

BURBOT BIOLOGY AND LIFE HISTORY

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Burbot Biology and Life History

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Abstract.—The burbot *Lota lota* is a holarctic member of the cod family Gadidae. Scales are cycloid, very small, and difficult to age. Burbot can attain lengths of 1 m and weights of 8 kg, but most are 300–600 mm and weights of 1–3 kg. Weights of burbot in Siberia reach up to 25–30 kg and ages of 15–20 years have been reported. Because of their long cylindrical shape they have low swimming endurance and even large fish cannot maintain themselves for more than 10 min in current velocities greater than 25 cm/s. Burbot spawn in lakes, rivers and streams. In lakes, spawning usually occurs over near-shore shallows (1.5–10 m deep) or over shallow off-shore reefs and shoals. There are, however, suggestions of deep-water spawning in the Great Lakes. The substrate is usually sand, gravel, or cobble and is relatively free of silt. In rivers, burbot spawn in low-velocity areas in main channels and in side channels behind deposition bars. The preferred substrate in rivers appears to be fine gravel, sand, or even fine silt, 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. Depending on the current, the semi-buoyant eggs may initially drift but eventually settle into interstices in the substrate. Burbot spawn in the winter or early spring, often under ice, and the spawning season is relatively short (2 or 3 weeks) and highly synchronized. Burbot spawn at low temperatures (1–4°C). The batch fecundity of burbot is enormous, and estimates of egg number vary from 6,300 to 3,477,699, depending on body size. Newly hatched burbot larvae are pelagic. At first, they drift passively in the water column, but as they grow and their swimming performance improves, they become more mobile. At about 11–23 d of age or 4.4–5.5 mm in total length the larvae migrate to the surface and begin exogenous feeding. Young burbot initially move to the land-water interface, then gradually move to deeper and colder water as they continue to grow. Adults are piscivorous and can consume substantial numbers of prey. Burbot populations vary in numbers. The most reliable adult population estimates come from lacustrine populations in Alaska, adult (>450 mm) density estimates range from 0.24 to 21.9 burbot ha⁻¹. The highest recorded adult densities are for Julian's Reef, southwestern Lake Michigan. Burbot biology is poorly understood and in many circumstances management is non-existent.

Description

Burbot *Lota lota* are easily distinguished from other Northern Hemisphere freshwater fish. They are elongate, laterally compressed, the head is somewhat flattened, there is a single barbel at the tip of the chin, and each nostril has a small single tube-like projection (Plates 1 and 2, page 17). Burbot also have two soft dorsal fins: the first is low and short, and the second also is low but much longer than the first. The anal fin is low and almost as long as the second dorsal fin. The caudal fin is rounded, the pectoral fins are fan shaped, and the pelvic fins are narrow with an elongate second fin ray. The pelvic fins are placed well for-

ward on the body and are located slightly in front of the pectoral fins. The mouth is wide, and the upper and lower jaws contain many small teeth. Adult burbot vary in color, but dorsally they usually have olive to brown or black vermiculations and the belly is crème to white. Young burbot are usually dark. Scales are cycloid, very small, and are not useful for aging. Burbot can attain lengths of 1 m and weights of 8 kg, but most are 300–600 mm with weights of 1–3 kg. Muus and Dahlstrom (1971) reported weights of burbot in Siberia up to 25–30 kg and ages of 15–20 years while one of the largest known burbot from British Columbia was 15.44 kg (Plate 3, p. 18). Because of their

long cylindrical shape they have low swimming endurance and even large fish cannot maintain themselves for more than 10 min in current velocities greater than 25 cm/s (Jones et al. 1974).

Taxonomy and Distribution

The burbot 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 (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. The geographic range of burbot 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 northwestern 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; 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. 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 studies (e.g., Billington and Hebert 1988; Grewe and Hebert 1988; Bernatchez and Dodson 1991; Taylor and Dodson 1994) support this interpretation. Paragamian et al. (1999), using mitochondrial DNA analysis, found that burbot in the Kootenai River in Idaho and British Columbia differed genetically from fish from the same river in Montana. 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 (Table 1). This suggests that variation in *Lota lota* has geographic patterning and, consequently, treating all burbot as a single taxon may be misleading.

Life History Stages

Spawning

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), rivers (Cahn 1936; Robins and Deubler 1955; Chen 1969; Sorokin 1971; Johnson 1981; Breeser et al. 1988; Evenson 1993b; Paragamian 2000) and streams (Arndt and Hutchinson 2000). 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, 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).

Season and Conditions. —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; Arndt and Hutchinson 2000; Evenson 2000; Paragamian 2000), and the spawning season is relatively short (2 or 3 weeks) and highly synchronized (Boag 1989; Arndt and Hutchinson 2000; Evenson 2000). However, Martin (1977) suggested that burbot in Kootenay Lake, B.C., begin spawning in early April and may continue into late May or early June.

Burbot spawn at low water temperatures (1–4°C: Fabricius 1954; McCrimmon and Devitt 1954; Hewson 1955; Lawler 1963; Meshkov 1967) and Kouril et al. (1985) indicated that a change in temperature from 0 to 2.5°C can delay spawning by 14 d. These field observations suggest that burbot eggs are adapted for maximal survival at temperatures between 0 and 2°C, yet Jager et al. (1981) indicated the optimal development temperature for burbot eggs is between 4 and 7°C and that mortality increases below 4°C. This anomalous result is unexplained.

There appear to be differences in 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 et al. 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.

Behavior.—The only description of actual gamete release is that of Fabricius (1954). He placed four ripe males and four ripe females in a

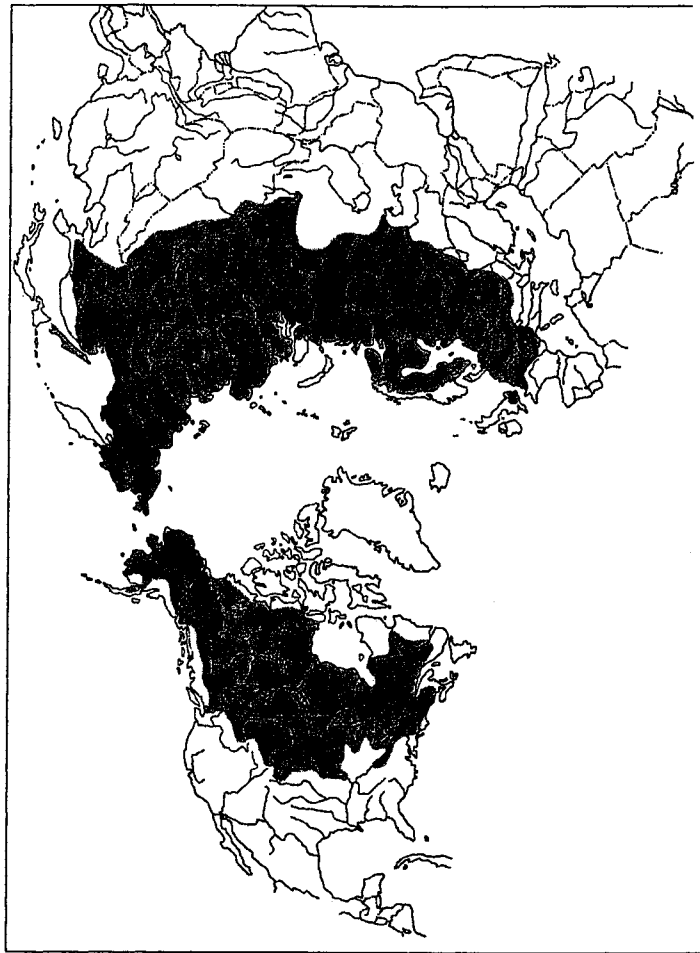


Figure 1. Circumpolar distribution of *Lota lota* (modified from Howes 1991).

large stream-tank and observed three separate spawning events. Each spawning event involved a single male and a single female, and included multiple gamete releases at 5- to 20-min 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 (Plate 2). 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.

Fecundity.—Like other cods, the batch fecundity of burbot is enormous, and estimates of egg number vary from 6,300 (Miller 1970) to 3,477,699 (Roach and Evenson 1993). Fecundity varies and average fecundity can vary substantially between lakes in the same geographic area (Boag

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

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

River system	Pyloric caeca				Caudal peduncle ratio			
	mean	range	SE	N	mean	range	SE	N
Columbia - Kootenay	57.33	35-7	10.42	40	1.50	1.3-1.8	0.27	40
Peace - Liard	82.62	45-10	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

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) estimated that about 15% of the female, and 17% of the male, age-7 or older burbot (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) estimated 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) noted that 5% of the adults on the spawning grounds were not ripe. These observations suggest that in northern populations some adults "skip" spawning on some years.

Egg Development, Hatching and Larvae

Egg Size.—Burbot eggs are round with a large oil globule, about 1 mm in diameter, but apparently range in diameter from 0.71 mm (Chen 1969) to 1.7 mm (Fish 1930). Some of this reported variation in egg size, however, may be due to differences in preservation technique. In Europe and Siberia egg diameter ranges from 0.88 to 1.14 mm (Nikolsky 1954; Meshkov 1967). Burbot eggs have been variously described as

demersal, semi-buoyant and buoyant; however, if the Fabricius (1954) observations on spawning are typical, these apparently contradictory descriptions may represent different stages in the process of fertilization and water hardening. He 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.

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. Jager et al. (1981) estimated that the optimal incubation regime for burbot lies between 1.0 and 7.0°C, 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) suggested that most of the incubation period (about 71-d) is spent at temperatures below 2°C. In Hemming Lake, Manitoba, Lawler (1963) suggested that incubation occurs 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) recorded an incubation period of 30-d 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) suggested an incubation period of 41-d at 2.0°C, and Meshkov (1967) reported 98–128 d 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). However, Jager et al. (1981) indicated 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) indicated that the eggs are tolerant of low salinities (1–6 ppt).

Larval Size.—Ghan and Sprules (1991) estimated that burbot larvae they collected in Lake Oneida, New York, had just begun exogenous feeding on April 18 and hatched four or five days earlier. These larvae ranged from 3 to 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 in Lake Michigan from mid-March to mid-June that ranged from 3.0 to 7.5 mm in length. Fischer (1999) estimated larval length at 3.56 ± 0.15 mm at hatching.

Shortly after hatching, larval densities can be high (up to 15/m² of surface area) but, within a month, densities drop to less than 1/m² (Ghan and Sprules 1991). This suggests that larval mortality rates are high.

Larval Habitat and Feeding

Larval Habitat.—In lakes, newly hatched burbot larvae are limnetic (Clady 1976; Ghan and Sprules 1991; Ryder and Pesendorfer 1992; Wang and Appenzeller 1998; Fischer 1999). 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 by June were no longer found in limnetic samples in Lake Oneida. This suggests that in lakes, larval burbot undergo a habitat shift in early summer. This shift occurs at lengths above 15.0 mm (Ghan and Sprules 1993).

Larval Feeding.—Fischer (1999) recognized several distinctive growth patterns on the otoliths of larval burbot. Through a combination of laboratory and field studies, Fischer established that in Lake Constance endogenous feeding (yolk sac stage) lasts about 11–23 d (until the larvae are about 4.4–5.5 mm in total length). This phase ends when the larvae migrate to the surface and begin exogenous feeding. Apparently the larvae remain in the limnetic zone for 16–27 d and, in Lake Constance, they undergo weak diel vertical migrations during this period (Wang and Appenzeller 1998). A third distinctive growth pattern occurs on the otoliths and lasts 11–32 d but this pattern does not mark the settlement of the larvae. Settlement is accompanied by the development of accessory growth centers on the sagittae. Settlement occurs 20–30 d, after the third otolith growth stage and appears to take 3–5 d. At settlement the larvae in Lake Constance are about 22 mm long.

In contrast to the Lake Constance data, field observations in Lake Oneida, New York, suggest that exogenous feeding starts about 5 d after hatching (Ghan and Sprules 1993). These same authors indicated that the first food items taken by larval burbot are rotifers. Ryder and Pesendorfer (1992) found that copepods and cladocerans were the first foods, and Wang and Appenzeller (1998) found that copepod nauplii were positively selected by the smallest free-foraging larvae. 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) suggested that once they start feeding the larvae select the largest prey items they can engulf. Hartmann (1983) indicated that burbot larvae go through two ontogenetic feeding

stages. From 5 to 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. Larval growth is rapid in May and June but slows in August (Ryder and Pesendorfer 1992).

Age-0 Burbot 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 age-0 burbot sheltered under stones and debris in shallow bays and along rocky shores during the day, but were out foraging at night. Fischer and Eckmann (1997) found that the distribution of juvenile burbot in the littoral zone of Lake Constance was strongly correlated with gravel substrate and the presence of large stones. Ryder and Pesendorfer (1992) also found age-0 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 limnetic 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) age-0 burbot are night-active in summer and day-active in winter (Kroneld 1976).

In rivers and streams, age-0 burbot also shelter in weed beds, under rocks, debris, and cutbanks during the day (Robins and Deubler 1955; Hanson and Qadri 1980). Here, they feed on amphipods, mayflies, stoneflies and the young of other fish (Robins and Deubler 1955; Bishop 1975; Hanson and Qadri 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 through-

out the winter (Boag 1989).

Subadult Habitat and Feeding

Subadult burbot occupy essentially the same habitat as the age-0 fish: shallow littoral environments with rocks, weeds or debris as cover. They primarily feed on insects but as they grow they progressively shift to 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). The age at sexual maturity varies both geographically and with sex. Generally, in both Europe and North America, northern populations (Chen 1969; Kirillov 1988; 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 was 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 1988; Boag 1989; Sandlund et al. 1985).

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 River system, for example, burbot populations are rare south of the 49th parallel except in deep oligotrophic lakes such as Kachees, Cle Elum and Chelan, Washington, or rivers, lakes and reservoirs in the headwaters of the Kootenay River in British Columbia and Idaho and Flathead River in Montana (Brown 1971; Simpson and Wallace 1978; Wydoski and Whitney 1979). In lakes, adult burbot are strongly associated with the bottom. Hackney (1973) reported a preferred summer temperature range of 10–12°C and suggested that adults avoid temperatures above 13°C. Thus, in the summer, burbot are usually below the thermocline (Sandlund et al. 1985; Kirillov 1988; 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). In some lakes, burbot move into shallow areas or rivers in late fall

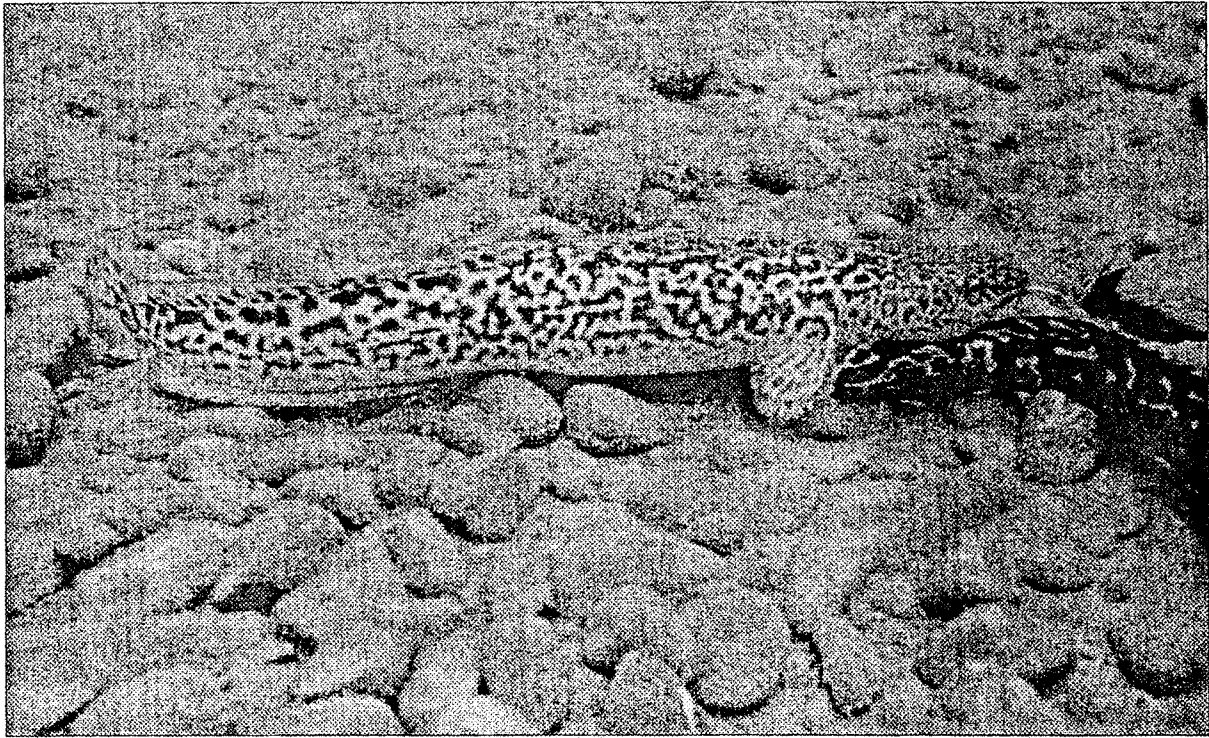


Plate 1. An adult burbot in an unnamed tributary to Columbia Lake, British Columbia. The burbot *Lota lota* is a holarctic member of the cod family Gadidae. Photo taken and contributed by Ernest Keeley of Idaho State University.

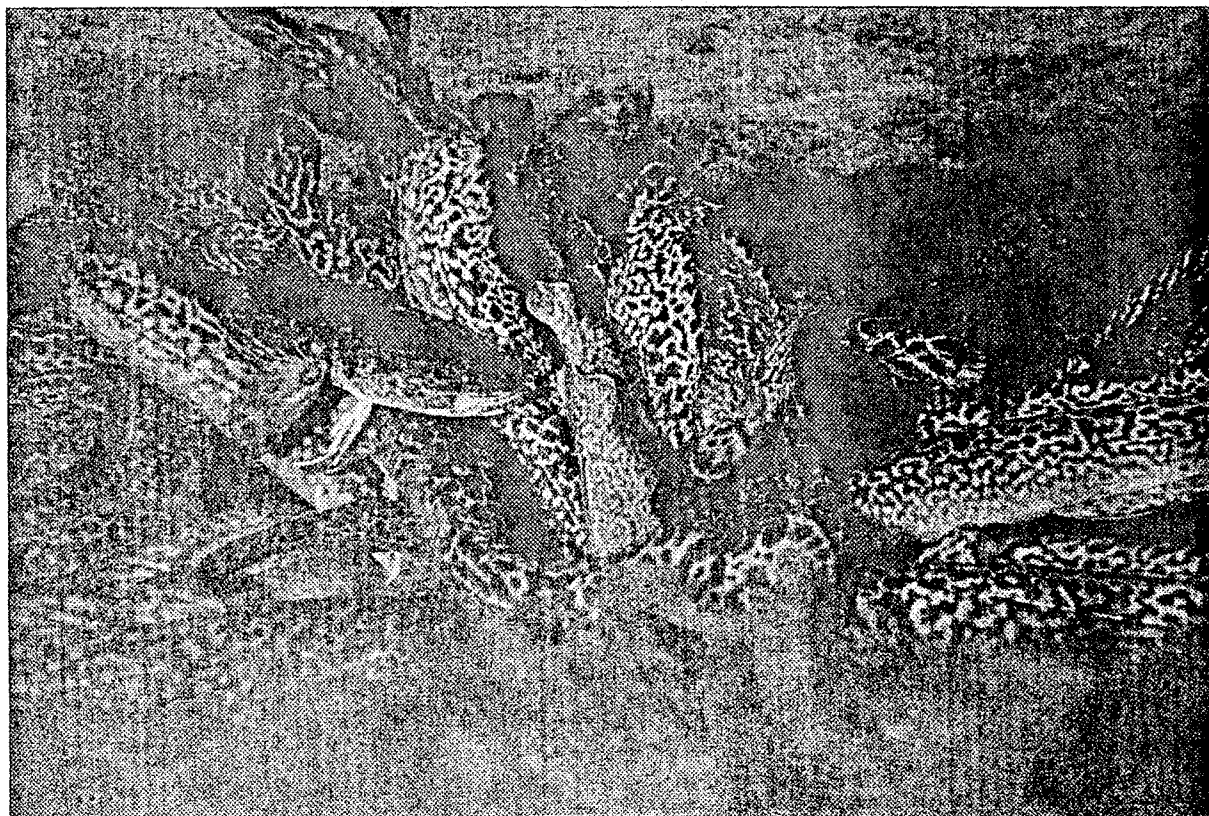


Plate 2. Spawning 'ball' of adult male and female burbot in an unnamed tributary to Columbia Lake, British Columbia. Burbot in this system are highly synchronized in their spawning migration to this tributary stream. Photo taken and contributed by Ernest Keeley of Idaho State University.

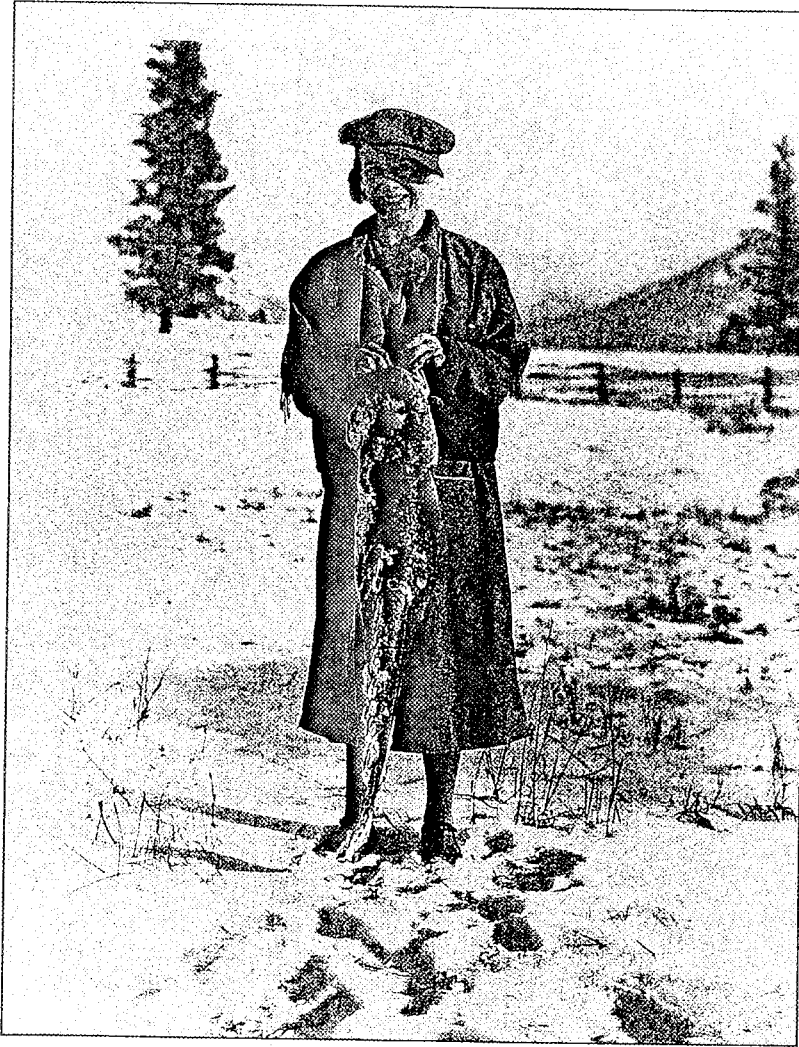


Plate 3. Circa 1923, Nellie Richardson holding a 15.44 kg burbot caught in Lake Windermere off the mouth of Windermere Creek, British Columbia, by her brother Harry E. Richardson Jr. This burbot was one of the largest known caught from British Columbia waters. Photo taken and contributed by Harry Richardson Jr. Photo from Ron and Belle Ede's photo collection and brought to our attention by Mark Stevenson.

(Lawler 1963; Anonymous 1985). These movements are thought to be part of a pre-spawning feeding migration. Carl (1995) used sonic tags to track adult burbot in Lake Opeongo, Ontario. He found that burbot were sedentary during daylight hours but started moving at dusk and were active until dawn. Movements were less in the summer and, although burbot sometimes were active at 20°C they moved to deeper, cooler water during the day. None of his tagged burbot were detected in less than 2 m of water.

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 1988; 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 are usually 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 1978; Bishop 1975; Magnin and Fradette 1977; Chisholm et al. 1989) indicated that over 80% of their diet consists of fish. In North America they take a wide spectrum of species including lampreys *Ichthyomyzon* and *Lampetra* spp., various whitefish *Coregonus* and *Prosopium*, grayling *Thymallus arcticus*, northern pike *Esox lucius*, suckers *Catostomus* spp., many species of Cyprinidae, sticklebacks (Gasterosteidae), trout-perch *Percopsis omiscomaycus*, yellow perch *Perca flavescens*, sculpins *Cottus* spp. and burbot. The proportion of fish in the diet is related to size, but even large burbot usually take some insects and macroinvertebrates. Also, diet can shift seasonally (Bailey 1972). For example, in Lake Koocanusa the

main winter prey fish for adult burbot is the largescale sucker (*Catostomus macrocheilus*) but in the spring yellow perch replace suckers as the main diet (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) noted 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 1978; Guinn and Hallberg 1990).

Pertinent Biological Characteristics

Migration and Homing.—Many lacustrine burbot populations are adfluvial (Sorokin 1971): 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 toward the spawning sites (Sorokin 1971). This migration involves travel rates of 1.5–2.0 km/d. 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 and Idaho (Paragamian 2000).

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 movements 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 River, burbot migrated from the main river into the Spillamacheen River to a spawning site that historically supported a popular spear fishery (G. Oliver, B.C. Ministry of Environment, personal communication). At the southeastern edge of their range, Robins and Deubler (1955) described 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 6 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 d. One individual, however, was recovered in the lake 117 km from the tagging site, and another individual left the lake and was recovered 90 d later 406 km away in the Slave River. Over nearly 3 years in Idaho and British Columbia (the Kootenai River and Kootenay Lake), Paragamian and Whitman (1996) tracked a mobile male burbot with sonic telemetry for over 450 km. In contrast, another burbot returned after each of three consecutive spawning seasons to the same pool (Paragamian and Whitman 1998).

Between lakes there is evidence of seasonal migrations that may be temperature mediated. Kennedy (1940) described 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. (1990) 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.

Population Densities.—Not surprisingly, bur-

bot 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 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 burbot ha⁻¹. The highest recorded adult densities are for Julian's Reef, southwestern Lake Michigan averaging 139 individuals ha⁻¹ (Edsall et al. 1993). Burbot remain as one of the last species considered in a fisheries program. Consequently, their management is poorly understood and, in many circumstances, non-existent.

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