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Burbot and large hydropower in North America: benefits, threats and research needs for mitigation

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Abstract In North America, burbot *Lota lota* (L.), interactions with hydropower are common, southern burbot populations are endangered and hydropower has been implicated in the decline. Thus, the objectives of this review were to identify threats and benefits of hydropower to riverine and reservoir dwelling burbot, assess overall impacts and identify key research needs for mitigation. Review findings suggest that while winter hydropower discharge regimes threaten riverine burbot spawning, burbot often successfully exploit reservoir environments. Further, while turbine entrainment has been hypothesised as a factor in the decline of burbot populations, low adult vulnerability to passage and a high resilience to juvenile removals likely mean risk to populations is low. Identified research needs include better definitions of flow and temperature requirements for riverine burbot and a quantification of the potential for reservoirs to act as source populations for downstream impacted zones. This review highlights the Pacific watershed focus of existing work and calls for status assessments and ecological research of burbot in North American Arctic and Atlantic watersheds where large hydropower and burbot interactions are common yet rarely studied.

KEYWORDS: entrainment, hydropower, *Lota lota*, regulated rivers, reservoirs.

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Introduction

Hydroelectric generating dams and their operations change natural lentic and lotic ecosystems to reservoirs and regulated rivers (Stanford *et al.* 1996; Rosenberg *et al.* 1997, 2000). These hydropower dams, their operations and their resultant habitat alterations (hereafter, together known as hydropower facilities) most commonly carry negative consequences for fish populations (Murchie *et al.* 2008). Approximately 1000 large hydropower dams (>10 m head height) are in operation in North America, with 596 in Canada (Environment Canada https://www.ec.gc.ca/eau-water/default.asp?lang=En&n=9D404A01-1) and 420 in the USA (Global Reservoir and Dam Database: http://www.gwsp.org/products/grand-database.html). Together hydropower accounts for around 60% (Smokorowski *et al.* 2011) and 3.1% (US Energy Information Administration http://www.eia.gov/totalenergy/data/monthly/pdf/sec1_5.pdf) of electricity production in Canada and the USA, respectively, and demand for hydropower is growing rapidly.

Hydropower facilities have many notable impacts on fisheries resources including disruption of the natural flow regime (Poff *et al.* 1997; Bunn & Arthington 2002; Lytle & Poff 2004; Poff & Zimmerman 2010), altered downstream thermal regimes (Webb & Walling 1993; Quinn *et al.* 1997; Olden & Naiman 2010), changes to community and trophic structure (Baxter 1977; Fernando & Holčík 1991) and disruption of habitat connectivity (Lucas & Baras 2001; Nilsson *et al.* 2005; Arthington *et al.* 2010). Furthermore, hydropower facilities can result in direct losses to fish populations through turbine entrainment (the involuntary passage of fish through turbines; Coutant & Whitney 2000) and habitat losses through reservoir drawdown and habitat dewatering (Cott *et al.* 2008; Nagrodski *et al.* 2012). As a species found in riverine (Evenson 1993, 1997) and lacustrine (McPhail & Paragamian 2000) habitats, burbot, *Lota lota* (L.), are potentially vulnerable to both upstream and downstream hydropower-related impacts. Indeed, populations towards the southern extent (~40°N) of the North American burbot range are threatened (Stapanian *et al.* 2010; Fig. 1); and hydropower facilities, which are concentrated in this region, have been implicated in the decline (Hardy & Paragamian 2013).

A Web of Science search (3 March 2015) for the terms ‘burbot’ and ‘lota lota’ identified the following: 456 burbot-specific manuscripts since 1994, compared to just 117 in the previous part of the 20th century, and five burbot-specific symposia since the year 2000 (Paragamian & Willis 2000; Paragamian & Bennett 2008; Paragamian & Stapanian 2011; Stapanian & Madenjian 2013; : Stapanian & Myrick 2015). However, while 372 burbot-specific papers have been published since McPhail and Paragamian’s (2000) comprehensive review of burbot biology and life history, few recent, burbot-specific synthesis papers exist (see Stapanian *et al.* 2008, 2010 for exceptions). Given the high potential for burbot–hydropower facility interactions in North America, a review of the effects of hydropower facilities on burbot populations is important for the future conservation of the species. In this study, a traits-based assessment approach (Rubach *et al.* 2011; Ĉada & Schweizer 2012) was used to review the threats and benefits of hydropower facilities to burbot populations. The effects of flow alterations, thermal habitat changes and disruption of downstream connectivity for riverine burbot populations below hydropower dams were assessed, and the consequences of turbine entrainment, reservoir drawdown, trophic depression and disruption of upstream connectivity for reservoir burbot populations were investigated. Next, information was synthesised to assess and compare impacts to populations and identify potential conservation issues. Finally, the review identified research needs for the following: the conservation of riverine burbot below hydropower facilities, management of burbot in reservoirs and the design of future hydropower facilities for burbot conservation.

Threats to river populations

Flow alterations

Decreasing winter discharges are an important trigger for pre-spawning migrations in fluvial burbot populations, with spawning occurring during low-flow periods in late winter (Breeser *et al.* 1988; Paragamian *et al.* 2005; Paragamian & Wakkinen 2008). In the Kootenai River, Idaho, pre-spawning migrations were significantly reduced when hydropower-regulated discharges exceeded 300 m s^{-1}, and burbot delayed migration and spawning failed to occur in years with high winter discharges (Paragamian *et al.* 2005). Successful spawning was only observed when drought conditions reduced winter discharge to an average of 174 m s^{-1} (Paragamian *et al.* 2005; Hardy & Paragamian 2013). Hydropeaking or ramping, where turbines are turned on or off in relation to diel and even hourly fluctuations in demand for electricity, results in highly variable flows and current velocity downstream of turbines; as a weak swimmer (Jones *et al.* 1974), burbot may be vulnerable to such unpredictable changes in velocity.

Thermal habitat change

As a winter-spawning (Cott *et al.* 2013b), winter-active, coldwater stenotherm (Shuter *et al.* 2012), burbot are

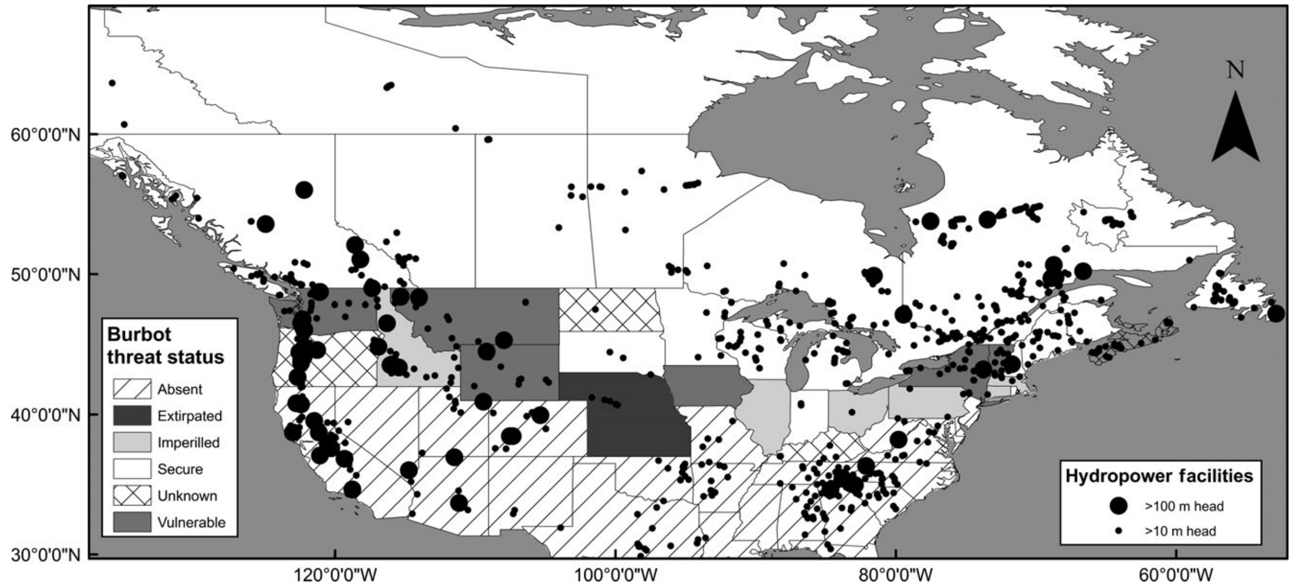

Figure 1. Range of burbot and distribution of large hydropower reservoirs in North America. Burbot provincial- and state-scale population status was based on information from Stapanian *et al.* (2010), with status updates for the Northwest Territories and Nunavut provided by Working Group on General Status of NWT Species (2011) and Beckett *et al.* (2012), respectively. Data on hydroelectric facilities from GRanD Database, available at http://atlas.gwsp.org.

potentially sensitive to increases in temperature associated with winter hydropower discharge regimes. Burbot spawn at 0–4 °C (McPhail & Paragamian 2000), and spawning cannot be induced at temperatures above 6 °C (Zarski *et al.* 2010). Successful egg incubation has been observed at temperatures ranging from 0–6 °C (McPhail & Paragamian 2000), with optimum hatch rates reported at 3.8 °C (Vught *et al.* 2008) and 3 °C (Taylor & McPhail 2000). One hundred percent egg mortality has been recorded at >8.1 °C (Vught *et al.* 2008), >6 °C (Taylor & McPhail 2000) and >5 °C (Zarski *et al.* 2010). In addition to acting as a physiological requirement for successful spawning and egg incubation, winter temperatures below 6 °C, have also been shown to act as an important trigger for burbot spawning migrations (Paragamian & Wakkinen 2008; Hardy & Paragamian 2013). Furthermore, the slow rate of cooling associated with reservoir thermal mass may have an impact on burbot reproductive success, as Zarski *et al.* (2010) showed that a fast rate of cooling from 6 °C to 1 °C significantly improved spawning success under hatchery conditions. For more northern riverine burbot populations, cooling induced by summertime hypolimnetic discharge has the potential to impact population fitness if temperatures fall below preferred temperatures of ~10 to 14 °C (Carl 1995; Rudstam *et al.* 1995 Pääkkönen & Marjomäki 2000; Pääkkönen *et al.* 2003). Researchers are increasingly recognising the importance of maintaining the natural temperature regime for ensuring ecosystem integrity (reviewed in Caissie 2006), and a natural thermal regime also appears to benefit burbot reproduction.

Barriers to upstream habitat connectivity

Large hydropower dams without fishways represent a barrier to upstream movements of all life stages of burbot. Successful passage of burbot has been recorded through low-head (<10 m) fishways, including vertical slot and Denil fishways in northern Canada (Schwalme *et al.* 1985), a vertical slot fishway in the Czech republic (Slavík & Bartoš 2002) and naturelike fishways in a Swedish project (Calles & Greenberg 2007). No published evidence of burbot fishway use on high-head dams (>10 m) was found, but this may be a consequence of the absence of fishway construction on high-head hydropower dams in Canada and the USA, which were not traditionally installed at the time of construction (Katopodis & Williams 2012; Hatry *et al.* 2013). Nonetheless, Vokoun and Watrous (2009) suggested that current velocities in most large fishways would present a serious challenge to burbot ascent. Jones *et al.* (1974) found large burbot (>50 cm) incapable of ascending 100 m over 10 min at velocities >0.25 m s^{-1}, and Vokoun and Watrous (2009) observed switching to sprint swimming at very low velocities of 4.7 body lengths sec^{-1}. Furthermore, burbot have been found to be weak jumpers, incapable of jumping heights equal to a single body length

(Gardunio 2014). Lacking site-specific data, any hydropower dam, regardless of fishway status with a head height of >10 m, is likely to represent a complete barrier to upstream migration.

Threats to reservoir populations

Turbine entrainment

Fish entrainment, the involuntary downstream movement of fish through water-release structures such as turbines (Ĉada *et al.* 1997; Coutant & Whitney 2000), can result in immediate or delayed mortality due to physical contact with passage structures, pressure changes or increased susceptibility to predation post-entrainment. While adult burbot entrainment has been noted (Skaar *et al.* 1996; Spence & Neufeld 2002; Dunnigan & Sinclair 2008; Spinelli 2010), burbot-specific entrainment vulnerability and passage mortality studies are rare (see Martins *et al.* 2013 for an exception). Lacking such studies, a traits-based assessment procedure (Ĉada & Schweizer 2012) was undertaken.

Autumn and winter movements of adult burbot include pre-spawning adfluvial migrations (Paragamian & Wakkinen 2008) and within-reservoir movements (Harrison *et al.* 2015). As a winter-active species (McPhail & Paragamian 2000; Harrison *et al.* 2013), burbot are often quiescent during the summer (Hölker *et al.* 2004). Consequently, turbine-passage exposure risk is likely highest during the autumn–winter period, which may explain the general pattern of increased autumn–winter adult entrainment described by Dunnigan and Sinclair (2008) and Martins *et al.* (2013). However, the time of entrainment appears to be site-specific, with Spinelli (2010) reporting elevated entrainment during the summer and autumn in Hauser Reservoir, Montana, and Spence and Neufeld (2002) observing entrainment in early spring (March) in Duncan Reservoir, British Columbia.

Life history strategy and associated movements can result in within-system variation in entrainment risk. Life history diversity within burbot populations includes littoral, deep-water and tributary spawning (Paragamian & Wakkinen 2008; Jude *et al.* 2013); and entrainment risk may differ among strategies. Burbot display large within-population individual differences in home range size, site fidelity and movement distances (Harrison *et al.* 2015). Different behavioural types may have unequal vulnerabilities to entrainment, with the more mobile, exploratory behavioural types with large home ranges being more at risk of encounters with turbine entrances, assuming that the turbine entranceway is within burbot depth use range.

As a benthic species (Cott *et al.* 2015), hypolimnetic-located turbine entrances may increase entrainment exposure for burbot. Burbot are night-active (Müller 1973; Kavaliers 1980; McPhail & Paragamian 2000; Fischer 2004; Harrison *et al.* 2013) and exhibit diel bank migrations between deep and shallow benthic habitat (Bergersen *et al.* 1993; Carl 1995; Harrison *et al.* 2013; Cott *et al.* 2015). Accordingly, risk of exposure may increase in shallower intake locations at night. Burbot depth use varies from <1 m to 180 m in a Columbia River reservoir (Harrison *et al.* 2013) and up to 366 m in Lake Superior (Boyer *et al.* 1989); consequently, no turbine entrance depth could be considered risk free.

As weak swimmers (McPhail & Paragamian 2000; Peake 2008), burbot may be vulnerable to high velocities around turbine intakes. Nevertheless, turbine entrance velocities may not be high enough to significantly challenge burbot. Data suggest that even for hydropower systems with a very large capacity, such as the Mica Dam in British Columbia, velocities in the forebay reach a maximum of ~0.2 m s^{-1} within 20 m of the turbine intake (Langford *et al.* 2012).

Insufficient entrainment data are available to make conclusive quantitative statements about burbot entrainment vulnerability. However, the low vulnerability to entrainment suggested by the traits-based approach is mostly supported by the limited available literature on annual entrainment removal rates (the proportion of tagged fish that become entrained, scaled to a single year, which is taken to represent the proportion of the reservoir population likely to be entrained). For example, Martins *et al.* (2013) calculated an annual entrainment removal rate of 0.7% through Mica Dam, British Columbia (based on a sample of 75 tagged fish monitored over 2 years), and a 1.6% annual removal rate through Libby Dam, Montana, was calculated based on observations of 40 burbot monitored over 18 months (Dunnigan & Sinclair 2008). The entrainment of 2 tagged burbot through Duncan Dam observed by Spence and Neufeld (2002), suggest a high annual removal rate (32%), but this estimated was calculated from a low number of tagged fish (15) were observed to for only 5 months. Further, while 6555 burbot were observed to by hydroacoustics to be entrained over 2 years at Hauser Dam (Spinelli 2010), upstream population size was not quantified and, therefore, removal rates could not be estimated.

Early life stage (ELS) burbot display a number of traits that may render them susceptible to turbine passage. ELS burbot undergo three distinct life stages: passive drifting in the early post-hatch larval stage (Jude *et al.* 2013); a juvenile pelagic phase with active swimming and diel vertical migration (Probst & Eckmann 2009; Donner & Eckmann 2011); and a settlement phase where burbot move from the profundal towards the littoral zone as they grow into subadults (Fischer 1999; Miler & Fischer 2004). For the larval passive drifting and juvenile pelagic phases, weak swimming ability (Wang & Appenzeller 1998) and pelagic habitat use are traits that suggest high vulnerability to entrainment (Coutant & Whitney 2000). Further, diel vertical migrations of the pelagic juveniles may influence entrainment vulnerability, depending on the relative depth of water intake locations and the diel cycle of turbine operations. Benthic habitat use and increased swimming ability of settlement-phase burbot (Fischer 1999; Miler & Fischer 2004) may result in reduced entrainment vulnerability. While turbine entrainment-specific research is lacking, a similar ontogenetic shift in entrainment vulnerability of ELS burbot has been observed in cooling water intakes in the Laurentian Great Lakes where Mansfield *et al.* (1983) noted high numbers of larval and juvenile pelagic burbot but low numbers of settlement-stage burbot entrained.

While examples of adult burbot surviving turbine passage have been reported through Libby Dam, Montana, USA (Dunnigan & Sinclair 2008) and Duncan Dam, British Columbia, Canada (Spence & Neufeld 2002), samples sizes of entrained fish have been too small to provide reliable estimates of mortality rates. Passage mortality of adult fish is species-specific, and swim bladder morphology is a key predictor of entrainment mortality (Brown *et al.* 2014), as rapid decompression is a significant stressor in turbine passage (Trumbo *et al.* 2014). As a deep-water physoclistous species (Bruesewitz *et al.* 1993), burbot are likely to have higher mortality than physostomous species (Brown *et al.* 2009, 2014). Further, the deep-water habitat use increases burbot susceptibility to barotrauma induced by turbine passage due to higher acclimation pressure (Stephenson *et al.* 2010; Brown *et al.* 2014). The suggested elevated vulnerability to barotrauma of adult burbot passing turbines is further evidenced by their high susceptibility to capture barotraumas (Bruesewitz *et al.* 1993; Neufeld & Spence 2004)).

For adult burbot, which can reach lengths of >100 cm (McPhail & Paragamian 2000), large body size may increase the likelihood of turbine-passage mortality, as larger fish are more susceptible to turbine strikes (Deng *et al.* 2005, 2007). Integument type is also a useful trait in predicting turbine-passage survival (Ĉada & Schweizer 2012), as passage through turbines can yield abrasive contacts with hard structures and shear stresses (Neitzel *et al.* 2004). Fishes such as burbot, which have a very thick mucus layer (Ashton *et al.* 2013) and small, hard-to-remove scales (McPhail & Paragamian 2000), tend to be less susceptible to damage and mortality from abrasions and shear stresses (Ĉada & Schweizer 2012). Nonetheless, while the thick integument may offer some protection, given their large size and high susceptibility to barotrauma, adult burbot turbine-passage mortality is likely high.

Given the known size dependency of entrainment-passage mortality (Ĉada 1990; Ĉada *et al.* 1997; Deng *et al.* 2005, 2007), juvenile settlement- and pelagic-stage burbot may have a higher passage survival than adult burbot. Juvenile burbot entrainment mortality has not been well studied, and the most comprehensive research into juvenile turbine-passage mortality has been on out-migrating salmonid species where turbine-passage mortality was found to be 7–13% through high-head dams in a 25-year study (Bickford & Skalski 2000). While entrainment-passage mortality likely differs among species, Bickford and Skalski (2000) provide the best available estimate of juvenile entrainment mortality. Although swim bladder morphology differences complicate cross-species comparisons, the small size of juvenile pelagic-phase burbot (25–40 mm, Fischer 1999) compared to the larger out-migrating salmonid smolts and the known size dependency of entrainment-passage mortality (Ĉada 1990; Ĉada *et al.* 1997; Deng *et al.* 2005, 2007) suggest similar mortality rates might be expected.

Larval entrainment mortality may be higher than for juveniles (Coutant & Whitney 2000) because less robust swim bladders render larval fish more susceptible to barotrauma (Brown *et al.* 2014). While mortality through high-head systems is often higher than through low-head systems (Ĉada & Schweizer 2012), estimates of larval mortality are limited to low-head systems. Ĉada (1990) reported ichthyoplankton mortality as low as ~5% through low-head turbines. Accordingly, although turbine-passage mortality of larval burbot through high-head dams is likely higher than the 5% estimate for low-head structures, turbine-passage mortality of ichthyoplankton, including larval burbot, is low (Coutant & Whitney 2000).

Reservoir drawdown

Many large hydropower impoundments in North America operate a winter drawdown regime, refilling the reservoir with the spring and summer runoff (Wantzen *et al.* 2008). For a winter spawner such as burbot (Cott *et al.* 2013a,b), this regime has the potential to adversely affect spawning success. Lacustrine burbot spawn in shallow water (<2 m), and winter drawdown may reduce available spawning habitat and increase the likelihood of egg stranding and freezing (Cott *et al.* 2008; Stapanian *et al.* 2010). Indeed, Bergersen *et al.* (1993) reported that a 13 m drawdown on Bull Lake, Wyoming, led to a virtual elimination of burbot spawning habitat. Winter drawdown can restrict access to reservoir tributaries for adfluvial spawners (Gaboury & Patalas 1984) including burbot (Spence & Neufeld 2002). In addition, drawdowns have been shown to reduce the availability of shelter for adult burbot (Fischer & Öhl 2005). Drawdowns also negatively impact the littoral benthic invertebrate community (Furey *et al.* 2006), which provide the main prey items for juvenile settlement-stage burbot. Further, the occupation of the littoral zone in lakes by subadult burbot (Taylor & McPhail 2000) suggests a vulnerability to stranding, which is common in juveniles of many species (Nagrodski *et al.* 2012).

Trophic depression

As a top predator (Cott *et al.* 2011), burbot are susceptible to shifts in the structure and function of the trophic community that result from river and stream impoundment (Baxter 1977; Rosenberg *et al.* 2000). Reservoir trophic depression is a common issue in upland reservoirs (Grimard & Jones 1982), particularly in the Pacific (Stockner & Shortreed 1985; Stockner & Macisaac 1996; Stockner *et al.* 2000) and Arctic watersheds (Stockner *et al.* 2005). In these systems, impoundment creates a short-lived trophic upsurge as nutrients leach from flooded lands (Matzinger *et al.* 2007) that is followed by long-term trophic depression as available nutrients are used and nutrient inputs are removed by hypolimnetic sediment deposition (Grimard & Jones 1982; Stockner *et al.* 2000). The elimination of littoral habitat and the littoral community associated with winter drawdown is thought to contribute to trophic depression (Stockner & Macisaac 1996). Trophic depression often causes crashes in the pelagic fish community (Stockner & Macisaac 1996; Bradford *et al.* 2000; Perrin *et al.* 2006) that comprise a high proportion of the diet of lacustrine burbot (Wagner 1972; Schram *et al.* 2006). Importantly, reservoir trophic depression may also act as a limiting factor for survival of ELS burbot (Hardy *et al.* 2008). Starvation is a key factor controlling larval survival, and sufficient nutrient availability is necessary for the production of burbot larvae foods (Ghan & Sprules 1993). Similarly, nutrient availability is important for the production of the larger zooplankton that account for the majority of juvenile pelagic-stage burbot diet (Wang & Appenzeller 1998).

Downstream connectivity

Given turbine entrainment mortality for adult burbot is likely high, large hydropower dams may act as an impermeable barrier to downstream connectivity for adult burbot. On the other hand, large hydropower dams likely are a more permeable barrier for downstream movements of ELS burbot, as turbine entrainment mortality of larval and juvenile individuals is fairly low (Ĉada *et al.* 1997; Coutant & Whitney 2000; Ĉada & Schweizer 2012; Brown *et al.* 2014).

Benefits to riverine populations

Hypolimnetic withdrawals that lower downstream summer water temperatures have the potential to benefit burbot populations. Burbot prefer temperatures ~10–14 °C (Carl 1995; Rudstam *et al.* 1995 Pääkkönen & Marjomäki 2000; Pääkkönen *et al.* 2003), burbot abundance is negatively correlated with mean stream temperatures >20 °C (Dixon & Vokoun 2009) and food consumption has been observed to slow at >20 °C (Hölker *et al.* 2004). Accordingly, in rivers where pre-dam temperatures often exceed these values, hypolimnetic releases may benefit burbot populations. Horton and Strainer (2008) hypothesised increases in burbot abundance in the Missouri River were associated with dam-derived habitat cooling. Similarly, colonisation of the Green River Drainage of the Upper Colorado River in Wyoming and Utah, where burbot are not native, has been attributed to downstream cooling from hypolimnetic discharges (Gardunio *et al.* 2011).

Benefits to reservoir populations

Dam construction impacts the upstream thermal regime, most notably in the impounded zone, where the thermal regime shifts from a riverine regime, typically characterised by daily, diel and seasonal fluctuations, to a much more stable lacustrine-type regime, often with summer and winter thermal stratification (Webb & Walling 1993; Olden & Naiman 2010). In general, during the summer, stratified impoundments result in a hypolimnion that provides cooler thermal habitat than would be found in the original river system. In contrast, summer epilimnion temperatures may be higher than summer river temperatures. Burbot are adapted to survive in both riverine and lacustrine systems (McPhail & Paragamian 2000), and the shift to a lacustrine-like thermal regime may not come at a significant fitness cost. Both juvenile and adult burbot have been hypothesised to gain a bio-energetic advantage by exploiting warm water within the epilimnion to hunt at night and by occupying the cold hypolimnion during the day to optimise energy gain during rest (Donner & Eckmann 2011; Harrison *et al.* 2013). Provided sufficient oxygen is available, the cold hypolimnetic layer may also provide an important summer daytime thermal refuge for burbot in systems where global warming is increasing thermal stress.

While pelagic fish communities may not exist in reservoirs immediately post-fill, the vacant pelagic zooplanktivorous niche is usually quickly filled as a result of stocking, recruitment from flooded natural lakes and pre-existing riverine species that can exploit a pelagic niche (Baxter 1977; Fernando & Holčík 1991). As a top piscivore, pelagic fishes form the majority of lacustrine adult burbot diet (Wagner 1972; Schram *et al.* 2006), and burbot appear to be able to exploit a similar niche in impoundments (Black *et al.* 2003).

Synthesis of overall impacts to riverine burbot populations

The hypolimnetic-withdrawal winter discharge regimes and the associated winter warming and elevated winter flow provide the most significant threat to riverine burbot downstream of hydropower facilities. Regulated discharge has been suspected as factor in the decline of burbot populations downstream of hydropower facilities (McPhail & Paragamian 2000; Stapanian *et al.* 2010), and high winter discharges and increased temperatures have been strongly linked to the collapse of the Kootenai River burbot population below Libby Dam in Idaho (Hardy & Paragamian 2013). As burbot are weak swimmers (Jones *et al.* 1974), large hydropower dams with or without fishways, likely represent an impassable upstream barrier to riverine burbot. Disruption of longitudinal connectivity may have adverse consequences for riverine burbot that sometimes migrate long distances (Evenson 1993, 1997). Genetically distinct stocks of burbot have been detected above and below natural barriers (Powell *et al.* 2008), and Underwood *et al.* (2015) suggested that although localised burbot movements between lakes and rivers on the same tributary are fairly common, even modest natural barriers can result in distinct populations within the same watershed.

In terms of benefits, cooling effects from hypolimnetic withdrawal can provide summertime thermal refuge to riverine burbot populations at the southern end of burbot range, and this may be especially important in the light of global warming. Nevertheless, in general, riverine burbot populations downstream of hydropower dams are much reduced in comparison to pre-dam conditions, as demonstrated for the Columbia River (Cope 2008) and the Missouri River below Garrison Dam (Stapanian *et al.* 2010). While the loss of habitat connectivity associated with dam construction may play a part in this decline, upstream connectivity disruption is likely not a significant threat compared to the effect of winter discharge regimes. Indeed, winter discharge regimes are the paramount hydropower-related threat to riverine burbot due to the disruption to spawning associated with elevated flows and temperatures during the late winter period.

Synthesis of overall impacts to reservoir burbot populations

While entrainment has been hypothesised as a possible factor in the decline of burbot populations in reservoirs (Stapanian *et al.* 2010; Hardy & Paragamian 2013), detailed data on the population-level effects of entrainment are lacking. Adult burbot entrainment has occasionally been reported, but research based on meaningful sample sizes and sufficient sampling periods (Martins *et al.* 2013), combined with the traits-based assessment, suggest adult entrainment removal rates are low.

While burbot population work has not been extensive, existing population models indicate burbot can sustain high removal rates. For example, Ahrens and Korman (2002) suggested that the west arm of the Kootenai Lake historical burbot population sustained an annual harvest of up to 20% per year. Further, burbot possess a number of the key demographic traits identified by Ĉada and Schweizer (2012) as indicative of a species capable of sustaining entrainment removal. Female burbot are highly fecund, often producing over 3 million eggs per year per individual (Roach & Evenson 1993), resulting in high numbers of larval and juvenile pelagic burbot (Ghan & Sprules 1993). Further, burbot reach sexual maturity early and at a small size (Stapanian & Madenjian 2007), are iteroparous and can live up to 20 years (Guinn & Hallberg 1990), ensuring high lifetime reproductive output. Given that available evidence suggests adult entrainment rates are fairly low and that population models (Ahrens & Korman 2002) and burbot life history traits indicate a certain amount of resilience to removals, threats to burbot populations from adult entrainment may be fairly low. Nonetheless, given that vulnerability to entrainment is site-specific (Coutant & Whitney 2000), site-by-site monitoring and assessments are recommended where possible. The large numbers of larval and juvenile pelagic burbot produced by this r strategist (Ghan & Sprules 1993; Roach & Evenson 1993) suggest that the potential for population-level impacts associated with ELS entrainment is also low. However, given that research into the entrainment vulnerability of ELS of resident species, including burbot, is limited (Ĉada & Schweizer 2012), entrainment needs measurement studies should consider site-specific differences and effects.

Given the importance of littoral habitat for subadults (Taylor & McPhail 2000), the importance of the littoral zone and shoreline for adult lacustrine burbot at night (Harrison *et al.* 2013; Cott *et al.* 2015) and the evidence that suggests lacustrine burbot spawn in the shallow littoral zone (McPhail & Paragamian 2000), damage to the littoral habitat as a result of winter drawdowns may be a more important threat to reservoir burbot than turbine entrainment. Similarly, because the main prey items for both ELS and adult burbot have been shown to be vulnerable to trophic depression (Stockner & Shortreed 1985; Stockner & Macisaac 1996; Stockner *et al.* 2000), reservoir trophic depression is also likely a greater threat to reservoir burbot populations than entrainment.

In terms of benefits, while comparisons with pre-dam conditions are not possible due to insufficient baseline data, hydropower reservoirs appear able to provide suitable thermal and trophic niches for burbot and support burbot populations. Opportunities to improve reservoir habitat for burbot exist, and efforts should be focused on the mitigation of the negative effects of winter drawdown on littoral habitat and the effects of reservoir trophic depression on burbot prey.

Research needs for mitigation of hydropower impacts

Burbot and hydropower outside of the Pacific Watershed

Much of the information about interactions between burbot and hydropower facilities in North America reviewed in this manuscript has been based on data from hydropower systems in the Pacific watershed, with much less information available on burbot in hydropower systems in Atlantic or Arctic drainages. Large hydropower dams (>10 m) and mega-dams (>100 m) are common across much of the North American burbot range (Fig. 1). Tellingly, no information could be found for the status of burbot populations above or below the four largest reservoirs in Canada, all of which lie in Arctic and Atlantic drainages within the range of burbot [Daniel-Johnson Dam in northern Quebec (ranked 5th largest reservoir in the world); Williston Reservoir, northern British Columbia (ranked 7th largest reservoir in the world) and Robert-Bourassa Reservoir and La Grande-3 Nord Reservoir both in northern Quebec (ranked 11th and 12th in the world, respectively)]. Indeed, the abundance of large hydropower dams (>10 m head height) and mega-dams (>100 m head height) within the North American range of burbot, which exist outside of the Pacific watershed, is evident in Fig. 1. Accordingly, given the evidence of negative impacts of hydropower facilities reviewed here, status assessments of burbot populations below and above hydropower dams in Atlantic and Arctic watersheds should be a priority for burbot conservation.

Environmental flows and thermal requirements of spawning riverine burbot

Given the interpretation that winter discharge is the primary threat of hydropower dams to riverine burbot populations, changes in dam operation are a priority for riverine burbot conservation. The operational changes required to mitigate hydropower discharge impacts are hard to implement (Hardy & Paragamian 2013), as winter drawdowns are required to prevent flooding from spring snowmelt, and the current drawdown and fill routine common in North America is driven by seasonal demand for power. The reluctance of hydropower authorities to change detrimental regimes has been illustrated by the Kootenai system, where power authorities have not implemented regimes requested for burbot conservation (Hardy & Paragamian 2013). Research to precisely define the timing and environmental flow and temperature requirements of spawning burbot is needed to design discharge regimes that can balance burbot conservation with hydropower objectives.

Potential for impoundments to act as source populations for downstream

This synthesis suggests that while hydropower reservoirs can support burbot populations, burbot populations below hydropower systems can be negatively impacted, in part due to reproductive disruption. Larval drift is an important dispersal mechanism for many fishes in both riverine (Lechner *et al.* 2014) and lacustrine systems (Höök *et al.* 2006), including burbot in the Laurentian Great Lakes (Jude *et al.* 2013) and in rivers (Fisher 2000). Successful downstream passage through turbines has been recorded for young-of-year fishes in the Danube River delta (Janáč *et al.* 2013), and data suggest upstream lake and reservoir systems can be sources for downstream recruitment of burbot (Paragamian *et al.* 1999; Hubert *et al.* 2008; Underwood *et al.* 2015). This traits-based assessment suggested that burbot produce large numbers of pelagic larvae in addition to juveniles that are vulnerable to entrainment (Ĉada & Schweizer 2012), that survival of entrained ELS burbot is likely high (Ĉada *et al.* 1997; Coutant & Whitney 2000; Ĉada & Schweizer 2012; Brown *et al.* 2014) and that upstream populations can probably withstand high ELS removal rates. Thus, the viability of reservoirs to act as source populations for downstream populations warrants further investigation. While quantification of burbot ELS entrainment rates might help establish levels of downstream passage, direct methods are logistically difficult in large reservoirs due to the difficulty associated with netting high-volume turbine outflows (Skaar *et al.*

1996). Further, laboratory-based simulations of turbine entrainment have potential to quantify passage survival (Richmond *et al.* 2014), but they cannot assess the ability of survivors to contribute to recruitment. Therefore, genomic sequencing and other genetic methods (see Hughes *et al.* 2009 for a review) may be the most practical approach to quantify downstream population connectivity. Should downstream population connectivity be quantified and established as a viable source of recruitment, then improvements to reservoir burbot productivity have the potential to at least partially compensate for the negative effects on downstream riverine burbot.

Fertilisation for reservoir trophic depression

In ultra-oligotrophic lakes and reservoirs suffering from trophic depression, fertilisation experiments have resulted in primary productivity increases and improved phytoplankton abundance (Stockner & Shortreed 1985; Stockner & Macisaac 1996; Stockner *et al.* 2000), increased zooplankton abundance (Thompson 1999), increases in pelagic fish production (Hyatt *et al.* 2004), and increased growth of a top predator, rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Johnston *et al.* 1999). While increased burbot growth was noted post-fertilisation in Arrow Lakes Reservoir in British Columbia (Arndt & Baxter 2006), more research is needed to understand the effects of fertilisation for burbot. However, given that pelagic fishes form the majority of lacustrine adult burbot diet (Wagner 1972; Schram *et al.* 2006), the prospects for increased burbot growth post-fertilisation are promising. The nutrient dependence of the phytoplankton, copepods and rotifers that are important ELS burbot prey items (Wang & Appenzeller 1998) also suggests nutrient restoration has potential for improving ELS recruitment in impoundments suffering from trophic depression. As a caveat, lake fertilisation can result in variable results (Hilborn & Winton 1993), fertilisation costs can be high and, while favourable cost–benefit ratios have been seen in sockeye, *Oncorhynchus nerka* (Walbaum) nursery lake fertilisation experiments (Guthrie & Peterman 1988; Maxwell *et al.* 2006), cost–benefit analysis has not been performed on fertilisation experiments for fishes of lower commercial value. Further, fertilisation has sometimes resulted in negative effects such as blue-green algae and ungrazable diatom blooms (Hyatt *et al.* 2004).

Life history of burbot in reservoirs

Burbot reservoir life history is an important knowledge gap (Dunnigan & Sinclair 2008). Burbot display several distinct life history strategies including deep-water spawning, reef spawning, tributary spawning and littoral spawning in natural lakes (Jude *et al.* 2013). While lake spawning and tributary spawning burbot may contribute to reservoir burbot stocks (Paragamian & Wakkinen 2008), the existence of each strategy and relative contribution to reservoir recruitment needs to be defined. Differing life history strategies likely have different implications for the management of reservoir drawdown, as littoral spawning could increase vulnerability to late winter drawdown egg habitat dewatering (Bergersen *et al.* 1993; Stapanian *et al.* 2010), and tributary spawners may be vulnerable to drawdown-imposed tributary access restriction. Accordingly, a greater understanding of the precise spawning habitat requirements of lake spawners is a necessary step in targeting spawning habitat improvement and drawdown mitigation works. Further, this research is needed to explain how reservoirs with large drawdowns such as Kinbasket and Arrow Lakes Reservoirs in British Columbia (Arndt & Baxter 2006; Harrison *et al.* 2013) can maintain burbot stocks. Improved understanding of the exact timing and location of reservoir burbot spawning events will be required to better design drawdown operational changes to reduce the likelihood of egg habitat dewatering. Equally, at the site scale, identification of tributary spawning locations is necessary to target access and habitat improvement works.

Considerations for future hydropower projects

Mitigation of the effects of existing hydropower facilities on fisheries is often difficult to achieve (Fraley *et al.* 1989), but many research opportunities exist to enable the design of future hydropower facilities with fewer impacts on burbot populations. While the upstream passage of burbot past existing hydropower facilities was not identified as the most significant threat to burbot populations in this review, habitat connectivity remains an important feature of sustainable hydropower facilities (Lucas & Baras 2001). Accordingly, more work is needed to investigate the effectiveness of fishways for non-salmonid species (Hatry *et al.* 2013) that will enable the design of fishways to pass weak swimmers such as burbot. ELS turbine-passage survival was identified in this review as likely important for population connectivity. Thus, research to test the burbot passage mortality of new turbine designs will be important, particularly for ELS. Initial work suggests new turbine designs can pass fish well (>98% survival of <20 cm fish) and actually improve power output (Hogan *et al.* 2014), but effects on burbot are yet to be quantified.

Conclusions

This review emphasises the threat to riverine burbot caused by winter discharge regimes. Accordingly, it was suggested that better definitions of the precise environmental flow and temperature requirements for successful riverine spawning are needed to design winter regimes suitable for meeting burbot conservation and hydropower objectives. Burbot appear capable of occupying and exploiting reservoir habitat. Nonetheless, contributions to recruitment from differing reservoir life history strategies are not well understood, and the effects of littoral habitat loss associated with winter drawdown need quantification. While entrainment of burbot has previously been hypothesised as a possible factor in burbot declines (Stapanian *et al.* 2010), this review suggests that the risk to burbot populations from adult entrainment is likely low due to low entrainment vulnerability and an ability to withstand relatively high removal rates. Further, given that the traits-based assessment suggest ELS burbot are vulnerable to entrainment and have high passage survival and populations can likely withstand high ELS removal rates, the ability of entrained ELS burbot to contribute to downstream recruitment needs quantification. In addition, if successful downstream passage can be confirmed, then research should focus on methods of improving ELS recruitment in reservoirs, such as fertilisation and spawning habitat improvements. Finally, an overarching theme that emerged from the synthesis of hydropower-related burbot work is the current Pacific watershed focus. Given the potential for hydropower facilities to result in consequences to burbot populations highlighted in this review, status and ecological assessments of burbot above and below hydropower facilities in Arctic and Atlantic watersheds regions should be prioritised to ensure the conservation of the species.

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