Worldwide status of burbot and conservation measures

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Abstract
Although burbot (Lota lota Gadidae) are widespread and abundant throughout much of their natural range, there are many populations that have been extirpated, endangered or are in serious decline. Due in part to the species’ lack of popularity as a game and commercial fish, few regions consider burbot in management plans. We review the worldwide population status of burbot and synthesize reasons why some burbot populations are endangered or declining, some burbot populations have recovered and some burbot populations do not recover despite management measures. Burbot have been extirpated in much of Western Europe and the United Kingdom and are threatened or endangered in much of North America and Eurasia. Pollution and habitat change, particularly the effects of dams, appear to be the main causes for declines in riverine burbot populations. Pollution and the adverse effects of invasive species appear to be the main reasons for declines in lacustrine populations. Warmer water temperatures, due either to discharge from dams or climate change, have been noted in declining burbot populations at the southern extent of their range. Currently, fishing pressure does not appear to be limiting burbot populations world-wide. We suggest mitigation measures for burbot population recovery, particularly those impacted by dams and invasive species.

Keywords burbot Lota lota, dams, fishery management, invasive species, water quality, worldwide stock status

Introduction
Circumpolar status and trends of burbot
Lota lota lota of Nearctic and Eurasia
Western Europe and the British Isles
Northern Europe, Scandinavia and Baltic Countries
Eastern Europe
Russia, Mongolia, and China
Alaska and north of Great Slave Lake, Canada
Lota lota maculosa of North America south of Great Slave Lake, Canada
Introduction

Burbot (Lota lota, Gadidae) is the only member of the cod family that lives exclusively in freshwater and it is one of only two freshwater fishes that have a circumpolar distribution, the other being northern pike (Esox lucius, Esocidae) (McPhail and Lindsey 1970). Burbot are thought to have evolved from a marine form of gadid that separated 10 million years ago from other forms of Lotinae. The oldest fossil burbot was found in Austria and was dated from the lower Pliocene (Cavender 1986). There is further evidence the genus inhabited freshwater as long as 5 million years ago (Pietschmann 1934; but see Van Houdt et al. 2003).

Burbot exhibit a wide, Holarctic distribution (Fig. 1). Phylogenetic studies of burbot confirmed two distinct forms worldwide (Hubbs and Shultz 1941). One form, L. l. maculosa (Le Sueur), occurs exclusively in North America, from south of Great Slave Lake, Canada to the southern limit of the species’ distribution. The other form, L. l. lota, comprises the remainder of the Nearctic range and the entire Eurasian range. Van Houdt et al. (2003, 2006) found three mitochondrial DNA clades of L. l. maculosa (L.), which arose from allopatric separation in different Wisconsinian glacial refugia. Powell et al. (2008) found all three clades in the northwestern USA and southwestern Canada.

Burbot have retained many characteristics of their marine ancestors. For example, the species prefers cool and cold waters, has a high fecundity, and spawns at low temperatures and in large schools with random dispersal of gametes (McPhail and Paragamian 2000). Adult burbot are benthic predators and inhabit large cool rivers of the north temperate region and the hypolimnion of large lakes, preferring temperatures of c. 10–14 °C (Cooper and Fuller 1945; Hackney 1973; Hoffman and Fischer 2002). Burbot are thought to be ecologically intermediate in thermal preference between cold-water salmonids (e.g., Hucho hucho and Salmo trutta, Salmonidae) and more thermophilic cyprinids (Nikčević et al. 2000) and can be classified as temperate mesotherms (Hokanson 1977). Burbot commonly spawn at temperatures ranging from 0 °C to <6 °C during winter (Becker 1983). The batch fecundity of burbot, like other cods (McPhail and Paragamian 2000), is enormous, ranging from 6300 eggs (Miller 1970) to more than 3.4 million eggs (Roach and Evenson 1993). Burbot spawn in large ‘balls’ with a few females at the centre surrounded by many males (Cahn 1936). Eggs and sperm are released as the ball moves through the water. The larvae are pelagic (Clady 1976; Jude et al. 1979; O’Gorman 1983; Ghan 1990). These cod-like characteristics were likely instrumental in their widespread distribution and persistence over the past 5 million years or more. However, as discussed below, they may have become a liability to many burbot populations because their specialization has made the species vulnerable to natural and anthropogenic habitat disturbances.

Commercial fisheries for burbot in Eurasia occur in Russia, Finland, Sweden, Estonia and Lithuania. With few exceptions (Muth and Smith 1974; McCart 1986; Rudstam et al. 1995; Hayes et al. 2008; Whitmore et al. 2008), commercial harvest of burbot in most of North America is generally restricted to incidental catches during fishing for other species (Branion 1930; Hewson 1955). Burbot are benthic predators and in many systems may function as a top predator (McPhail and Paragamian 2000). There are recreational fisheries for burbot in several European countries, especially countries around the Baltic Sea (Tolonen and Lappalainen...
In parts of the USA and Canada, burbot have long been targeted by indigenous peoples and recreational anglers as food fish (Paragamian et al. 2000; Van Schubert and Newman 2000; Arndt 2001; Prince 2001, 2007; Ahrens and Korman 2002; Kootenai Valley Resource Initiative (KVRI) Burbot Committee 2005; Lheidli T’enneh First Nation 2007). However, in most of North America, burbot have not been as popular with recreational anglers as other predatory species of similar size (Quinn 2000). Although burbot meat is palatable (Branion 1930), low in fat and nutritious (Tack et al. 1947; Addis 1990; Stapanian et al. 2008 and references therein), burbot is not popular as a food fish in many parts of North America, due mainly to its appearance and slimy exterior texture (Cahn 1936; Hewson 1955; Lawler 1963; Bailey 1972; Muth and Smith 1974), problems with preservation and a lack of prepared products (Stapanian and Kakuda 2008 and references therein). The overall lack of commercial and sport interest in burbot has undoubtedly contributed to its being ignored or regarded as a ‘trash’ fish by some management agencies (Quinn 2000; but see Paragamian et al. 2000).

Burbot population dynamics are not well described and in many waters, they are not incorporated in assessment or management plans (Paragamian 2000b). Although burbot are abundant throughout much of their natural range (Muth and Smith 1974; Bruesewitz and Coble 1993; Evenson and Hansen 1991; Edsall et al. 1993), there are many populations that have been extirpated, endangered or are in serious decline (Maitland and Lyle 1990, 1996; Keith and Allardi 1996; Argent et al. 2000; Arndt and Hutchinson 2000; Paragamian et al. 2008). When burbot populations...
become threatened, remedial actions may not be implemented until after the population has become stock limited (Paragamian et al. 2008).

In this article, we survey the status of burbot populations from all over the world. We explore some of the reasons why burbot populations vary across their distribution and factors responsible for population change. We investigate reasons why some burbot populations are endangered or declining, some have recovered and some do not recover despite management measures. Finally, we synthesize those management practices that have resulted in successful rehabilitation and identify remedial actions for those populations. Our objective is to formulate a more global approach to restore a native predator in much of its range.

**Circumpolar status and trends of burbot**

*Lota lota lota* of Nearctic and Eurasia (Table 1)

Western Europe and the British Isles

Burbot are extirpated from the United Kingdom (UK), probably as a result of pressure on habitats (Pinnegar and Engelhard 2008). The species occurred in the Trent, Tame, Dove, Derwent, Nene, Great Ouse, Little Ouse, Cam, Thet, Waveney, Skeme, Esk and Foss rivers (Marlborough 1970; Pinnegar and Engelhard 2008). Burbot remains are found among archaeological excavations throughout the UK (Barrett et al. 2004). The last confirmed capture of burbot in the UK was on 14 September 1969 in the lower reaches of the Great Ouse River, and the species is listed in the UK’s Biodiversity Action Plan (T. Worthington, University of Southampton, personal communication). Similarly, in Belgium burbot have been considered to be extirpated since 1970 and are subject to introduction programmes (Dillen et al. 2008; Vught et al. 2008). Burbot have been extirpated in parts of Germany, but specimens have been found in the Danube, Ruhr, Elbe, Oder, and Rhine rivers and in Lake Constance (Harsányi and Aschenbrenner 1992; Fladung et al. 2003; Dillen et al. 2005; Wolter 2007). Reintroduction programmes of burbot have begun in Germany and the UK (Harsányi and Aschenbrenner 1992; T. Worthington, University of Southampton, personal communication).

Burbot are endangered and protected in the Netherlands and their numbers are probably still declining (De Nie 1997). The species is extremely rare, but specimens have been reported in the

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Table 1 Worldwide status of burbot (*Lota lota maculosa* in North America south of Great Slave Lake, Canada to the southern extreme of its range in North America; *L. l. lota* in Eurasia and the remainder of the species’ Nearctic range).
have been introduced elsewhere (e.g., known (Bianco and Ketmaier 2001; Dillen and Iseo) in Italy, the status in that country is not known (Kirchhofer et al. 2007). Populations are presently considered not threatened in coastal waters of the Baltic Sea and inland rivers and lakes in this region. Burbot are common but probably declining in Finland (Anttila 1973; Rask et al. 1995; Pulliainen et al. 1999; Tammi et al. 1999; Anonymous 2008), Sweden (Herrmann et al. 1993; Olofsson et al. 1995) and Estonia (Pihl and Turovski 2003; Kangur et al. 2007).

Burbot occur in lakes and rivers, and in coastal waters of the Baltic Sea in Lithuania (Kesminas and Virbickas 2000; Balkuviené et al. 2003; Repecka 2003), although there is some evidence that climate change is associated with the decline of burbot in some areas. In the Curonian lagoon, warmer winters have had negative effects on burbot reproduction (Švagždys 2002). The status of burbot in Denmark and Norway is unknown, but in both the countries, burbot inhabits rivers and lakes (Jensen 1988; Hesthagen et al. 1998; Folsvik and Brevik 1999; Tammi et al. 2003; Carl et al. 2007). There is some evidence that the species is threatened by pollution in parts of its range. Organotin compound levels in burbot muscle tissue showed an obvious trend, being higher in freshwaters situated in urban and rural areas in southern Norway than those in lakes in more isolated and remote areas in central and northern Norway (Folsvik and Brevik 1999). Similarly, elevated levels of polybrominated diphenyl ethers (PBDEs) were found in burbot from lakes Røgden and Mjøsa (Mariussen et al. 2008). There are recreational fisheries for burbot in Denmark and Norway.

In Finland, burbot populations have declined or have been extirpated in 16% of the lakes due to eutrophication (Anttila 1972; Tammi et al. 1999). For example, in Lake Hiidenvesi, which is the second largest lake (30.3 km²) in southern Finland, few adult burbot occur in the least eutrophic basin (Olin and Ruuhijärvi 2005), but burbot larvae were found in four of the five lake basins (Kjellman et al. 2000). Farther north, to the Bothnian Bay, sterility in adult burbot was caused by effluents from pulp mills (Pulliainen et al. 1999). The River Kyrönjoki, emptying into the Northern Quark of the Gulf of Bothnia, is episodically acidified due to excavation and drainage of sulphuric soil layers in the catchment area. The diadromous burbot of the river currently reproduce in the estuary and the resident population of the river has vanished (Hudd et al. 1983; Urho et al. 1998). The decline in burbot catches in the area was due to the acidification-limited survival of burbot larvae (Kjellman 2003). In southern Finnish lakes, burbot larvae were found...
in lakes having pH between 5.6 and 7.1 (50% probability of occurrence), while no larvae were found below or above this range (Urho et al. 1998).

In southern and central Finnish lakes, Rask et al. (1995) estimated that acidic precipitation was associated with the extinction of 180–380 burbot populations and negatively affected 110–220 more. However, in the northernmost Finnish Lapland, no clear effects of acidification on burbot and Eurasian minnow (Phoxinus phoxinus, Cyprinidae) were found in 13 rivers caused by the sulfur emissions from Russian Kola Peninsula (Erkinaro et al. 2001).

Pollution has undoubtedly contributed to declines in other burbot populations in Finland. For example, the sea area close to Helsinki has been one of the most polluted along the Finnish coast. Anttila (1973) reported that the local whitefish, burbot and northern pike populations had decreased or disappeared, while populations of many cyprinid species have increased. The water quality has improved since 1975 (Kaupilia et al. 2005), but Lappalainen & Pesonen (2000) showed that the recovery in local fish communities has been very slow and that burbot have not returned to the area.

Winter drawdown (c. 1.7 m) of Lake Koitere in Finland had negative effects on burbot (Tarvainen et al. 2006). In two other Finnish reservoirs, burbot was the most abundant species for c. 10 years after filling (Koivisto et al. 2005). Since that time, the burbot stocks decreased and other fish species became more dominant; northern pike in Lake Kalajärvi and roach (Rutilus rutilus, Cyprinidae) in Lake Kyrkösjärvi. In eight regulated lakes the combined proportion of littoral fish species including young burbot was much lower than in five reference lakes (Sutela and Vehanen 2008). However, other variables such as nutrient level and lake size besides the winter drawdown may have affected the fish community simultaneously. Similar shifts in fish domination and the final decline of burbot have also been noted in several other reservoirs elsewhere (Mutenia 1985; Jensen 1988; Avakyan et al. 2002).

Similarly, acidification, pollution and invasive species are associated with declines in burbot populations in Sweden. Acidification has negatively affected burbot in rivers and lakes in Sweden (Herrmann et al. 1993; Olofsson et al. 1995; Norberg et al. 2008). Svärdson (1976) suggested that the decline in burbot catches in Lake Vättern during 1957–73 was associated with concentrations of polychlorinated biphenyls (PCBs). The decline in burbot was concurrent with an increase in the abundance of ruffe (Gymnocephalus cernuus, Percidae). Introduced signal crayfish (Pacifastacus leniusculus, Astracidae) have been suggested as negatively affecting burbot and other benthic fishes in Sweden (Josefsson and Andersson 2001 and references therein). Although damming of rivers has been shown to affect burbot populations elsewhere, burbot were observed both to ascend and descend through two human-made fishways in the River Emån in southern Sweden (Calles 2005).

Eastern Europe
Burbot populations in Poland are vulnerable due to damming and pollution (Brylnska et al. 2002; Penczak and Kruk 2005; Kruk 2007a,b). In the Warta River, damming affected negatively burbot both in tail- and backwaters (Penczak and Kruk 2005). Burbot and wels (Silurus glanis, Siluridae) are becoming extirpated as a result of impoundment and accompanying effects. The high variation in flow and increased poaching when the river bed is uncovered can lead to local extinction (Kruk and Penczak 2003). Rheophilic burbot, stone loach (Barbatula barbatula, Balitoridae), gudgeon (Gobio gobio, Cyprinidae), chub (Squalius cephalus, Cyprinidae) and dace (Leuciscus lewiscus, Cyprinidae) are most abundant in the upper section of the river. These species are nearly absent in the middle section, which is the most polluted, and occur in comparatively low numbers in the downstream section, which is moderately disturbed (Kruk 2007a). The main reasons for the recorded declines in fish biomasses were water pollution and impoundment of the river (Kruk 2004).

Burbot populations in Slovakia occur in the River Danube (Copp et al. 1994). Due mainly to pollution and damming, these populations are also vulnerable (Holcik 2003). In the Czech Republic, burbot populations occur in the rivers Morava and Ohre (Slavík and Bartoš 2002; Lusk et al. 2004; Jurajda et al. 2006). Although these populations are vulnerable to the effects of damming and pollution, the constructions of fishways have had positive effects on burbot in the Czech Republic (Slavík and Bartoš 2002). The decline of burbot in Slovenia is thought to be caused by river regulation, in combination with pollution (Veenhiet 2000; Šlekovec et al. 2004). Burbot occur in the River Drava, Lake Cerknica, Rak Creek and the lower reach of Cerkniščica Creek. Fishing for burbot is prohibited in Slovenia. Burbot are rare or endangered in Bulgaria (River Danube: Vassilev and Pehlivanov...
2005) and vulnerable in Hungary (Biró et al. 2003; Anonymous 2005).

**Russia, Mongolia and China**

Burbot are common in much of the species’ range in Russia but populations have declined or have been extirpated in some places due to damming, eutrophication, competition from invasive species and pollution (Zhadin and Gerd 1963; Kirillov 1988; Volodin 1994; Chershnev 1996; Reshetnikov et al. 1997; Zhulidova et al. 2002; Allen-Gil et al. 2003; Andrianova et al. 2006; Kotev 2007). Known burbot populations occur in the rivers Kolyma, Anadyr and Penzhina and rivers near Novosibirsk in Siberia; rivers on Sakhalin and the Shantar Islands; and in Lake Baikal. Burbot were extirpated from Lake Guseinov as a result of eutrophication and the occurrence of invasive species that occupied the same trophic niche as burbot (Pisarsky et al. 2005). Similarly, burbot populations have either declined or disappeared from some Russian reservoirs (Avakyan et al. 2002; Andrianova et al. 2006). For example, in the Sheksninskii Pool of Rybinskoe Reservoir, emergency dumping of sewage effluent reduced the reproduction potential of burbot by about half (Volodin 1994). By contrast, despite a considerable technogenic load to Lake Kostomuksha, pike, roach, bleak (*Alburnus alburnus*, Cyprinidae) and burbot have survived in the lake (Sidorov et al. 2003).

The status of burbot is unknown in Mongolia and China. Populations in Mongolia have been recorded in Bur Lake and the Khalkhin River in the Amur drainage, the Selenge and Orkhon river basins, and in Hövsgöl, Ugii, Terhiyn Tsagaan lakes (Dulmaa 1999; Ocok et al. 2006). In western China, burbot occurs in Erqishi River system, where it is commercially fished. Besides this river system, burbot occurs also in Lake Ulungur (Walker and Yang 1999).

**Alaska and north of Great Slave Lake, Canada**

Burbot are endemic to most watersheds in Alaska and to many of the arctic drainages of Canada, although specific information on distribution is lacking for many areas. Fluvial populations have been documented in large glacial systems in Alaska, such as the Yukon (Evenson 1993), Kuskokwim (Andrews and Peterson 1983), Susitna (Sundet and Wenger 1984) and Copper rivers (Schwanke and Bernard 2005) as well as in many clear, run-off rivers draining into the Arctic Ocean (Bendock 1979). Lacustrine populations have also been documented throughout northern, central and south central Alaska (Bendock 1979; Lafferty et al. 1991). In northern Canada, burbot populations are distributed in suitable habitats in the continental portions of the Northwest and Yukon Territories exclusive of most northern portions and are thought to be absent from the Canadian Archipelago (Scott and Crossman 1973). Fluvial populations along the Canadian Arctic coast have been documented from the Mackenzie River east as far as the Coppermine River. Burbot from these populations and from arctic coastal populations in Alaska are known to enter the brackish waters of the Arctic Ocean (Walters 1955).

Overall, habitats supporting burbot populations in this region are unperturbed and healthy and burbot are widely distributed and abundant. In addition, many of the lake and river systems are remote and receive little fishing pressure. Therefore, few populations have been impacted to a level leading to substantial population declines.

However, in Alaska, there have been a number of road-accessible lacustrine populations impacted by sport fisheries that have led to substantial reductions in abundance. Harvest of burbot increased, on average, 30% annually from 1977 to 1983, coinciding with an increase in human population following construction of the Trans Alaska Pipeline. Statewide sport harvests peaked in 1985 exceeding 27 000 burbot, but recent harvests have typically been <10 000 (Howe et al. 1995; Jennings et al. 2007). The majority of this harvest was taken from numerous small-to-moderate-sized lakes throughout central and south central Alaska and from the Tanana River. Stock assessments of lacrustine populations in the mid-1980s (Bernard et al. 1993) led to estimates of sustainable yield for many of the lakes that were either being, or likely would be, exceeded with existing regulations (Parker et al. 1989). Consequently, more restrictive regulations were adopted for many of the lakes that reduced the daily creel limit. In addition, baited set-lines were prohibited as a legal method of sport fishing for most lakes in central Alaska. These restrictive regulations were effective at maintaining yields at sustainable levels. Concurrent with the assessments of Alaskan lakes, an assessment programme for fluvial populations of burbot indicated that the river populations were very large compared to harvest and that seasonal movements of mature burbot mitigated the impacts of fisheries that were concentrated spatially and temporally (Evenson 1993, 2000). Therefore,
the restrictive regulations put in place for the lake populations were not enacted for the river populations.

*Lota lota maculosa* of North America south of Great Slave Lake, Canada (Table 1)

Western Canada south of Great Slave Lake

Burbot are endemic to western Canada, typically east of the coastal range (McPhail and Lindsey 1970; Scott and Crossman 1973, 1998). In British Columbia (BC), burbot are common in most of the large drainages: typically flowing southwest to the Pacific Ocean and North to the Arctic Ocean (McPhail and Carveth 1993; Nelson and Paetz 1992). There are a few records of burbot from the lower Fraser River west of the coast range. However, these burbot are thought to have emigrated from east of the coast range and the population has never established at a self-sustaining level (McPhail and Carveth 1993). In Alberta, Saskatchewan and Manitoba burbot are also common in most of the large drainages that flow north to the Arctic Ocean, east to Hudson Bay and southwest to the Atlantic Ocean. Burbot in these drainages are more common in large, deep lakes as well as many of the larger river systems (Nelson and Paetz 1992). Although burbot are common in many of the Rocky Mountain foothill streams, they are rare in the Rockies (Nelson and Paetz 1992).

It is unlikely that the overall range of burbot in western Canada has changed significantly in the last century (McPhail 1997; McPhail and Paragamian 2000; Van Schubert and Newman 2000; Spence and Neufeld 2002; Reddecopp et al. 2003; Lheidli T’enneh First Nation 2007; Prince 2007). Although some populations appear to be stable (Arndt and Baxter 2006), little is known about the status of most populations and many of those that have been evaluated show evidence of declines (Paragamian et al. 2000; Prince 2001, 2007; Ahrens and Korman 2002; Bisset and Cope 2002). Recreational interest is strong in most of BC today (Lheidli T’enneh First Nation 2007; British Columbia (BC) Ministry of Environment 2008; Prince and Cope 2008). However, in Alberta and Saskatchewan, most captures are incidental in the recreational pursuit of other sport fish. (K. Bodden, Alberta Ministry of Sustainable Resource Development [AMSRD], personal communication; M. Cope and T. Johnston, Saskatchewan Ministry of Environment, personal communication. Sport fishing regulations in Alberta contain an exemption for wastage of burbot, in which anglers are not legally required to retain harvested burbot for consumption (Alberta Sustainable Resource Development 2008). These incidental catches of burbot in Alberta waters can exceed 25 000 kg year⁻¹. In Manitoba, burbot were removed from some lakes as part of a ‘rough fish’ removal programme (Anonymous 1964).

Populations in BC, Alberta, Saskatchewan and Manitoba are thought to be generally secure, but have not been assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The only exception is the Kootenay Lake and River population in BC, which has been Red Listed (S1) by BC’s Conservation Data Centre (BC CDC). However, this assessment, should be interpreted with caution. The combined effects of low regard for burbot as a sport fish in many regions (Ford et al. 1995), a lack of standardized methods for completing population assessments (Bernard et al. 1993; Paragamian 2000a; Prince 2007; Neufeld 2008), and decompression-related mortality when retrieving burbot from depth (Gitschlag 1986; Bruesewitz and Coble 1993; Neufeld and Spence 2004) have resulted in few stock assessments targeting burbot. This lack of trend information for many burbot stocks has left some populations vulnerable to overfishing (Prince 2007, Prince 2008; K. Bodden, AMSRD, personal communication). In addition, burbot are even more susceptible to overfishing because much of the angling effort typically occurs over spawning or feeding congregations (Martin 1976; Ahrens and Korman 2002; Prince 2008).

Remedial actions for overfishing have typically included closure of the fishery, either entirely or for the spawning period when burbot are most vulnerable, or reductions in the daily harvest quota (Martin 1976; Prince 2007; Prince 2008; B. Jantz, C. Spence, and C. Williamson, BC Ministry of Environment, personal communication). Although there are many examples of these remedial techniques in both BC and Alberta (Alberta Sustainable Resource Development 2008; British Columbia (BC) Ministry of Environment 2008; K. Bodden, AMSRD, personal communication), little targeted monitoring has been performed to assess the response. In Alberta, many of the fisheries that have been impacted by harvest have not seen a major resurgence in angler numbers typically seen when other species recover.

Dams may have had a negative effect on burbot populations in the region. Although some reservoirs
in southern BC appear to have healthy burbot populations (Arndt and Baxter 2006), winter drawdown for power production and flood control has been hypothesized as a significant risk factor to burbot reproductive success (BC Hydro 2005a,b). In particular, burbot eggs deposited from shallow spawning events may become dewatered during spring drawdown, resulting in high egg mortality. On Duncan Reservoir in BC, Spence & Neufeld (2002) found that 17% of tagged adult burbot were entrained in the space of 5 months and remained alive after entrainment. No fish passage upstream exists for burbot at Duncan Dam. Although the population trend has not been established, densities in Duncan reservoir are much lower than nearby reservoirs (Arndt and Baxter 2006; Neufeld 2006). The lower population density in Duncan Reservoir may be associated with its drawdown regime.

The burbot population in Kootenay Lake, BC collapsed starting in the early 1970s and studies since 1998 indicate that few, if any, adult burbot remain today (Spence 1999; Neufeld 2005). Modelling results suggest recruitment failure was the most likely cause of collapse and angling pressure resulted in removing the remaining adults. Recruitment failure was most highly associated with decreases in mean summer density of copepods, which are thought to be an important food item for larval burbot (Ryder and Pesendorfer 1992; Hardy et al. 2008). Although alternate hypotheses have been proposed, it is likely that decreases in copepod density are linked to increases in introduced mysis shrimp (Mysis relicta, Mysidae), which are copepod predators and competitors, in combination with reductions in lake productivity after construction of upstream dams (Duncan and Libby Dams: Zylbut 1967; Northcote 1972; Binsted and Ashley 2006). Remediation for the decrease in copepods has included adding nutrients to Kootenay Lake as part of a larger ecosystem rehabilitation project (Ashley et al. 1999; Schindler et al. 2007). This lake fertilization project has resulted in increased copepod densities close to levels at the time of historic recruitment. Although suitable conditions for larval survival may now exist, few adult burbot remain in this population today (Spence 1999; Neufeld 2005) and there is little chance it will recover on its own.

**USA Pacific Northwest to the Great Lakes States**

Burbot are endemic to the northern tier of states of the Pacific Northwest east to the Laurentian Great Lakes bounding the border with Canada, ranging as far south as Kansas, Iowa, Nebraska and Wyoming (McPhail and Lindsey 1970). This area includes the upper Mississippi, Missouri, Saskatchewan and Columbia River systems. They are also found in large deep lakes and reservoirs (Brown 1971; Wydoski and Whitney 2003; Hubert et al. 2008). The southern extent of their range is limited to below Gavins Point Dam in Nebraska (Bouc 1987). Burbot are also uncommon in Iowa but found in border rivers (Harlan et al. 1987) and in Kansas, there are only a few records from the Missouri and Kansas rivers (Cross 1967). To the north, burbot are endemic to the Missouri River and its tributaries in North and South Dakota, Montana and to the upper Columbia of Washington (Wydoski and Whitney 2003).

In Washington, there were no regulations to manage burbot until 1998. The species is generally not a popular gamefish and there is no evidence of overharvest (Bonar et al. 1997). Burbot are seldom found in Oregon and the species is not included in Oregon’s fishing regulations.

In Idaho, burbot are found only in the Kootenai River of the upper Columbia (Simpson and Wallace 1982). Prior to the construction of Libby Dam in 1972, the annual harvest of burbot from the Kootenai River by sport anglers, particularly during winter setline fishing, and commercial fishers in Idaho may have been in the tens of thousands of kg (Paragamian et al. 2000). Three commercial fishers alone harvested an estimated 2150 kg in 1958 (Idaho Department of Fish and Game [IDFG] Regional Archives, unpublished data). During 1979–82, the estimated burbot harvest declined to <250 fish per year (Partridge 1983). Burbot regulations in Idaho were not restrictive until 1983, when a two-fish limit was adopted. This limit was followed until 1992 when the fishery was closed because the burbot population was nearing collapse (Paragamian et al. 2000). The burbot population in the Kootenai River continued to diminish despite closure of the fishery (Paragamian 2000a). The primary reasons for the loss of burbot recruitment in the Kootenai River are likely the increased winter temperatures and discharge from the dam (Paragamian 2000a; Paragamian et al. 2005), which are in part responsible for disruption or delay in burbot spawning migration and spawning synchrony (Paragamian and Wakkinen 2008). Winter discharges in the Kootenai River are now three to four times that of pre-Libby Dam conditions and water temperatures post-Libby Dam are warmer by
up to 4 °C (Partridge 1983). In Montana, Skaar et al. (1996) reported entrainment of fishes through Libby Dam, where burbot were the second most abundant species through the turbines.

In Wyoming, burbot are generally limited to the cooler water of high elevation lakes and rivers including the Wind/Bighorn watershed, Boysen Reservoir, the main stem of the Wind River and several natural lakes and tributaries (Hubert et al. 2008). Burbot have been extirpated from the Tongue River in Wyoming as a result of construction of the Tongue River Reservoir in Montana and past pollution (Eiserman 1964). Hubert et al. (2008) believed that the low densities of burbot in Wyoming were due to the cumulative effects of exploitation and entrainment to canals. Emigration of burbot from reservoirs and fluvial portions of some watersheds in Wyoming is due to water diversion structures and canals and thought to be limiting stock numbers (Hubert et al. 2008). Hubert et al. (2008) also indicated that large numbers of burbot emigrate annually from natural lakes that have been modified for water storage by construction of dams. Hubert et al. (2008) also cited the diversion of water during the irrigation season between the Wind River Diversion Dam and the mouth of the Little Wind River and in Bull Lake Creek as major factors of burbot mortality. Most burbot in Wyoming are believed to die at the end of the irrigation season. Extreme winter drawdowns of Bull Lake, Wyoming were implicated as a source for failed reproduction by exposing sand and gravel habitat leaving only silt habitat for burbot spawning (Bergersen et al. 1993). Concerns about burbot populations due to increasing angler exploitation and overharvest of stocks led the Wyoming Game and Fish Department to implement more restrictive regulations during the late 1940s through the 1960s, such as shorter fishing seasons, lower creel limits, restrictions on minimum length and a closure of the special winter fisheries on lakes where burbot spawn (Krueger and Hubert 1997).

Burbot decreased in the angler creel and electrofishing surveys during 1998–2007 in North Dakota, below Garrison Dam on the Missouri River (P. Bailey, North Dakota Game and Fish Department, personal communication), but the reason for the decline is not known. However, burbot numbers in the creel were apparently higher in the late 1990s during higher water and an abundant smelt entrainment. Anglers fish for post-spawning burbot as they enter tributaries of the Missouri River in North Dakota (Quinn 2000) and burbot remain vulnerable to exploitation. By contrast, burbot are not popular in South Dakota and there are no regulations to manage them, although they are common in lakes Oahe and Sharpe (Quinn 2000). In Nebraska, Hesse (1993) recommended that burbot be protected and fishing closed because they were found to be vulnerable to angler harvest during the spawning season. In Iowa and Kansas, burbot are of little consequence in the fisheries. The species is uncommon in these states, likely due to upper water temperature limits (Harlan et al. 1987).

Great Lake States of USA

Burbot are found in hundreds of inland lakes and streams throughout Minnesota (P. Jacobson, Minnesota Department of Natural Resources [MNDNR], personal communication). Although fish communities in Minnesota inland lakes are assessed using standard gillnet surveys, burbot catch is so infrequent that temporal trends are difficult to discern in most lakes. However, for Mille Lacs Lake, the survey data clearly showed a greater-than-80% decrease in burbot abundance during 1979–2007 (T. Jones, MNDNR, personal communication). The trend toward warmer water temperatures beginning in 1980 is suspected of causing this decline in burbot abundance in Mille Lacs Lake (T. Jones and P. Jacobson, MNDNR, personal communications). On the basis of the reports by anglers, burbot abundance in Lake of the Woods has substantially declined over the last 20 years (D. Topp, MNDNR, personal communication). Reasons for this decrease are unclear.

Burbot are widespread throughout the inland waters of northern Wisconsin, where they occur in hundreds of lakes and streams (J. Lyons, Wisconsin Department of Natural Resources [WIDNR], personal communication). By contrast, burbot are generally rare in the southern inland waters of Wisconsin. As burbot are not regularly caught by WIDNR biologists during their standard assessment surveys of inland waters, reliable information on temporal trends in burbot abundance from these standard surveys is not available (J. Lyons, WIDNR, personal communication). Burbot are regularly seen beneath the ice by winter anglers on Lake Winnebago. By the early 1960s, a programme to remove ‘rough fish’ from Lake Winnebago had begun (M. Schrage, WIDNR, personal communication). Fryke nets were set under the ice to catch these rough fish. The removal programme targeted freshwater drum (Aplodinotus grunniens, Sciaenidae);
however, burbot represented a substantial portion of the fyke-net catch. The removal programme was terminated in the early 1980s. Commercial harvest of burbot from Lake Winnebago plummeted between the early 1960s and the early 1980s and this decrease was attributable to the rough fish removal programme (M. Schrage, WIDNR, personal communication). According to the results of special surveys targeting burbot in the early 2000s, the burbot population in Lake Winnebago has fully recovered from the effects of the rough fish removal programme.

Burbot are found in inland waters of both the Lower Peninsula and Upper Peninsula of Michigan (L. Wang, Michigan Department of Natural Resources, personal communication). Just as in Wisconsin and Minnesota, no special regulations are imposed on anglers fishing for burbot. Also, the status of burbot in the inland waters of Michigan remains unknown because burbot are not effectively sampled by the regular fish surveys.

Laurentian Great Lakes

Burbot occur in all of the Great Lakes, but in Lake Erie the species is restricted to the colder and deeper eastern portion of the lake (Scott and Crossman 1973; Trautman 1981). Burbot populations collapsed in four of the five Laurentian Great Lakes between 1930 and the early 1960s (Stapanian et al. 2008). Collapses in Lakes Michigan, Huron and Ontario were associated with sea lamprey (Petromyzon marinus, Petromyzontidae) predation, whereas the collapse in Lake Erie was likely due to a combination of over-exploitation, decreased water quality and habitat degradation. Burbot population density in Lake Superior has remained relatively low and stable since 1978.

Since the decline of burbot, many changes occurred in the Great Lakes, including reductions in sea lamprey through control efforts, reductions in alewives, stocking native and non-native salmonines, and controls on commercial fishing. Perhaps the most important management effort, in terms of its influence on the fishery of the Great Lakes, has been sea lamprey control (Smith and Tibbles 1980). Sea lamprey abundance has been dramatically reduced in all five of the Great Lakes as a result of control efforts.

Alewife (Alosa pseudoharengus, Clupeidae) predation has been implicated in the decline of certain Great Lakes fish stocks, mainly by preying on their pelagic fry (Smith 1970; Brandt et al. 1987; Eck and Wells 1987; Brown et al. 1987; Luecke et al. 1990; O’Gorman and Stewart 1999). Eshenroder & Burnham-Curtis (1999) concluded that when alewifes are abundant in the Great Lakes, they inhibit the natural succession of native species in the Great Lakes.

Intensive salmonine stocking in the 1960s and 1970s and the subsequent predation led to reductions in alewife abundances in Lakes Michigan, Huron and Ontario (Madenjian et al. 2002; Madenjian et al. 2005a,b; Mills et al. 2003; Dobiesz et al. 2005). However, alewife abundance in Lake Ontario has remained considerably higher than alewife abundances in Lakes Michigan and Huron (O’Gorman and Stewart 1999; Madenjian et al. 2003). Alewife abundance in Lake Erie has remained low, owing mainly to the species’ intolerance to the adverse water temperature regimes that exist under typical winter conditions in Lake Erie (Ryan et al. 1999).

Recovery of burbot populations occurred in Lakes Michigan and Huron during the 1980s and in Lake Erie during the 1990s (Stapanian et al. 2006, 2008). Control of sea lampreys was a requirement for recovery of burbot populations in these three lakes. Declines in alewife abundance appeared to be a second requirement for burbot recovery in Lakes Michigan and Huron (Stapanian et al. 2008). High populations of adult lake trout (Salvelinus namaycush, Salmonidae) in the Great Lakes have been shown to serve as a buffer species against sea lamprey predation and thus contribute to the recovery of other native species, including burbot in Lakes Huron and Erie (Swink and Fredericks 2000; Stapanian and Madenjian 2007) and lake whitefish (Coregonus clupeaformis, Coregonidae) (Madenjian et al. 2002). This buffering effect facilitated recovery of the burbot populations in Lakes Huron and Erie (Stapanian et al. 2008). Although sea lampreys have been controlled in Lake Ontario, alewives are probably still too abundant to permit burbot recovery (Stapanian et al. 2008).

USA east and south of the Laurentian Great Lakes

Burbot are endemic to the northern tier of states in the eastern USA bordering Canada west to the Great Lakes, and occur in isolated populations or appear in historic records from several other states as far south as Maryland and Kentucky. Although this region supports burbot populations in multiple waters, burbot are rarely included in agency assessments and status and abundance trends of...
populations or changes in distribution patterns are largely unknown. As in much of their range in North America, burbot are generally not highly valued by anglers in this region. However, some exceptions occur, in several waters in Maine (Roy 2001) and New Hampshire (Quinn 2000).

In the northernmost states of the region, burbot typically occur in large, deep lakes and associated tributaries, but their distribution further south is primarily associated with large river systems (Whitworth et al. 1968; Cooper 1983; Halliwell et al. 2001; Hartel et al. 2002). In Maine, burbot are widely distributed in lakes and ponds, particularly in the northern regions of the state, and are also found in the headwaters of the Kennebec, Penobscot and St. John Rivers (Roy 2001). Burbot are also widely distributed in the colder lakes of New Hampshire, primarily in the central and northern regions of the state, and have been reported from all of the state’s major watersheds, with riverine populations most prevalent in the northern part of the state (Scarola 1973; New Hampshire Fish and Game Department (NHFGD) 2005). In Vermont, burbot are most common in rivers and streams in the northern part of the state, but also occur in some lakes of that region as well as tributaries to Lake Champlain and the Connecticut River (Langdon et al. 2006). Burbot in the Connecticut River extend south into Massachusetts and Connecticut, where they are considered rare (Whitworth et al. 1968; Hartel et al. 2002). Burbot have also been reported from the Housatonic River drainage in both Massachusetts and Connecticut (Whitworth et al. 1968; Hartel et al. 2002).

Burbot are widely distributed in New York State, occurring in both lakes and river systems (Smith 1985). Lake populations of burbot in New York include Lake Champlain, Oneida Lake, some of the Finger Lakes, as well as other smaller lakes, chiefly in the St. Lawrence and Susquehanna drainages. Jackson et al. (2008) attributed the recent decline in burbot abundance in Oneida Lake to global climate warming. Burbot are also found above downstream barriers in the Raquette River system of the St. Lawrence and in the headwaters of the Susquehanna and Allegheny rivers (Robins and Deubler 1955; Smith 1985).

Isolated records of burbot in the Susquehanna River exist from both Pennsylvania (Cope 1879) and Maryland (Kazyak and Raesley 2003). In Pennsylvania, burbot are a species of special concern and also occasionally found in the Susquehanna River (Argent et al. 2000), but modern records of burbot from Pennsylvania are primarily restricted to the headwaters of the Allegheny River (Cooper 1983). In Kentucky, the burbot has been sporadically reported in the lower Ohio River system, but no evidence of reproduction exists for burbot (Clay 1975; Burr and Warren 1986).

Canada north and east of the Laurentian Great Lakes
Burbot are found throughout eastern Canada as far north as the Arctic drainage, that of Hudson Bay and east to Newfoundland and Labrador (Scott and Crossman 1973). In Ontario, burbot numbers were thought to be stable, at least into the early 1960s (MacKay 1963), and Scott (1967) characterized burbot as common in deep lakes and large rivers of the province. Burbot populations are secure in Québec, New Brunswick and Newfoundland and Labrador. Burbot are not highly regarded in eastern Canada, although a few commercial fisheries exist. During 1930–72, commercial fishers on Lake of the Woods in Minnesota, USA and Ontario, Canada annually harvested from 82 565 to over 400 000 burbot (Muth and Smith 1974). Burbot have been removed from some lakes in Ontario as part as part of ‘rough fish’ removal programmes (Smedley 1998). A removal programme in Lake Simcoe resulted in catches of almost 6000 kg in 1954, but the programme was discontinued due to a lack of identified use for the fish (MacCrimmon and Skobe 1970). The lack of popularity of burbot in eastern Canada and the disdain for the species by anglers fishing for more popular sportfish is partially responsible for the lack in interest regarding their status. In Ontario, burbot are often caught coincidentally while angling for lake trout (MacKay 1963).

Synthesis of causes for decline and mitigating measures
Habitat change, especially from dam construction and pollution, was overwhelmingly the most important reason for declines in burbot abundance in rivers and streams worldwide. Dams have been shown to change habitat complexity, alter river discharge and temperatures on a temporal and spatial scale, and have contributed to the decline of many species of fish (Stanford et al. 1996). Overfishing is still a problem in some areas and undoubtedly contributed to declines in burbot abundance at the local level. However, overfishing...
does not appear to be limiting burbot populations worldwide. Further, the comparatively poor swimming stamina of burbot (Jones et al. 1974) may limit its movement of burbot from one water body to another due to water velocity gradients across culverts or other structures. In lakes, adverse effects of exotic species and pollution appear to be the main factors for decreases in burbot abundance. In the Laurentian Great Lakes, invasions of exotic fishes have apparently led to substantial increases in both mortality of adult burbot and mortality of burbot fry.

Mitigation measures for burbot populations impacted by dams are lacking. A conservation strategy (Kootenai Valley Resource Initiative (KVRI) Burbot Committee 2005; Ireland and Perry 2008) was prepared to outline measures necessary to rehabilitate the burbot population of the Kootenai River. The Conservation Strategy indicated that operational discharge changes at Libby Dam are required during winter to provide suitable conditions for burbot migration. Paragamian et al. (2005) and Paragamian & Wakkinen (2008) recommended that discharge for burbot pre-spawning migration and spawning should range from 113–300 m$^3$ s$^{-1}$ and average 176 m$^3$ s$^{-1}$ for a minimum of 90 days (mid-November through mid-February) in the Kootenai River. Temperature should decline to $<5 \, ^{\circ}C$ by the first week in November and maintained from 1 to $4 \, ^{\circ}C$ for the duration of December through February, which includes the migration and spawning season. However, implementation has not occurred and unless it occurs, it is likely burbot in the Kootenai River will be extirpated (Paragamian et al. 2008). However, in the interim, development involving artificial propagation technology may serve to reestablish burbot stocks (Jensen et al. 2008).

The specialization of burbot to cold, oligotrophic conditions may make it more vulnerable to anthropogenic change. Warmer water temperatures, due either to discharge from dams or climate change, have been noted in declining burbot populations at the southern extent of their range. Some of these declines appear to be due to warmer summer water temperatures thought to reflect climate change (Jackson et al. 2008). Although Columbia Lake at the extreme upper end of the Columbia River drainage is not the southern bound of burbot range in western North America, this shallow lake is at the extreme side of temperature tolerance for burbot survival (Ford et al. 1995; Taylor 2002). By contrast, Horton & Strainer (2008) considered possible benefits of dams that cooled riverine habitats below and provided lacustrine habitats within impoundments. Although no historical distribution data existed for burbot, Horton & Strainer (2008) hypothesized burbot numbers in a section of the Missouri River below dams of three upstream reservoirs increased because the upstream reservoirs provided comparatively cooler summer water temperatures downstream.

Our review also suggests that burbot populations are fully capable of recovering from over-exploitation once fishing pressure has been relaxed. For example, once more restrictive regulations were placed on burbot fisheries, burbot populations in Alaskan lakes exhibited recoveries. These regulation changes included reducing the daily limit and prohibiting the use of baited set-lines. The Lake Winnebago case history provided another example of burbot populations recovering from over-exploitation. Once the rough fish removal programme was terminated in the early 1980s, the burbot population in Lake Winnebago exhibited a strong recovery during the late 1980s and through the 1990s. By contrast, total protection of burbot in Kootenay Lake, BC from fishing has not led to population restoration.

The case histories for the Laurentian Great Lakes clearly illustrate that burbot populations can recover when appropriate fisheries management actions are taken. As previously mentioned, the burbot populations in Lakes Michigan, Huron, Erie and Ontario had collapsed by 1960, due in part to high populations of sea lamprey and alewife. Chemical control of sea lampreys began in the late 1950s and was effective in reducing sea lamprey abundance in all five Great Lakes (Christie and Goddard 2003; Mullett et al. 2003). To reduce alewife abundance in Lakes Michigan, Huron and Ontario, large-scale salmonine stocking programmes were launched as early as 1965 by Great Lakes fishery managers (Madenjian et al. 2008). These salmonine stocking programmes led to dramatic increases in salmonine abundances, which in turn led to dramatic increases in the consumption of alewives by salmonines. These salmonine stocking programmes were effective in substantially reducing alewife abundance in Lakes Michigan, Huron and Ontario (Madenjian et al. 2008). A decrease in the abundance of the sea lamprey led to recovery of the burbot population in Lake Erie, and decreases in the abundances of both

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sea lamprey and alewife led to recovery of the burbot populations in Lakes Michigan and Huron (Stapanian et al. 2008). Thus, management action to control these two invasive fish species was instrumental in the recovery of burbot populations in three of the Laurentian Great Lakes. Apparently, alewife abundance in Lake Ontario is still too high to allow for burbot recovery in that lake (Stapanian et al. 2008). Increasing the lakewide biomass of salmonines to further reduce alewife abundance should eventually result in a recovered burbot population in Lake Ontario (Madenjian et al. 2008).

Although burbot are widespread in distribution, they are locally sensitive to disturbances of habitat conditions and fish community structure. Capacity for recovery when appropriate management actions are taken indicates that threatened populations recover. Burbot appear to serve as an excellent indicator species in much of their range, and monitoring of populations could provide valuable insights into the magnitude of perturbations resulting from both intentional and unintentional actions. Burbot in marginal habitats may also serve as an early indicator of the impacts of climate change on coldwater fish species. However, because burbot are not held in high regard as a sport or commercial species in much of their range, information on population status is frequently limited or nonexistent. The ability to measure responses to recovery efforts and identify future threats will be dependent on expanded efforts to assess burbot status in waters where they occur. Thus, it will be important to develop standardized methods to assess stock status of burbot populations in consideration of juvenile and adult abundance.

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