the species is primarily a freshwater fish.

Along with the pike (*Esox lucius*), the burbot has the widest longitudinal range of any freshwater fish. It extends in an almost continuous distribution from the British Isles eastward across Europe and Asia to the Bering Strait (Berg 1949). On the North American side of the strait, burbot range eastward from the Seward Peninsula in Alaska (McPhail and Lindsey 1970), to New Brunswick on the Atlantic coast (Scott and Crossman 1973). Given this wide geographic distribution, it is not surprising that the species' taxonomy is confused. Originally, European and North American burbot were considered separate species: *Lota lota* (Linnaeus) in Europe, and *Lota lacustris* (Walbaum) in North America. However, Gunther (1862) reduced all burbot to a single widespread species (*Lota lota*) but, later, Hubbs and Schultz (1941) argued for the existence of at least three subspecies: *Lota lota lota* in Europe and most of Siberia, *Lota lota lacustris* (= *maculosa*) in eastern North America, and a new subspecies, *Lota lota leptura*, in north-western North America and eastern Siberia. Most recent authors (e.g., Lindsey 1956; Lawler 1963; McPhail and Lindsey 1970; Scott and Crossman 1973; Morrow 1980; Simpson and Wallace 1978; Wydoski and Whitney 1979, and Nelson and Paetz 1992) have not used subspecific designations.

This does not imply that burbot are genetically uniform throughout their immense geographic range or, even, that subspecific names are unwarranted, but only that the traits that supposedly characterize the different subspecies are unreliable. Indeed, it would be remarkable if a fish with a North American range that includes three, and perhaps four, glacial refugia (Figure 2) was not divisible into geographic forms. Certainly, most species whose preglacial ranges were fragmented by glaciation now show geographic patterns in morphology that suggest survival in multiple refugia (McPhail and Lindsey 1970), and recent molecular

Figure 1. Circumpolar distribution of *Lota lota* (after Svetovidiv 1948).

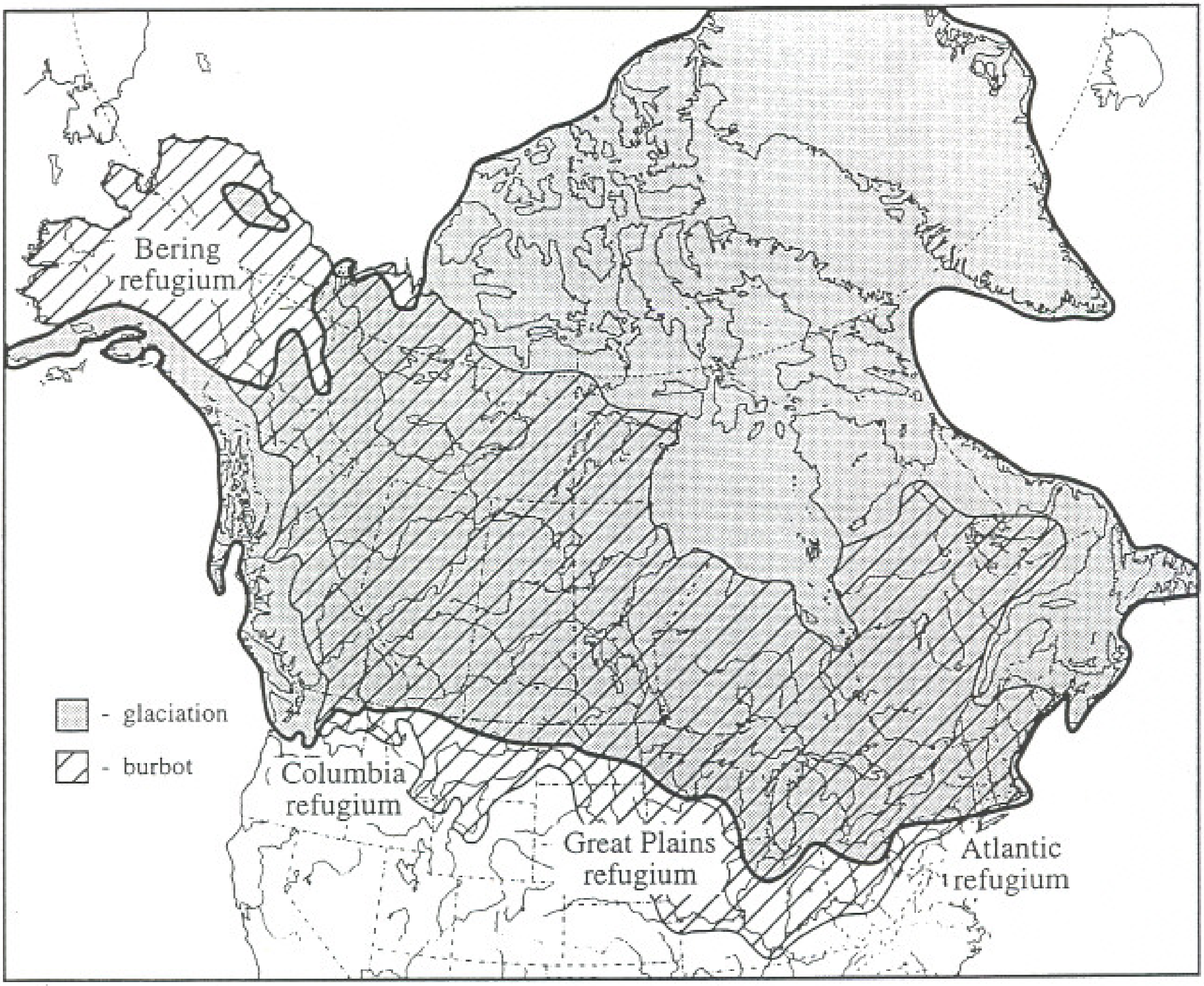



studies (e.g., Billington and Hebert 1988; Grewe and Hebert 1988; Bernatchez and Dodson 1991; Taylor and Dodson 1994) support this interpretation. In addition, Chen (1969) demonstrated that burbot from the interior of Alaska (Hubbs and Schultz's *Lota lota leptura*) consistently differ in a number of morphological traits from burbot found elsewhere in North America. This suggests that variation in *Lota lota* has geographic patterning and, consequently, treating all burbot as a single taxon may be misleading. Clearly, it is time for a review, using modern techniques, of the taxonomy of burbot.

For burbot, however, questions about geographic variation are of more than taxonomic interest. Published accounts of the species' basic life-history (e.g., spawning times, egg size, incubation regimes, migration patterns, age at maturity, sexual dimorphism, and growth patterns) indicate considerable variability. Since life-history data provide the basic foundation for all management, mitigation, and habitat compensation programs, any concept that organizes the often contradictory burbot life-history data into a rational pattern deserves serious consideration. In North America, the notion that burbot survived glaciation in more than one refugium provides a useful framework for organizing life-history data. The presence of fossil burbot in unglaciated areas of the Yukon (Cumbra et al. 1981) indicates that the species survived the last (Wisconsin) glaciation in the Bering refuge, while relict populations well south of the southern limits of continental glaciation argue for the survival of burbot in several refugia to the south of the Laurentide and Cordilleran Ice-sheets (Lee et al. 1980). Thus, glaciation severed gene flow between fish in these different refuges, and these isolated populations probably were exposed to different selection regimes in the different refugia. Consequently, the populations diverged and genetic differences (morphological, ecological and behavioural) accumulated between burbot in the different refugia. Postglacially, these newly evolved forms dispersed into glaciated areas and eventually re-established a continuous distribution. Where different forms came into postglacial contact, they probably hybridized and established suture zones. There is, however, a growing body of evidence that outside of these suture zones the different forms retain their basic characteristics. For example, Snyder (1979) describes two types of burbot larvae from the Great Lakes region (Figure 3). One type is confined to the lower Great Lakes (below Niagara Falls) and the other type to the upper Great Lakes, the upper Mississippi and Missouri systems. Snyder argues that the two types of larvae represent two species. This seems improbable, but the geographic distribution of the two larval types in the Great Lakes follows a pattern of genetic variation typical of species that survived glaciation in both the Atlantic and Mississippi refuges (Bernatchez and Dodson 1991).

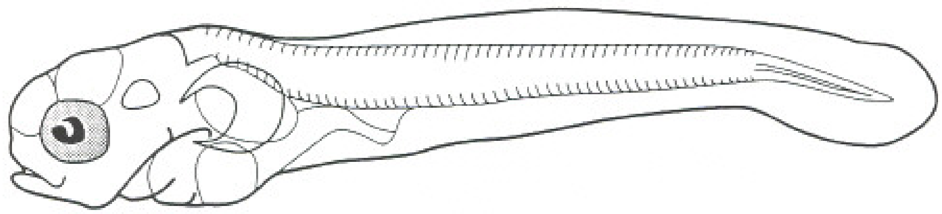
In British Columbia, burbot are widely distributed and could have colonized the province from at least three unglaciated areas (Figure 4): the Columbia; the Great Plains, and the Bering refugia. Comparison of burbot from the Columbia and Mackenzie systems reveals significant regional differences in pyloric caeca number and caudal peduncle ratio that are relatively consistent within each geographic region (Table 1). These differences are concordant with the hypothesis that each area was colonized from a different refugium: the Columbia-Kootenay burbot from the Columbia refugium, and the Liard-Peace burbot from the Great Plains refugium.

Figure 2. Approximate limits of Wisconsin glaciation, the four major ice-free refugia, and the North American distribution of Burbot (*Lota lota*).

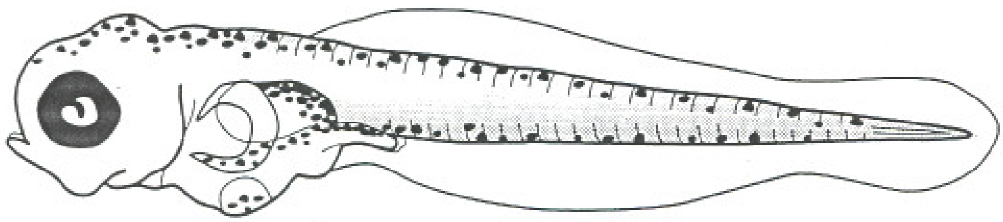



In addition, burbot in the upper Liard River (above Liard Canyon) may have originated from the Bering refugium. Burbot certainly survived glaciation in the Yukon system (Cumbra et al. 1981), and there is evidence from other species that the upper Liard was colonized from the Yukon system (Lindsey et al. 1981; McPhail and Carveth 1992).

Figure 3. The two types of larval burbot from eastern North America (after Snyder 1979).



**A.** *Lota lota* , Lake Erie (4.5 mm TL).



**B.** *Lota lota* , Mississippi River, Minnesota (4.7 mm TL).

Figure 4. The approximate distribution of burbot (*Lota lota*) in BC and the three potential sources of postglacial colonists: 1) Columbia, 2) Great Plains, and 3) Bering refugia.

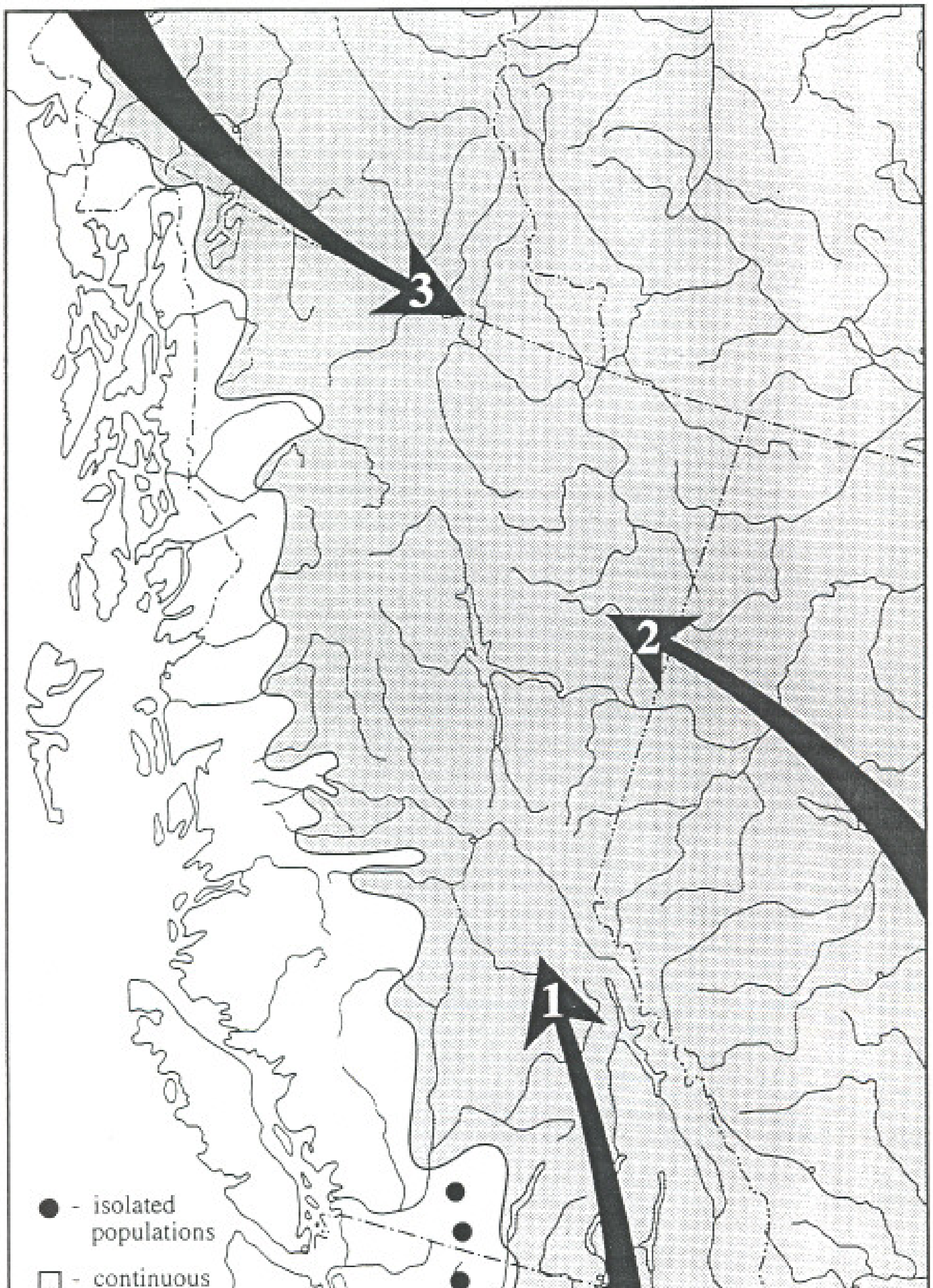


Table 1. Morphological comparison of burbot from the upper Columbia, Mackenzie (Peace-Liard) and Yukon river systems.

| River system | Pyloric caeca | | | | Caudal peduncle ratio | | | |
|---|---|---|---|---|---|---|---|---|
| | mean | range | SE | N | mean | range | SE | N |
| Columbia - Kootenay | 57.33 | 35-76 | 10.42 | 40 | 1.50 | 1.3-1.8 | 0.27 | 40 |
| Peace - Liard | 82.62 | 45-107 | 15.31 | 30 | 1.98 | 1.4-2.5 | 0.36 | 30 |
| Yukon* | 115.9 | 67-168 | 21.82 | 114 | 1.94 | 1.4-2.5 | 0.35 | 176 |

* Yukon data from the Tanana River, Alaska (Chen 1969).

## 2.0 BURBOT LITERATURE

Robins and Deubler (1955) attempted a complete bibliography on *Lota lota* from its description in 1758 up to 1954. Their review covered papers on the taxonomy, anatomy, ecology, fisheries and life-history of burbot, but did not include faunal lists that merely mentioned the presence of the species. For this period (almost 200 years) they listed 256 publications as significant contributions to knowledge about burbot. Sixty-one percent of this literature dealt with North American burbot, and 39% with European and Siberian burbot. Of the North American references, only one (McCray 1952, a popular magazine article on the Kootenay Lake ling fishery) specifically referred to burbot in British Columbia. A recent, more eclectic, burbot bibliography (Pearse 1987) list 599 references. This includes the 256 references in Robins and Deubler plus about 340 references since 1955. Pearse's compilation includes about equal numbers of European and North American papers. From 1987 to 1993 approximately 70 articles on burbot appeared in the primary literature (abstracted journals and conference proceedings). In this recent literature, the proportion of North American to European and Siberian articles is about 28% North American and 72% European and Siberian. This change reflects a growing interest in burbot as a commercial and recreational species in Scandinavia, Russian and the Danube countries. No articles in the recent primary literature deal specifically with burbot in British Columbia, but there is a growing literature on

Alaskan burbot. Again, this reflects their relative importance as a recreational resource in the interior of Alaska.

In recent years another source of information on burbot has become increasingly important. This is the so called "grey" literature. The "grey" literature consists of consultants reports, government reports, and unpublished theses. This "grey" literature is growing, but accessing it is a vexing problem. Usually these reports have a limited distribution, and are rarely deposited in major libraries, and almost never appear in standard abstracts. Consequently, there is no efficient way to find this material and, as a result, it is often over-looked. Unfortunately, in British Columbia, and in the surrounding provinces, territories and states, most of the recent information on burbot life histories, ecology and management is in this "grey" literature.

## 3.0 BIOLOGY OF RELEVANT LIFE HISTORY STAGES

### 3.1 SPAWNING

#### 3.1.1 Areas and habitat characteristics

Burbot spawn in both lakes (Clemens 1951b; McCrimmon and Devitt 1954; Robins and Deubler 1955; Meshkov 1967; Boag 1989; Ghan and Sprules 1991) and rivers (Cahn 1936; Robins and Deubler 1955; Chen 1969; Sorokin 1971; Johnson 1981; Breeser et al. 1988; Evenson 1993b). In lakes, spawning usually occurs over near-shore shallows (1.5-10 m deep: Clemens 1951b; McCrimmon 1959; Johnson 1981; Boag 1989) or over shallow off-shore reefs and shoals (McCrimmon 1959). There are, however, suggestions of deep water spawning in the Great Lakes (e.g., Clemens 1951b). The substrate is usually sand, gravel, or cobbles and is relatively free of silt (McCrimmon and Devitt 1954; Chen 1969; Sorokin 1971; Boag 1989). In rivers, burbot spawn in low velocity areas in main channels (Breeser et al. 1988) and in side channels behind deposition bars (Sorokin 1971). The preferred substrate in rivers appears to be fine gravel, sand, or even fine silt (G. Oliver, pers. comm.), but coarse gravel and cobbles are used in lakes. There is no site preparation and the eggs are broadcast into the water column well above the substrate (Fabricius 1954). Depending on the current, the semi-buoyant eggs may initially drift but eventually settle into interstices in the substrate (Sorokin 1971).

#### 3.1.2 Season and conditions

Most authors agree that burbot spawn in the winter or early spring, often under ice, (December to early March: Bjorn 1940; Clemens 1951b; McCrimmon and Devitt 1954;

Lawler 1963; Meshkov 1967; Chen 1969; Johnson 1981; Kouril et al. 1985; Sandlund et al. 1985; Breeser et al. 1988; Boag 1989), and that the spawning season is relatively short (2 or 3 weeks) and highly synchronized (Boag 1989). In Kootenay Lake, however, Martin (1977) suggests that burbot begin spawning in early April and continue into late May or early June. If so, this is the latest, and most protracted, spawning season recorded for burbot; however, elsewhere in the Kootenay region (e.g., Kootenay River at Fort Steele, and Columbia Lake) burbot spawn in late January or February (G. Oliver, pers. comm.).

Not surprisingly, burbot spawn at low temperatures (1° - 4°C : Fabricius 1954; McCrimmon and Devitt 1954; Hewson 1955; Lawler 1963; Meshkov 1967) and Kouril et al. (1985) indicate that a change in temperature from 0° to 2.5°C can delay spawning by 14 days. These field observations suggest that burbot eggs are adapted for maximal survival at temperatures between 0° and 2°C; yet Jager et al. (1981) indicate that the optimal development temperature for burbot eggs is between 4° and 7°C and that mortality increases below 4°C. So far, this anomalous result is unexplained.

There is disagreement about the time of day when burbot spawn, and it may vary with region. Because spawning usually occurs under ice, observations on actual gamete release are rare; however, most faunal works state that burbot spawn at night (Carl, Clemens and Lindsey 1959; Scott and Crossman 1973; Simpson and Wallace 1978; Morrow 1980). In contrast, all of the spawnings that Fabricius (1954) observed in a large stream-tank occurred during the morning or in the evening. In Alberta, Boag (1989) observed burbot through a hole in the ice and noticed that the water became cloudy about mid-morning. He suggests that the cloudy water results from the release of milt, and infers that spawning occurred at this time. In the Kootenay River, at Fort Steele, burbot spawn at night at depths in excess of one metre (G. Oliver, pers. comm.).

### 3.1.3 Behaviour

Because of the difficulty of observing spawning burbot, the only description of actual gamete release is that of Fabricius (1954). He placed four ripe males and four ripe females in a large stream-tank and observed three separate spawning bouts. Each spawning bout involved a single male and a single female, and included multiple gamete releases at 5 to 20 minute intervals. Gamete release occurred above the substrate and the semi-buoyant fertilized eggs slowly settled to the bottom. In contrast to these tank observations, field observations on burbot spawning indicate aggregations. Cahn (1936) describes a large "ball" with one or two females at the center surrounded by many males. Eggs and sperm are released as this "ball" writhes about in the water column. Similar "writhing balls", each involving more than 12 individuals, have been observed in Dutch Creek, a tributary to Columbia Lake (G. Oliver, pers. comm.). Other observations are less dramatic but agree that spawning involves more than just a pair of fish (McCrimmon 1959; Boag 1989).

3.1.4 Fecundity

Like other cods, the batch fecundity of burbot is enormous (Table 2), and estimates of egg number vary from 6,300 (Miller 1970a) to 3,477,699 (Roach and Evenson 1993). Clearly, fecundity is variable and, apparently, average fecundity can vary substantially between lakes in the same geographic area (Boag 1989). As in most fish, there is a positive relationship between length, and to a lesser degree age, and fecundity (Roach and Evenson 1993). Thus, large individuals produce more eggs than small individuals, but in burbot the effect of size on fecundity is not as pronounced as it is in many fish (Boag 1989; Roach and Evenson 1993).

Not all adult fish spawn every year. Evenson (1990) estimates that about 15% of the female, and 17% of the male, burbot aged 7 or older (i.e., adults) collected from the Tanana River, Alaska, from November to mid-February would not have spawned in the year they were sampled. Similarly, Pulliainen and Korhonen (1990) estimate that about 30% of the adult burbot in their samples did not spawn every year. In Alberta, Boag (1989) calculated that 5% of the adults in Cold Lake and 1.5% of the adults in Lac Sainte Anne did not spawn on consecutive years, and in Lake Winnipeg, Manitoba, Hewson (1955) notes that 5% of the adults on the spawning grounds are not ripe. These observations suggest that in northern populations some adults "skip" spawning on some years.

3.2 EGG DEVELOPMENT, HATCHING AND LARVAE

3.2.1 Egg size

Burbot eggs are round with a large oil globule and variously described as demersal, semi-buoyant and buoyant; however, if Fabricius's observations on spawning are typical, these apparently contradictory descriptions may represent different stages in the process of fertilization and water hardening. Fabricius (1954) noted that spawning occurs above the substrate and, when first fertilized, the eggs appear to be neutrally buoyant but the movements of the spawning adults keep the eggs suspended in the water column. Thus, for a short while the eggs are suspended, but gradually they sink and drift along the bottom until they lodge in interstices in the sand or gravel. The eggs are not adhesive.

Variation in egg diameter is not as easily explained as the differences in buoyancy. Some of the recorded differences in egg diameter certainly reflect differences in preservation and measuring techniques, and in the state of maturation at the time the eggs were measured. For example, often it is unclear if the measurements were made on extruded eggs or eggs still in the ovaries and, if extruded, whether the eggs were fertilized or not. Even allowing for these sources of error, however, there appears to be geographic patterning in size of burbot eggs in North America (Table 3). Generally, mean egg diameter in eastern North American

Table 2. Fecundity estimates in North America burbot.

| Average fecundity | Range | Region | Author |
|---|---|---|---|
| ----- | 160,000 - 670,000 | Lake Erie | Fish 1930 |
| 812,282 | 268,832 - 1,154,014 | Lake Superior | Bailey 1972 |
| 364,342 | 142,442 - 1,380,640 | Minnesota | Muth 1973 |
| 448,134 | 74,810 - 1,362,102 | Manitoba | Lawler 1963 |
| 620,620 | 64,498 - 1,444,122 | Wyoming | Bjorn 1940 |
| 933,944 | 15,498 - 1,675,102 | Wyoming | Williams 1958 |
| 462,000 | 230,000 - 1,000,000 | Wyoming | Miller 1970a |
| 16,000 | 6,300 - 29,900 | Wyoming | Miller 1970b |
| 504,980 | ----- | Alberta | Boag 1989 |
| 701,320 | ----- | Alberta | Boag 1989 |
| 969,986 | 23,937 - 3,477,699 | Alaska | Roach and Evenson 1993 |

populations is greater than that found in western North American (including Alaska) populations. Since in most fishes larval size is a function of egg size, this pattern suggests that newly hatched burbot may be slightly larger in eastern North America than they are in western North America. In Europe and Siberia egg diameter ranges from 0.88-1.14 mm (Nikolsky 1954; Meshkov 1967).

3.2.2 Development rate

As in most fish, development rate and zygote mortality are functions of temperature: development rate usually is faster at higher temperatures; while, zygote mortality usually increases on either side of some optimal development temperature. The only estimate of the optimal development temperature for burbot is that given in Jager et al. (1981). They estimate that the optimal incubation regime for burbot lies between 1.0° and 7.0°C,

Table 3. Egg diameter in North American burbot populations.

| Locality | Author | mean egg diameter (mm) |
|---|---|---|
| Lake Erie | Fish 1930 | 1.7 |
| Minnesota | Cahn 1936 | 1.25 |
| Minnesota | Muth and Smith 1974 | 1.12 |
| Manitoba | Lawler 1963 | 0.50 |
| Wyoming | Williams 1958 | 0.76 |
| Wyoming | Miller 1970a | 0.86 |
| Wyoming | Bjorn 1940 | 1.04 |
| Alberta | Boag 1989 | 0.92 |
| Alberta | Boag 1989 | 0.79 |
| Alaska | Chen 1969 | 0.71 |
| Alaska | Roach and Evenson 1993 | 0.53 |

and that on either side of 4.0°C zygote mortality sharply increases. Yet, most of the natural incubation regimes inferred for both North American and European populations are below 4.0°C. For example, in Lake Simcoe, McCrimmon (1959) suggests that most of the incubation period (about 71 days) is spent at temperatures below 2°C. In Hemming Lake, Manitoba, Lawler (1963) suggests incubation occurs at below 4.0°C and, in Ontario, Ryder and Pesendorfer (1992) measured temperatures of 1.0°C in shallow bays in the early spring. Under hatchery conditions in Wyoming, Bjorn (1940) records an incubation period of 30 days at a constant 6.1°C. In Europe, most authors (e.g., Andersson 1942; Meshkov 1967; Sorokin 1971) agree that incubation occurs at temperatures less than 4.0°C. Andersson (1942) suggests an incubation period of 41 days at 2.0°C, and Meshkov (1967) gives 98-128 days at close to 0°C.

Burbot eggs sometimes hatch under the ice (Ryder and Pesendorfer 1992), and in eastern North America larvae are usually present, and feeding, by mid-April (McCrimmon 1959; Ghan and Sprules 1993). Yet, Jager et al. (1981) indicate that the larvae require temperatures above 8°C to survive. Some populations spend several months in brackish water, but no population is known to spawn in brackish water. Populations in the Gulf of Bothnia migrate to rivers to spawn, although both Jager et al. (1981) and Johnson (1981) indicate that the eggs are tolerant of low salinities (1-6 ppt).

3.2.3 Larval size

Not surprisingly, the small eggs of burbot produce small larvae. Ghan and Sprules (1991) estimated that larvae they collected in Lake Oneida, New York, had just begun exogenous feeding on April 18 and had hatched four or five days earlier. These larvae ranged from 3-4 mm in total length. McCrimmon (1959) reported a mean larval length of 4.6 mm in Lake Simcoe, and Mansfield et al. (1983) collected larvae that ranged from 3.0-7.5 mm in length in Lake Michigan from mid-march to mid-June.

Shortly after hatching, larval densities can be high (up to 15/m$^2$ of surface area) but, within a month, densities have dropped to less than 1/m$^2$ even though the larvae have not dispersed throughout the entire lake (Ghan and Sprules 1991). This suggests high larval mortality rates.

## 3.3 LARVAL HABITAT AND FEEDING

3.3.1 Larval habitat

In lakes, newly hatched burbot larvae are pelagic (Clady 1976; Ghan and Sprules 1991; Ryder and Pesendorfer 1992). At first, they drift passively in the water column, but as they grow and their swimming performance improves, they become more mobile. In Lake Oneida, from April 19 to May 9 the modal depth of larvae was approximately at 7.5 m, but by May 17 they had moved to the surface. In Ontario, Ryder and Pesendorfer (1992) observed larvae high in the water column. Small schools of larvae moved inshore and were observed feeding during the day. In early spring and early summer (March to mid-June) in Lake Michigan, Mansfield et al. (1983) found the maximum concentration of larvae at depths of 3.0-7.5 m, and Clady (1976) and Ghan and Sprules (1991) found that larvae consistently disappeared from pelagic samples in Lake Oneida in June. This suggests that in lakes, larval burbot undergo a habitat shift in early summer. This shift occurs at sizes above 15.0 mm (Ghan and Sprules 1993).

Apparently, little is known about the larval ecology of fluvial populations, although G. Oliver (pers. comm.) notes that in the upper Columbia quiet water areas often are found downstream of major spawning sites, and that these areas could provide nursery sites for larvae. Also, burbot spawn near the outlet of St. Mary Lake near Kimberly, British Columbia and, apparently, some larvae are displaced downstream. This downstream displacement is inferred from the presence of small burbot in downstream tributaries that are ice-bound at spawning time (G. Oliver, pers. comm.).

### 3.3.2 Larval feeding

Field observations suggest that exogenous feeding starts about 5 days after hatching and that the first food items are rotifers (Ghan and Sprules 1993), or copepods and cladocerans (Ryder and Pesendorfer 1992). Vatcha (1990), however, raised hatchlings in the laboratory and found that the larvae first eat phytoplankton and do not switch to copepod nauplii until the third day of exogenous feeding. Ghan and Sprules (1993) suggest that once they start feeding the larvae select the largest prey items they can engulf. Hartmann (1983) indicates that burbot larvae go through two ontogenetic feeding stages. From 5-14 mm the number of particles in the gut increases with fish size, but from 15 mm to transformation (about 30 mm) the number of particles in the gut remains relatively constant while particle size increases with fish size. Regardless of the details of initial feeding, larval growth is rapid in May and June but tapers off in August (Ryder and Pesendorfer 1992). At about 30 mm the larvae switch from day active to night active and take up a solitary, benthic existence.

## 3.4 YOUNG-OF-YEAR HABITAT AND FEEDING

Girsa (1972) demonstrated that burbot larvae are first photo-positive but, at about 40 mm, they reverse their response to light and become photo-negative. In lakes, this change appears to trigger a shift from a schooling, diurnal life to a nocturnal, solitary, benthic life. Lawler (1963) and Boag (1989) observed that young-of-year burbot sheltered under stones and debris in shallow bays and along rocky shores during the day, but were out foraging at night. Ryder and Pesendorfer (1992) also found young-of-the-year in shallow water (0.5 to 3.0 m). Again, these burbot fingerlings were night-active, and sheltered during the day under rocks and debris where they excavated small burrows. The change from pelagic to benthic life is accompanied by a shift in major prey items: larvae 3-10 mm long fed primarily on copepods and cladocerans; those 11-20 mm took zooplankton and dipterans; those 21-30 mm contained 60% zooplankton and 30% amphipods; those 31-40 mm contained 85% amphipods, while larger fingerlings contained mostly amphipods and insects (Ryder and Pesendorfer 1992). At high latitudes (i.e., above the Arctic Circle) young-of-year burbot are night-active in summer and day-active in winter (Kroneld 1976).

In rivers and streams, young-of-year burbot also shelter in weed beds, under rocks, debris, and cutbanks during the day (Robins and Deubler 1955; Hanson and Quadri 1980). Here, they feed on amphipods, mayflies, stoneflies and the young of other fish (Robins and Deubler 1955; Bishop 1975; Hanson and Quadri 1980).

Burbot grow rapidly in their first year and, depending on food resources and length of growing season, they can reach 110-120 mm in total length by late fall (Chen 1969; Sandlund et al. 1985). Apparently, they continue to grow throughout the winter (Boag 1989).

## 3.5 SUBADULT HABITAT AND FEEDING

Subadult burbot occupy essentially the same habitat as the young-of-the year: shallow littoral environments with rocks, weeds or debris as cover. They feed mainly on insects but, as they grow, they progressively shift towards a diet dominated by fish (Clemens 1951a; Beeton 1956; Bishop 1975: Nagy 1985; Sandlund et al. 1985; Guthruf et al. 1990). Subadult burbot grow rapidly until the onset of sexual maturity after which growth rate declines (Boag 1989; Bruesewitz et al. 1989). The age at sexual maturity varies both geographically and with sex. Generally, in both Europe and North America, northern populations (Chen 1969; Kirillov 1988b; Evenson 1990) reach maturity later (4-7 years) than southern populations (3-4 years: Robins and Deubler 1955; Lelek 1980; Boag 1989). In Czechoslovakia, the onset of sexual maturity is negatively correlated with the average annual temperature in different regions (Bastl 1985). Most authors agree that males mature about a year before females (Bjorn 1940; Clemens 1951b; Kirillov 1988b; Boag 1989; Sandlund et al. 1985).

## 3.6 ADULT HABITAT AND FEEDING

Burbot are a northern species and, at the southern edges of their range, they typically inhabit deep lakes or cool rivers and reservoirs associated with mountainous areas. In the Columbia system, for example, burbot populations are rare south of the 49$^{th}$ parallel except in deep oligotrophic lakes like Kachees, Cle Elum and Chelan or rivers, lakes and reservoirs in the headwaters of the Kootenay and Flathead rivers in Idaho and Montana (Brown 1971; Simpson and Wallace 1978; Wydoski and Whitney 1979). In lakes, adult burbot are strongly associated with the bottom, and the areas used appear to be temperature dependent. Hackney (1973) gives the preferred summer temperature range as 10°-12°C and suggests that adults avoid temperatures above 13°C. Thus, in the summer, burbot are usually below the thermocline (Sandlund et al. 1985; Kirillov 1988a; Carl 1992; Edsall et al. 1993). In Lake Superior, burbot regularly occur to depths of 300 m where they construct extensive burrows in the substrate (Boyer et al. 1989, 1990). A preliminary underwater television survey in Okanagan Lake also suggests burbot build burrows in the substrate under deep water (B. Shepherd, pers. comm.). In some lakes, burbot move into shallow areas or even into rivers in late fall (Lawler 1963; R. L. & L./EMA 1985). These movements are thought to be part of a pre-spawning feeding migration.

The habitats used by adult burbot in rivers are not clear. They are a common fluvial species in northern rivers where summer temperatures rarely exceed 18°C(Chen 1969; Hatfield et al. 1972; Bishop 1975; Breeser et al. 1988; Kirillov 1988a; Hvengaard and Boag 1993) but relatively uncommon in southern rivers where summer temperatures often exceed 20°C. In southwestern rivers, they are restricted to high altitude, cool systems (e.g., the upper Kootenay in Idaho, Montana and British Columbia, and the upper Missouri in Montana and Wyoming). In northern rivers, adult burbot are associated with main channels and appear to prefer turbid water (Chen 1969; Hatfield et al. 1972; Breeser et al. 1988), although they often enter tributaries in the fall. In the Baltic, and the Mackenzie Delta, burbot regularly enter brackish water in the summer (Preble 1908; Percy 1975; Mueller 1982) but return to rivers in the fall.

Adult burbot usually are characterized as piscivores, and most authors (Clemens 1951a; Rawson 1951; Nikolsky 1954; Hewson 1955; Bonde and Maloney 1960; Lawler 1963; Bailey 1972; Hatfield et al. 1972; Nelichik 1972; Bishop 1975; Magnin and Fradette 1977; Chisholm et al. 1989) indicate that over 80% of their diet consists of fish. In North America they take a wide spectrum of species including lampreys, various whitefish, grayling, pike, suckers, many species of minnows, sticklebacks, trout-perch, yellow perch, sculpins and burbot. The proportion of fish in the diet is related to size, but even large burbot usually take some insects and macro-invertebrates. Also, diet can shift seasonally (Bailey 1972). For example, in Lake Koocanusa (Libby Reservoir) the main winter forage fish for adult burbot is the largescale sucker (*Catostomus macrocheilus*) but in the spring yellow perch (*Perca flavescens*) replace suckers as the main diet item (Chisholm et al. 1989).

The life span of burbot varies geographically, but the general pattern is for northern populations to contain older fish than southern populations. In Quebec, for example, Magnin and Fradette (1977) note that individuals older than 7 years are rare in populations at 45° N, but in populations at 55° N most adults are 8 to 12 years old. The maximum ages recorded in northern populations are about 20-22 years (Hatfield et al. 1972; Nelichik 1972; Guinn and Hallberg 1990). Lengths of over 1 m and weights up to 24 kg have been recorded from Lake Onega (Berg 1949) but such large individuals are uncommon (Keleher 1961).

## 4.0 OTHER RELEVANT BIOLOGICAL FEATURES

### 4.1 MIGRATION AND HOMING

Many lacustrine burbot populations are adfluvial (Sorokin 1971; G. Oliver, pers. comm.): they live in lakes but migrate to rivers to spawn. In Lake Baikal, burbot enter river mouths in September when temperatures reach 10° -12°C and in October they move further upstream towards the spawning sites (Sorokin 1971). This migration involves travel rates of 1.5-2.0 km/day. Spent fish return to the lake in March. Similar adfluvial spawning migrations occur in eastern North America (Robins and Deubler 1955) and in the Kootenay region of British Columbia (G. Oliver, pers. comm.). From Columbia Lake, a spawning migration has ascended Dutch Creek in February to the same site for many years but, when that site was channeled, they shifted to another spring-fed tributary characterized by fine gravels over-lying clay (G. Oliver, pers. comm.). This observation suggests that if burbot are homing to a specific spawning site, they can shift from a disturbed site to a suitable alternative site if such is available.

Fluvial populations of burbot also migrate long distances to specific spawning sites (Tripp et al. 1981). Evenson (1993a) radio tagged burbot in the Tanana River, Alaska. He found that small burbot (<450 mm) on average moved about 17 km, but that large burbot (>650 mm) on average moved about 57 km. The longest movement was 255 km. In addition, small burbot showed no seasonal pattern to their movements; whereas, large burbot made their greatest moves at freeze-up and ice-out. This pattern suggests a spawning migration, and Evenson was able to infer the location of a number of spawning sites in both the main river and in tributaries. In the upper Columbia, burbot migrated from the main river into the Spillamacheen River to a spawning site that historically supported a popular spear fishery (G. Oliver, pers. comm.). At the southeastern edge of their range, Robins and Deubler (1955) describe a downstream migration of fluvial adults in the late fall and early December in the Susquehanna River, New York and Pennsylvania. Presumably, this is a spawning migration and the adults return to the headwaters from March to May.

After spawning in rivers tributary to the Gulf of Bothnia, adult burbot descend into brackish water and spend about six months in the sea (maximum salinity 6 ppt) before returning to the rivers (Johnson 1981). Apparently, juveniles make a similar migration but at a different time (August to January). There also is evidence of a regular migration of burbot in the Mackenzie Delta to brackish areas in the outer delta (Percy 1975).

Except for spawning migrations, burbot in both rivers and lakes appear to be relatively sedentary. In the Slave River, some radio tagged burbot moved upstream (40-280 km) but others remained in the release area or moved short distances downstream (R. L. &L./EMA

1985). Keleher (1963) studied the movements of tagged burbot in Great Slave Lake. Two thirds of the recovered tagged fish were found within 10 km of the original tagging site, even though the average time at large was 581 days. One individual, however, was recovered in the lake 117 km from the tagging site, and another individual left the lake and was recovered 90 days later 406 km away in the Slave River. A few burbot have been tagged in the Peace River and a few in the Columbia River below Keenleyside Dam, and they appear not to move long distances, but there are too few data to detect any pattern.

Between lakes there is evidence of seasonal migrations that may be temperature mediated. Kennedy (1940) describes burbot movements between two lakes connected by a short channel. The lakes had different seasonal temperature regimes (one was cooler than the other) but burbot appeared to move in both directions. In Lake Michigan, Bruesewitz et al. (1989) noted the seasonal movement of tagged fish from Green Bay into Lake Michigan proper. In contrast, in Alaska, Lafferty et al. (1990) found only limited movement of tagged fish between connected, and closely adjoining, lakes.

## 4.2 STOCKS

The presence of lacustrine, adfluvial and fluvial life-history forms in the same system (e.g., the upper Columbia) argues that within a region burbot probably are divisible into genetically discrete demes or stocks. Even within large lakes there is evidence of stock structure. Hewson (1955) found significant length-weight differences between burbot spawning at different sites in Lake Winnipeg, and Sorokin (1971) describes differences in run timing between different rivers entering Lake Baikal. The most extreme case of stock differentiation is that reported by Nelichik (1978). He argues that there are two morphologically and ecologically distinguishable forms of burbot in the upper Tuloma Reservoir, Kola Peninsula: a lacustrine form and a fluvial form. The central part of the reservoir covers what was a lake (Lake Notozero), while two other regions were originally river channels. The lacustrine form occupies the former lake area and differs from the other two regions in vertebral, gill raker, and pyloric caeca numbers as well as in several morphometric traits. In addition, there are differences between the forms in rate of growth and fecundity. The samples were collected five to nine years after the reservoir was filled, and the persistence of the two forms, in spite of opportunities for interbreeding to erode the differences, suggests that their morphologies adapt them to alternative niches: lacustrine and fluvial. Curiously, no one in North America has examined different ecological forms of burbot for morphological and genetic differences, even though in systems like the Columbia, there are clearly fluvial, adfluvial and lacustrine populations (G. Oliver, pers. comm.). If Nelichik's results are general, the life histories of the different ecological forms of burbot may be sufficiently different as to require separate management strategies.

## 4.3 POPULATION SIZE AND CONTROLS

Not surprisingly, burbot populations vary in numbers. The most reliable adult population estimates come from lacustrine populations in Alaska where an extensive stock assessment program, based on tagging and CPUE (catch per unit effort) data, has operated since the mid-1980s (Bernard et al. 1991; Lafferty et al. 1990, 1991, 1992; Evenson 1993b; Parker 1993; Lafferty and Bernard 1993). Across a variety of lakes, adult (>450 mm) density estimates range from 0.24-21.9 per hectare of surface area. The highest recorded adult densities are for Julian's Reef, southwestern Lake Michigan. Here, densities range from 0 to 571 (average 139) per hectare of lake bottom (Edsall et al. 1993). Given the large batch fecundity of burbot, larval densities should be high. In Oneida Lake, New York, Ghan and Sprules (1991) estimated larval abundances, shortly after egg hatch in mid-April, of between 14 and 15 larvae per square metre of lake surface. Within a month, density had dropped by 50% and continued to decline up to June when the larvae shifted from a pelagic to a benthic mode of life. Ryder and Pesendorfer (1992) report a similar rapid decline in the relative abundance of larvae from hatch to the shift to a benthic life. Carl (1992), assuming a 1% survival from larvae to benthic settlement, estimated that there should be about 24 young-of-the-year per metre of suitable shoreline. The actual recruitment to shallow inshore areas was estimated at less than 50 young over 29 kilometres of shore. He concluded that burbot numbers are limited by recruitment. Although their assessment method estimates subadult (<450 mm) to adult (>450 mm) recruitment, workers in Alaska (Lafferty and Bernard 1993; Parker 1993) also conclude that recruitment is limiting burbot populations. In contrast to the high mortality rates of larvae, adult survival usually is high (0.5-1.0, average 0.70; Lafferty et al. 1991, 1992).

Many authors (e.g., Clemens et al. 1923; Clemens 1951b; Chisholm et al. 1989) have observed a broad diet overlap between burbot and other piscivorous fish (e.g., walleye, lake trout, bull trout) and inferred a competitive interaction between burbot and these species. Day (1983) tested this notion by comparing numbers and growth of an unexploited burbot population in a lake with an exploited lake trout population. He found that burbot numbers increased and growth rate decreased as lake trout numbers declined. These responses are consistent with the hypothesis that a lake trout-burbot interaction is controlling burbot numbers. In contrast, Carl (1992) detected no changes in burbot growth or numbers at a time when lake trout numbers increased by about 20%. This apparent contradiction may reflect differences in the fish communities in the two lakes, and Carl (1992) suggests that predation by planktivores on larval burbot may be responsible for the apparent "recruitment bottleneck" in burbot.

Also, it is possible that cannibalism is an important population control mechanism in burbot. Chen (1969) notes that at some times of the year young burbot are a major food item of adults in the Tanana River, Alaska. Given the high survival and longevity of adults, cannibalism, if common, could explain the characteristic low recruitment of burbot populations.

## 5.0 ENVIRONMENTAL IMPACTS ON BURBOT HABITAT

### 5.1 IMPOUNDMENTS

A repeated pattern in Europe, Siberia and North America is the increase in burbot density that accompanies the creation of reservoirs. Typically, burbot are reported as rare before impoundment but become a dominant species a few years after impoundment (Borgstroem and Loekensgard 1984; Kirillov 1988b; Chisholm et al. 1989). An explanation for this phenomenon may be increased larval survival in reservoirs. There are no data on larval survival in rivers but, since early larvae drift passively with current (Ghan and Sprules 1991), larval survival to demersal settlement probably is lower in flowing water than in an impoundment. In addition, forage species (e.g., minnows, suckers and perch) usually increase in reservoirs and, typically, the forage base used by adult burbot increases after impoundment (Kirillov 1988b; Chisholm 1989). Together, increased larval survival and increased adult foraging opportunities may explain the observed increases in burbot density after impoundment.

Although burbot populations often increase after impoundment, the downstream effects of impoundment can be detrimental (Hildebrand 1991; Paragamian 1993). Obvious downstream effects of impoundment are changes in temperature and flow regimes. Most burbot populations spawn from mid-January through February at water temperatures well below 4°C. Impoundment causes significant rises in winter temperatures and this may delay maturation (Kouril et al. 1985) and increase egg mortalities. In addition, many burbot populations have pre-spawning migrations, and apparently they increase their food intake before moving to their spawning sites (Chen 1969). Whether temperature and flow regimes influence the timing of these pre-spawning migrations is unknown but, taken together, increased winter temperatures and changes in flow regimes probably negatively influence burbot reproductive success (Paragamian 1993).

Another common impact of impoundment in northern and temperate regions is an increase in mercury levels in fish. For example, the creation of the South Indian Reservoir in northern Manitoba was accompanied by increases in mercury contamination in burbot (Bodaly et al. 1988). In the Parsnip Reach of Williston Lake (a Peace system reservoir), 21 percent of the burbot sampled exceed the federal guideline of 0.5 ppm mercury per kg (Watson 1992).

## 5.2 PIPELINES

Gas and oil pipelines are seldom a serious threat to burbot. Seismic exploration and pipeline construction may increase turbidity in effected waters, and adult burbot are sensitive to turbidity. Indeed, they show a strong preference for turbid over clear water (Chen 1969). At spawning time, however, burbot usually seek clear water and the eggs, once they settle, are susceptible to smothering. This is may be a problem in northeastern British Columbia, where pipeline construction in muskeg areas often occurs in winter. Since burbot spawn during the winter, construction silt at this time is potentially lethal to eggs and larvae. Leakage of petroleum derivatives into streams, and the subsequent tainting of burbot flesh, is a potential problem. Findings of burbot accumulating petroleum aromatics (Morgan et al. 1987) are further substantiated by complaints registered in the Mackenzie system near Norman Wells regarding tainted burbot flesh (Lockhart et al. 1987).

## 5.3 OTHER IMPACTS

Forest industry wastes and paper mills are sources of mercury contamination in burbot (Klein et al. 1987; Bagge and Hakkari 1992). Because of their position in the food chain, burbot can accumulate a sufficient mercury load to be unfit for human consumption (Sandlund et al. 1987); however, there is little direct effect on burbot themselves and Bagge and Hakkari (1992) note that burbot and perch are the only fish that still reproduce in an area heavily contaminated with paper mill effluent.

Severe acidification of lakes is often accompanied by marked declines in burbot populations (Gunn 1982) but, with lime treatment, Berqquist (1991) documents the successful recolonization of 25-50% of the lakes where burbot went extinct. In contrast, after the Schweizerhalle chemical spill in the upper Rhine, burbot have not recolonized the area where they occurred before the accident (Mueller and Meng 1990).

Climate change may be a factor in the restriction and gradual loss of burbot at the southern edge of their geographic distribution. Basically, burbot are a cold water species and their preferred summer temperature lies between 9° and 12°C (Ferguson 1958; Hackney 1973; Bruesewitz 1990). Above 12°C both subadults and adults shift their distribution to below the thermocline (e.g., Edsall et al. 1993). If this option is not available, even in northern lakes, summer kills may occur (Lafferty et al. 1992). Indirect evidence for the importance of temperature is the sporadic distribution of burbot at the southern edges of their range. For example, in the Okanagan system burbot are present in Okanagan and Skaha lakes but absent from the shallower lakes in the system (University of British Columbia Fish Museum records). In the same vein, on the east slope of the Rocky Mountains in Wyoming and Montana, burbot are common at altitude but absent down on the warmer plains (Simon 1946; Brown 1971). In

Britain, burbot have disappeared over the last decade (Maitland and Lyle 1990) and, although the causes of their extinction are not clear, increasing summer water temperatures are part of the picture.

Little is known about the impacts of fish introductions on burbot. Perhaps, it is coincidence that the decline of burbot in the Columbia River downstream of Keenleyside Dam occurred at the same time that introduced walleye (*Stizostedion vitreum*) populations were starting to build (Hildebrand 1991).

## 5.4 SPORTS FISHERIES

Until recently, recreational fisheries for burbot in western North America were largely unregulated. In British Columbia, burbot were taken through the ice with set-lines and by jigging, but in some areas (e.g., the East Kootenays) spearing burbot on their spawning grounds was a popular pastime. In British Columbia, the fishery is now regulated (five to ten fish per day), spearing is banned, and set-lines are only authorized in regions six (Skeena) and seven (Omineca-Peace) (G. Oliver, pers. comm.). In northern British Columbia, some burbot are still taken in subsistence fisheries, and in northern Alberta and the Northwest Territories subsistence and dog food fisheries for burbot are locally important (R. L. & L./EMA 1985).

Recreational fisheries for burbot in the lakes and rivers of southern British Columbia share a similar pattern of exploitation: a period of abundance that extended into the 1960s and 70s followed by a period of dramatic declines in the 1980s. The thriving Kootenay Lake burbot fishery described by McCray (1952) and Martin (1977) is now almost non-existent (D. Atagi, pers. comm.). To a lesser extent, the burbot fishery in Okanagan Lake is also in decline (J. Baxter, pers. comm.), and the size of burbot has declined in Windermere and Columbia lakes (G. Oliver, pers. comm.). The causes of declines in these lacustrine populations are difficult to assess: changes in the limnology of the lakes (especially Kootenay Lake), destruction of spawning sites, and over-fishing are confounded in most cases. However, the decline in burbot size in Windermere and Columbia lakes suggests that over-fishing is an important contributor to the declines. There is also evidence of declines in fluvial populations. Before the construction of Keenleyside Dam at the outlet of lower Arrow Lake, there was a winter burbot fishery in the Columbia River near Castlegar. This fishery lasted into the mid-1980s and then collapsed. In 1980/81 burbot made up 2.2% of the total catch in an extensive survey of the Columbia River between Castlegar and the US border, but in a similar 1991 survey they made up less than 0.1% of the total catch (Hildebrand 1991).

In Idaho and Montana there is a similar pattern of collapse in the recreational fisheries (Paragamian 1993), and in Washington the burbot population in Banks Lake declined to the point that an introduction of Montana burbot was attempted (P. Mongillo, pers. comm.). The best documented collapses of recreational burbot fisheries are those in a series of lakes in the Tanana system in Alaska (Lafferty et al. 1990, 1991, 1992; Lafferty and Bernard 1993). Several of these lakes supported unregulated recreational fisheries into the mid-1980s. The fisheries then collapsed and gear restrictions and limits were imposed. The burbot populations in these lakes are monitored annually but, interestingly, the populations are slow to recover and have not yet returned to pre-collapse levels.

This repeated pattern of collapse under intense recreational harvest suggests that burbot fisheries are susceptible to recruitment over-fishing. Given their life-history, this is not surprising. Burbot are a long lived species with enormous fecundity, but larval mortality is high and recruitment to the adult population is low. Fish with these characteristics are easily over-exploited. There is, however, evidence that depleted burbot populations can rebound. In Scandinavia, acid rain eliminated burbot from a large number of lakes, but with lime treatment burbot returned to 25-50% of these lakes (Berqquist 1991). In the same vein, burbot populations in Lake Michigan were greatly depressed during the peak Sea lamprey years, but they rebounded after the institution of lamprey control measures (Bruesewitz et al. 1989). In Alaska, where unregulated fisheries dramatically reduced burbot numbers in several lakes, they appear to be slowly increasing after the institution of gear and catch restrictions (Parker 1993).

## 6.0 OPPORTUNITIES FOR HABITAT COMPENSATION AND IMPROVEMENT

### 6.1 SPAWNING AND EGG DEVELOPMENT HABITATS

In British Columbia, almost all reported burbot spawning sites are in flowing water. This does not mean that all British Columbia burbot spawn in rivers and streams; it probably reflects the relative conspicuousness of fluvial spawning runs compared to spawning aggregations in lakes, especially lakes with ice covers. In rivers, the preferred spawning sites are associated with slow water. Such areas are deposition sites and, consequently, the substrate is usually made up of fine material. This places the demersal eggs at some risk from siltation, but burbot spawn in mid- to late-winter (a time of clear water and low flows). Where burbot have abandoned a traditional spawning site (e.g., the west channel of Dutch Creek just above Columbia Lake), the loss of the spawning run coincided with human activities that altered the flow and substrate characteristics of the site (G. Oliver pers. comm.). Presumably, if we knew what aspects of the environment burbot were cueing on in their choice of spawning sites these could be duplicated to produce artificial spawning sites in cases where human activities have destroyed the natural sites. Using the same information, it may be possible to restore traditional spawning site that have been damaged or, in some cases, to enlarge natural spawning sites and increase larval production. However, any program to modify existing spawning sites should be viewed with caution, and not attempted without a study of the characteristics of preferred local spawning sites and the major local causes of larval mortality.

## 6.2 LARVAL MORTALITIES

The available evidence indicates that burbot suffer high larval mortalities (Clady 1976; Ghan and Sprules 1991; Carl 1992; Ryder and Pesendorfer 1992). This "larval bottleneck" may be a major factor controlling burbot population density. There is little that human intervention can do to lessen this mortality. For many marine fish, including several species of cods, the initiation of feeding is a "critical period" of high mortality. Theoretically, if burbot larvae go through such a "critical period", it might be possible to provide an artificial pulse of phytoplankton followed by a pulse of zooplankton through some kind of lake or stream fertilization program. Since burbot often hatch under the ice, such a program would be expensive and the technical obstacles formidable.

## 6.3 JUVENILE HABITAT

The transition from pelagic to demersal life is a period of high mortality for burbot (Carl 1992), but why this is so is not clear. One possibility is that suitable cover is limited. On a rocky, debris strewn shore this seems unlikely but in littoral areas with little or no cover, newly transformed burbot may suffer high mortalities. Under such conditions, it may be feasible to add cover (e.g., hollow cement building blocks). On a small scale, such manipulations are easy to perform and assess, and they may increase the survival of juveniles. Similarly, the addition of instream cover in quiet water areas (e.g., side channels, pools, or areas behind deposition bars) might improve juvenile survival in rivers. If, however, there is adequate cover and the mortality associated with the transition to demersal life is inflicted by predators (e.g., sculpins and subadult burbot) there is little that can be done to reduce this source of mortality.

## 6.4 SUBADULT AND ADULT HABITAT

Not much can be done to improve adult and subadult habitats. Subadult burbot may be subject to predation by large piscivores (e.g., lake trout, bull trout, and adult burbot), but once they recruit to the adult population the main source of mortality appears to be fishing. In terms of water quality, burbot are robust and survive well under conditions that are lethal to many species (Bagge and Hakkari 1992). They are, however, sensitive to high temperatures and low oxygen, and in Alaska there is evidence for adult mortalities in shallow warm lakes when the temperature exceeds 12°C and oxygen saturation drops to about 40% (Lafferty et al. 1992).

## 6.5 BASIC BIOLOGICAL INFORMATION

In both the Columbia-Kootenay and Peace-Liard systems, there is a need for basic life-history information. This information should be gathered on both lacustrine and fluvial populations. This is particularly true of the Columbia system. There is no published account of the biology of burbot in the Columbia system, yet the unglaciated portions of the Columbia probably were a refuge for this species. Consequently, burbot in the Columbia system probably differ in some aspects of their biology from burbot elsewhere in North America. Whether such differences would influence a management strategy is unknown, but we should find out.

In contrast, burbot in the Peace-Liard system probably are similar in their biology to the burbot of northern Alberta; however, upper Liard burbot may be derived from the Bering refuge and be closer, biologically, to burbot in Alaska than to burbot in Alberta.

## 6.6 ESSENTIAL BIOLOGICAL RESEARCH

In most fisheries, an understanding of the factors that govern recruitment is a crucial component in the development of a management strategy. Burbot are no exception. They appear to pass through a series of "bottlenecks" in their life-history and, in British Columbia, information on these critical stages is almost non-existent. The larval stage may be important in establishing later recruitment patterns and an effort should be made to investigate their larval ecology, especially in rivers. The transition from water column to bottom life is potentially another critical stage. Again, information on this phase of their life-history would be useful. Finally, the interaction between adults, subadults and juveniles needs investigation. There is no clear evidence of year-class dominance in burbot, but the low recruitment to the adult population suggests that predation by adults may limit recruitment.

Given the history of collapses that suggest recruitment over-fishing in burbot, some method of assessing adult numbers and recruitment of subadults to the breeding population is essential. Here, the Alaskan experience is invaluable, and British Columbia should take advantage of the assessment techniques developed in Alaska (e.g., Bernard et al. 1993) and apply these to populations in both the Peace-Liard and Columbia-Kootenay regions.

## 6.7 PUBLIC EDUCATION

In British Columbia, burbot do not benefit from a high reputation as a recreational species. Locally, there are fisheries (especially ice fisheries) for burbot, but generally they are regarded as an inferior species. For those who get beyond their admittedly unappetizing exterior, however, burbot are an excellent food fish. Perhaps, stressing their close relationship to cod, and their unique status as the only truly freshwater species of cod would help their reputation. In addition, they are biologically interesting: they are one of the few of species of freshwater fish in British Columbia that spawns in mid-winter, and the only species with a prolonged larval stage. For these reasons alone, in this time of growing interest and concern for biodiversity, they deserve more attention than they have had in the past.

## ACKNOWLEDGEMENTS

Alaska Department of Fish and Game: Bob Lafferty; British Columbia Ministry of Environment, Lands and Parks: Chris Bull, Ted Down, Jay Hammond, Gerry Oliver, Eric Parkinson, and Bruce Shepherd; Washington Department of Fisheries: Paul Mongillo; Idaho Fish and Game: Vaughn Paragamian; BCHydro: Gary Birch; R. R. & L. Ltd.: Gary Ash, Larry Hildebrand and Curtiss McLeod; Department of Fisheries and Oceans: Gordon Ennis and Cathy Gee; University of British Columbia: Dana Atagi, James Baxter, David Ghan, and Gordon Haas; Diana McPhail did the maps and figures.

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