Impacts of waterpower management on select fish in the Ottawa River, Canada, with an emphasis on lake sturgeon
Impacts of waterpower management on select fish in the Ottawa River, Canada, with an emphasis on lake sturgeon

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Legend

$C_F$ – foraging component

$C_{F,A}$ – adult foraging component

$C_{F,J}$ – juvenile foraging component

FWIN – Fall walleye index netting

HSI – habitat suitability index

HSM – habitat suitability index model

$k$ – intrinsic growth length (Von Bertalanffy growth equation)

$L_\infty$ - asymptotic length (Von Bertalanffy growth equation)

NSCIN – nearshore community index netting

TL - total length

$t_0$ – theoretical age at which length is 0 (Von Bertalanffy growth equation)
Abstract

The impacts of waterpower management on select fish in the Ottawa River are examined in this study and are presented in four manuscripts: 1) a systematic review of published literature on water power management; 2) examining potential causes of variation in lake sturgeon abundance among river reaches; 3) community structure and abundance among water management regimes; and 4) evaluating the predictive power of a lake sturgeon habitat suitability model at multiple scales.

1) Three meta-analyses were completed: (i) macroinvertebrate abundance is lower in zones or areas that have been dewatered due to water fluctuations or low flows (overall effect size -1.64 (-2.51/-0.77; 95% CI)); (ii) a hypolimnetic draw reduces the abundance of aquatic communities (overall effect size -0.84 (-1.38/-0.33; 95% CI)) and macroinvertebrates (overall effect size -0.73 (-1.24/-0.22; 95% CI)) downstream of a dam; (iii) altered flows has a negative effect on the abundance fluvial specialists (-0.42 (-0.81/-0.02; 95% CI) but does not affect habitat generalists (overall effect size -0.14 (-0.61/0.32; 95% CI)).

2) Three main stressors were examined to explain variation in lake sturgeon abundance among river reaches: contaminants, commercial harvest and water power management. Results were consistent with water power management impeding lake sturgeon recovery: abundance was significantly greater in unimpounded river reaches; growth rates were significantly greater in impounded reaches suggesting food was not limiting; and size/age structure in managed reaches was skewed to larger, older fish suggesting recruitment was impaired.
3) Variation in community structure and abundance was assessed for 11 fish species among three water management regimes: winter reservoirs, run-of-the-river and unimpounded. Littoral zone benthivores were significantly lower in abundance in winter reservoirs whereas species that are planktivorous for portions of their life were significantly greater. Lake sturgeon was the only fast water spawning species affected in run-of-the-river reaches.

4) The predictive power of a lake sturgeon habitat suitability model was assessed by paired net sets in good (habitat suitability index (HSI)>0.6) and poor (HSI<0.3) habitat. Lake sturgeon catch-per-unit-effort (CUE) was significantly greater for adults and juveniles in good habitat however, predictive power of the model was low ($r^2 < 0.18$). Standard index netting lake sturgeon CUE corresponded with overall foraging component which suggests the model is a good predictor of sturgeon abundance at multiple scales.

Résumé

Les effets de la gestion de l’énergie hydraulique sur certaines espèces de poissons présentes dans la rivière des Outaouais sont examinés dans cette étude et présentés dans quatre manuscrits : 1) examen systématique des textes publiés sur la gestion de l’énergie hydraulique; 2) examen des causes possibles de la variation de l’abondance de l’esturgeon jaune parmi les tronçons de la rivière; 3) structure et grosseur des populations parmi les divers régimes hydrauliques; 4) évaluation du pouvoir prévisionnel, à plusieurs échelles, d’un modèle d’indice de qualité de l’habitat de l’esturgeon jaune.
5) Trois méta-analyses pourraient être réalisées : i) l’abondance des macro-invertébrés est inférieure dans les zones qui ont été drainées en raison d’un faible débit ou d’une fluctuation des niveaux de l’eau (effet global : -1,64 [-2,51/-0,77; IC 95 %]); ii) un retrait hypolimnique réduit l’abondance des communautés aquatiques (effet global : -0,84 [-1,38/-0,33; IC 95 %]) et celle des macro-invertébrés (effet global : -0,73 [-1,24/-0,22; IC 95 %]) en aval d’un barrage; iii) la modification des débits réduit l’abondance des espèces nécessitant un habitat spécialisé (-0,42 [-0,81/-0,02; IC 95 %]), mais ne se répercute pas sur les espèces généralistes (effet global : -0,14 [-0,61/0,32; IC 95 %]).

6) Trois facteurs d’agression ont été examinés pour expliquer la variation de l’abondance de l’esturgeon jaune parmi les tronçons de la rivière : les polluants, la récolte commerciale et la gestion de l’énergie hydraulique. Les résultats indiquent que la gestion de l’énergie hydraulique nuit à la repopulation de l’esturgeon jaune : l’abondance était considérablement supérieure dans les tronçons sans barrage-réservoir; les taux de croissance étaient considérablement supérieurs dans les tronçons où les eaux sont retenues, ce qui laisse entendre que la nourriture n’était pas limitée à ces endroits; la structure par taille et par âge dans ces tronçons penchait du côté des poissons plus grands et plus âgés, ce qui laisse entendre que le recrutement y était affaibli.

7) La variation de la structure et de l’abondance a été examinée pour 11 espèces de poissons dans trois régimes de régularisation des eaux : les tronçons ayant un réservoir d’hiver, les tronçons ayant une centrale au fil de l’eau et les tronçons sans barrage-réservoir. Les espèces benthophages étaient bien moins abondantes
dans les réservoirs d'hiver, alors que les espèces qui se nourrissent de plancton pendant des parties de leur vie l'étaient bien plus. L'esturgeon jaune est le seul poisson à frayer en eau courante qui est touché dans les tronçons ayant une centrale au fil de l'eau.

8) Le pouvoir prévisionnel d'un modèle de qualité de l'habitat de l'esturgeon jaune a été examiné au moyen de filets mis bout à bout dans un bon habitat (indice de qualité de l'habitat > 0,6) et dans un habitat médiocre (indice < 0,3). Dans un bon habitat, l'indice de captures par unité d'effort était considérablement supérieur pour les adultes et les jeunes, mais le pouvoir prévisionnel du modèle était faible ($r^2 < 0,18$). Pour l'esturgeon jaune, l'indice de captures par unité d'effort (déterminé au moyen d'un filet normalisé) correspondait au composant alimentation, ce qui laisse entendre que le modèle réussit bien à prédire l'indice d'abondance de l'esturgeon jaune à plusieurs échelles.
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Finally, my daughters Erika and Nicola who provided the motivation to complete my thesis.
Chapter I. Overview of thesis and impacts of waterpower management on river ecosystems.
Rivers in North America have been exploited for centuries, initially as a means of transportation for exploring new lands then later for the movement of goods (e.g. furs) to markets. Alterations to rivers in the form of dams began when large materials (e.g. logs) were transported downstream to mills and/or markets. Many chutes were constructed to circumvent rapids and dams were constructed to alter flow patterns; dams were essential to store excess water during freshet and released during periods of low flows (e.g. late summer). Flowing waters were eventually harnessed to produce hydro-electricity which brought further and arguably the greatest alterations to river. Large scale projects dramatically altered the way rivers flow across the landscape. Impacts to the aquatic environment occurred with the hydro-electric development of rivers. Intuitively, these impacts may vary depending on how the river is managed (i.e., run-of-the-river, peaking etc.). In this doctoral thesis, I examine the impacts of different water management regimes on select fish in the Ottawa River, Canada. I focus on lake sturgeon (*Acipenser fulvescens*) as i) they are one of the only large-bodied, migratory species remaining in decent numbers in the Ottawa River; and ii) are purportedly drastically affected by dams. In this chapter, I qualitatively review existing literature on the impacts of dams, specifically hydro-electric dams, at multiple scales (Table I-1). Then, I review changes to the Ottawa Rivers as a result of hydro-electric development and finally review life history of lake sturgeon and potential effects of waterpower management.

My thesis is presented as a series of manuscripts as submitted to peer reviewed scientific journals. Co-authors are included on each manuscript although I am the lead author. In the first manuscript entitled *Meta-analysis of the ecological impacts of*
freshwater power management, we conducted a systematic review of the impacts of dams and water power management on aquatic ecosystem. Published studies in peer reviewed journals were reviewed for relevant articles. Studies were included in the meta-analysis when effect sizes could be determined from the presented information. The meta-analysis focused on three different effects: (1) changes in macroinvertebrate density associated with dewatering; (2) differences in macroinvertebrate and fish community structure and abundance associated with hypolimnetic draw; (3) differences in fish communities, in particular changes in abundance of fluvial specialists and habitat generalists, between natural and managed river flows.

In the next manuscript entitled *Variation in lake sturgeon abundance and growth among river reaches in a large regulated river*, we examine why lake sturgeon have not substantially recovered in all Ottawa River reaches. Three primary anthropogenic stressors have been identified as potentially limiting lake sturgeon populations including 1) commercial harvest; 2) contaminants; and 3) water power management. Two hypotheses (1 & 3) were tested by comparing lake sturgeon abundance and growth among the different reach types; the third hypothesis (2) was tested by assessing contaminant loads in lake sturgeon of various sizes and examining effects on growth and condition.

In the next manuscript entitled *Variation in the large-bodied fish community structure and abundance among reaches subject to different management regimes in a large river*, we use data collected from standardized index netting using both trapnets and gillnets to
compare demographic and life history attributes (relative abundance, growth, condition, mortality and recruitment) of select large-bodied fish species among different water management regimes. The hypothesis that water management regime is a major determinant of fish community structure leads to specific predictions about the how life history attributes should vary among reaches both within and among groups of species (trophic guilds).

In the final manuscript entitled *Evaluation of the predictive power of a lake sturgeon habitat suitability model at multiple scales*, we: develop a spatially explicit form of the lake sturgeon HSM; apply this version to three reaches of the Ottawa River using spatially explicit measurements of the model’s key variables (substrate type, water depth and velocity) to generate spatially explicit predicted habitat suitabilities; and test the predictive power of the model by correlating predicted habitat suitability with observed lake sturgeon abundance at two different spatial scales: within-reach and among-reach. The initial intent was to assess if habitat availability differed among managed versus unimpounded Ottawa River reaches however model validation was pertinent before this comparison could occur.

I. History of dam construction and operation

1.1 Global

Dams and weirs have been constructed on streams and rivers for centuries (Hoffmann 2005); commencing in the late 1800s or early 1900s, they were constructed along rivers
for navigational and hydro-electrical purposes. Large dams (>15 m foundation to crest) have been primarily constructed since the 1950’s (Chao 1995; Rosenberg et al. 2000) with the number of large dams constructed worldwide peaking in the 1970’s (Rosenberg et al. 2000). By the early 1900s, most large rivers in temperate regions had already been modified to some extent and have been subjected to increasing alterations during the 20th century (Welcomme 1995). In comparison, fewer dams have been constructed in the tropics although these areas are currently experiencing increased development pressure (Pringle et al. 2000).

I. 2 North American and Canada

The United States has more than 5000 large dams, or approximately 58 per 100,000 km² of land area; Canada, on the other hand, has over 700 large dams or approximately 7.5 per 100,000 km² of land area (Pringle et al. 2000). Large dam development peaked in North America in the 1960s (Pringle et al. 2000); in contrast, Canada shows two peaks in large dam construction, one in the 1950s, another in the 1970s (Figure I - 1). The most suitable sites have now been developed in Canada (Baxter and Glaude 1980; Dynesius and Nilsson 1994; Rosenberg et al. 1995; 1997) although there is still further development potential on remote northern rivers (Rosenberg et al. 1995).

II. Impacts of Dams

II. 1. Methodological problems in determining impacts
General knowledge on the ecological impacts of dams has been limited due to the lack of baseline data prior to dam construction (Nelson 1965; Gehrke et al. 1999; Pringle et al. 2000). Moreover, unimpacted rivers which would serve as true controls for comparative studies no longer exist (Gehrke et al. 1999). Additionally, it is often difficult to distinguish the effects of dams and waterpower management from the effects of other correlated disturbances within a river catchment (Gehrke et al. 1999; Bunn and Arthington 2002). Finally, most studies of ecological impacts have focused on economically important species (Pringle et al. 2000) and as such, probably cannot provide comprehensive effects assessments.

II 2. Hydrological impacts
II 2.1 Global Scale

An estimated 7% of freshwater flowing to the ocean is impeded by approximately 40,000 large dams and more than 800,000 small dams throughout the world (Nilsson and Berggren 2000) causing the estimated retention of $4 - 5 \text{ Gt yr}^{-1}$ of sediment worldwide (Vorosmarty et al. 2003). Most large dams in the world are in Asia, with China containing the majority of the dams (Dudgeon 2000). Global surface area of all reservoirs is estimated to be approximately 1.5 million km$^2$ (St. Louis et al. 2000); world wide reservoir storage estimated at 10,000 km$^3$ of water (Chao 1991; Nilsson and Berggren 2000). Sea levels have purportedly been lowered by about 3 cm over the past 40 years attributed to reservoirs (Chao 1995). An estimated 6% of the world’s river runoff no
longer reaches the ocean, lost mainly to irrigation and evaporation from reservoirs (Dynesius and Nilsson 1994).

The extra mass from the concentration of reservoirs at high altitudes (i.e., northern temperate zone) has purportedly slightly altered the planet’s axis and speed of the earth’s rotation (Chao 1991; 1995). Reservoirs are also considered to be a significant source of greenhouse gases (CO₂ and CH₄) to the atmosphere (Rosenberg et al 1995; 1997; St. Louis et al. 2000; Friedl and Wuest 2002) with an average flux of 1400 mg·m⁻²·d of CO₂ and 20 mg·m⁻²·d of CH₄ from temperate reservoirs (St. Louis et al. 2000). Total flux from reservoirs is estimated to account for approximately 4% of the anthropogenic greenhouse gases flux (St. Louis et al. 2000).

II 2.2 Regional Scale

Dams are designed and managed to reduce flow variability in the rivers downstream (i.e., provide water when required and reduce peak flows hence control flooding) by increasing water level fluctuations in upstream reservoirs (Baxter and Glaude 1980; Nilsson and Berggren 2000). As a result, many rivers have been transformed into a series of storage reservoirs and run-of-the-river impoundments (Nilsson and Berggren 2000) changing the characteristics of the system from lotic to lentic (Friedl and Wuest 2002). The increased mass of impounded water has purportedly increased seismic activity in the vicinity of reservoirs, an effect that appears to be greater when impoundments are large and exceed 100 m in height (Baxter and Glaude 1980).
One of the greatest impacts of dams is the alteration of water flow from the natural regime (Poff et al. 1997). Flows in North America are generally greatest during the freshet and lowest during the summer and winter months. Under most water management regimes, water is stored during the freshet and then released when flows are traditionally low (i.e. winter). This reduces the peaks in flows and spreads the freshet over a longer period of time (Liu and Yu 1992; Poddubny and Galat 1995; Rosenberg et al. 1995; Zhong and Power 1996; Rosenberg et al. 1997). Reduction of peak flows often reduces the incidence of flooding which can adversely affect floodplain species (species that rely on the floodplain for a portion of their life cycle; Mirza and Ericksen 1996). Changes to the natural flow regime are not restricted to North America; monsoon rains are captured in Asia during August and September and are released later during periods of low water (Dudgeon 2000).

Flows can vary within a river depending on the water management regime. Run-of-the-river systems have little storage and therefore pass water as it enters the reach thereby emulating natural water flows (Baxter and Glaude 1980). Peaking systems on the other hand, pass water through the turbines during periods of high energy demand (generally early morning and early evening) causing large and rapid variations in flows (Fisher and LaVoy 1972; Baxter and Glaude 1980). Thus, although there is generally a decreased seasonal variation in flows in managed systems, it is generally accompanied with an increase in the diurnal variation in flows (Baxter and Glaude 1980; Gehrke et al. 1999).
II 2.3 Local Scale

The effects of an impoundment are felt at several scales. At the local scale, evaporation generally increases due to the increased surface area of reservoirs in comparison to natural rivers (Dynesius and Nilsson 1994). This not only reduces the amount of water available downstream but may also affect local microclimate. Climate (e.g. ambient air temperature, precipitation and wind) can be affected by reservoirs not only within the vicinity of the impoundment but some distance upstream and downstream from the reservoir; the effect purportedly extending equal to the distance wind has traveled over water (Baxter and Glaude 1980). Large tracts of upland area are often flooded during the creation of a reservoir which can often lead to an increase in anaerobic bacterial production. As a result, methylmercury levels often increase both within the water column itself and in biota, an effect that may last for a 20 – 30 year period following creation of the reservoir (Rosenberg et al. 1997).

Biodiversity, both on local and global scales, can be affected by dams (Poff et al. 1997; Rosenberg et al. 1997). Fluvial specialists, species requiring flowing water habitats under a natural flow regime (Kinsolving and Bain 1993), are generally the imperilled native fish in large altered systems whereas habitat generalists, species capable of inhabiting a variety of habitats and adjusting to local conditions (Kinsolving and Bain 1993), generally become the introduced species (Galat and Zweimüller 2001). Many of North America’s listed species (special concern, threatened or endangered) of fish (Williams et al. 1989) are fluvial specialists. Riparian areas can also be affected from alterations to

Dams alter habitat and flood natural rapids that may have been traditionally used for spawning (Zhong and Power 1996; Nilsson and Berggren 2000). Several species of fish spawn in shallow, fast-moving waters, areas that are usually sites for dam construction because they are generally areas of greatest hydraulic head (Auer 1999a). Post construction sites may be dramatically altered, often rendering them unsuitable for spawning (Auer 1999a).

Dam construction and management almost always affects the natural flow regime, thereby altering habitat dynamics and creating new conditions to which many native species are poorly adapted (Poff et al. 1997). Altered flows generally results in the displacement of fluvial specialists by habitat generalists (Poff et al. 1997; Galat and Zweimüller 2001; Pegg and Pierce 2002; Černý et al. 2003) and has been identified as one of the leading stressors causing decline of numerous freshwater species (Richter et al. 1997). Dams may enhance (Nilsson and Berggren 2000; Bunn and Arthington 2002) or reduce (i.e., act as barriers to migratory fish (Geen 1974; Baxter and Glaude 1980)) the likelihood of colonization by exotic species, depending on the species in question and the context. Altered flows can also affect predator-prey relationships by concentrating species during periods where they would normally have some protection under a natural flow regime (Power et al. 1996), disrupts the timing of spawning by altering environmental cues necessary for gonadal development and/or spawning (Humphries and
Lake 2000) and affects survival of larval fish (Humphries and Lake 2000; Freeman et al. 2001).

Impoundments can significantly alter temperature, dissolved gases, nutrients, turbidity and toxicants in headponds (Baxter and Glaude 1980; Olmsted and Bolin 1996) which can negatively affect the aquatic environment immediately downstream. Dissolved gas supersaturation (i.e., gas bubble disease), resulting from the release of deep, cool upstream waters can lead to mortalities in downstream aquatic fauna (Weitkamp and Katz 1980) specifically in shallow waters (Weitkamp et al. 2003). Thermal regimes in both upstream and downstream sections from dams are altered from natural conditions (Spence and Hynes 1971; Zhong and Power 1996). Subtle changes such as the timing of ice-on and ice-off are altered in regulated rivers, generally with impoundments freezing earlier and breaking up later in the year than unregulated rivers (Baxter and Glaude 1980). Standing water generally absorbs more solar radiation, thereby increasing water temperatures in impoundments and enhancing thermal stratification (Wetzel 2001). Water temperatures can be dramatically affected downstream of dams depending on where water is drawn from the upstream water column. Downstream water temperatures may decrease if drawn from the hypolimnion of large dams (Baxter and Glaude 1980; Liu and Yu 1992) or increase if drawn from the epilimnion (Baxter and Glaude 1980).

II 3 Ecological impacts of dams

II 3.1 Effects on aquatic ecosystem function
Dams act as sediment traps, decreasing downstream turbidity (Liu and Yu 1992) and sediment load (Liu and Yu 1992; Zhong and Power 1996), changing systems that were once allochthonous systems into autotrophic reservoirs (Friedl and Wuest 2002). Upstream reservoirs may have an eutrophication effect on downstream reaches (Camargo et al. 2005). Moreover, the loss of high peak flows during freshet can reduce the ability of flowing waters to wash materials deposited in the main river by tributaries at confluences, which can in turn result in the formation of deltas (Baxter and Glaude 1980) hence changing the geomorphology of the river.

II 3.2 Effects on aquatic ecosystem structure

Dams fragment and isolate fish populations by eliminating connectivity between reaches and/or rivers (Auer 1996a; Bruch 1998; Baker and Borgeson 1999; Bevelhimer 2002). Migratory species (e.g. anadromous species) may be unable to migrate for spawning or nursing purposes either because insufficient water is passed through the dam or the dam acts as a barrier for distribution to upstream reaches (Geen 1974; Rochard et al. 1990; Liu and Yu 1992; Mirza and Ericksen 1996; Zhong and Power 1996; Cada 1998; Gehrke et al. 1999; Dudgeon 2000; Nilsson and Berggren 2000; Williot et al. 2002). Isolated fish populations may be restricted to areas that no longer provide suitable habitat for all life stages of the species (Beamesderfer 1988) and therefore may be at greater extirpation risk, because events inducing high mortality or reduced reproduction cannot be offset by immigration (Winston et al. 1991). It is not surprising, therefore, that migratory species
have often decline following dam construction in river main stems (Zhong and Power 1996; Aarts et al. 2004).

Macroinvertebrates can be affected by water power management. The operation of dams can affect the diversity and density of macroinvertebrates through dewatering productive littoral zones (Fillion 1967; Benson 1975; Gilason 1985; Ploskey 1986; Blinn et al. 1995) and through abnormal changes in water temperature or chemical characteristics of water downstream from a dam with a hypolimnetic draw (Casado et al. 1989). While there may be a general decline in density and diversity, some resilient species (e.g. *Ephemeroptera*) may actually benefit from water power management activities and increase in abundance (Spence and Hynes 1971; Geen 1974).

In addition to habitat fragmentation, dam construction and operation can have direct effects on both fish mortality and reproduction. Migratory fish that become concentrated at the base of dams as a result of a barrier effect are vulnerable to over-exploitation (Zhong and Power 1996; Williot et al. 2002); they become congregated in areas that anglers can easily access (Williot et al. 2002). Fish that spawn at the base of dams are subjected to additional stresses. Drastic diurnal fluctuations in flows below dams can dewater spawning areas leaving their eggs exposed to desiccation (Il’ina and Gorgeyev 1972; Gaboury and Patalas 1984; Humphries and Lake 2000). Drastic and rapid changes in flows or water levels may affect downstream passage of many individuals causing entrainment (stranding in less than ideal conditions; Geen 1974; Cada 1998; Pringle et al. 2000) which artificially increases mortality of spawning fish impacts future spawning.
stocks (especially species with traditionally low adult mortality). Lower temperatures from hypolimnetic draws may affect spawning phenology or reduce the quality of spawning habitat (Baxter and Glaude 1980; Gaboury and Patalas 1984; Liu and Yu 1992; Zhong and Power 1996; Bunn and Arthington 2002), as well as affecting growth and survival. For example, growth of largemouth bass (*Micropterus dolomieu*), a warmwater species, was negatively correlated with discharge from a dam with a hypolimnetic draw (Hickman and Hevel 1986). Contrarily, higher flows and water temperatures during winter months improved habitat conditions (Zhong and Power 1996) and therefore may benefit some fish species in terms of feeding, growth and survival.

Benthic invertebrate communities are also affected near dams, either because of large flow fluctuations or temperature changes. Thermal changes in the river can affect the development of invertebrates by disrupting (delaying) their normal life cycle (Lehmkuhl 1972; Geen 1974; Pardo et al. 1998; Bunn and Arthington 2002). This effect can extend considerable distances (113 km) downstream (Lehmkuhl 1972) and result in the invertebrate communities resembling first order streams (Hauer and Stanford 1982). An effect on the benthos can have a bottom up effect on benthivores abundance and condition (e.g. Chiasson et al. 1997; Beamish et al. 1998).

### III Water management on the Ottawa River

The Ottawa River (Figure I – 2) is one of the most highly regulated catchment basins in Canada (Telmer 1996). Alterations to the river started soon after European settlement.
The first dam on the river was constructed at Carillon in 1870 to aid the log drives and for navigation purposes (Legget 1975). The first power plants were constructed at Chaudière Falls in the 1890’s to supply power to industry and residents in Ottawa (Hincks 1978). Hydro-electric development along the Ottawa River was gradual until the 1940s. Bryson Dam was the first large hydro-electric dam constructed on the main course of the Ottawa River and was operational by 1925 (Kennedy 1970), Chats Generating Station (G.S) was operational by 1931 (Biggar 1991). An agreement signed by the Ontario and Quebec governments in 1943 to allocate the undeveloped water power sites on the Ottawa River (Ottawa River Engineering Board 1965) was the impetus to the greatest changes along the river. Large dams were constructed in the late 1940’s at Portage du Fort, Rolphton and Mattawa, each dam extensively flooding land (Biggar 1991). The last large dam on the main course of the river was constructed at Carillon in 1964 (Lafrenière 1984; Hydro-Quebec 1996). Currently, there are 43 dams within the Ottawa River watershed, downstream of Lake Temiscaming (Environment Canada et al. 1985), forming more than 14 billion m$^3$ of water storage capacity (Ottawa River Regulation Planning Board 1984). Hydroelectric dam operations on the Ottawa River are primarily run-of-the-river, peaking, winter reservoirs or a combination of management regimes. Dams and natural rapids help delineate river reaches; nine river reaches are recognized between Carillon and the outflow of Lake Temiskaming (Haxton and Chubbuck 2002).

Water power management has had a dramatic effect on flow variability in the Ottawa River: the ratio of maximum to minimum flow declined from 10:1 to 5:1 by 1930 (Legget 1975); peak flows at Chats G.S. (formerly Chats Falls) have declined 30.7% from pre-
impoundment conditions; summer flows have declined 34.5%; and, winter flows have increased 56.2% (Figure I - 3).

IV Lake sturgeon

IV 1 Life history

Acipenseriformes encompasses the 27 extant sturgeon species worldwide in four genera (Billard and Lecointre 2001). Sturgeon are known from the Lower Jurassic period of Europe (Bemis et al. 1997) and are purportedly the most threatened vertebrate group on the planet (Ludwig 2006). They are unique among vertebrates in that they can all hybridize and produce viable young if their spawning period and spawning grounds overlap (Birstein et al. 1997a; Billard and Lecointre 2001). Many sturgeon species are polyploids (Ludwig et al. 2001); polyploidization is believed to have played a significant role in speciation of Acipenser (Birstein et al. 1997a). Lake sturgeon (Acipenser fulvescens) are polyploids, reportedly tetraploids (Ludwig et al. 2001; Robinson and Ferguson 2004) or octoploids (Bemis et al. 1997; Birstein et al. 1997b; Robinson and Ferguson 2004) although octoploidy has been questioned (Pyatskowit et al. 2001).

Lake sturgeon spawn in Canada from early May to late June at temperatures between 13°C and 18°C (Harkness 1923; Scott and Crossman 1973; Nichols et al. 2003); peak spawning temperatures have been reported between 10°C and 14°C or 15°C in southerly populations (Kempinger 1988; Auer 1996b; Peterson et al. 2002), 12°C and 15°C in the St. Lawrence River (LaHaye et al. 1992) or 11.5°C and 16°C in Wisconsin (Bruch 2002).
Two separate spawning bouts may sometimes occur in a single season (Auer and Baker 2002; Bruch 2002; Nichols et al. 2003). Preferred spawning areas are shallow with fast flowing water over a rubble substrate (Scott and Crossman 1973; Kempinger 1988) but may also be found in deep water (9 – 12 m; Manny and Kennedy 2002; Caswell et al. 2004). Eggs are released over rock rubble (Bruch 2002) and incubate for 8 – 14 days (Kempinger 1988; LaHaye et al. 1992); duration of the incubation period is temperature dependent decreasing with increasing temperatures (Smith 2003). Egg loss can be high with a natural hatch rate estimated to be less than 1% (Nicols et al. 2003). Optimal survival and development of lake sturgeon eggs is between 14°C - 17°C whereas total egg mortality occurs at temperatures greater than about 20°C (Wang et al. 1985). Yolk-sac larvae emerge about 11 days post peak spawn (LaHaye et al. 1992) or 13 – 19 days post peak spawn (Smith 2003; Smith and King 2005). As with incubation, larval emergence is temperature dependent. Water temperature of 15°C appears to be important for initiating drift (Smith 2003). Peak drift occurs nocturnally between 2100 and 0200 hrs (Kempinger 1988; D’Amours et al. 2001; Smith 2003). Duration of the drift can extend up to 40 days (Auer and Baker 2002).

Lake sturgeon growth is rapid for the first five years of life and declines thereafter (Harkness 1923). Post juvenile growth is considered to be relatively slow requiring many years to attain adult size (Scott and Crossman 1973; Magnin 1977; Threader and Brousseau 1986). Growth rates of males and females are similar until about age 20, after which female growth rates generally exceed males (Bruch 1998). There is a considerable geographical variation in growth across the species range; much of this variation is
latitudinal (Royer et al. 1968; Beamish et al. 1998; Fortin et al. 1996; Noakes et al. 1999) and has been linked to the energetics of growth under different temperature regimes (Power and McKinley 1997). Age at sexual maturity is from 12 – 20 years for males, 14 – 33 years for females (Scott and Crossman 1973). Under natural conditions, spawning is periodic: males spawn every 2 or 3 years whereas females spawn every 4 – 6 years (Scott and Crossman 1973; Kempinger 1988) or 4 – 7 years (Roussow 1957). Natural mortality of mature lake sturgeon is low (Threader and Brousseau 1986; Houston 1987) and therefore, they can be long lived. The oldest known-age lake sturgeon was 154 years caught in Lake of the Woods (Scott and Crossman 1973); the largest lake sturgeon documented was 140 kg, measuring 2.4 m caught in Batchewana Bay, Lake Superior (Harkness and Dymond 1961).

Productive shoals of rivers and lakes are habitats commonly used for foraging by sturgeon. Depth preferences are generally 4.6 – 9.2 m (Harkness and Dymond 1961; Scott and Crossman 1973), 4 to 8 m (Smith 2003) however, lake sturgeon have been caught in depth of 43 m (Harkness and Dymond 1961; Scott and Crossman 1973). Lake sturgeon are benthivores feeding primarily on aquatic invertebrates (Harkness 1923; Harkness and Dymond 1961; Scott and Crossman 1973; Magnin 1977; Kempinger 1996; Chiasson et al. 1997; Beamish et al. 1998; Jackson et al. 2002) but are also known to be opportunistic feeders (i.e., feeding on fish: Harkness 1923; Beamesderfer and Farr 1997).

Lake sturgeon are potamodromous, migrating strictly within freshwater to spawning areas, with migration movements that may exceed 200 km (Kempinger 1988; Rusak and
Mosindy 1997; Auer 1999b). Downstream migrations purportedly are primarily to foraging areas (Bemis and Kynard 1997).

**IV 2 History of population declines**

Lake sturgeon is indigenous to North America and was historically considered abundant (Harkness and Dymond 1961; Scott and Crossman 1973). Numbers have declined precipitously across their range to the level where they are considered at risk in many states and provinces (Williams et al. 1989; Carlson 1995; Kempinger 1996; Ferguson and Duckworth 1997; Baker and Borgeson 1999; Williamson 2003). Commercial harvests, generally peaking in the late 1800s, initiated the decline of many populations (Harkness and Dymond 1961; Brousseau 1987; Houston 1987; Holzkamm and McCarthy 1988). Given their life history traits (low recruitment, slow growth, late maturity, periodic spawning, long life expectancy, low adult mortality), sturgeon populations are sensitive to an increase in adult mortality and therefore declined (Boreman 1997; Beamesderfer and Farr 1997; Crouse 1999; Secor and Waldman 1999; Gross et al. 2002). Concurrent with commercial harvest were dramatic changes to their habitat: rivers became dumping grounds for refuse or effluent and many dammed for hydro-electric, flood control and/or navigational purposes. Consequently, lake sturgeon have not been able to recover to historical levels (Houston 1987; Auer 1996a; Baker and Borgeson 1999). These pressures were not unique to lake sturgeon, but to all sturgeon species worldwide (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997; Billard and Lecointre 2001). For example, European sturgeon (*Acipenser sturio*) declined by the twelfth century as a result
of overfishing and barriers along rivers (Hoffmann 2005). Most sturgeon species are considered to be in some level of threatened status primarily from anthropogenic stressors (Billard and Lecointre 2001).

IV 3 Lake sturgeon and dams

For several reasons, lake sturgeon are expected to be a (freshwater) species particularly susceptible to the effects of dam construction and operation. First, they are migratory, with often large distances separating spawning, nursing and overwintering habitats (Harkness and Dymond 1961; Houston 1987; Rochard et al. 1990; Beamesderfer and Farr 1997; Ferguson and Duckworth 1997; Baker and Borgeson 1999; Williot et al. 2002). Second, high quality spawning habitat is precisely that which is often eliminated or degraded by dam operations, and there is accumulating evidence that regulated flows can disrupt normal spawning patterns (Fernández-Pasquier 1999). Third, many species of sturgeon have been extirpated or are at high risk of extirpation in rivers that have extensive mainstream impoundments (Pringle et al. 2000). While these rivers have also been exposed to other anthropogenic stresses, many of these stresses have been reduced substantially: today, the commercial harvest of lake sturgeon is regulated in all jurisdictions, and indeed prohibited in many; most industrial and domestic effluent has primary treatment at the very least; debris from log mills is no longer dumped into the rivers; and log drives, which were a source of bark contamination and habitat alterations from sunken logs, have ceased. Dams however, are still present on the majority of rivers. While dam construction had an initial impact on fish, their associated water management
regimes continue to influence fish populations. Rivers that have had dams removed and return to a natural flow regime are often re-colonized by migratory species and/or fluvial specialists (Hart et al. 2002).
Table I-1. Summary of the impacts water power management have on both hydrological and ecological processes and the scale of impact.

<table>
<thead>
<tr>
<th>Impact Class</th>
<th>Type of Impact</th>
<th>Impact(s)</th>
<th>Scale</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrological</td>
<td>flow attenuation</td>
<td>2/3 of fresh flowing water impeded</td>
<td>global</td>
<td>Nilsson and Berggren 2000</td>
</tr>
<tr>
<td>Hydrological</td>
<td>flow attenuation</td>
<td>sea levels have dropped by 3 cm</td>
<td>global</td>
<td>Chao 1995</td>
</tr>
<tr>
<td>Hydrological</td>
<td>flow attenuation</td>
<td>6% of river runoff no longer reaches ocean</td>
<td>global</td>
<td>Dynesius and Nilsson 1994</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>planet’s axis and speed of earth’s rotation altered</td>
<td>global</td>
<td>Chao 1991; 1995</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>increase green house gas emission</td>
<td>global</td>
<td>Rosenberg et al 1995; 1997; St. Louis et al. 2000</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>departure from natural flow regime</td>
<td>local</td>
<td>Baxter and Glaude 1980</td>
</tr>
<tr>
<td>Ecological</td>
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<td>climate change (temperature, precipitation, wind etc.)</td>
<td>local</td>
<td>Baxter and Glaude 1980</td>
</tr>
<tr>
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<td>reservoir creation</td>
<td>increased methylation resulting in increased methlymercury levels in the water body and food web</td>
<td>local</td>
<td>Rosenberg et al. 1997</td>
</tr>
<tr>
<td>Ecological</td>
<td>dam construction</td>
<td>alters spawning habitat at dam site and floods rapids upstream</td>
<td>local</td>
<td>Zhong and Power 1996; Nilsson and Berggren 2000</td>
</tr>
<tr>
<td>Ecological</td>
<td>altered flow regime</td>
<td>decline of riverine specialists, increase of habitat specialists and invasive species</td>
<td>local</td>
<td>Poff et al. 1997; Pegg and Pierce 2002; Černý et al 2003; Nilsson and Berggren 2000; Bunn and Arthington 2002</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>alters temperature regimes, dissolved gases, nutrients, turbidity and toxicants</td>
<td>local</td>
<td>Olmsted and Bolin 1996</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>thermal stratification rivers with previous homogenous water temperatures</td>
<td>local</td>
<td>Wetzel 2001</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>alters downstream temperatures from hypolimnetic or epilimnetic draws</td>
<td>local</td>
<td>Baxter and Glaude 1980; Liu and Yu 1992</td>
</tr>
<tr>
<td>Hydrological</td>
<td>reservoir creation</td>
<td>sedimentation, decreased turbidity, reduced sediment load downstream</td>
<td>local</td>
<td>Lui and Yu 1992; Zhong and Power 1996</td>
</tr>
<tr>
<td>Impact Class</td>
<td>Type of Impact</td>
<td>Impact(s)</td>
<td>Scale</td>
<td>Reference</td>
</tr>
<tr>
<td>--------------</td>
<td>----------------</td>
<td>--------------------------------------------------------------------------</td>
<td>----------------</td>
<td>--------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Ecological</td>
<td>fragmentation</td>
<td>isolate fish populations; eliminate connectivity between reaches/rivers</td>
<td>local, regional</td>
<td>Auer 1996a; Bruch 1998; Baker and Borgeson 1999; Bevelhimer 2002</td>
</tr>
<tr>
<td>Ecological</td>
<td>fragmentation</td>
<td>fish population decline; change in fish assemblage</td>
<td>local</td>
<td>Winston et al. 1991; Gehrke et al. 1999</td>
</tr>
<tr>
<td>Ecological</td>
<td>fluctuating flows</td>
<td>dewatered spawning areas affects recruitment</td>
<td>local</td>
<td>Gaboury and Patalas 1984; Humphries and Lake</td>
</tr>
<tr>
<td>Ecological</td>
<td>hypolimnetic draw</td>
<td>affect timing of spawning or conditions for spawning</td>
<td>local</td>
<td>Baxter and Glaude 1980; Gaboury and Patalas 1984; Lui and Yu 1992; Zhong and Power 1996; Bunn and Arthington 2002</td>
</tr>
<tr>
<td>Ecological</td>
<td>hypolimnetic draw</td>
<td>impact development of invertebrate; offset life cycle</td>
<td>local</td>
<td>Lehmkuhl 1972; Geen 1974; Pardo et al 1998; Bunn and Arthington 2002</td>
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</table>
Figure I - 1. Number of large dams (> 15 m from foundation to crest) constructed in Canada by decade. Data obtained from the Canadian Dam Association (www.cda.ca) current to 2003.
Figure 1-2. Ottawa River reaches with dams and generating stations (GS) highlighted.
Figure 1 - 3. Mean monthly flows at Chats Generating Station (G.S.) for three periods of time. Pre-1932 represents historical flow conditions prior to the construction of Chats G.S.; 1932 – 47 represents the time after Chats G.S. was constructed and prior to development of large dams (Chenaux G.S., Rolphton G.S. and Otto Holden G.S); 1948 – 1994 represents the period post hydro-electric development on the Ottawa River. Data for this graph were obtained from the Hydat database.
Chapter II. Meta-analysis of the ecological impacts of freshwater power management

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Abstract

Systematic meta-analyses were conducted on the ecological impacts of water power management including 1) effects of dewatering on macroinvertebrates; 2) effects of a hypolimnetic release on the downstream aquatic community and macroinvertebrates; 3) effects of flow modification on fluvial and habitat generalists. Our meta-analysis indicate that in general: (1) macroinvertebrate abundance is lower in zones or areas that have been dewatered due to water fluctuations or low flows (overall effect size -1.64 (-2.51/-0.77; 95% CI)); (2) a hypolimnetic draw reduces the abundance of aquatic (fish and macroinvertebrates) communities (overall effect size -0.84 (-1.38/-0.33; 95% CI)) and macroinvertebrates (overall effect size -0.73 (-1.24/-0.22; 95% CI)) downstream of a dam; (3) altered flows has a negative effect on the abundance of fluvial specialists (-0.42 (-0.81/-0.02; 95% CI) but does not affect habitat generalists (overall effect size -0.14 (-0.61/0.32; 95% CI)). Fail safe Ns suggest that many (>100) null effect studies would be required to change the results of the meta-analyses.
Introduction

While the effects of dam construction, impoundments and water management have been reviewed several times (e.g. Geen 1974; Baxter and Glaude 1980; Ploskey 1986; Prosser 1986; Rosenberg et al. 2000), to date there has been no systematic meta-analysis of these effects. A meta-analysis is a statistical technique that synthesizes results from separate, independent studies to derive general conclusions (Gurevitch and Hedges 1993). The power of a meta-analysis is that it can provide the magnitude and direction of an effect of a perturbation (Gurevitch and Hedges 1993) overcoming the qualitative and subjective shortcomings of literature reviews and discussion papers (Osenberg et al. 1999).

The meta-analysis presented here focuses on three potential impacts of water power management. First, we address the impacts of dewatering on macroinvertebrate communities. Water level fluctuations during peaking operations or water drawdown during periods of low flow may result in exposure or dewatering of the littoral zone or other shallow areas, usually the most productive areas within a waterbody. Benthic invertebrates inhabiting these shallow areas are purportedly negatively affected by dewatering (Fillion 1967; Benson and Hudson 1975; Gislason 1985; Ploskey 1986; Blinn et al. 1995). Macroinvertebrates, which are generally not particularly mobile, are stranded and die from asphyxiation and desiccation (Ploskey 1986; Moog 1993), leading to an impoverished (both in terms of abundance and diversity) macroinvertebrate community (Paterson and Fernando 1969; Fisher and LaVoy 1972; Munn and Brusven 1991; Englund and Malmqvist 1996; Ogbeibu and Oribhabor 2002). These effects in turn have
the potential to influence fish productivity, especially the abundance and growth of benthivores that feed primarily in the littoral zone.

Second, we consider the effects of hypolimnetic water release from dams on both macroinvertebrate and fish abundance downstream. Epilimnetic or hypolimnetic draws tend to increase or decrease, respectively, downstream temperatures depending upon time of year. Hypolimnetic draws are often cold and oxygen deprived (Fowler 1978), and there is some evidence that aquatic communities subjected to a hypolimnetic draw decline in productivity (Edwards 1978); reproduction and growth rates of warmwater species are reduced (Fry and Hanson 1968; Hickman and Hevel 1986; Clarkson and Childs 2000); communities shift from warmwater to coolwater (Fry and Hanson 1968); and fish biomass declines (Edwards 1978; Casado et al. 1989) as does species richness (Casado et al. 1989; Quinn and Kwak 2003). Macroinvertebrate biomass and diversity may also be reduced by a hypolimnetic draw (Casado et al. 1989). Only hypolimnetic draws are considered in this study due to the lack of published literature on other draws that fit the criteria established for the meta-analysis.

Finally, we consider the effects of dams, both upstream and downstream, on two specific fish classes: fluvial specialists and habitat generalists. There is evidence that after impoundments have been created or when flows deviate from the natural regime, species selective to flowing water habitats ("fluvial specialists" - Kinsolving and Bain 1993) generally decline and are replaced by habitat generalists (Zhong and Power 1996; Peñáz et al. 1999; Marchetti and Moyle 2001; Herbert and Gelwick 2003; Quinn and Kwak
2003; Aadland et al. 2005). This has been attributed to the ability of habitat generalists to tolerate high variability in flows and habitat conditions or changes from lotic to lentic conditions compared to the reduced adaptive capacity of fluvial specialists (Kinsolving and Bain 1993; Aadland et al. 2005).

Methods

Meta-analysis was conducted as specified by Gurevitch and Hedges (1993). We used a mixed effects model: a fixed effects model assumes there is one true effect size shared by all of the studies in the same class, and given the heterogeneity in designs and endpoints in our sample of studies, this assumption was unwarranted.

Data retrieval

Literature searches were conducted primarily using online database search engines such as Web of Science or EBSCO Host Electronic Journal Service. Search keywords included “water power management”; “dams AND fish”; “dams AND invertebrates”; “dams AND macroinvertebrates”; “water level fluctuation”; “water drawdown”; “water drawdown AND fish”; “water drawdown AND (macro)invertebrates”; “minimum flow”; “natural flow regime”; “flows AND fish”; “flows and invertebrates” “hydroelectric dams”; “reservoir”; “peaking facilities”; “run-of-the-river facilities”; “dewatering AND macroinvertebrates”; “hypolimnetic release”; “hypolimnetic draw”; “fluvial specialist”; “habitat generalist”. In addition, articles listed in the bibliographies of retrieved articles,
and which appeared (on the basis of the title or review of the article) to pertain to water power management and aquatic environments were also reviewed. To be included in the analysis: 1) the study had to be relevant (i.e., pertained to water power management or effects of dams on the aquatic environment); 2) the study contained a control group and an experimental group from which an effect could be estimated; 3) the necessary statistics (mean, standard deviation or some estimate of precision, and sample size for control and experimental groups) were provided or could be determined from data and/or figures presented in the publication (e.g. means and S.E. provided by histograms (Munn and Brusven 1991; Weisburg et al. 1990; Liebig et al. 1997)); and 4) the study was published in a peer reviewed scientific journal or a special publication which comprised a set of peer reviewed articles.

Mean abundance was selected as the primary endpoint of interest, as most studies included estimates of abundance (Table II-1). A few studies included estimates of species richness and/or diversity; these studies invariably did not include an estimate of variance, nor could one be determined with the data supplied. Consequently, these studies were excluded from the meta-analyses. Only one endpoint (e.g. abundance) was used when multiple endpoints were reported during a study (e.g. abundance and biomass of a species) to ensure independence (Gurevitch and Hedges 1993). Several studies pooled species (e.g. fluvial specialists) when reporting on a specific endpoint (e.g. abundance) whereas other studies reported on individual species; in the latter case, all species were treated separately in the meta-analysis. Only studies that specifically identified fluvial specialists or habitat generalists in their study were used in that particular meta-analysis.
Study design

Articles satisfying our selection criteria were reviewed for sample size ($N^c$: control group; $N^e$: experimental group); estimates of the mean ($\bar{X}^c$) and ($\bar{X}^e$) for control and experimental groups respectively) and some estimate of precision, generally a standard deviation ($S^c$: control group; $S^e$: experimental group).

In clinical medicine involving randomized control trials, experimental and control groups are well defined, and invariably are represented by arms of the clinical study. In ecological studies, however, experimental designs are much more variable. Studies of the impacts of dams, impoundments or water management on river ecosystems range from classical BACI (before – after designs on a single river, to comparison of (putatively) affected ("impacted") with unaffected ("control") reaches within a river (e.g. Young et al. 1976; Munn and Brusven 1991; Hauer and Stanford 1982)), to comparison of rivers with dams and/or water power management to those without (e.g. Scullion et al. 1982; Kinsolving and Bain 1993; Englund and Malmqvist 1996). Because no single class of experimental designs included a sufficient sample of studies, study designs were pooled in most analyses however, where possible we attempted to determine (a posteriori) whether general results held within a particular class of experimental designs.

As the objective was to detect a difference between control and experimental treatments, whether positive or negative, we used two-tailed tests of null hypotheses with the type I
error rate set at \( \alpha = 0.05 \). A meta-analysis was determined to be significant if zero was not included in the 95\% CI for reported (or estimated) effect sizes (Gurevitch and Hedges 1993).

The sample for meta-analysis includes studies and experiments (Table II -1), the latter corresponding to comparisons with different endpoints for example, different species or taxa (e.g. fluvial specialists, habitat generalists). As such, the number of experiments per study ranges from 1 (where, for example, only one species or one taxon was investigated) to several (where, for example, abundances of several different taxa were estimated in control and experimental sites). Using several experiments from a single study could potentially give rise to non-independence (Gates 2002). We addressed this problem in two ways. First, we estimated the magnitude of the problem by computing the intraclass correlation for each meta-analysis, using studies as groups to estimate the between-group variation in effect size, and experiments within studies to estimate the within-group variation in effect size for studies with multiple experiments. Second, to examine the potential effects of multiple experiments per study on estimated effect sizes, we conducted a bootstrap analysis as follows: (1) for each study with multiple experiments, one experiment was selected at random resulting in a sample of \( n \) (equals the number of studies) experimental-control pairs, with one experiment per study; (2) for each pair \( i \), we estimated the effect size \( d_i \) and computed the mean effect size and associated variance over the sample; (3) steps (1) and (2) were repeated 1000 times, sampling with replacement, to generate a distribution of sample means and variances, from which we calculated the average (bootstrapped) sample mean effect size and associated variance;
(4) steps (1) – (3) were repeated for sample size \( N = n + j \), \( j = 1, 2, \ldots, n_{max} - 1 \), where \( n_{max} \) is the total number of experiments in the sample (i.e. the sum of all experiments for each study); with the \( j = N - n \) additional experiments being sampled randomly with replacement from those studies with multiple experiments. By assessing the change in estimated mean effect size and associated variance with changing \( N \), we obtained a quantitative estimate of the effect of multiple experiments per study on the first two moments of the effect size distribution.

Forest plots were generated for each meta-analysis to assess the effect of time on the overall effect size using publication year as the time index. Effect size \( (d_i) \) and 95% CIs were calculated by incrementally incorporating results from experiments from each publication year. Publication bias was assessed by funnel plots (Gates 2002; Pai et al. 2004), Egger’s statistics (Egger et al. 1997) and fail-safe \( N \) (Rosenthal 1995). Funnel plots were constructed by plotting the estimated effect size \( (d_{ij}) \) against the precision \( (v_{ij}) \) of the estimated effect size (Gates 2002). Funnel symmetry was determined by a regressing \( v_{ij} \) on \( d_{ij} \) and using the intercept as a measurement of asymmetry – the greater the deviation of the intercept from zero, the greater the funnel asymmetry and therefore the greater the potential publication bias (Egger et al. 1997). Fail-safe \( N \) is the number of studies reporting no effect that would be required to reduce the estimated overall effect size to one indistinguishable from zero: if the number of additional studies required to accept the null hypothesis is small, the meta-analysis may well be contaminated by the file drawer effect (Rosenthal 1995). Finally, a Kruskal-Wallis test was conducted on
effect size by study design (i.e., BACI or C/I) to assess if study design had an effect on the results.

Unweighted meta-analysis

Many studies were excluded from the formal meta-analysis due to (1) inadequate or missing statistical information (e.g. estimates of precision, sample size); (2) inadequate design (i.e. did not include adequate controls for control-experimental comparison); (3) no or insufficient empirical data provided (which would apply in the case of reviews and modeling studies); or (4) inadequate endpoint resolution (studies that, for example, considered all species or did not differentiate among different guilds) (Figure II - 1). Nonetheless, these studies still have some value, and as such, were included in an unweighted meta-analysis and a vote counting meta-analysis.

An unweighted meta-analysis was conducted for all publications including those that did not provide an estimate of the precision of $\overline{X}^e$ and $\overline{X}^c$. Sample size ($N^c$ and $N^e$) was required for inclusion in the unweighted meta-analysis. The effect size in the unweighted analysis, $U_{ij}$, was given by

\begin{equation}
U_{ij} = \ln \left( \frac{\overline{X}^e + 1}{\overline{X}^c + 1} \right)
\end{equation}
where $U$ is the effect size of the $i$th class in the $j$th study. This is a variation of Osenberg et al. (1997; Eq. 4) who calculated the effect size similarly except they divided the mean of the control treatment by the mean of the experimental treatment. Calculating the effect size by Eq. 1 provides the proper direction of the effect (i.e., negative or positive). One is added to the numerator and denominator to account for samples with a mean of zero. To ensure the addition of one to the numerator and denominator did not influence results, studies with a mean of zero were removed from the analysis, the effect size was recalculated in the standard manner, and results from the two methods were compared.

The cumulative effect of the unweighted meta-analysis was given by

$$U_i = \frac{\sum_{j=1}^{k} U_{ij}}{n}$$

A bootstrap (1000 iterations), sampling with replacement, was conducted using the studies included in the unweighted meta-analyses to calculate variance; the 95% CIs of the estimated overall effect size was given by the 2.5 and 97.5 percentiles of the bootstrapped effect-size distribution.

**Vote counting**

Vote counting is the method whereby the number of statistically significant results in support of or refuting a specified hypothesis is counted (Gates 2002). In this instance, a positive (negative) vote was scored if there was a significant (non-significant) reported
difference between the control and experimental groups or if the publication definitively stated an effect was detected but did not provide an explicit comparison. Directionality of the result was documented (i.e., difference between the control and the experiment: difference <0, score = -1; difference > 0, scored = +1). Only one score was determined for each published article (i.e., studies were not stratified into experiments as done in the true meta-analysis) based on the overall effect. Articles reporting summaries of other studies were not included in these analyses. Vote counting was conducted separately for studies included in and excluded from the formal meta-analyses, to evaluate potential biases.

Results

Of the 185 studies examined, only thirty-three met all inclusion criteria (Table II - 2; Appendix A), with the lack of required statistics (e.g. measure of variance) being the primary reason for exclusion (Figure II - 1).

Dewatering has a significant impact on the abundance of macroinvertebrates in affected areas (Table II - 2) with macroinvertebrate abundance declining in dewatered areas. This general conclusion was supported both by an unweighted meta-analysis (Table II - 3) and vote counting (Figure II - 2).

Weighted meta-analysis indicated that hypolimnetic draws were associated with a significant impact (Table II - 2), with both fish and macroinvertebrate density declining
in downstream areas affected by a hypolimnetic draw. This conclusion was supported both by unweighted meta-analysis (Table II - 3) and vote counting (Figure II - 2). Modification of Osenberg’s et al. (1997) equation to allow for inclusion of studies in which either control or experimental sites was zero, did not affect the outcome of the unweighted meta-analysis (Table II - 3). Effect size was heterogeneous between classes (fish and macroinvertebrates; $\chi^2 = 32.6$ d.f = 1 $P <0.001$) in the weighted meta-analysis.

Modification of the natural flow regime was associated with a decline of fluvial specialists (Table II - 2) but does not appear to significantly affect habitat generalists (Table II - 2). Unweighted meta-analysis (Table II - 3) supported the weighted meta-analyses; vote counting supported the fluvial specialist meta-analysis but suggested that the abundance of habitat generalists increased in areas with modified flows (Figure II - 2).

Intra-class correlations indicate an independence of effect size for all meta-analyses with multiple experiments except for the effect of modification of natural flow on habitat generalists ($R = 0.72$; Table II - 2). Mean effect size and assessed significance did not change significantly when multiple experiments from individual studies were included in the meta-analysis for the effects of dewatering on macroinvertebrates and modification of natural flow on fluvial specials and habitat generalist (Table II - 4). However, for the effect of hypolimnetic draw on the aquatic community and macroinvertebrate abundance, the inclusion of multiple experiments did result in a detected effect (Table II - 4).
Confidence limits generally narrowed on Forest plots with the additional studies from later years (Figure II - 3). Significance of the meta-analysis was determined during early years of publication and remained consistent throughout; additional studies added over time had small effects on the overall results with the exception of the effects of modification of natural flows on fluvial specialist where significance of the effect changed with the addition of studies (Figure II - 3c)

Funnel plots suggests publication bias for each meta-analysis (Figure II - 4). Egger’s test for funnel symmetry suggests bias for all meta-analyses except effect of hypolimnetic draw on aquatic community (Table II - 4). However, fail-safe Ns were sufficiently large for all meta-analyses to suggest that many unpublished studies without a significant or a negative effect would be required to obtain a null effect (Table II - 2).

In all meta-analyses, we combined different study designs. The effect of this variability and, in particular, the biases it may introduce to the estimated effect sizes cannot be determined with the present sample. However, if one considers experiments as independent, one can compute average estimated effect sizes and associated 95% CIs for each class of experimental designs (Figure II - 5): this analysis shows that overall effect size was similar (or of the same sign) among study design and that CIs overlapped. Nonparametric analysis did not detect a significant difference between study design for the effects of dewatering ($\chi^2 = 0.536$, d.f. = 1, $P = 0.464$) or the effects of flow deviation on fluvial specialists ($\chi^2 = 2.65$, d.f. = 1, $P = 0.104$) and habitat generalists ($\chi^2 = 2.12$, d.f. = 1, $P = 0.145$). This suggests that while variability in study design may well have
influenced the precision of overall effect size estimates, it does not appear to have introduced substantial bias.

Discussion

Our meta-analyses indicates that in general: (1) macroinvertebrate abundance is lower in zones or areas that have been dewatered due to water fluctuations or low flows (overall effect size -1.64 (-2.51/-0.77; 95% CI)); (2) a hypolimnetic draw is associated with reduced abundance of downstream fish and aquatic invertebrates (overall effect size -0.84 (-1.38/-0.33; 95% CI)) and macroinvertebrate abundance (overall effect size -0.73 (-1.24/-0.22; 95% CI)); (3) altered flows were associated with a reduced abundance of fluvial specialists (-0.42 (-0.81/-0.02; 95% CI) but did not significantly affect the abundance of habitat generalists (overall effect size -0.14 (-0.61/0.32; 95% CI)).

Effects of dewatering on macroinvertebrates

The finding that macroinvertebrate abundance is generally lower in dewatered areas supports the general literature that macroinvertebrate abundance and density is affected by dewatering (Paterson and Fernando 1969; Fisher and LaVoy 1972; Munn and Brusven 1991; Englund and Malmqvist 1996; Ogbeibu and Oribhabor 2002) which in turn suggests that benthivorous fish inhabiting such areas will also be affected (Gippel and Stewardson 1998). Benthivore fish with life stages that rely on productive shallow areas (i.e., not necessarily benthivores with deep water niches) may be most affected as these
areas are generally the most affected by fluctuating water levels (i.e., dewatering). Low abundance of benthic invertebrates would be expected to affect growth, recruitment and ultimately benthivore abundance (Chiasson et al. 1997). Consistent with this prediction, benthivores and fish species that are benthivores for part of their life history (e.g. channel catfish), were absent or in very low abundance in reservoirs of the Ottawa River that experience drawdowns during the winter months (Haxton and Findlay, unpublished data) as has been observed in other systems (Miller and Paetz 1959; Nelson 1965). Taken together, these results suggest that in areas experiencing extensive dewatering (i.e., managed as winter reservoirs), alterations to the current water management regime (e.g. change to a run-of-the-river system) would be necessary to restore macroinvertebrate productivity if the objective is to manage littoral zone benthivores. Other rehabilitation efforts for littoral feeding benthivores (e.g. spawning shoal enhancement) would be expected to have minimal effects if littoral zone macroinvertebrate productivity was not first rehabilitated.

Effects of a hypolimnetic draw on invertebrate and fish abundance

Our analysis indicates that hypolimnetic releases are associated with downstream declines in both macroinvertebrate and fish abundance. This effect can extend some distance (70 km +) downstream before recovery occurs (Edwards 1978; Lessard and Hayes 2003). In contrast, Lessard and (Hayes 2003) showed fish species diversity increased in streams below dams with an epilimnetic release, although cold water species declined. Releases from isothermal reservoirs may not have significant impacts on the
aquatic community if temperature of released waters approximated that of the receiving environment (Smalley and Novak 1978) however, epilimnetic releases could have a detrimental downstream effect if the water was heated above normal receiving water temperature (Smalley and Novak 1978; Baxter and Glaude 1980). Our results suggest a general decline in downstream productivity in waters receiving a hypolimnetic release.

Changes to the thermal properties of water may not be the only factor affecting downstream communities. Changes to the chemical properties of water from hypolimnetic releases such as dissolved gas supersaturation (Baxter and Glaude 1980; Crunkilton et al. 1980; Weitkamp and Katz 1980; Olmsted and Bolin 1996), anoxia (Olmsted and Bolin 1996), hydrogen sulphide (Baxter and Glaude 1980), turbidity (Liu and Yu 1992), nutrients (Liu and Yu 1992; Zhong and Power 1996), and sediment loading (Baxter and Glaude 1980; Liu and Yi 1992; Zhong and Power 1996) can all have an impact, whether positive or negative, on downstream fauna. The causal mechanisms responsible for the detected effects are unknown: it is conceivable that differences are attributable to changes in oxygen, to changes in sedimentation patterns, etc., but the meta-analysis per se sheds no light on the causal mechanisms for the detected difference. These effects may be contributing to the impacts of a hypolimnetic draw; a separate meta-analysis could not be conducted for each due to the paucity of data.

Downstream areas affected only by thermal changes (i.e., chemical composition is not altered, sediment loading is negligible) may be better suited for the introduction and management of coldwater species (Nelson 1965; Fry and Hanson 1986; Olmsted and
Bolin 1996; Peñáz et al. 1999; Quinn and Kwak 2002). However, if attempting to manage for the native species that may not necessarily be coldwater selective, the location of release in terms of changes to the thermal properties of water is pertinent to ensure continuity with upstream and downstream reaches.

**Effects of flow alteration on fluvial specialists and habitat generalists**

Several researchers have suggested that modification of flows from natural regimes negatively affects fluvial specialists, whereas habitat generalists purportedly thrive in altered ecosystems (Poddubny and Galat 1995; Zhong and Power 1996; Marchetti and Molye 2001; Stanford and Ward 2001; Brown and Ford 2002; Aarts et al. 2004; Aadland et al. 2005). Our analysis indicates that flow alterations do not significantly affect habitat generalist abundance. This discrepancy may, in part, simply reflect different endpoints. For example, under flow modification, the proportion of the community represented by habitat generalists may increase (e.g. Quinn and Kwak 2003; Aadland et al. 2005) as fluvial specialists decline however, overall abundance measured by CUE may not change significantly (for example, the composition of *Lepomis auritus* (a habitat generalist) changed from 16% to 1.9% whereas their density changed from 1.4 to 1.5 per 100 m² pre and post flow modification respectively (Travnichek et al. 1995)). Many studies could not be included in this meta-analysis as they did not meet the criteria for inclusion however, the unweighted meta-analysis (which incorporated several of these studies) supported the weighted meta-analysis.
Meta-analysis issues

Many studies were excluded from weighted meta-analysis because they did not meet the inclusion criteria. Even so, more qualitative techniques (unweighted and vote counting) corroborated weighted meta-analysis results. The exception is the effect of modification of natural flows on habitat generalists which was not corroborated by vote counting. This issue may pertain to the metric used and was addressed in the previous section.

Our sample of studies included those in which only one endpoint was assessed (e.g. one species – Auer 1996; one habitat guild – Weisberg et al. 1990) and those for which multiple endpoints were assessed (e.g. abundance of 23 different species in Travnichek et al. 1995). In the analysis, each of these endpoints (called experiments) was considered an independent study. As such, studies with multiple endpoints may have a strong influence on the overall results, a common situation in ecological meta-analyses (Gates 2002). Our results suggest that this is a potential problem in at least one of the analyses: the results of this analysis must be interpreted cautiously; even though the unweighted meta-analysis and vote counting techniques corroborated the weighted meta-analysis results.

Funnel plots and Egger’s statistic provide evidence of publication bias in several meta-analyses. Conversely, relatively large associated fail-safe Ns indicate considerable tolerances for future null results, i.e., the overall conclusions from the meta-analyses are not threatened (Rosenthal 1995). In addition, detecting non-effects are equally as important to detecting effects therefore should be as publishable (i.e. the file drawer effect may be negligible in these meta-analyses).
The meta-analyses in this study were all based on abundance as the endpoint; too few studies reporting species richness or diversity met the criteria for inclusion. These metrics probably would not have changed the results observed except for possibly habitat generalists; one may expect a significant increase in habitat generalist richness and diversity as a result of flow alteration.

Conclusions

Meta-analysis is an effective, systematic technique that combines results from independent studies. For fisheries management where studies generally have low statistical power, a meta-analysis may help reduce uncertainty in fisheries management (Myers and Mertz 1998). In the context of waterpower management, fisheries management objectives should be clearly identified prior to new developments or modification of flow regime. The results of our meta-analyses analyses suggest that if the objectives are to maintain a native fish community, then the appropriate water management regime must be implemented. For fluvial specialists, this means maintaining as natural a flow as possible, that is, a run-of-the-river system. This still does not address issues with migratory species or habitat alteration resulting from dam construction. Draw location should be chosen so as to have minimal effect on the temperature of downstream receiving waters. Large reservoirs with deep hypolimnetic draws may however still have effects due to changes to the chemical properties of water and dams in general will have an effect on sedimentation processes. Extensive drawdowns (i.e., reservoirs) should be
avoided as a management regime if the objective is to maintain macroinvertebrates and benthivores occupying the littoral zone niche in the community.
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Table II - 1. Characteristics of each meta-analysis including study design, control and experimental sites, study endpoints and the associated indicators.

<table>
<thead>
<tr>
<th>Study design</th>
<th>Question</th>
<th>Control</th>
<th>Experimental</th>
<th>Taxon</th>
<th>Endpoint</th>
<th>Indicator (N,E)**</th>
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</thead>
<tbody>
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<td>Among-reach, within river comparison</td>
<td>I</td>
<td>natural flow regime</td>
<td>impoundment</td>
<td>macroinverts</td>
<td>taxon</td>
<td>indicator</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>upstream</td>
<td>downstream</td>
<td>fish</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>natural flow regime</td>
<td>altered flow</td>
<td>fish (fluvial specialists)</td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Before-After construction</td>
<td>I</td>
<td>before</td>
<td>after</td>
<td>macroinverts</td>
<td>taxon</td>
<td>indicator</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>before</td>
<td>after</td>
<td>fish</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>before</td>
<td>after</td>
<td>fish (fluvial specialists)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>before</td>
<td>after</td>
<td>fish (habitat generalists)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

I – effects of dewatering on macroinvertebrates; II- effects of a hypolimnetic draw; III effects of modification of natural flow

** N-number of studies; E – number of experiments
Table II - 2. Number of published studies (N) and experiments (E), estimated effect size based on mixed effects model, and associated 95% confidence intervals (CI), intraclass coefficient ($R$) and fail-safe N for each weighted meta-analysis.

<table>
<thead>
<tr>
<th>Meta-analysis</th>
<th>N (studies)</th>
<th>E (experiments)</th>
<th>Effect size (95% Cls)*</th>
<th>$R$</th>
<th>Fail-safe N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effect of dewatering on macroinvertebrates</td>
<td>10</td>
<td>13</td>
<td>-1.64 (-2.51/-0.77)</td>
<td>0.23</td>
<td>544</td>
</tr>
<tr>
<td>Effect of hypolimnetic draw on aquatic community</td>
<td>6</td>
<td>17</td>
<td>-0.84 (-1.38/-0.33)</td>
<td>-0.08</td>
<td>176</td>
</tr>
<tr>
<td>Effect of hypolimnetic draw on macroinvertebrate abundance</td>
<td>4</td>
<td>15</td>
<td>-0.73 (-1.24/-0.22)</td>
<td>-0.08</td>
<td>109</td>
</tr>
<tr>
<td>Effect of modification of natural flow on fluvial specialists</td>
<td>8</td>
<td>20</td>
<td>-0.42 (-0.81/-0.02)</td>
<td>0.03</td>
<td>102</td>
</tr>
<tr>
<td>Effect of modification of natural flow on habitat generalists</td>
<td>5</td>
<td>16</td>
<td>-0.14 (-0.61/ 0.32)</td>
<td>0.72</td>
<td>n/a</td>
</tr>
</tbody>
</table>

*based on number of experiments
Table II - 3. Number of published studies (N) and experiments (E), estimated effect size \((U_i)\) and associated 95% confidence intervals (CI) for each unweighted meta-analysis with and without modification to Osenberg’s et al (1999).

<table>
<thead>
<tr>
<th>Meta-analysis</th>
<th>N (studies)</th>
<th>E (experiments)</th>
<th>(U_i) - Effect size (95% CIs)</th>
<th>Effect size without modification to equation</th>
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<tr>
<td>Effect of dewatering on macroinvertebrates</td>
<td>10</td>
<td>13</td>
<td>-1.07 (-1.47/-0.61)</td>
<td>-1.41 (-2.82/-1.45)</td>
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<tr>
<td>Effect of hypolimnetic draw on aquatic community</td>
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<td>17</td>
<td>-1.27 (-1.94/-0.61)</td>
<td>-0.18 (-2.07/-0.67)</td>
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<tr>
<td>Effect of hypolimnetic draw on macroinvertebrate abundance</td>
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<td>15</td>
<td>-1.32 (-2.05/-0.59)</td>
<td>-1.32 (-2.09/-0.63)</td>
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<tr>
<td>Effect of modification of natural flow on fluvial specialists</td>
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<td>20</td>
<td>-1.02 (-1.44/-0.64)</td>
<td>-0.86 (-1.43/-0.39)</td>
</tr>
<tr>
<td>Effect of modification of natural flow on habitat generalists</td>
<td>5</td>
<td>16</td>
<td>-0.24 (-0.61/0.109)</td>
<td>-0.18 (-0.96/0.19)</td>
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</tbody>
</table>
Table II - 4. Average effect size ($d$) with standard deviation and probability from a bootstrap (1000 iterations with replacement) for each meta-analysis with different numbers of experiments.

<table>
<thead>
<tr>
<th>Meta-analysis</th>
<th>E (# of experiments)</th>
<th>Average $d$</th>
<th>Standard deviation</th>
<th>$P$</th>
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<tr>
<td>Effect of dewatering on macroinvertebrates</td>
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<td></td>
<td>12</td>
<td>-0.71</td>
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</tr>
<tr>
<td></td>
<td>11</td>
<td>-0.73</td>
<td>0.28</td>
<td>0.012</td>
</tr>
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<td></td>
<td>10</td>
<td>-0.74</td>
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<td>0.020</td>
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<td>Effect of hypolimnetic draw on aquatic</td>
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<td>-0.63</td>
<td>0.26</td>
<td>0.011</td>
</tr>
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<td>community</td>
<td>16</td>
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<td>0.014</td>
</tr>
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<td></td>
<td>15</td>
<td>-0.62</td>
<td>0.27</td>
<td>0.012</td>
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<tr>
<td></td>
<td>14</td>
<td>-0.62</td>
<td>0.27</td>
<td>0.018</td>
</tr>
<tr>
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<td>13</td>
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<td>0.023</td>
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<td>12</td>
<td>-0.65</td>
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<td>0.34</td>
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</tr>
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<td>8</td>
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<tr>
<td></td>
<td>13</td>
<td>-0.59</td>
<td>0.28</td>
<td>0.021</td>
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<td>0.047</td>
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<td>0.07</td>
<td>0.006</td>
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<td>0.009</td>
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<td>14</td>
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<td>0.08</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>-0.21</td>
<td>0.08</td>
<td>0.011</td>
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<td></td>
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<td>0.015</td>
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<td>-0.21</td>
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<td></td>
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<td>-0.21</td>
<td>0.11</td>
<td>0.022</td>
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<td>9</td>
<td>-0.21</td>
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<tr>
<td></td>
<td>8</td>
<td>-0.21</td>
<td>0.12</td>
<td>0.041</td>
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</table>

Effect of modification of natural flow on

<p>| Effect of modification of natural flow on | 16       | -0.04       | 0.13        | 0.243|
|                                        | 15       | -0.04       | 0.10        | 0.276|</p>
<table>
<thead>
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<th>Meta-analysis</th>
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<th>Average $d$</th>
<th>Standard deviation</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>habitat generalists</td>
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<td>-0.04</td>
<td>0.09</td>
<td>0.229</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>-0.04</td>
<td>0.09</td>
<td>0.265</td>
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<tr>
<td></td>
<td>12</td>
<td>-0.04</td>
<td>0.07</td>
<td>0.252</td>
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<td></td>
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<td>0.07</td>
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<td>-0.03</td>
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<td>-0.03</td>
<td>0.07</td>
<td>0.278</td>
</tr>
<tr>
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<td>-0.03</td>
<td>0.06</td>
<td>0.244</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>-0.03</td>
<td>0.06</td>
<td>0.248</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-0.03</td>
<td>0.06</td>
<td>0.230</td>
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</tbody>
</table>
Table II - 5. Egger’s test for funnel symmetry for each meta-analysis.

<table>
<thead>
<tr>
<th>Meta-analysis</th>
<th>Intercept</th>
<th>95% CI</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effect of dewatering on macroinvertebrates</td>
<td>-0.82</td>
<td>-1.61/-0.003</td>
<td>0.04</td>
</tr>
<tr>
<td>Effect of hypolimnetic draw on aquatic community</td>
<td>0.26</td>
<td>-0.13/0.66</td>
<td>0.17</td>
</tr>
<tr>
<td>Effect of hypolimnetic draw on macroinvertebrate abundance</td>
<td>0.38</td>
<td>0.18/0.58</td>
<td>0.001</td>
</tr>
<tr>
<td>Effect of modification of natural flow on fluvial specialists</td>
<td>0.17</td>
<td>0.01/0.32</td>
<td>0.04</td>
</tr>
<tr>
<td>Effect of modification of natural flow on habitat generalists</td>
<td>0.15</td>
<td>0.04/0.27</td>
<td>0.012</td>
</tr>
</tbody>
</table>
Figure II - 1. Limitations precluding the use of extracted studies in either weighted or unweighted meta-analyses: inadequate or incomplete statistical data (A); inadequate design (B); few or no empirical data (C); inadequate endpoint resolution (D).
Figure II - 2. Number of studies included (+) or not included (-) in formal meta-analysis that reported an effect of dewatering on macroinvertebrates (A); hypolimnetic draw on the aquatic communities (B); modification of natural flows on fluvial specialists (C) or habitat generalists (D). Studies not included in weighted meta-analysis were used either in unweighted meta-analysis or vote counting analysis.
Figure II - 3. Forest plots for the effects of dewatering on macroinvertebrates (a); a hypolimnetic draw on the aquatic community (b); and modification of natural flow on fluvial specialists (c) and habitat generalists (d).
Figure II - 4. Funnel plots for the effects of (a) dewatering on macroinvertebrates, (b) a hypolimnetic draw on the aquatic community, modification of natural flow on (c) fluvial specialists and (d) habitat generalists. The dashed line represents the overall estimated effect size for each meta-analysis.
Figure II - 5. Effect size classified by study design (Before-After (B/A); Control-Impact (C/I)) for each meta-analysis: effects of (A1) dewatering on macroinvertebrates based on B/A designs; (A2) dewatering on macroinvertebrates based on C/I design; (B1) a hypolimnetic draws on the aquatic community based on B/A design; (B2) a hypolimnetic draws on the aquatic community based on C/I design; (C1) modification of natural flow on fluvial specialists or habitat generalists based on B/A design; (C2) modification of natural flow on fluvial specialists or habitat generalists based on C/I design. The number of studies and experiments ($N_1, N_2$) in each class are included.
Chapter III. Variation in lake sturgeon abundance and growth among river reaches in a large regulated river

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Abstract

Lake sturgeon stocks are well below historical levels across their natural range. In this study, we examine why lake sturgeon have not substantially recovered to historical levels in a large regulated river (Ottawa River, Canada). Three primary anthropogenic stressors have been identified as potentially limiting lake sturgeon populations including 1) commercial harvest, 2) contaminants, and 3) water power management. Two hypotheses (1 & 3) were tested by comparing lake sturgeon abundance and examining growth among different reaches types; the third hypothesis (2) was tested by assessing contaminant loads in lake sturgeon of various sizes and examining effects on growth and condition.

Relative abundance, growth, mortality and mean size of lake sturgeon were not significantly different among river reaches with (n = 6) and without a commercial harvest (n = 3) in the Ottawa River. Mercury was the only contaminant of the many tested that was elevated in lake sturgeon samples. Neither growth nor condition was affected with increasing mercury contamination. Relative abundance of lake sturgeon was significantly greater in unimpounded reaches than impounded reaches. Lake sturgeon grew significantly faster in impounded (n = 6) than unimpounded reaches (n = 3) possibly suggesting density dependent compensation. Water power management appears to be the primary factor affecting lake sturgeon populations in the Ottawa River.
Introduction

Sturgeon are purportedly the most threatened vertebrate group on the planet (Ludwig 2006). Acipenseriformes, comprising 27 extant species (including two species of paddlefish), are widespread throughout the northern hemisphere, and all species are imperilled (Billard and Lecointre 2001; Pikitch et al. 2005). Extinction threats include commercial harvest (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997; Billard and Lecointre 2001), habitat deterioration and loss (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997; Billard and Lecointre 2001), population isolation and habitat fragmentation, especially by dams (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997; Billard and Lecointre 2001), and poaching (i.e., for caviar; Ludwig 2006).

Lake sturgeon (Acipenser fulvescens) are endemic to North America and were historically abundant (Harkness and Dymond 1961; Scott and Crossman 1973). However, populations have declined precipitously throughout their range and are currently considered at risk in many states and provinces (Williams et al. 1989; Carlson 1995; Kempinger 1996; Ferguson and Duckworth 1997; Baker and Borgeson 1999; Williamson 2003). Sturgeon life history traits, including low recruitment, slow growth, late maturity and periodic spawning not only render populations susceptible to increased adult mortality – as occurred, for example, with the large commercial harvests in the late 1800s (Prince 1905; Harkness and Dymond 1961; Brousseau 1987; Houston 1987; Holzkamm and McCarthy 1998) – but have also inhibited population recovery (Boreman 1997; Beamesderfer and Farr 1997; Crouse 1999; Secor and Waldman 1999; Gross et al. 2006).
2002). Large commercial harvests in many cases were accompanied by deterioration in water quality and loss or degradation of habitat and population isolation by dams constructed for hydroelectric development, flood control or navigation. Although some of these stresses have been ameliorated, sturgeon populations in general have not recovered to historical levels (Houston 1987; Auer 1996a; Baker and Borgeson 1999).

While at one time considered abundant in the Ottawa River (Small 1883; Dymond 1939) lake sturgeon numbers declined dramatically during the early part of the 20th century (Toner 1943). A commercial lake sturgeon fishery, established in 1881, peaked at a harvest of 28 780 kg in 1898 (Dymond 1939) and declined thereafter; although a commercial fishery still exists in portions of the Ottawa River, sturgeon harvest is currently at least an order of magnitude smaller than at the turn of the century. A reduction in sturgeon harvest across Ontario was attributed to stressed (overexploited) populations - less than 1/3 of the quota issued across Ontario were filled in 1984 primarily due to low sturgeon abundance and not necessarily due to market value (Brousseau 1987). The first part of the 20th century until the early 1970’s also saw a dramatic reduction in water quality in the Ottawa River associated with adjacent land use practices (primarily agriculture and forestry), untreated municipal sewage discharge, use of the river for garbage disposal (Ontario Water Resources Commission and Quebec Water Board 1971), the presence of massive log drives, which exceeded one million cords in the late 1800’s to early 1900’s (Ottawa River Engineering Board 1965) and the construction of a number of pulp mills with untreated discharge (Ontario Water Resources Commission and Quebec Water Board 1971). Dams were constructed along
the river and in major tributaries between the 1880’s and 1964 (Ottawa River Engineering Board 1965) altering habitat and potentially isolating and fragmenting sturgeon populations.

Since the 1970s, the river has experienced changes that might be expected to reduce stress on sturgeon populations. All discharge from pulp and paper mills, as well as all municipal sewage, receives primary if not secondary or tertiary treatment. Moreover, more than 90% of municipal sewage is subject to phosphorus removal (Environment Canada et al. 1989). Log drives on the Ottawa River ceased in 1990 and therefore no longer litter the river bottom with sunken logs and wood debris. Commercial harvest for lake sturgeon has all but ceased; all commercial licenses on the Ontario portion of the river were bought out in the late 1980s, and the Quebec portion has had only two licensees since the early 1990’s with quotas set at 0.1 kg/ha (Henri Fournier, Ministère des Ressources naturelles et de la Faune du Québec, pers. comm.). Yet lake sturgeon populations in the Ottawa River have still not recovered to anything close to historical levels – indeed, there is little evidence of any population recovery in some river reaches whatever.

Preliminary assessment of current lake sturgeon populations in the Ottawa River was conducted by Haxton (2002). Variation in lake sturgeon abundance was observed among river reaches verifying that recovery has not occurred in all river reaches. At least three (not mutually exclusive) hypotheses can be advanced to explain the lack of recovery: (1) that although commercial harvesting has declined dramatically, given historical declines
and sturgeon life history, it is still sufficiently high to prevent population recovery; (2) population recovery is hampered by high contaminant levels and their attendant impacts on growth and reproduction; (3) the possibility of population recovery to anything approaching historical levels is effectively precluded by the current water management regime on the river. We investigate these hypotheses below.

**Study site**

This study was conducted in nine reaches of the Ottawa River, Canada (Figure III - 1). Ottawa River is a large, highly altered, managed system. The full course of the river extends 1,130 km from the headwaters at Lake Capitmitchigama in Québec to the confluence at the St. Lawrence River (Legget 1975) forming a natural provincial border between Ontario and Québec for approximately 580 km from Lake Temiscaming to Carillon (Chapman and Putnam 1984). The river has a watershed of over 146,000 km², 65% within Quebec, a mean annual flow of 1,968 m³/s and has a vertical descent of 365 m (Telmer 1996) making it ideal for hydro-electric production. This study is restricted to the nine reaches downstream of Lake Temiscaming to the Carillon Dam (Figure III - 1). Reaches are delineated by the presence of dams or sets of rapids. Six of the nine river reaches are controlled by dams although water management regimes (Table III - 1) and water level fluctuations vary among these reaches (Figure III - 2). Water flows, obtained from several locations along the river, increase from upstream to downstream but show similar patterns that follow a natural flow regime with the greatest flows occurring in spring, the lowest flows occurring during the summer months and then increasing again.
during the fall (Figure III - 3). Water flows were not substantially altered after the construction of Chats Generating Station in 1932 but changed dramatically after the construction of Chenaux G.S., Rolphoton G.S and Otto Holden G.S. (Table III - 1) with a 42% increase in flows in during the winter months and 25% decrease in peak flows during the freshet (Figure III - 4).

Methods

Two of the three hypotheses were tested by comparing sturgeon population attributes in different reaches which vary either in the level of commercial harvest or water management regimes. Thus, reaches were classified as either unimpounded or impounded (hypothesis 3); unimpounded reaches (Upper Allumette Lake, Lower Allumette Lake and Lac Coulonge) are those where a dam is not present (Table III - 1). Riparian areas were not flooded or altered as a result of dam construction, and natural rapids exist (e.g. Allumette Rapids); impounded reaches (Lac Dollard des Ormeaux, Lac Deschênes, Lac des Chats, Lac du Rocher Fendu, Holden Lake and Lac la Cave) are those with a dam where extensive areas have been flooded and where dam operations influence water levels and flows directly. If lake sturgeon population recovery is inhibited by the current water management regime, then impounded reaches should, on average, show lower abundance and/or recruitment compared to unimpounded reaches.

To test hypothesis (2), reaches were classified as either having a lake sturgeon commercial harvest (Lac Deschênes, Lac des Chats, Lac du Rocher Fendu, Lac Coulonge, Lower Allumette Lake and Upper Allumette) or not (Lac la Cave, Holden
Lake and Lac Dollard des Ormeaux; Table III - 1). All river reaches at one time supported a commercial harvest. Commercial harvest of lake sturgeon in Lac Dollard des Ormeaux was closed in 1992 due to overexploitation and mercury burden (Fortin et al. 1992); Lac la Cave and Holden Lake did not produce any sturgeon in 1987 despite a quota of 800 kg (Fortin et al. 1992) and the commercial fisheries were subsequently closed. If recovery is inhibited by ongoing commercial harvest, we would expect lower abundance in reaches with a commercial harvest versus those without as a consequence of increased mortality. Moreover, because harvest usually results in removal of large, more commercially valuable individuals (Houston 1987), the average size of lake sturgeon will be smaller in those reaches with versus without an existing commercial harvest.

The contaminant exposure hypothesis was evaluated in two ways. First, if contaminants are negatively affecting sturgeon populations, one potential effect may be through reduced growth and/or condition. This can be evaluated by testing whether in Ottawa River lake sturgeon, growth and/or condition declines with increasing contaminant loading. Second, because estimates of body burden are available for other North American lake sturgeon populations, we can assess (1) whether there is any relationship between Hg burden and population status (e.g. declining, stable, increasing) and (2) where Hg burden of Ottawa River sturgeon fits in this relationship – if indeed any such relationship exists. Contaminant sample sizes were not sufficient to examine among reach variation, even when categorized as impounded and unimpounded.
Netting Assessment

Nearshore Community Index Netting (NSCIN) and Fall Walleye Index Netting (FWIN) were used to sample fish communities. NSCIN used randomly set trapnets from early August through early October (water temperature > 13°C; Stirling 1999). Unbaited trapnets, 1.8 m trapnets with 36.5 m leads and 2.4 m trapnets with 61.0 m leads (3.8 cm mesh) were used. Water depths were restricted to 1.7 - 3.5 m for the 1.8 m trapnets and 2.3 - 4.7 m for the 2.4 m trapnets. The shoreline of each reach was partitioned into 2000 m sections, numbered and then randomly chosen. Trapnets were set at a random locations perpendicular to the shore at least 500 m apart for a 24 hr period. At the end of the sampling period, each net was lifted, all fish were identified, enumerated, measured, weighed, an aging structure obtained for select species and then released and then the nets were reset in another randomly chosen location. Attempts were made to sample each reach with at least 40 net sets. No sampling sites were reused if possible; if not possible, a minimum of four days must have lapsed from the previous netting before the sampling site was reused (two sites were reused in this study). NSCIN was conducted from 1998 – 2004.

FWIN uses randomly set monofilament gillnets in the fall when surface water temperatures are between 10°C and 15°C. Gillnets had eight panels of different (25 – 152 mm stretched) mesh and were set perpendicular to the shore. Nets were randomly set in two depth strata, 2 to 5 m and 5 to 15 m, with each depth stratum sampled equally (Morgan 2002). Sample sites were determined by partitioning the reach into 1 km x 1 km numbered quadrats and randomly selecting a quadrat. Nets were fished overnight and
picked up early the following day (generally an 18 – 24 hour net set). FWIN is a lethal sampling technique for most species, with the exception of lake sturgeon and channel catfish. Nets were then reset in another random location. FWINs were conducted from 1998 – 2003. Catch per unit effort (CUE - number of lake sturgeon caught per net night) was estimated for each site for both NSCIN and FWIN.

To increase sample size, lake sturgeon that were sampled during spawning assessment (Haxton 2006; Haxton, unpublished data) or outside of standardized index netting projects (Haxton, unpublished data) were included in our analysis of growth, but not in any other analyses.

Total length (to the nearest mm), fork length and weight (to the nearest 100 grams) were measured for all lake sturgeon. A one cm section of the leading pectoral ray was extracted for aging. Commencing 2001, a numbered monel tag was attached to the anterior portion of the dorsal fin of each lake sturgeon. All lake sturgeon except for those taken for contaminant analysis were live released. Pectoral rays were dried for at least 30 days and then 60 μm sections were extracted using a Buehler low speed isomet saw (Wilson 1987). Pectoral ray sections were examined under a 25X power microscope and annuli counted. Translucent bands are deposited during summer growth and opaque bands during winter growth (Noakes et al. 1999). A drop of mineral oil was used to illuminate the zones. Ages were estimated from undamaged pectoral rays. Ages were not validated but were estimated by multiple readers; the final decision on age was assigned by the lead author.
Von Bertalanffy’s growth curves (Ricker 1975) were constructed for lake sturgeon with parameters determined by a least squares non linear regression using Solver in Microsoft Excel (Microsoft Corporation, Redmond, CA); constraints were placed on parameters ($L_\infty$: 100 (min.), 150 (max.); $k$: 0.001 (min.), 1.0 (max.); $t_0$: -3 (min.), 0 (max.)) to ensure convergence. Age-size data were pooled over reaches within a water management regime or commercial harvest category (e.g. impounded or unharvested) to estimate Von Bertalanffy’s growth parameters, as for individual reaches, sample sizes were often too small to permit sufficiently precise estimates of growth parameters. Von Bertalanffy’s growth curves were then constructed for lake sturgeon in unimpounded reaches, reaches under water power management, reaches commercially harvested and reaches without a commercial harvest. Bootstrapped confidence intervals on estimated growth parameters were obtained by sampling with replacement $n$ individuals (where $n$ is the size of actual sample), estimating growth parameters, and estimating the CIs based on the parameter distribution over the 1000 trials.

Catch curves were constructed for each sampling technique to assess gear selectivity (Van den Avyle 1993). Size classes were partitioned into 5 cm (total length) bins and plots constructed of log$_{10}$ frequency versus size class. Lake sturgeon were considered fully vulnerable to gear at the mode of the frequency distribution. A $t$-test was conducted on the total length of the lake sturgeon caught by different depth strata in the FWIN to determine if they were size selectivity based on gear depth.
Annual mortality was determined from age class frequency distributions with ages grouped in 5 year intervals. Instantaneous mortality ($z$) was calculated by regressing the logarithm of age class frequency on age on the descending limb of the catch curve (Ricker 1975). Annual mortality ($A$) was determined from $A = 1 - e^{-2z}$ (Ricker 1975).

Bootstrapped confidence intervals on estimated mortality were obtained by sampling with replacement $n$ individuals (where $n$ is the size of actual sample), estimating mortality, and estimating the CIs based on the mortality estimate distribution over the 1000 trials.

Forty-eight lake sturgeons from five reaches were collected for contaminant analysis. A 500 g sample of epaxial muscle was sent to the Ontario Ministry of Environment for contaminant analysis, specifically organochlorine pesticides which are widely used in insecticides, polychlorinated biphenyls (PCBs) which have many industrial uses (Ministry of the Environment 2005) and inorganic substances such as mercury which can bioaccumulate in fish (Fiest et al. 2005; Webb et al. 2006). Samples were therefore tested for mercury, PCBs, heptachlor, aldrin, mirex, photomirex, hexachlorocyclohexane ($\alpha$-BHC, $\beta$-BHC, $\gamma$-BHC), $\alpha$-chlordane, $\gamma$-chlordane, toxaphene, hexachlorobenzene, octachlorostyrene, trans-nonachlor, cis-nonachlor, oxychlordane, o,p$'$-DDT, p,p$'$-DDD, p,p$'$-DDT and p,p$'$-DDE. Detection limits are summarized in Table III - 2 (Ministry of the Environment 2005). $[Hg]$ and length data from: four stable Ontario lake sturgeon populations (Abitibi River, Kenogami River, Mattagami River and Moose River) were obtained from the Ontario Ministry of Environment, Wisconsin populations (including Chippewa River, Menominee River and Wisconsin River. Sample size for each Wisconsin waterbody was too small for individual analyses therefore data were pooled).
from Wisconsin Department of Natural Resources and from the St. Lawrence River from Quebec’s Ministry of Natural Resources.

**Statistical analysis**

The correlation between lake sturgeon abundance in each reach as estimated by the two different netting techniques was calculated using Kendall’s Tau rank correlation. Poisson regression was conducted to determine if there was an interaction between netting techniques and reach type (commercially harvested or not, impounded or unimpounded); if an interaction existed, then further CUE analysis using netting technique would have to be conducted separately. Poisson regression was then used to determine if there was a detectable difference in lake sturgeon CUE between impounded and unimpounded river reaches and reaches with and without a commercial harvest, with netting technique (i.e., FWIN and NSCIN) included as a factor in fitted regression models.

Principal component analysis (PCA) was conducted using log₁₀ total length and log₁₀ age of lake sturgeon from samples. A cumulative distribution graph was constructed from PC1 for impounded and unimpounded river reaches and for commercially harvested and non-commercially harvested reaches; differences in the shape of the curve would identify differences in age-size distribution. Von Bertalanffy growth curves were estimated for unimpounded and impounded reaches, and reaches with and without a commercial harvest, and compared using Kimura’s Likelihood Ratio test (Haddon 2001). Generalized linear models (GLM) was also fitted to log₁₀ transformed total length (dependent) in
relation to $\log_{10}$ age and reach type (unimpounded versus impounded, with and without a commercial harvest) as factors to assess growth.

Generalized Linear Model was conducted to determine if Hg body burden differed between sexes or reach types using $\log_{10}[Hg]$ as the dependent, $\log_{10}$ total length and sex or reach type (unimpounded versus impounded, with and without a commercial harvest) as factors. To determine if $[Hg]$ affects lake sturgeon growth, PCA was conducted on $\log_{10}$ total length and $\log_{10}$ weight; GLM was then conducted with PC1 scores as the dependent, $\log_{10}$ age and $Hg$ concentration as independents. GLM was also conducted to determine if there was a relationship between $[Hg]$ and size from different robust lake sturgeon populations (i.e., does Hg accumulate faster in some populations than others?). Total length and $[Hg]$ were $\log_{10}$ transformed. Finally, a correlation of $\log_{10}$ length and $[Hg]$ was conducted on each population to determine if variation was excessively high in Ottawa River due to samples coming from multiple river reaches.

Statistical analysis was conducted using SYSTAT 11 (SYSTAT Software Inc., Richmond, CA); Poisson regressions were conducted using S-PLUS 6.2 (Insightful Corporation Seattle, Washington). Significance was determined at $P = 0.05$.

**Results**

Sporadic harvest records notwithstanding, there is little doubt that commercial harvest has declined dramatically in the Ottawa River since the turn of the century (Figure III -
During the course of the study, we captured 758 lake sturgeon in six of the nine reaches using standardized index netting (Figure III - 6); 312 by FWIN and 446 by NSCIN (Table III - 3) with lake sturgeon CUE based on FWIN and NSCIN being positively correlated \((r = 0.76, \text{ d.f.} = 7, P = 0.018)\) across river reaches (Figure III - 6). Lake sturgeon were fully vulnerable to FWIN nets at 80 cm total length (TL) however FWIN nets were selective for lake sturgeon less than 115 cm TL (Figure III - 7). There was also selectivity of the gear due to depth as significantly smaller lake sturgeon were caught in the deeper depth (5 – 15 m) strata \((t = 4.07, \text{ d.f.} = 125, P < 0.001)\). Lake sturgeon were fully vulnerable to NSCIN nets at 85 cm TL and sampled larger lake sturgeon (Figure III - 7). There was an interaction between reach and netting technique (Poisson regression; d.f. = 883 \(P < 0.001\)) between impounded and unimpounded reaches, therefore CUE analysis was conducted separately for each netting technique. Lake sturgeon CUE was significantly greater in unimpounded reaches than impounded reaches using both FWIN (Poisson regression; d.f. = 376 \(P < 0.001\)) and NSCIN (Poisson regression; d.f. = 507 \(P < 0.001\); Figure 8). Both size \((\chi^2 = 99.5, \text{ d.f.} = 21, P < 0.001)\) and age \((\chi^2 = 65.6, \text{ d.f.} = 9, P < 0.001)\) distributions varied between impounded and unimpounded reaches, with smaller, younger fish occurring more frequently in unimpounded reaches (Table III - 4; Figure III - 9). Von Bertalanffy growth curves were significantly different between unimpounded and impounded reaches (Figure III - 10; \(F = 55.16, \text{ d.f.} = 550, P < 0.001\)); difference in the curves was influenced primarily by \(t_0\) \((\chi^2 = 9.56, \text{ d.f.} = 1, P = 0.001)\). Growth – as estimated by the slope of the regression of \(\log_{10}\) length on \(\log_{10}\) age - was significantly greater (GLM \(F_{1,552} = 33.29, P < 0.001\) in impounded than unimpounded reaches.
There was an interaction between reach and netting technique (Poisson regression; d.f. = 883, \( P<0.001 \)) among reaches with and without a commercial harvest therefore CUE analysis was conducted separately for each netting technique. Lake sturgeon CUE from NSCIN was significantly greater in river reaches with a commercial harvest than without (Poisson regression d.f. = 507, \( P<0.001 \); Figure III - 8) but was not significantly different using FWIN (Poisson regression d.f. = 376, \( P = 0.561 \)). Mean total length of lake sturgeon was significantly greater in river reaches with a commercial harvest than without a commercial harvest (Table III - 4; \( t \)-test; \( t = 4.088 \) d.f. = 745, \( P<0.001 \)). Both size (\( \chi^2 = 33.9 \), d.f. = 21, \( P = 0.037 \)) and age (\( \chi^2 = 28.9 \), d.f. = 9, \( P = 0.001 \)) distributions were significantly different between commercially harvested and non commercially harvested reaches with populations skewed to larger fish in commercially harvested reaches (Table III - 4; Figure III - 11). Von Bertalanffy growth curves were not significantly different between reaches with versus without a commercial harvest (Figure III -12; \( F = 0.45 \), d.f. = 550, \( P=0.72 \)). Growth was not significantly different between commercially harvested versus not harvested reaches (GLM \( F_{1,552} = 3.66 \), \( P=0.056 \)) nor was the intercept (ANCOVA: \( F_{1,553} = 0.31 \), \( P = 0.58 \)). Annual estimated mortality was 18.8% (14.2 - 21.4%; 95% CI) in reaches without a commercial harvest, compared to 20.4% (17.0 - 22.1%; 95% CI) for those with a harvest.

Because of the comparatively small number of reaches from which sturgeon were sampled, a factorial analysis of the effect of impounded versus unimpounded, and the presence/absence of a commercial harvest, is not possible. However, the fit of a Poisson
model using solely water management reach type (impounded versus unimpounded; Deviance residual = 452.5, d.f. = 885), commercial harvest reach type (presence versus absence of a commercial harvest; Deviance residual = 67, d.f. = 885) compared to the fit with reach as the sole predictor (Deviance residual = 747.5, d.f. = 885), indicates that variation explained by water management regime (60.5%) is a far better predictor of among-reach CUE than commercial harvest (9.0%).

Of 21 contaminants assayed, only 3 had at least one sample above detection limit: total PCB ranged from 20 - 120 ng/g; DDT and metabolites ranged from 2 - 170 ng/g; and total mercury ranged from 0.06 - 0.68 µg/g (Table III - 2), with mercury the most commonly detected contaminant. Total mercury concentration increased with total length ($r^2 = 0.17; \text{d.f.} = 47 \ P = 0.002$; Figure III - 13) with no detectable difference between sexes with respect to either the intercept ($F_{1,41} = 0.04, P = 0.84$) or the slope ($F_{1,41} = 0.04, P = 0.84$) of this relationship; there was no detectable differences between reach type with respect to the intercept ($F_{1,44} = 2.68 P = 0.109; F_{1,44} = 0.62 P = 0.435$) or slope ($F_{1,44} = 2.67 P = 0.109; F_{1,44} = 0.65 P = 0.43$) for reaches with or without a commercial harvest and impounded or unimpounded reaches respectively (Figure III -13). Total length and weight were highly correlated for lake sturgeon sampled for contaminant analysis; PC1 explained 90.9% of the variation. There was no effect of Hg body burden detected on growth (slope ($F_{14,11} = 0.71, P = 0.71$) or intercept ($F_{18,1} = 0.73, P = 0.40$)).

Slopes of the relationship between $[Hg]$ and total length among populations across North America were significantly different (GLM: $F_{6,468} = 5.043 P < 0.001$). However, for a
given size, Hg body burden in Ottawa River lake sturgeon were not unusually high
against a background of contaminant levels for lake sturgeon in populations (Figure III -
14). Variation in body burden in relationship to size in the Ottawa River was not
excessive in comparison to other North American populations (Table III - 5).

Discussion

Despite the reduction in several likely stressors over the past several decades, lake
sturgeon in several Ottawa River reaches show few signs of recovery. The hypothesis
that recovery is being impeded by the already substantially reduced commercial harvest
was not supported: reaches still supporting a commercial harvest not only have greater
sturgeon CUE, but sturgeon in these reaches are, on average, larger than those in reaches
without a current harvest; and annual mortality was not significantly greater. All reaches
at one time supported a commercial harvest, with all fisheries except those in current
operation being closed by the early 1990s. Our assumption is that all river reaches were
subjected to the same level of harvest (i.e., the rate of population depletion was not
greater in any particular river reach). Without reach specific commercial harvest data, our
assumption cannot be tested. Nonetheless, lake sturgeon that were too small for the
commercial harvest when it was operational should be currently present in the population
and have grown into harvestable size. Yet more than 15 years later, populations in those
reaches where commercial operations were eliminated are still dramatically smaller than
those in reaches where harvesting currently occurs. Thus, while commercial harvesting
may well have contributed – perhaps substantially - to historical sturgeon decline, there is
no evidence that the current small commercial take is impeding recovery in the Ottawa River.

Lake sturgeon are susceptible to bioaccumulation of persistent contamination in the environment due partially to their longevity (Fiest et al. 2005; Webb et al. 2006). Mercury has been linked to poor reproductive physiology (Fiest et al. 2005; Webb et al. 2006) and poor growth and condition (Fiest et al. 2005) in lake sturgeon however, relationships in these studies were weak and very few mature fish were included; the two mature male sturgeon that were included did not display any effects in terms of gondaosomatic index from increased mercury burden (Webb et al. 2006). While reproductive physiology was not examined during this study, there was no evidence of significant effects of mercury burden on growth or condition, and Hg body burden did not appear to be elevated in impounded compared to unimpounded reaches as observed in the Columbia River (Feist et al. 2005). Moreover, contaminant levels in Ottawa River sturgeon are well within the range of concentrations present in considerably more robust sturgeon populations in other North American rivers. In fact, mercury burden was greater at a given size in the Ottawa River than in a river which intuitively one would expect higher contamination (e.g. St. Lawrence River). This may be a function of growth as lake sturgeon in the St. Lawrence River grow faster than in the Ottawa River (Fortin et al. 1992). Or, it may be a function the chemical properties of the water (e.g. dissolved organic carbon, calcium) due to the location of the river (e.g. located on the Precambrian shield versus off shield). This is beyond the scope of this study but definitely warrants further study. As such, there is at present little evidence that sturgeon recovery in the
Ottawa River is being impeded by contaminant stress. A similar conclusion was reached for lake sturgeon in the Lower Saskatchewan River (Findlay et al. 1996).

Our results are consistent with the hypothesis that water power management is impeding sturgeon recovery, as has been suggested for white sturgeon (Acipenser transmontanus) in the Columbia River (Beamesderfer et al. 1995; Beamesderfer and Farr 1997). Food availability, poor spawning habitat and changes in flow and temperature were the identified stressors responsible for poor recruitment (Feist et al. 2005). While relative abundance of lake sturgeon was greater in unimpounded Ottawa River reaches, estimated growth was greater in impounded reaches suggesting that prey was not limiting for lake sturgeon within these reaches. This, combined with the observed reduced abundance, suggests that recruitment relating to spawning habitat is impaired in impounded reaches.

Lake sturgeon are potamodromous and will migrate long distances between foraging, overwintering and spawning areas (Harkness and Dymond 1961; Houston 1987; Rochard et al. 1990; Beamesderfer and Farr 1997; Ferguson and Duckworth 1997; Baker and Borgeson 1999; Williot et al. 2002). In the Ottawa River, movement can occur downstream from impounded reaches, but there are no fishways to facilitate upstream movement. Movement can occur among the unimpounded reaches as the rapids present are not considered a major barrier (i.e., not a falls) and therefore there is a concern the same fish were being sampled in different reaches (i.e., pseudo-replication). During the time this study was conducted, 794 lake sturgeon were tagged (includes tagging from concurrent work on spawning areas - e.g. Haxton 2006); 628 of these lake sturgeon were
tagged in unimpounded reaches. Although recapture rates were low, all were caught in
the same reach they were originally sampled (Haxton unpublished data). Lake sturgeon
are generally sedentary (Fortin et al. 1993) and are often recaptured in the location they
were originally tagged (Dumont et al. 1987). Even with the removal of a barrier on a
smaller river, lake sturgeon remained within a 32 km section (Borkholder et al. 2002).
Lake sturgeon tracked for 2.5 years in the Ottawa River remained within the same section
of a reach despite the potential of extensive movement both upstream and downstream
with the absence of barriers (Haxton 2003). While barriers were not present and
movement of fish possible between unimpounded reaches, the aforementioned studies
suggest that this was not occurring on a regular basis and therefore pseudo-replication is
not considered to be a major issue in this study.

Although dams form barriers to migrating species, and can limit access to historical
spawning areas, sturgeon will spawn at the base of dams (Harkness and Dymond 1961;
Khoroshko 1972; Kempinger 1988; Auer 1996b; Auer 1999; Cooke and Leach 2004;
Duncan et al. 2004). Lake sturgeon have been documented to spawn at the base of dams
in all of the impounded Ottawa River reaches (e.g. Dubrieuil and Cuerrier 1950; Haxton
2006). There are several tributaries to the Ottawa River which lake sturgeon could spawn;
however, many of these tributaries are also dammed. Spawning success will depend on
flow variability downstream of dams and the presence of suitable spawning habitat
White sturgeon recruitment was negatively affected in impounded reaches (Beamesderfer
et al. 1995). Mitigation techniques could be employed that could enhance recruitment
(LaHaye et al. 1992) such as ensuring adequate flows are provided during spawning through to drift, ensuring suitable habitat is available immediately downstream or providing passage over dams to historical spawning site (assuming they have not been altered from impoundment effects).

The conclusion that sturgeon recovery in the Ottawa is being impeded primarily by reduced recruitment in impounded reaches should be regarded as tentative. In reaching this conclusion, we have inferred putative causal effects of water power management from variation in indices of sturgeon population condition among different reaches and clearly, this variation is not solely attributable to the nature of water management in a particular reach. Additional evidence could potentially be provided by similar findings in other river sturgeon populations (e.g. sturgeon abundance is reduced in impounded rivers but not unimpounded reaches) but clearly, the lack of similar finding in other systems does not militate against its veracity in the Ottawa River. A much more powerful test of the hypothesis would involve creating additional high quality spawning habitat ensuring suitable flows are provided during the spawning period in several impounded and unimpounded reaches; the prediction is then that recruitment relative to levels before habitat creation, recruitment and abundance in the following years will increased substantially more in impounded than unimpounded reaches. We are currently investigating the possibility of conducting such an experiment on the Ottawa River.
Conclusions

Water power management appears to have the greatest influence on the relative abundance of lake sturgeon within the Ottawa River reaches and is therefore currently limiting population recovery. While at one time commercial harvest probably limited lake sturgeon numbers, it does not currently appear to be controlling populations. Mercury levels are elevated in lake sturgeon in the Ottawa River relative to other organic contaminants tested but do not appear to be affecting populations. This study provides evidence that water power management affects lake sturgeon recovery in the Ottawa River; however it does not explore how or why water power management limits recovery.
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References

Auer, N. 1996a. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Canadian Journal of Fisheries and Aquatic Sciences 53: 152-160.


Table III - 1. Characteristics of Ottawa River reaches including water management regime, water level fluctuation, area flooded as a result of dam construction and commercial fisheries.

<table>
<thead>
<tr>
<th>Reach</th>
<th>Length (km)</th>
<th>Surface Area (ha)</th>
<th>Mean Depth (m)</th>
<th>% littoral zone</th>
<th>Natural Rapids Present</th>
<th>Dam controlled</th>
<th>Year constructed</th>
<th>Water Level Fluctuation (m)</th>
<th>Water Management</th>
<th>Area Flooded (km²)</th>
<th>Commercial lake sturgeon fisheries</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac Dollard des Ormeaux</td>
<td>113.1</td>
<td>14 414</td>
<td>6.1</td>
<td>64.6</td>
<td>No</td>
<td>Carillon G.S.*</td>
<td>1964</td>
<td>1.5</td>
<td>Run-of-the-river/ Peaking (winter)</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Lac Deschenes</td>
<td>52.8</td>
<td>10 900</td>
<td>5.2</td>
<td>62.5</td>
<td>Yes</td>
<td>Chaudière Falls G.S.</td>
<td>1880's</td>
<td>0.9</td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>0.1 kg ha^-1**</td>
</tr>
<tr>
<td>Lac des Chats</td>
<td>40.0</td>
<td>7 513</td>
<td>4.9</td>
<td>61.4</td>
<td>No</td>
<td>Chats Falls G.S. Chenaux G.S.</td>
<td>1932</td>
<td>0.34</td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>0.1 kg ha^-1**</td>
</tr>
<tr>
<td>Lac du Rocher Fendu</td>
<td>31.1</td>
<td>3 893</td>
<td>7.9</td>
<td>50.1</td>
<td>Yes</td>
<td>G.S.</td>
<td>1950</td>
<td>1.6</td>
<td>Peaking</td>
<td>7.4</td>
<td>0.1 kg ha^-1**</td>
</tr>
<tr>
<td>Lac Coulonge</td>
<td>18.1</td>
<td>2 888</td>
<td>3.8</td>
<td>76.0</td>
<td>Yes</td>
<td>n/a</td>
<td>1950</td>
<td>0.72</td>
<td>n/a</td>
<td>n/a</td>
<td>0.1 kg ha^-1**</td>
</tr>
<tr>
<td>Lower Allumette Lake</td>
<td>22.3</td>
<td>4 613</td>
<td>2.9</td>
<td>81.5</td>
<td>Yes</td>
<td>n/a</td>
<td>1950</td>
<td>0.72</td>
<td>n/a</td>
<td>n/a</td>
<td>0.1 kg ha^-1**</td>
</tr>
<tr>
<td>Upper Allumette Lake</td>
<td>76.9</td>
<td>13 212</td>
<td>10.1</td>
<td>54.5</td>
<td>Yes</td>
<td>n/a</td>
<td>1950</td>
<td>0.72</td>
<td>n/a</td>
<td>45.6</td>
<td>n/a</td>
</tr>
<tr>
<td>Holden Lake</td>
<td>90.0</td>
<td>7 592</td>
<td>16.8</td>
<td>24.5</td>
<td>No</td>
<td>Rolphton G.S. Otto Holden G.S.</td>
<td>1952</td>
<td>2.3</td>
<td>Reservoir - winter drawdown</td>
<td>13.7</td>
<td>n/a</td>
</tr>
<tr>
<td>Lac la Cave</td>
<td>49.0</td>
<td>3 028</td>
<td>19.7</td>
<td>21.3</td>
<td>No</td>
<td>G.S.</td>
<td>1952</td>
<td>3.3</td>
<td>Reservoir - winter drawdown</td>
<td>n/a</td>
<td></td>
</tr>
</tbody>
</table>

+ % area < 5 m; *G.S. - generating station; **Quebec portion of the river
Table III - 2. Levels (ng/g) of selected contaminants in 48 lake sturgeon from the Ottawa River and corresponding detection limits (Ministry of Environment 2005).

<table>
<thead>
<tr>
<th>Compound</th>
<th>Detection Limit (ng/g)</th>
<th>N (number samples &gt; DL)</th>
<th>Average concentration (SD)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>polychlorinated biphenyls (total)</td>
<td>20</td>
<td>36</td>
<td>52.9 (29.7)</td>
<td>20 – 120</td>
</tr>
<tr>
<td>Heptachlor</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aldrin</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mirex</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Photomirex</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>α-BHC</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>β-BHC</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>γ-BHC</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>α-chlordane</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>γ-chlordane</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Toxaphene</td>
<td>50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hexachlorobenzene</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>octachlorostyrene</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>trans-nonachlor</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cis-nonachlor</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oxychlordane</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>o,p'-DDT</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p,p'-DDD</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.p'-DDT</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.p'-DDE</td>
<td>1</td>
<td>35</td>
<td>27.8(35.4)</td>
<td>2 – 170</td>
</tr>
<tr>
<td>Hg*</td>
<td>48</td>
<td></td>
<td>0.29 (0.15)</td>
<td>0.06 – 0.68</td>
</tr>
</tbody>
</table>

*μg/g
Table III - 3. Number, mean total length and mean weight (SD) of lake sturgeon caught by sampling technique in each Ottawa River reach.

<table>
<thead>
<tr>
<th>River Reach</th>
<th>Sampling Technique</th>
<th>Year(s)</th>
<th>No. of sturgeon sampled</th>
<th>Mean total length (cm)</th>
<th>Mean weight (g)</th>
<th>No. of nets set</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac Dollard des Ormeaux</td>
<td>FWIN</td>
<td>2001/2002</td>
<td>127</td>
<td>76.1 (15.0)</td>
<td>2133 (1591)</td>
<td>106</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>2004</td>
<td>1</td>
<td>71.0</td>
<td>1100</td>
<td>40</td>
</tr>
<tr>
<td>Lac Deschênes</td>
<td>FWIN</td>
<td>2003</td>
<td>0</td>
<td></td>
<td></td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>2000/2002</td>
<td>0</td>
<td></td>
<td></td>
<td>80</td>
</tr>
<tr>
<td>Lac des Chats</td>
<td>FWIN</td>
<td>2002/2003</td>
<td>1</td>
<td>73.2</td>
<td>1828</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>1998</td>
<td>11</td>
<td>109.9 (20.4)</td>
<td>8450 (4773)</td>
<td>42</td>
</tr>
<tr>
<td>Lac du Rocher Fendu</td>
<td>FWIN</td>
<td>2002/2003</td>
<td>3</td>
<td>78.1 (3.1)</td>
<td>2599 (148)</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>1997/2000</td>
<td>26</td>
<td>79.8 (16.3)</td>
<td>2655 (1790)</td>
<td>65</td>
</tr>
<tr>
<td>Lac Coulonge</td>
<td>FWIN</td>
<td>2002/2003</td>
<td>42</td>
<td>58.5 (15.3)</td>
<td>1184 (1078)</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>1998</td>
<td>39</td>
<td>72.8 (18.6)</td>
<td>2079 (1438)</td>
<td>43</td>
</tr>
<tr>
<td>Lower Allumette Lake</td>
<td>FWIN</td>
<td>2002/2003</td>
<td>53</td>
<td>72.9 (13.0)</td>
<td>2007 (1226)</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>1998</td>
<td>113</td>
<td>83.9 (10.3)</td>
<td>2904 (1258)</td>
<td>39</td>
</tr>
<tr>
<td>Upper Allumette Lake</td>
<td>FWIN</td>
<td>1999/2000</td>
<td>86</td>
<td>81.8 (8.6)</td>
<td>2505 (974)</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>2001/2002</td>
<td>256</td>
<td>86.7 (11.2)</td>
<td>3267 (1427)</td>
<td>136</td>
</tr>
<tr>
<td>Holden Lake</td>
<td>FWIN</td>
<td>1998</td>
<td>0</td>
<td></td>
<td></td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>2003/2004</td>
<td>0</td>
<td></td>
<td></td>
<td>48</td>
</tr>
<tr>
<td>River Reach</td>
<td>Sampling Technique</td>
<td>Year(s)</td>
<td>No. of sturgeon sampled</td>
<td>Mean total length (cm)</td>
<td>Mean weight (g)</td>
<td>No. of nets set</td>
</tr>
<tr>
<td>--------------</td>
<td>--------------------</td>
<td>---------</td>
<td>-------------------------</td>
<td>------------------------</td>
<td>-----------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Lac la Cave</td>
<td>FWIN</td>
<td>1998</td>
<td>0</td>
<td></td>
<td></td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>NSCIN</td>
<td>2004</td>
<td>0</td>
<td></td>
<td></td>
<td>16</td>
</tr>
</tbody>
</table>
Table III - 4. Mean total length and age with standard deviations and von Bertalanffy growth parameters with 95% CI's for different reach types.

<table>
<thead>
<tr>
<th></th>
<th>Unimpounded</th>
<th>Impounded</th>
<th>Commercially harvested</th>
<th>Unharvested</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_{\text{inf}}$ (95% CI)</td>
<td>113.8</td>
<td>147.3 (140.9/150)</td>
<td>128.9</td>
<td>119.1</td>
</tr>
<tr>
<td></td>
<td>(107.9/120.0)</td>
<td>(121.3/137.4)</td>
<td>(101.0/145.0)</td>
<td></td>
</tr>
<tr>
<td>$k$ (95% CI)</td>
<td>0.075</td>
<td>0.066</td>
<td>0.061</td>
<td>0.087</td>
</tr>
<tr>
<td></td>
<td>(0.067/0.085)</td>
<td>(0.061/0.073)</td>
<td>(0.054/0.069)</td>
<td>(0.053/0.131)</td>
</tr>
<tr>
<td>$t_0$ (95% CI)</td>
<td>-2.99 (-2.99/3.0)</td>
<td>-0.85 (-0.29/-1.36)</td>
<td>-3</td>
<td>-1.54 (0/-3)</td>
</tr>
<tr>
<td>mean total length (SD)</td>
<td>84.1 (16.3)</td>
<td>96.7 (25.4)</td>
<td>87.9 (19.2)</td>
<td>76.1 (16.4)</td>
</tr>
<tr>
<td>mean age (SD)</td>
<td>16.2 (6.3)</td>
<td>17.1 (7.6)</td>
<td>16.9 (6.6)</td>
<td>11.7 (4.5)</td>
</tr>
</tbody>
</table>
Table III - 5. The correlation ($r$) between mercury concentration and length in various North American sturgeon populations.

<table>
<thead>
<tr>
<th>Population</th>
<th>Sample size</th>
<th>$R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abitibi River</td>
<td>104</td>
<td>0.72</td>
</tr>
<tr>
<td>Kenogami River</td>
<td>20</td>
<td>0.45</td>
</tr>
<tr>
<td>Mattagami River</td>
<td>147</td>
<td>0.13</td>
</tr>
<tr>
<td>Moose River</td>
<td>89</td>
<td>0.72</td>
</tr>
<tr>
<td>Ottawa River</td>
<td>48</td>
<td>0.41</td>
</tr>
<tr>
<td>St. Lawrence River</td>
<td>21</td>
<td>0.34</td>
</tr>
<tr>
<td>Wisconsin</td>
<td>53</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Figure III - 1. River reaches and dam locations on the Ottawa River (GS = generating station); location of Ottawa River in relationship to Lake Ontario and the St. Lawrence River (insert).
Figure III - 2. Monthly deviations around the mean annual water level among Ottawa River reaches based on water levels records from 1950 to 2005. Unimpounded reaches (Upper Allumette, Lower Allumette and Lac Coulonge) are grouped.
Figure III - 3. Monthly deviations in flow around mean annual flow at various locations on the Ottawa River based on flow data from 1950 - 2005.
Figure III - 4. Mean monthly water flow at Chats G.S. before and after hydro-electric development in 1932; extensive hydro-electric development occurred in upstream locations during the late 1940’s.
Figure III - 5. Reported annual commercial harvest (kg) of lake sturgeon from the Ottawa River from 1880 – 2005. Zero catches represents missing data except for 1956, 1971 – 1974, 1984–1986 and 1989. For the years 1956-1975, commercial harvests are for both the Ottawa River and southern Ontario inland lakes. During the periods (1964 - 1974) where harvest data exists for both the Ottawa River and southern Ontario inland lakes, the Ottawa River harvest represented on average, 33.5% (+/- 49% SD) of the total harvest. Inset: current commercial harvest of lakes sturgeon from 2000 to 2005 - dashed line represents annual quota.
River reach

Figure III - 6. Average (+/- 1 SE) lake sturgeon CUE (# sturgeon per net night) in different Ottawa River reaches as estimated by FWIN and NSCIN from 1998 through 2005.
Figure III - 7. Frequency of different size classes in samples from FWIN (gillnets) and NSCIN (trapnets).
Figure III - 8. Average (+/- 1 SE) lake sturgeon CUE (sturgeon per net night) as estimated from FWIN and NSCIN in impounded and unimpounded reaches and commercially harvested and non-commercially harvested reaches of the Ottawa River.
Figure III - 9. Cumulative distribution graph of the first principal component (size) in impounded and unimpounded reaches of the Ottawa River.
Figure III - 10. Fitted von Bertalanffy growth curves for lake sturgeon in unimpounded reaches and reaches of the Ottawa River.
Figure III - 11. Cumulative distribution graph of the first principal component (size) in reaches of the Ottawa River for which a commercial harvest is present or absent.
Figure III - 12. Fitted von Bertalanffy growth curves for lake sturgeon in reaches of the Ottawa River for which a commercial harvest is present or absent.
Figure III - 13. Mercury concentration in relationship to total length of lake sturgeon from various Ottawa River reaches.
Figure III - 14. Mercury concentration in relation to size (total length) of lake sturgeon from various populations across North America.
Chapter IV. Variation in large-bodied fish community structure and abundance among reaches subject to different management regimes in a large river.

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Abstract

We investigate variation in life history traits (growth, condition, mortality and recruitment) and relative abundance of 11 large-bodied fish species among three water management regimes (unimpounded, run of the river and winter reservoirs) in a large regulated river (Ottawa River, Canada). If waterpower management has an effect on fish, then i) we would expect to detect community structuring among water management regimes; and ii) species with similar life history traits should be affected in a similar manner. Large-bodied fish communities were assessed using two different standard index netting techniques, one using trapnets and the other gillnets. Community structure could be discriminated based on species caught in nets using Discriminant Function Analysis (26% Jackknifed misclassification rates using trapnets and 24% using gillnets) and neural networks (78.8% correct overall classification rate using trapnets and 76.0% using gillnets) therefore water management regimes affect community structure in the Ottawa River. Littoral zone benthivores were significantly lower in abundance (P<0.001) or absent in winter reservoirs whereas the abundance of planktivores or species that were planktivorous at young ages were significantly greater than unimpounded river reaches. Growth, condition and mortality of did not vary among reach types except smallmouth bass were in better condition in winter reservoirs than unimpounded reaches. Lake sturgeon recruitment was impaired in run-of-the-river reaches whereas recruitment for other species that spawn in fast water were not affected.
Introduction

North American rivers have been exploited for centuries, initially as a means of transportation for exploring new lands and later for the movement of goods (e.g. furs) to market. River alterations commenced when they were used as a means to transport materials such as timber downstream to mills and/or markets; dams were essential to store excess water during peak flows and provide water during periods of low flow with chutes constructed to circumvent rapids. The complexity and size of dams increased over time. Currently, the United States for example, has more than 5000 large (> 15 m foundation to crest) dams, or approximately 58 per 100,000 km$^2$ of land area. Canada, on the other hand, has over 700 large dams or approximately 7.5 per 100,000 km$^2$ of land area (Pringle et al. 2000). The most suitable sites have now been developed in Canada (Baxter and Glaude 1980; Dynesius and Nilsson 1994; Rosenberg et al. 1995; 1997) although further development potential still exists in remote northern rivers (Rosenberg et al. 1995).

Dams are designed and managed to reduce flow downstream variability (i.e., provide water when required and reduce peak flows hence control flooding) by increasing water level fluctuations in upstream reservoirs (Baxter and Glaude 1980; Nilsson and Berggren 2000). As such, many rivers have been transformed into a series of storage reservoirs and run-of-the-river impoundments (Nilsson and Berggren 2000), producing increasingly lotic – and decreasingly lentic - systems (Friedl and Wuest 2002). Because a major impact of dams is the alteration of the natural regime (Poff et al. 1997), a common
consequence is the displacement of fluvial specialists, species restricted to flowing water habitats (Kinsolving and Bain 1993), by habitat generalists (Poff et al. 1997; Galat and Zweimüller 2001; Pegg and Pierce 2002; Černý et al. 2003; Kinsolving and Bain 1993). Fish community complexity downstream of dams is reduced due to the unnatural flow fluctuations that are produced (Bain et al. 1988) although a partial recovery of the community, specifically fluvial specialists, can occur as the effects of the dam are dissipated (Kinsolving and Bain 1993). While community structure in two large rivers was related to flow regimes, human alterations appeared to have a stronger influence on the fish communities (Pegg and Pierce 2002).

Many other factors attributed to dams and their operations in addition to altered flow regime affects the aquatic ecosystem. The physiochemical properties of water within a river system may be altered including dissolved gas supersaturation (Baxter and Glaude 1980; Crunkilton et al. 1980; Weitkamp and Katz 1980; Olmsted and Bolin 1996), anoxia (Olmsted and Bolin 1996), elevated hydrogen sulphide (Baxter and Glaude 1980), increased turbidity (Liu and Yu 1992), increased nutrient status (Liu and Yu 1992; Zhong and Power 1996), and sediment loading (Baxter and Glaude 1980; Liu and Yi 1992; Zhong and Power 1996). Dams, which act as barriers, fragment or isolate fish populations by eliminating connectivity between reaches and/or rivers (Auer 1996; Bruch 1998; Baker and Borgeson 1999; Bevelhimer 2002). Isolated populations may be restricted to areas that no longer provide suitable habitat for all life stages of the species (Beamesderfer 1988) and therefore are subjected to greater extirpation risk, as circumstances inducing high mortality or low reproduction cannot be offset by
immigration (Winston et al. 1991). Anadromous species are generally adversely affected by barriers (Welcomme et al. 1989; Poddubny and Galat 1995) and are often absent in sections upstream of dams (Reyes-Gavilán et al. 1996). Habitat is altered in both the location and upstream of dams which may include flooding of natural rapids that may have traditionally been used for spawning (Edwards et al. 1989; Zhong and Power 1996; Auer 1999; Nilsson and Berggren 2000). Reservoirs may undergo water drawdowns during the winter months exposing extensive areas and reducing aquatic macroinvertebrates density and diversity (Currier 1954; Fillion 1967; Fisher and LaVoy 1972; Hunt and Jones 1972; Benson 1973; Trotzky and Gregory 1974; McAfee 1980; Blinn et al. 1995; Prus et al. 1999; Richardson et al. 2002). In contrast, density and biomass of zooplankton and phytoplankton generally increase when rivers are regulated (Pinel-Alloul et al. 1982; Lui and Yu 1992) and are rarely directly affected by water level fluctuations (McAfee 1980; Ploskey 1986). As a result, impoundments generally become autotrophic (Cortes et al. 2002). Unsurprisingly, dams have been implicated as major factors in the decline of many freshwater species (Richter et al. 1997).

Most studies of the impacts of dams on fish communities have inferred these effects by comparing communities in dammed versus undammed rivers (e.g. Bain et al. 1988; Kinsolving and Bain 1993; Gehrke and Harris 2001; Herbert et al. 2003) or before and after dam construction or flow modification (e.g. Travernicheck et al. 1995; Cerny et al. 2003). Another experimental approach is within-river comparison, in which reaches subject to different flow regimes are compared. While studies on systems as such have been conducted (e.g. Kinsolving and Bain 1993; Pegg and Pierce 2002) few of this design
have been conducted on large river systems (Pegg and Pierce 2002). Here we compare abundance and community structure of select large-bodied fish among reaches in a large river operated under different management regimes: unimpounded, winter reservoirs, and run-of-the-river in the Ottawa River. We examine variation in several endpoints (relative abundance, growth, recruitment, mortality, and condition) and assess the extent to which variation in fish community structure among reaches can be attributed to life history characteristics.

**Methods**

**Study site**

The Ottawa River is a large (in places 3 km wide, maximum depth 100 m) waterbody with a watershed of over 146,000 km² and a mean annual flow of 1,968 m³/s (Telmer 1996). The study was conducted in seven Ottawa River reaches (Figure IV - 1; Table IV - 1) including: three unimpounded reaches (Lac Coulonge, Lower Allumette Lake, Upper Allumette Lake); two run-of-the-river reaches (Lac Deschênes and Lac des Chats); and two reaches managed as winter reservoirs (Holden Lake and Lac la Cave).

**Run-of-the-river**

Run-of-the-river systems are water management operations that pass water as it enters the impoundment (i.e., inflows equal outflows). There is generally limited to no storage
capacity in the headponds (water above dam) within run-of-the-river systems and therefore water is passed primarily through the generating station or through sluice gates in periods of excessive flows; therefore, upstream water management practices can influence flows released from a run-of-the-river system. No extensive flooding of the terrestrial environment occurred during the creation of the impoundment (at least on the Ottawa River (Haxton and Chubbuck 2002)) and therefore habitat within the reaches was not extensively altered. Changes to habitat may have occurred since impoundment due to shoreline development or log drives but these would not be restricted to run-of-the-river systems. Under this management regime, alterations to fish habitat are expected to be minimal except for changes that occurred at the site of the dam, and changes that occur due to varying flows immediately downstream of a hydroelectric facility.

**Winter Reservoirs**

River reaches that are managed as winter reservoirs generally support large dams, have had extensive terrestrial flooding resulting from the construction of the dam, and are subjected to extensive water drawdowns from January until March. Water drawn during the winter months provides suitable flows for energy production during periods of low flow; in addition, these reservoirs provide storage capacity during the periods of high flow (e.g. freshet), which aids in flood prevention in downstream areas. Reservoir water levels in this study are drawn down as much as 4.0 m, de-watering extensive areas (e.g. Holden Lake 1053 ha; Lac la Cave 459 ha; Haxton unpublished data) during the winter months.
Unimpounded reaches

Unimpounded reaches have not undergone extensive flooding; natural rapids exist within the reaches which generally define the extent of the reach; and water is not impeded by a man-made barrier. Flows are controlled by a series of dams upstream and therefore are altered from a natural flow regime; flows are greater in winter post dam construction than pre-dam conditions, and significantly reduced during the freshet period (Figure IV - 2).

Predicted responses

If extensive dewatering reduces benthic invertebrate abundance in winter reservoirs, as has been shown in other systems (Currier 1954; Fillion 1967; Fisher and LaVoy 1972; Hunt and Jones 1972; Benson 1973; Trotzky and Gregory 1974; McAfee 1980; Blinn et al. 1995; Prus et al. 1999; Richardson et al. 2002), and benthivores are limited by prey availability (e.g. Chiasson et al. 1997), then benthivore abundance and growth should be lower in winter reservoir reaches compared to unimpounded reaches. By contrast, if in winter reservoirs plankton abundance is higher compared to unimpounded reaches, then so too should be the relative abundance and growth of planktivorous species or those that are planktivorous at an early life stage. The main impact in run-of-the-river reaches should be spawning success of species that spawn in fast water due to the operations of dams. Abundance of fast water spawners, generally migratory species, should be lower than unimpounded reaches whereas growth, condition and mortality should be consistent.
Species that are nest spawners or spawn on flooded vegetation should not be affected by barriers and therefore should have similar life history traits as those in unimpounded reaches. Life history traits of these species should not vary from unimpounded reaches as prey should not be limited.

**Sampling techniques**

We examined variation in the abundance, growth, recruitment, mortality and condition of eleven species (Table 2): lake sturgeon (*Acipenser fulvescens*), northern pike (*Esox lucius*), walleye (*Sander vitreus*), sauger (*Sander canadense*), smallmouth bass (*Micropterus salmoides*), pumpkinseed (*Lepomis gibbosus*), channel catfish (*Ictalurus punctatus*), brown bullhead (*Ameiurus nebulosus*), shorthead redhorse (*Moxostoma macrolepidotum*), silver redhorse (*Moxostoma anisurum*) and common white sucker (*Catostomus commersoni*).

Nearshore Community Index Netting (NSCIN) and Fall Walleye Index Netting (FWIN) were used to sample fish communities. NSCIN used randomly set trapnets from early August through early October (water temperature > 13°C; Stirling 1999). Unbaited trapnets, 1.8 m trapnets with 36.5 m leads and 2.4 m trapnets with 61.0 m leads (3.8 cm mesh) were used. Water depths were restricted to 1.7 - 3.5 m for the 1.8 m trapnets and 2.3 - 4.7 m for the 2.4 m trapnets. The shoreline of each reach was partitioned into 2000 m sections, numbered and then randomly chosen. Trapnets were set at a random locations perpendicular to the shore at least 500 m apart for a 24 hr period. At the end of the
sampling period, each net was lifted, all fish were identified, enumerated, measured, weighed, an ageing structure obtained for select species and then released; nets were then reset in another random location. Attempts were made to sample each reach with at least 40 net sets. No sampling sites were reused if possible; if not possible, a minimum of four days must have lapsed from the previous netting before the sampling site was reused (two sites were reused in this study). NSCIN was conducted from 1998 – 2004.

FWIN uses randomly set monofilament gillnets in the fall when surface water temperatures are between 10°C and 15°C. Gillnets had eight panels of different (25 – 152 mm stretched) mesh and were set perpendicular to the shore. Nets were randomly set in two depth strata, 2 to 5 m and 5 to 15 m, with each depth stratum sampled equally (Morgan 2002). Sample sites were determined by partitioning the reach into 1 km x 1 km numbered quadrats and randomly selecting a quadrat. Nets were fished overnight and picked up early the following day (generally an 18 – 24 hour net set). FWIN is a lethal sampling technique for most species, with the exception of lake sturgeon and channel catfish. Nets were then reset in another random location. FWINs were conducted from 1998 – 2003.

Due to netting gear selectivity (netting techniques have different success at sampling species, e.g. smallmouth bass are not as vulnerable to gillnets as trapnets therefore will be underrepresented in gillnet samples), analysis was conducted using NSCIN catch data on channel catfish, smallmouth bass, lake sturgeon, *Moxostoma* sp. and common white sucker: whereas analysis was conducted using FWIN catch data on walleye, sauger,
northern pike, lake sturgeon and common white sucker. In what follows, shorthead redhorse and silver redhorse samples were combined due to suspected identification problems by field crews.

Catch-per-unit-effort (CUE) - number of fish caught per net set (generally over a 24 hour period), was calculated for each net in a reach. Total length (to the nearest mm), fork length and weight (to the nearest 10 g; sturgeon to the nearest 100 g) were measured for all fish. Ageing structures extracted include: a small section of the pectoral ray from lake sturgeon; otoliths from walleye in the FWIN sample; scales were taken from northern pike, smallmouth bass and sauger. Scales from NSCIN samples were all aged by the same lab (Aqua-Tech Services, Westport, ON), whereas otoliths and scale samples from FWIN samples were aged at Ontario Ministry of Natural Resource’s ageing lab in Thunder Bay. All lake sturgeon were aged following Wilson (1987); ages were estimated independently by three assessors. Intraclass correlation coefficient among assessors was 0.07 (i.e., there was little agreement among assessors on ages). The final age assessed for each individual was determined by the lead author. Attributes and/or aging structures were not obtained for *Moxostoma* sp., common white sucker, brown bullhead, channel catfish and pumpkinseed.

Spawning lake sturgeon were assessed over several years in different river reaches (Holden Lake 2006; Lower Allumette Lake 2001 and 2004; Lac Deschênes 2001, 2003 and 2004). Lake sturgeon were sampled by gillnets set for short durations in areas of congregations (Haxton 2006). Lengths at age data from these surveys were used in these
analyses to increase the sample size of lake sturgeon, especially from run-of-the-river and winter reservoir reaches, exclusively for growth analysis. Sturgeon samples from different years of the same spawning shoal were pooled for these analyses.

Instantaneous mortality \( (z) \) was calculated from the slope of the line on the descending limb of the frequency of the age class on a logarithmic scale versus the age (Ricker 1975; Lester et al. 1991). The slope was determined from the greatest represented age class to the least represented (where \( n > 5 \); Van den Avyle 1993). Annual mortality \( (A) \) was determined by \( A = 1 - e^{-z} \) (Ricker 1975). We used a bootstrap with replacement to determine variation in \( A \). With a sample size \( n \) individuals, we obtained a random sample of \( n \) individuals with replacement, estimated \( A \), and then calculated CIs based on the distribution of this estimated parameter over the 1000 trials. Annual mortality was calculated for each species for each reach using the technique that was most selective for that species. Samples were pooled i) for reaches where the same technique was conducted in consecutive years; ii) by water management regime for species when samples size was inadequate by reach within regime to calculate \( A \).

Recruitment was assessed by constructing cumulative total length frequency diagrams for each species based on water management regime. Total length frequencies were determined on 5 cm or 10 cm intervals. Curves that were similar for a species suggest that recruitment among different water management regimes is comparable.
Statistical analysis

To examine the influence of sampling technique and water management regime on each species, we used Poisson regression treating net stations as observations, CUE for each species as the dependent variable, and netting technique (two levels, FWIN or NSCIN) and management regime (3 levels) as independent variables. Discriminant function analysis (DFA) was conducted to determine if community structures could be discriminated based on water management regime using catch data for each net. Discriminant function analysis was run separately for each netting technique; catch data for all species for each net were used as the predictors; water management regime was used as the grouping variable based on equal priors. Neural network was also conducted on the catch data for each netting technique for similar reasons as for DFA. The data was randomly separated into training and testing; 70% was allocated to training and 30% to testing on each run. Monte-Carlo was conducted for 1000 iterations. Acceptable level of absolute difference was set at 0.5.

A hierarchical cluster analysis was conducted to determine how fish species grouped based on their CUEs within water management regimes. Catch-per-unit-effort was averaged for each species within each water management regimes using the netting technique selective for that species (both FWIN and NSCIN CUEs were used for lake sturgeon and common white sucker). Catch-per-unit-efforts were standardized for each species among water management regimes and Euclidean distances were calculated.
A nested ANOVA was conducted on the CUE of all species (individually) among water management regimes using the different assessment techniques; river reach was used as the nested factor. CUE for each net within a water management regime was used in this analysis. CUE data were transformed \((\log_{10}(\text{CUE}+1))\) to meet the assumptions of an ANOVA. Bonferroni pairwise comparisons were conducted when a significant difference was determined. Poisson regression was used as an alternate statistical technique when the assumptions of an ANOVA could not be satisfied; river reach was used as a nested factor in the Poisson regression. When a significant difference was detected, Poisson regression was re-run comparing water management regimes to unimpounded reaches since we are really only interested in these comparisons (i.e., run-of-the-river vs. winter reservoirs is not necessarily the topic of interest). To control for experiment wise error, the critical value is divided by the number of cases (always 2 in this study); therefore significance is determined at \(P = 0.025\).

To assess growth, Generalized Linear Models (GLM) were fitted with \(\log_{10}\) total length as the dependent, \(\log_{10}\) age as the covariate and water management regime as a factor. Generalized Linear Models nesting reach within water management regime could not be conducted due to insufficient samples in some reaches therefore GLMs were fitted with \(\log_{10}\) total length as the dependent variable, \(\log_{10}\) age as the independent variable and river reach as a factor for each water management regime to assess growth within water management regime. A cluster analysis was conducted to determine how species grouped based on growth. Slopes from length at age relationships were standardized for each species among water management regimes and Euclidean distances were calculated.
Generalized Linear Models were conducted to assess differences in mortality rates ($A$) for each species among water management regimes. Age was used as a covariate, water management regime as a factor and logarithm of the age class frequency as the dependent.

Statistical analysis was conducted using SYSTAT 11 (SYSTAT Software Inc., Richmond, CA); Poisson regressions were conducted using S-PLUS 6.2 (Insightful Corporation Seattle, Washington). Significance was determined at $P = 0.05$.

**Results**

Over the seven reaches, FWIN (NSCIN) sampled 30 (24) species and 3,805 (20,791) individuals (Appendix B). Jackknifed misclassification rates using discriminant function analysis for discriminating community structure among water management regimes were 26% using NSCIN and 24% using FWIN (Figures IV - 3 and IV - 4). Correct classification rates based on neural network were 79% using NSCIN and 76% using FWIN (Table IV - 4)

Catch-per-unit-effort depended on netting technique for common white sucker (Poisson regression d.f. = 2, 642 $P<0.001$), *Moxostoma* sp. (Poisson regression d.f. = 2, 642 $P<0.001$), brown bullhead (Poisson regression d.f. = 2, 642 $P = 0.017$), channel catfish (Poisson regression d.f. = 2, 642 $P<0.017$) and pumpkinseed (Poisson regression d.f. = 2,
Sturgeon spawning assessment sampled 279 individuals from three separate reaches: Lac Deschênes (n = 73); Lower Allumette Lake (n = 176); and Holden Lake (n = 30).

Catch-per-unit-effort

Hierarchical clustering of species based on average CUE for each water management regime showed three major clusters (i) walleye, northern pike, sauger, common white sucker, smallmouth bass, and *Moxostoma* sp.; and (ii) lake sturgeon, channel catfish, brown bullhead; and (c) pumpkinseed (Figure IV - 5). Species in the first cluster were generally most abundant in winter reservoirs and least abundant in run-of-the-river reaches (Figure VI - 6).

Catch-per-unit-effort was significantly different among water management regimes for northern pike (Poisson regression d.f. = 2, 241 P = 0.001), walleye (ANOVA: $F_{2,237} = 19.04 P<0.001$), sauger (Poisson regression; d.f. = 2, 241 $P < 0.001$), smallmouth bass (Poisson regression d.f. = 2, 401 $P < 0.001$) and common white sucker (Poisson Regression d.f. = 2, 401 $P < 0.001$) whereas *Moxostoma* sp. CUE was not (ANOVA $F_{2,401} = 1.77 P=0.171$; Figure IV - 6). Walleye, sauger, smallmouth bass and common
white sucker CUE were significantly greater in winter reservoirs than unimpounded
reaches (Bonferroni pairwise comparison \( P<0.05 \); Poisson regression d.f. = 1, 187,
\( P<0.001 \); Poisson regression d.f. = 1,280 \( P < 0.001 \); Poisson regression, d.f. = 1, 187,
\( P < 0.001 \) respectively); northern pike, walleye, smallmouth bass, common white sucker
CUE were significantly greater in unimpounded reaches than run-of-the-river reaches
(Poisson regression d.f. = 1, 188 \( P = 0.003 \); Bonferroni pairwise comparison \( P<0.017 \);
Poisson regression d.f. = 1, 338 \( P<0.001 \); Poisson regression, d.f. = 1,188 \( P = 0.021 \)
respectively) whereas sauger CUE was significantly greater in run-of-the-river than
unimpounded reaches (Poisson regression d.f. = 1,188 \( P<0.001 \)).

Species in the second major cluster were most abundant in unimpounded reaches and
absent or in very low relative abundance in winter reservoirs (Figure IV - 7). Lake
sturgeon (FWIN: Poisson regression d.f = 2, 241 \( P < 0.001 \) and NSCIN: Poisson
regression d.f. = 2, 401 \( P < 0.001 \)), channel catfish (ANOVA: \( F_{2,397} = 135.3 \ P<0.001 \)),
brown bullhead (Poisson Regression d.f. = 2, 401 \( P < 0.001 \)) and pumpkinseed (Poisson
regression d.f. = 2, 401 \( P < 0.001 \)) CUE were significantly different among water
management regimes. Channel catfish and brown bullhead CUE were significantly
greater in unimpounded reaches than winter reservoirs (Bonferroni pairwise comparison
\( P<0.001 \); Poisson regression d.f. = 1,280, \( P<0.001 \) respectively); no lake sturgeon or
pumpkinseed were sampled in winter reservoirs. Lake sturgeon and brown bullhead
(Poisson regression d.f. = 1,338 \( P<0.001 \)) CUE were significantly greater in
unimpounded reaches than run-of-the-river; whereas pumpkinseed were significantly
greater in run-of-the-river than unimpounded reaches (Poisson regression d.f. = 1,338 \( P < 0.001 \)).

Variation in CUE was greater in river reaches within water management regimes than among water management regimes for northern pike whereas it was opposite for all other species (Table IV - 5).

**Growth**

Hierarchical clustering of species based on growth (slope of length at age relationship) for each water management regime showed two major clusters (i) walleye, northern pike, sauger, and smallmouth bass and (ii) lake sturgeon (Figure IV - 8).

Northern pike, walleye, sauger and smallmouth bass growth did not vary significantly (Figure 9; GLM \( F_{1,510} = 3.07 \ P = 0.08 \); GLM \( F_{2,1897} = 2.91 \ P = 0.055 \); GLM \( F_{1,289} = 0.17 \ P = 0.679 \); GLM \( F_{2,1491} = 2.73 \ P = 0.066 \) respectively) among water management regimes. However, walleye, sauger and smallmouth bass growth varied significantly among reaches within unimpounded reaches but not within other water management regimes (Table IV - 6). While the slopes of lake sturgeon length at age were not significantly different among water management regimes (GLM \( F_{2,522} = 1.67 \ P = 0.19 \)), the intercepts were significantly different (GLM \( F_{2,522} = 4.73 \ P = 0.009 \)). Intercepts of unimpounded reaches were significantly less than winter reservoirs and run-of-the-river

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reaches (Bonferroni pairwise comparison $P < 0.05$). There was no difference between winter reservoir and run-of-the-river reaches (Bonferroni pairwise comparison $P = 0.88$).

**Fish Condition**

Condition did not vary significantly among water management regimes for northern pike (Figure 9; GLM $F_{2,567} = 0 P = 0.716$) or walleye (GLM $F_{2,1495} = 0.47 P = 0.624$).

Condition varied significantly among water management regimes for sauger (GLM $F_{2,295} = 12.77 P < 0.001$), however, Bonferroni pairwise comparison could not detect a difference in condition among water management regimes ($P > 0.05$). Condition varied significantly for smallmouth bass (GLM $F_{2,1499} = 50.51 P < 0.001$); condition of smallmouth bass in winter reservoirs was greater than unimpounded and run-of-the-river reaches ($P < 0.001$) and greater in run-of-the-river reaches than unimpounded reaches ($P < 0.001$). Condition varied significantly among river reaches for: northern pike within unimpounded and winter reservoirs; sauger within unimpounded reaches; and smallmouth bass within run of the river reaches (Table IV - 6).

**Mortality**

Mortality estimates varied by species among water management regimes (Table IV - 7), however, this variation was not statistically significant for northern pike (GLM $F_{2,11} = 0.17 P = 0.845$), walleye (GLM $F_{2,17} = 3.56 P = 0.051$), sauger (GLM $F_{2,15} = 0.97 P = 0.401$), or smallmouth bass (GLM $F_{2,18} = 1.23 P = 0.316$).
Recruitment

Based on size frequency distribution, northern pike and walleye recruitment was comparable among water management regimes (Figures IV - 10a and d respectively). Small sauger were more prevalent in run-of-the-river and winter reservoirs than unimpounded reaches (Figure IV - 10b) suggesting good recruitment. Small smallmouth bass were more prevalent in run-of-the-river reaches than winter reservoirs and natural reaches (Figure IV - 10c). Few small lake sturgeon were sampled in run-of-the-river reaches, the distribution was skewed to larger fish (Figure IV - 10e) suggesting recruitment issues. No lake sturgeon were sampled in winter reservoirs during index netting also suggesting recruitment problems.

Discussion

Considerable variation in large-bodied fish community structure exists between reaches subject to different management regimes in the Ottawa River. As predicted, relative abundance of some benthivores were significantly lower in winter reservoirs, however, not all benthivores were affected. Littoral zone benthivores were present in only very low abundances in winter reservoirs despite the preponderance of certain species (e.g. channel catfish) run-of-the-river reaches. Other metrics for these species could not be assessed due to the small sample size from these reaches. *Moxostoma sp.* and common white suckers were abundant in these reaches contradicting our predictions. In contrast,
piscivores or species that were planktivores at younger life stages increased substantially within winter reservoirs supporting our predictions. Northern pike, walleye, sauger condition and growth showed little among-regime variation but considerable within-regime (among reach) variation, suggesting that water management is of lesser importance than more local factors for growth and condition of these species. Smallmouth bass condition varied among water management regimes; their condition was greater in winter reservoirs compared to run-of-the-river and unimpounded reaches supporting the hypothesis that habitat generalists fair better in altered systems. Our prediction of reduced abundance of species that spawn in fast water in run-of-the-river reaches was supported by lake sturgeon but not by any of the other species. However, growth, condition and mortality predictions were supported for all species. Our results also suggest that recruitment is limited for sauger in unimpounded river reaches, for lake sturgeon in winter reservoirs and run-of-the-river reaches and in contrast, favourable for smallmouth bass in winter reservoirs.

Littoral feeding benthivores (lake sturgeon, channel catfish, brown bullhead and pumpkinseed) were very low in abundance in winter reservoirs whereas other benthivores (common white sucker and *Moxostoma* sp.) were abundant. Channel catfish are near the northern extent of their natural range (Scott and Crossman 1973; Mandrak and Crossman 1992) which may be their limiting factor; however they are found in the Mattawa River, a tributary in the upper end of Holden Lake (Stephen Belfry, Ministry of Natural Resources, North Bay pers. comm.). Juvenile catfish, juvenile lake sturgeon (Ecologistics Limited 1987; Kempinger 1988; Holtgren and Auer 2004) and pumpkinseed (Bain et al.
1988; Vila-Gispert and Moreno-Amich 1998) feed in the littoral zone, the area most affected by a winter drawdown. Dewatering can impair the nursery function of these nearshore waters (Scheidegger and Bain 1995). Impacts on nursery areas or prey abundance will affect benthivore survival and therefore recruitment (Kempinger 1988; Poddubny and Galat 1995; Chiasson et al. 1997; Snyder and Minshall 2005).

All species that feed on macroinvertebrates were grouped as benthivores *a priori* in this study. This proved to be incorrect as macroinvertebrate abundance would be most affected in the areas subjected to dewatering; as such, benthivores that feed in deeper waters are less likely to be affected. Common white sucker have wide flexibility in the zone (i.e., littoral zone, epilimnion, metalimnion and hypolimnion) in which they feed (Logan et al. 1991) or what they consume (e.g. zooplankton; Saint-Jacques et al. 2000). Limited literature exists on the life history ecology of *Moxostoma* sp.; these species may be as robust as common white suckers in fulfilling their nutrient requirements and therefore would not necessarily be affected by a winter drawdown and reduction of prey abundance in shallow waters. Therefore, benthivores were further segmented based on niche *a posteriori* to help understand the effects of a winter drawdown.

Planktivorous (phytoplankton or zooplankton) or piscivorous species would not be affected by the loss of benthic invertebrates. Macroinvertebrates are minor diet items for young-of-the-year sauger (Nelson 1968) and walleye (Jackson et al. 1992) as they feed primarily on zooplankton prior to becoming piscivorous, although walleye are described as opportunistic and will feed on invertebrates (Ryder and Kerr 1978). Previous walleye
and sauger diet studies in the Ottawa River showed a preference for cyprinids (Osterberg 1978). Young-of-the-year bass prey on insects but also feed on zooplankton (Stephenson and Momot 1991). Young-of-the-year northern pike initially feed on zooplankton and macroinvertebrates (Bry 1996) and then become primarily piscivorous (Stephenson and Momot 1991; Casselman and Lewis 1996). Older northern pike are opportunistic predators and will feed on macroinvertebrates if prey is scarce (Casselman 1996).

Planktivorous fish generally benefit from the construction of a reservoir (Nelson 1965; Welcomme et al. 1989) which is consistent with observations in this study. Relative abundance of walleye, sauger and northern pike was greater in winter reservoirs than natural reaches whereas northern pike abundance in run-of-the-river and winter reservoirs were similar. Sauger abundance have been reported to decline after impoundment whereas walleye abundance increase (Nelson and Walburg 1977) although sauger are considered being the best adapted of the percids to high fluctuating water regimes (Jeffrey and Edds 1999). Increased walleye abundance in winter reservoirs may be an artefact of fishing pressure; downstream reaches are closer to population centres and receive greater fishing pressure. However, this is unlikely to be true of sauger as walleye are the preferred species for anglers in the Ottawa River (Ontario Ministry of Natural Resources and Gouvernement du Quebec Faune et Parcs 1999).

Lake sturgeon abundance was low in run-of-the-river and winter reservoir reaches. Size distribution in run-of-the-river reaches were skewed to larger individuals compared to unimpounded reaches, indicating reduced recruitment. This is consistent with findings for
other species of sturgeon (Beamesderfer et al. 1995; Paragamian et al. 2005). For example, while white sturgeon (*Acipenser transmontanus*) spawning was documented downstream of hydroelectric dam, there was limited recruitment. Juveniles of hatchery origin survived in this reach (Paragamian et al. 2005) thereby suggesting that survival of eggs or larvae during drift was the bottleneck. Some other fast water spawners (walleye and common white suckers) also showed reduced abundance in run-of-the-river reaches, while others, especially *Moxostoma* sp. and sauger exhibited greater abundance. While all of these species spawn in fast water, several may also spawn on wave swept shorelines (e.g. walleye; Jennings et al. 1996) and hence are classified as habitat generalists (Table 2). Spawning requirements for these species do not appear as stringent as for lake sturgeon, as they have been observed or documented in smaller tributaries and other areas with minor flows, whereas lake sturgeon have only been observed in the main river channel.

This study adds to a growing body of evidence, based on a range of different experimental designs, that dam operations have substantial effects on fish community structure and abundance, whether in small or large river systems. Winter reservoirs showed reduced carrying capacity for littoral zone feeding benthivore species but increased carrying capacity for planktivores (at least for species that were planktivorous for a portion of their life). Insofar as reduced abundance of benthivores in winter reservoirs relates to reduced benthic invertebrate abundance in areas dewatered during winter drawdown, it is unlikely that significant mitigation of these impacts can be effected with drastic changes to operating regimes. Likewise, run-of-the-river reaches
showed reduced recruitment for lake sturgeon, a fluvial dependent species. Such changes to fish communities can have positive socioeconomic effects (i.e., increase the abundance of game fish thereby attracting more anglers) however, and conversely, these changes can adversely affect biodiversity and native fish communities. Waterpower is and will continue to be an important source of energy. Clearly defined fisheries management objectives should be established prior to new developments and/or on existing operations to ameliorate the impacts on native fish communities.

Conclusions

Water management regime can affect community structure as demonstrated by DFA and neural network. Most notable were littoral zone benthivores in winter reservoirs whereas planktivores (or those species that were planktivorous at early life stages) were abundant. Some planktivores demonstrated increased growth which both could be related to prey availability. Fragmentation or reduced recruitment seemed to affect lake sturgeon in run-of-the-river reaches whereas recruitment did not appear impaired for other fast water spawners. Base flows associated with a large river may be suitable for these fast water spawners. Fish abundance was generally lower in run-of-the-river reaches which may be related to stable water levels throughout the year. Management efforts could possibly address recruitment problems in run-of-the-river reaches (e.g. spawning shoal rehabilitation and release of appropriate flows during spawning periods) but drastic changes to operating regime would be required in winter reservoirs to increase benthos productivity. Failure to change from winter drawdowns would suggest that these reaches
should not be managed for benthivores (i.e., rehabilitative efforts such as in run-of-the-river reaches or stocking should not be employed as they will be wasted). Future hydro-electric development on rivers should be cognisant of water management regimes and the effects they may have on inhabiting native species.

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### Table IV. Characteristics of Ottawa River reaches including water management regime, water level fluctuation, area flooded as a result of impoundment.

<table>
<thead>
<tr>
<th>Reach</th>
<th>Length (km)</th>
<th>Surface Area (ha)</th>
<th>Mean Depth (m)</th>
<th>Mean % littoral zone</th>
<th>Rapids Present</th>
<th>Dam Name</th>
<th>Wave-controlled</th>
<th>Dam Name</th>
<th>Wave-controlled</th>
<th>Condition</th>
<th>Fluctuation (m)</th>
<th>Water Management</th>
<th>Area Flooded (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac Deschênes</td>
<td>52.8</td>
<td>10,900</td>
<td>5.2</td>
<td>62.5</td>
<td>Yes</td>
<td>Chaudière Falls</td>
<td>1880's</td>
<td>0.9</td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Lac des Chats</td>
<td>40.0</td>
<td>7,513</td>
<td>4.9</td>
<td>61.4</td>
<td>No</td>
<td>Chats Falls</td>
<td>1932</td>
<td>0.34</td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
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<td>Lac Coulonge</td>
<td>18.1</td>
<td>2,888</td>
<td>3.8</td>
<td>76.0</td>
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<td>G.S.</td>
<td>n/a</td>
<td>n/a</td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Lower</td>
<td>22.3</td>
<td>4,613</td>
<td>2.9</td>
<td>81.5</td>
<td>Yes</td>
<td>G.S.</td>
<td>n/a</td>
<td>n/a</td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>n/a</td>
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<tr>
<td>Upper</td>
<td>76.9</td>
<td>13,212</td>
<td>2.9</td>
<td>81.5</td>
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<td>n/a</td>
<td>Run-of-the-river</td>
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<td>n/a</td>
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</tr>
<tr>
<td>Allumette Lake</td>
<td>90.0</td>
<td>7,952</td>
<td>10.1</td>
<td>54.5</td>
<td>Yes</td>
<td>G.S.</td>
<td>1950</td>
<td>2.3</td>
<td>Reservoir - winter drawdown</td>
<td>45.6</td>
<td>3.0</td>
<td>4.1</td>
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<td>Holden Lake</td>
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<td>19.7</td>
<td>24.5</td>
<td>No</td>
<td>G.S.</td>
<td>1952</td>
<td>3.3</td>
<td>Reservoir - winter drawdown</td>
<td>45.6</td>
<td>3.0</td>
<td>4.1</td>
<td>13.7</td>
</tr>
<tr>
<td>Lac la Cave</td>
<td>49.0</td>
<td>3,028</td>
<td>19.7</td>
<td>24.5</td>
<td>No</td>
<td>G.S.</td>
<td>1952</td>
<td>3.3</td>
<td>Reservoir - winter drawdown</td>
<td>45.6</td>
<td>3.0</td>
<td>4.1</td>
<td>13.7</td>
</tr>
<tr>
<td>*&lt; 5 m deep</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Run-of-the-river</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>
Table IV - 2. Selected life history characteristics of fish species examined in study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Characteristics</th>
<th>Trophic level</th>
<th>Macrohabitat</th>
<th>Reproductive guild</th>
<th>Migratory</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake sturgeon</td>
<td></td>
<td>benthivore</td>
<td>fluvial dependent</td>
<td>fast water - lithophi -</td>
<td>yes</td>
</tr>
<tr>
<td><em>Acipenser fulvescens</em></td>
<td></td>
<td></td>
<td></td>
<td>pelagophil</td>
<td></td>
</tr>
<tr>
<td>Northern pike</td>
<td></td>
<td>piscivore</td>
<td>generalist</td>
<td>fast water - flopped</td>
<td>no</td>
</tr>
<tr>
<td><em>Esox lucius</em></td>
<td></td>
<td></td>
<td></td>
<td>vegetation - phytophils</td>
<td></td>
</tr>
<tr>
<td>Walleye</td>
<td></td>
<td>piscivore</td>
<td>generalist</td>
<td>fast water -</td>
<td>yes</td>
</tr>
<tr>
<td><em>Sander vitreus</em></td>
<td></td>
<td></td>
<td></td>
<td>lithophi</td>
<td></td>
</tr>
<tr>
<td>Sauger</td>
<td></td>
<td>piscivore</td>
<td>generalist</td>
<td>fast water -</td>
<td>yes</td>
</tr>
<tr>
<td><em>Sander canadense</em></td>
<td></td>
<td></td>
<td></td>
<td>lithophi</td>
<td></td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td></td>
<td>piscivore</td>
<td>generalist</td>
<td>nest spawner -</td>
<td>no</td>
</tr>
<tr>
<td><em>Micropterus dolomieu</em></td>
<td></td>
<td></td>
<td></td>
<td>lithophi</td>
<td></td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td></td>
<td>benthivore</td>
<td>generalist</td>
<td>nest-spawner -</td>
<td>no</td>
</tr>
<tr>
<td><em>Lepomis gibbosus</em></td>
<td></td>
<td></td>
<td></td>
<td>polyphils</td>
<td></td>
</tr>
<tr>
<td>Channel catfish</td>
<td></td>
<td>benthivore</td>
<td>generalist</td>
<td>nest spawner -</td>
<td>no</td>
</tr>
<tr>
<td><em>Ictalurus punctatus</em></td>
<td></td>
<td>(juvenile)/</td>
<td></td>
<td>speleophils</td>
<td></td>
</tr>
<tr>
<td>Brown bullhead</td>
<td></td>
<td>benthivore</td>
<td>generalist</td>
<td>nest spawner -</td>
<td>no</td>
</tr>
<tr>
<td><em>Ameirurus nebulosus</em></td>
<td></td>
<td>(juvenile)/</td>
<td></td>
<td>speleophils</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>omnivore</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(adult)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Silver redhorse</td>
<td></td>
<td>benthivore</td>
<td>generalist</td>
<td>fast water -</td>
<td>yes</td>
</tr>
<tr>
<td><em>Moxostoma anisurum</em></td>
<td></td>
<td></td>
<td></td>
<td>lithophi</td>
<td></td>
</tr>
<tr>
<td>Shorthead redhorse</td>
<td></td>
<td>benthivore</td>
<td>generalist</td>
<td>fast water -</td>
<td>yes</td>
</tr>
<tr>
<td><em>Moxostoma macrolepidotum</em></td>
<td></td>
<td></td>
<td></td>
<td>lithophi</td>
<td></td>
</tr>
<tr>
<td>Common white sucker</td>
<td></td>
<td>benthivore/</td>
<td>generalist</td>
<td>fast water -</td>
<td>yes</td>
</tr>
<tr>
<td><em>Catostomus commersoni</em></td>
<td></td>
<td>planktvore</td>
<td></td>
<td>lithophi</td>
<td></td>
</tr>
</tbody>
</table>
Table IV - 3. Endpoints (Catch per unit effort (CUE-1), growth (2), condition (3) and mortality (4)) and sample size (n, number of sampled individuals, pooled over netting techniques) for each of the seven sampled Ottawa River reaches.

<table>
<thead>
<tr>
<th>Species</th>
<th>Lac la Cave</th>
<th>Holden Lake</th>
<th>Upper Allumette Lake</th>
<th>Lower Allumette Lake</th>
<th>Lac La Chou</th>
<th>Lac des Chats</th>
<th>Lac Deschênes</th>
</tr>
</thead>
<tbody>
<tr>
<td>lake sturgeon*</td>
<td>1(2)</td>
<td>1,2,3 (30)</td>
<td>1,2,3 (518)</td>
<td>1,2,3 (166)</td>
<td>1,2,3 (81)</td>
<td>1,3 (17)</td>
<td>1,2,3 (73)</td>
</tr>
<tr>
<td>northern pike</td>
<td>1,2,3,4</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (98)</td>
<td>1,2,3,4 (153)</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (87)</td>
<td>1,2,3,4 (43)</td>
</tr>
<tr>
<td>walleye</td>
<td>1,2,3,4</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (177)</td>
<td>1,2,3,4 (355)</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (123)</td>
<td>1,2,3,4 (46)</td>
</tr>
<tr>
<td>Sauger</td>
<td>1,2,3,4</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (68)</td>
<td>1,2,3,4 (72)</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (34)</td>
<td>1,2,3,4 (48)</td>
</tr>
<tr>
<td>pumpkinseed smallmouth bass</td>
<td>1,2,3,4</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (58)</td>
<td>1,2,3,4 (439)</td>
<td>1,2,3,4</td>
<td>1,2,3,4 (34)</td>
<td>1,2,3,4 (48)</td>
</tr>
<tr>
<td>channel catfish</td>
<td>1 (0)</td>
<td>1 (0)</td>
<td>1 (0) (101)</td>
<td>1 (79) (1127)</td>
<td>1 (79)</td>
<td>1 (79)</td>
<td>1 (367)</td>
</tr>
<tr>
<td>brown bullhead Moxostoma sp.</td>
<td>1 (0)</td>
<td>1 (2)</td>
<td>1 (6017) (277)</td>
<td>1 (3) (6017)</td>
<td>1 (140)</td>
<td>1 (3)</td>
<td>1 (188)</td>
</tr>
<tr>
<td>common white sucker</td>
<td>1 (52)</td>
<td>1 (132)</td>
<td>1 (163) (166)</td>
<td>1 (39) (166)</td>
<td>1 (188)</td>
<td>1 (22)</td>
<td>1 (102)</td>
</tr>
</tbody>
</table>

* sturgeon sample size includes individuals caught during spawning assessment
Table IV – 4. Neural network overall correct classification rates for testing and training runs with ± 1 S.D. (in parentheses) using NSCIN and FWIN data. Acceptable level of absolute difference was set at 0.5.

<table>
<thead>
<tr>
<th></th>
<th>NSCIN</th>
<th>FWIN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Testing</td>
<td>78.8 (4.7)</td>
<td>76.0 (2.5)</td>
</tr>
<tr>
<td>Training</td>
<td>72.2 (5.5)</td>
<td>68.2 (4.3)</td>
</tr>
</tbody>
</table>
Table IV - 5. Variation in species CUE in river reaches within water management regimes in comparison to variation among water management regimes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Measurement</th>
<th>Among water management regimes</th>
<th>Among reaches within water management regimes</th>
</tr>
</thead>
<tbody>
<tr>
<td>northern pike</td>
<td>Deviance</td>
<td>13.8</td>
<td>45.0</td>
</tr>
<tr>
<td>Walleye</td>
<td>Mean-square</td>
<td>2.9</td>
<td>2.3</td>
</tr>
<tr>
<td>Sauger</td>
<td>Deviance</td>
<td>99.0</td>
<td>20.0</td>
</tr>
<tr>
<td>smallmouth bass</td>
<td>Deviance</td>
<td>296.7</td>
<td>126.2</td>
</tr>
<tr>
<td><em>Moxostoma</em> sp.</td>
<td>Mean-square</td>
<td>2.3</td>
<td>0.5</td>
</tr>
<tr>
<td>common white sucker</td>
<td>Deviance</td>
<td>69.0</td>
<td>22.5</td>
</tr>
<tr>
<td>brown bullhead</td>
<td>Deviance</td>
<td>2356.3</td>
<td>1755.8</td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td>Deviance</td>
<td>385.4</td>
<td>279.6</td>
</tr>
</tbody>
</table>
Table IV - 6. Variation in growth rate and condition (weight/length) among river reaches within water management regimes for northern pike, walleye, sauger and smallmouth bass based on generalized linear model.

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameter</th>
<th>Unimpounded</th>
<th>Run of river</th>
<th>Winter reservoirs</th>
</tr>
</thead>
<tbody>
<tr>
<td>northern pike</td>
<td>growth</td>
<td>$F_{2,272} = 1.21$</td>
<td>$F_{1,102} = 2.01$</td>
<td>$F_{1,136} = 0.64$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.299$</td>
<td>$P = 0.159$</td>
<td>$P = 0.424$</td>
</tr>
<tr>
<td></td>
<td>condition</td>
<td>$F_{2,275} = 8.69$</td>
<td>$F_{1,148} = 0.32$</td>
<td>$F_{1,136} = 5.87$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.576$</td>
<td>$P = 0.017$</td>
</tr>
<tr>
<td>Walleye</td>
<td>growth</td>
<td>$F_{2,310} = 7.71$</td>
<td>$F_{1,116} = 0.74$</td>
<td>$F_{1,471} = 0.25$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.391$</td>
<td>$P = 0.616$</td>
</tr>
<tr>
<td></td>
<td>condition</td>
<td>$F_{2,964} = 0.26$</td>
<td>$F_{1,99} = 1.14$</td>
<td>$F_{1,423} = 2.01$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.771$</td>
<td>$P = 0.289$</td>
<td>$P = 0.157$</td>
</tr>
<tr>
<td>Sauger</td>
<td>growth</td>
<td>$F_{2,62} = 3.07$</td>
<td>$F_{1,95} = 0.22$</td>
<td>$F_{1,132} = 2.18$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.001$</td>
<td>$P = 0.643$</td>
<td>$P = 0.142$</td>
</tr>
<tr>
<td></td>
<td>condition</td>
<td>$F_{2,62} = 3.33$</td>
<td>$F_{1,95} = 2.61$</td>
<td>$F_{1,132} = 1.21$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.042$</td>
<td>$P = 0.110$</td>
<td>$P = 0.274$</td>
</tr>
<tr>
<td>smallmouth bass</td>
<td>growth</td>
<td>$F_{2,920} = 10.31$</td>
<td>$F_{1,243} = 0.80$</td>
<td>$F_{1,329} = 0.01$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.371$</td>
<td>$P = 0.917$</td>
</tr>
<tr>
<td></td>
<td>condition</td>
<td>$F_{2,920} = 0.35$</td>
<td>$F_{1,242} = 5.56$</td>
<td>$F_{1,329} = 1.96$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.705$</td>
<td>$P = 0.019$</td>
<td>$P = 0.163$</td>
</tr>
</tbody>
</table>
Table IV - 7. Annual estimated mortality of northern pike, walleye, sauger and smallmouth bass with 95% CIs (in parentheses) among different water management regimes.

<table>
<thead>
<tr>
<th>Water management</th>
<th>northern pike</th>
<th>walleye</th>
<th>sauger</th>
<th>smallmouth bass</th>
</tr>
</thead>
<tbody>
<tr>
<td>unimpounded</td>
<td>0.29</td>
<td>0.41</td>
<td>0.16</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>(0.22/0.43)</td>
<td>(0.38/0.46)</td>
<td>(0.06/0.27)</td>
<td>(0.28/0.37)</td>
</tr>
<tr>
<td>run of river</td>
<td>0.23</td>
<td>0.17</td>
<td>0.06</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>(0.10/0.40)</td>
<td>(0.06/0.29)</td>
<td>(0/0.14)</td>
<td>(0.22/0.34)</td>
</tr>
<tr>
<td>winter reservoir</td>
<td>0.33</td>
<td>0.48</td>
<td>0.22</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>(0.21/0.46)</td>
<td>(0.42/0.50)</td>
<td>(0.09/0.36)</td>
<td>(0.32/0.46)</td>
</tr>
</tbody>
</table>
Figure IV - 1. Ottawa River reaches included in the study with locations of dams along the river (G.S. = generating station). Satellite imagery depicts location of the Ottawa River in relationship to Lake Ontario and the St. Lawrence River (insert).
Figure IV - 2. Mean monthly water flow at Chats G.S. prior and post hydro-electric development in 1932. Extensive hydro-electric development occurred in upstream locations during the late 1940's.
Figure IV - 3. Biplots of net locations based on discriminant function analysis of fish community structure for different water management regimes using (a) NSCIN and (b) FWIN.
Figure IV - 4. Community structure Jackknifed misclassification rates of netting techniques based on water management using discriminant function analysis.
Figure IV - 5. Hierarchical cluster analysis of species based on CUE (technique as per gear selectivity) pooled over study reaches within management regimes. Sturgeon and common white sucker (CWS) with extension pertains to different netting techniques (n – NSCIN; f – FWIN)
Figure IV - 6. Catch-per-unit-effort with ± 1 S.E. of select species by netting technique among water management regimes.
Figure IV - 7. Catch-per-unit-effort with ± 1 S.E. of select species by netting technique among water management regimes.
Figure IV - 8. Hierarchical cluster analysis of select species based on growth rates among water management regimes.
Figure IV - 9. Growth (slope of log10 length – log10 age regression) and condition (slope of log10 weight – log10 length regression) ± 1 S.E. for northern pike, walleye, sauger, smallmouth bass and lake sturgeon (condition not included) among different water management regimes.
Figure IV - 10. Cumulative total length frequency diagrams for (a) northern pike; (b) sauger; (c) smallmouth bass; (d) walleye; and (e) lake sturgeon among water management regimes.
Chapter V. Evaluation of the predictive power of a lake sturgeon habitat suitability model at multiple spatial scales

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Abstract

Habitat suitability index models (HSM) have been developed and used for fish but few have been independently validated. Given the importance of HSMs in habitat management and conservation policy, the extent to which such models predict population parameters (e.g. abundance or recruitment) is a pertinent issue. Here, we: develop a spatially explicit form of the lake sturgeon HSM, apply this version to three reaches of the Ottawa River using spatially explicit measurements of the model’s key variables (substrate type, water depth and velocity) to generate spatially explicit predicted habitat suitabilities; and test the predictive power of the model by correlating predicted habitat suitability with observed lake sturgeon abundance at two different spatial scales: within-reach and among-reach. Model validation was conducted by paired samples using short set gillnets in predicted good (HSI >0.6) and poor habitats (HSI < 0.3) habitat. Substrate composition and depth were obtained at each netting location to evaluate potential inaccuracies associated with the spatial interpolation of habitat data and to also generate actual habitat suitability (versus predicted based on spatial interpolation). Correlations between predicted and observed habitat values were generally low ($R^2$<0.16). The lake sturgeon HSM was based on adult and juvenile foraging habitat. Significantly more lake sturgeon were caught in good habitat ($P<0.001$) suggesting foraging habitat is a good predictor of adult and juvenile abundance however, the predictive power of the model was low ($R^2 < 0.18$). Attempts to improve the predictive power of the HSM specific to the Ottawa River by discriminant function analysis and generalized additive models were ineffective.


**Introduction**

In Canada and the United States, habitat loss and degradation (McAllister et al 1985; Beamish et al. 1986) are the most pervasive risks to aquatic biodiversity in general, and to species of concern in particular. Mitigating these risks requires that we both characterize the habitat requirements of species of concern and manage human activities so as to maintain habitat of sufficient quality and quantity to ensure species persistence. To this end, many habitat suitability index models (HSMs) have been developed: the USGS alone has developed HSMs for 158 species including 53 species of fish after a large initiative in the 1980s (USGS website: [http://www.nwrc.usgs.gov/wdb/pubhsi/hsiintro.htm](http://www.nwrc.usgs.gov/wdb/pubhsi/hsiintro.htm)) and many more fish HSMs have been developed independent of the USGS initiative (e.g., Threader et al 1998; Rebuc et al. 1999; Guay et al. 2003).

Habitat suitability index models have been developed: to evaluate the quality and quantity of habitat for a variety of species (O’Neil et al. 1988); to assess the impact of management – both past or future - activities (O’Neil et al. 1988; Bray 1996; Brooks 1997; Roloff and Kernohan 1999); to assess changes in habitat quantity or quality (Bray 1996), and to link population changes to habitat supply (Chu et al. 2006). The strength of habitat models lies in their ability to explicitly represent limiting habitats which can then be used as concrete targets for conservation action and protection (Boisclair 2001). But while HSMs have been extensively used to manage habitat for fish species of interest or concern, very few have been independently validated (Layher and Maughan 1985;
Brooks 1997; Rubec et al. 1999; Ortigosa et al. 2000), although this appears to be gaining momentum especially with new geographical information systems tools available (e.g. Morris and Ball 2006; Vinagre et al. 2006).

The issue of validation is critical. Many HSMs were developed on the basis of expert opinion, often using data that were at best, unsystematically collected (Rubec et al. 1999). Moreover, the performance of those (comparatively few) HSMs that have been subjected to independent validation is inconsistent (Roloff and Kernohan 1999) to the point where their general reliability has been questioned (Cole and Smith 1983). Finally, often in cases where validation has been assessed, the data used to construct the model were also used in the validation process, a form of pseudo-replication, leading to overestimated model performance (Olden et al. 2002).

Moreover, an important issue in wildlife and fisheries management is the scale-dependence (or lack thereof) of habitat suitability models (Reyjol et al. 2001; Store and Jokimäki 2003) although certain ecological parameters may have different affects on a species at different scales (Graf et al. 2005; Legalle et al. 2005). Habitat protection, rehabilitation or remediation can, at least in principle, be done at a wide range of spatial scales: for example, for fish in large rivers, protection and rehabilitation efforts can occur within reaches, among reaches within rivers, or among rivers. Many HSMs are developed at comparatively large scales (Threader et al. 1996; Rothley 2001) but conservation and rehabilitation efforts often occur at smaller (local) scales (e.g. Mathys et al. 2006; Vinagre et al. 2006). Thus the question naturally arises as to extent to which an HSM
developed at large (e.g. among river) scales can be applied at smaller (e.g. among reach within-river) scales to inform local habitat protection or remediation efforts.

A habitat suitability index model (HSM) has been developed for lake sturgeon (*Acipenser fulvescens*; Threader et al. 1998) adhering to the USGS format based primarily on expert opinion and existing literature. The model was developed at a larger scale for medium sized, slow flowing rivers in northern Ontario (e.g. Moose River basin) and has nominally tested on several rivers throughout the province. Here, we: develop a spatially explicit form of the lake sturgeon HSM; apply this version to three reaches of the Ottawa River using spatially explicit measurements of the model’s key variables (substrate type, water depth and velocity) to generate spatially explicit predicted habitat suitabilities; and test the predictive power of the model by correlating predicted habitat suitability with observed lake sturgeon abundance at two different spatial scales: within-reach and among-reach.

**Methods**

The lake sturgeon HSM has two sub-models, one for reproduction, and the other for foraging; here we evaluate only the foraging submodel. This model includes three habitat variables: bottom substrate, water depth and water velocity that were considered key variables influencing the distribution and abundance of lake sturgeon in foraging habitats (Threader et al. 1998) based on an extensive literature review and discussions with fisheries specialist working in the field (Threader et al. 1998).
The foraging component ($C_F$) of the habitat suitability model comprises adult ($C_{F-A}$) and juvenile ($C_{F-J}$) foraging habitat. In the HSM, bottom substrate ($V_{bs}$) is the only variable that determines the quality of adult foraging habitat and is used as a surrogate for benthos production, the assumption being that habitat which is more productive for benthic invertebrates represents better foraging habitat for lake sturgeon (Threader et al. 1998). In the original model (Threader et al. 1998), suitability indices for adult and juvenile foraging were presented for each substrate type (Table V - 1), with suitability ranging from 0 (completely unsuitable) to 1 (most suitable). $V_{bs}$ is given by:

$$V_{bs} = \sum_i s_{ij} c_i,$$

(1)

where $j$ is age class (adult or juvenile); $i$ is the substrate type, $k$ is the number of substrate types, $s_{ij}$ is the suitability index of substrate $i$ for age class $j$ and $c$ is the proportion of the area under consideration of substrate type $i$.

Juvenile foraging habitat ($C_{F-J}$) is based on bottom substrate (Table V - 1; $V_{bs,j}$), water foraging depth (Figure V - 1; $V_d$) and juvenile foraging water velocity (Figure V -1; $V_v$). The juvenile foraging component is a geometric mean given by:

$$C_{F-J} = (V_{bs,j} \times V_d \times V_v)^{1/3}.$$

(2)

The overall $C_F$ was the minimum value of $C_{F-A}$ or $C_{F-J}$. 

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The lake sturgeon HSM (Threader et al. 1998) was developed as an aspatial model and as such, has two important limitations. First, fish habitat management and conservation is often spatially explicit, that is, designed to mitigate habitat threats or conserve optimal values at particular locations within a waterbody (Rubec et al. 1999). In such circumstances, the practical utility of an HSM is based on its ability to predict habitat suitability – and, presumably, species abundance or likelihood of occurrence - at particular sites or locations (e.g., Vinagre et al. 2006). Second, an important empirical issue in HSM validation is the extent to which models developed for one spatial scale (e.g., river basins or rivers) can be applied - with reasonable predictive power - to other scales. All else being equal, HSMs whose predictive power is: (a) reasonably good; and (b) independent of scale over the range of scales germane to most habitat management issues, will be more valuable than those for which condition (a) applies only at a narrow range of scales. To address these two issues, a spatially explicit version of the sturgeon HSM was created in ArcMap 8.3 (ESRI, Redlands, CA) as has been done for other species (e.g., Rubec et al. 1999; Ortigosa et al. 2000).

Development of a Spatial Application

The spatial application was developed by generating (a) look-up tables for habitat suitability and substrate class (Table V - 1); and (b) equations expressing suitability as a function of current velocity and depth (Figure V – 2; Threader et al. 1998). Rasters (a data source that uses a grid structure to store geographic information) at 10 m spatial
resolution were developed for each substrate (e.g., clay, silt, sand, detritus, gravel, rubble, boulder and bedrock) and water depth. This allowed us to calculate a habitat suitability index for each pixel using the appropriate elements. For example, when calculating $C_{F,A}$, each pixel (the smallest unit of information in an image or raster) of each raster was multiplied by its corresponding suitability index (SI); the scores for each pixel in each raster were then summed to provide a value for that pixel in the output raster ($0 \leq x \leq 1$ where $x$ is the HSI score for that pixel). The overall $C_F$ is the mean of all pixels in the reach based on the minimum value of $C_{F,J}$ or $C_{F,A}$ in a pixel:

\[ C_F = \frac{1}{n} \left( \sum \limits_i s_{ij} c_i \right), \quad (3) \]

where $i$ is the substrate type, $k$ is the number of substrates, $s_{ij}$ is the suitability index of the $i$th substrate for age class $j$, $n$ is the number of pixels in the area of interest and $c_i$ is the proportion of pixels in the area of interest that have a substrate type $i$.

**Determination of habitat variables**

Habitat sampling stations were set up in three Ottawa River reaches: Lower Allumette, Upper Allumette Lakes and Lac des Chats (Figure V -1). Distances between stations was initially set at 100 m but due to homogeneity of habitat in relatively close proximity, was increased to 300 m or at locations observed changes in habitat (e.g., relief in bathymetry; vegetative community etc.). In total, 680 stations were sampled in Lac des Chats, 154 in Lower Allumette Lake and 126 in Upper Allumette Lake.
At each station, an Aqua Vu (an underwater video camera) was used to describe bottom substrate (e.g., % boulders, rock rubble, detritus, logs, etc.); a sample of bottom substrate was collected using an Eckmann dredge in soft bottom locations. Bottom substrate at a sampling station was characterized as percent composition of different substrate types (e.g., 50% clay, 30% sand, 20% detritus). Data were captured directly into an attribute table on a Pencentra hand held data logger with Global Positioning System (GPS) capabilities and were downloaded as a point shapefile at the end of each sample day using autosync to a personal computer. ArcMap was used on the Pencentra to permit navigation on the waterbody and collection of GPS locations for each sample station. Due to the depth and width of the river, current velocity was considered to be slow, well within the suitability range established for juvenile sturgeon (i.e., < 40 cm/s; Figure V - 2); measurements taken by Ontario Power Generation using a RDI Acoustic Doppler Current Profiler in Lower Allumette Lake (downstream of rapids in the widening of the river) indicates flows were generally less than 40 cm/s during mid summer. Water velocity measurements were therefore not taken at each sample site. As such, \( V_v \) was set to 1 for all sample locations (i.e., flows were assumed to be between 10 – 40 cm/s during validation which was conducted during periods of low flow, mid to late July).

Point shapefiles were interpolated using kriging in ArcInfo 8.3 (ESRI, Redlands, CA) to calculate rasters for each substrate type at 10 m resolution; a search radius of 12 points and a maximum distance of 750 m were the constraints placed on the kriging process. Existing bathymetry maps of the Ottawa River produced by Canadian Hydrographic...
Services (Ottawa, Ontario) were georeferenced in ArcMap 8.3, digitized as point files, and interpolated using topogrid to produce a depth raster.

**Substrate validation**

Accuracy of substrate rasters was assessed by means of 156 test plots randomly located throughout the three reaches. Substrate was sampled as described above at each test location. Universal Transverse Mercator (UTM) coordinates were obtained at each location using a Garmin eTrex (Garmin International Inc, Olathe, Kansas) and a shapefile was created for all test locations. Interpolated (predicted) values for each substrate raster at each test location were obtained using Hawth’s Analysis Tools version 2.10 (Beyer 2004) in ArcMap. A 100 m buffer (50 m radius) was created around each location (sample point) and the average HSI value for this area, based on interpolated habitat variables, was calculated using the zonal statistics procedure in ArcMap. In this manner, for each test plot, we had both the actual substrate as assessed through direct sampling and the estimated substrate derived from interpolation, allowing us to examine the predictive accuracy of substrate interpolation. In addition, each sample site was expressed as a vector of Euclidean distance from the origin. Two distances were therefore calculated at each sample site: one for observed substrate type; and one for predicted substrate type. These distances were then correlated to assess the predictive power of the interpolations.
HSM evaluation

The HSM was evaluated on two Ottawa River reaches: Lower Allumette Lake and the lower portion of Upper Allumette Lake. Rasters were produced for adult and juvenile foraging suitability based on interpolated substrate designations. Model validation was conducted using paired, short set gill nets in areas classified as low (HSI scores 0 – 0.3; herein referred to as poor habitat) and high predicted suitability (HSI scores 0.6 – 1.0; herein referred to as good habitat) for both adult and juvenile foraging habitat separately. We selected the extremes of the predicted habitat gradient to maximum the chances of detecting the predicted relationship between habitat quality and abundance, if indeed any such relationship exists: if no differences in abundance are observed at the two extremes of the (predicted) habitat suitability gradient, then the model has little predictive power. Abundance of juveniles and adults in the appropriate habitats were assessed with small mesh gillnets (2.5 to 15.2 cm) and large (17.8 to 30.5 cm) mesh gillnets, respectively. Netting was conducted between 8:00 am and 6:00 pm from July 26 – August 11, 2004 and July 10 – July 21, 2006 to concentrate efforts when lake sturgeon are foraging (i.e., not at spawning grounds). Two nets of the same mesh composition were set within 500 m of each other for 90 – 120 minutes: one net in (predicted) poor suitability habitat; and the other in good (predicted) suitability habitat, for both juvenile and adult habitat separately; netting sites were determined based predicted habitat and the ability to meet the aforementioned criterion (i.e., different habitat types within 500 m). Nets were set for short duration to maximize the likelihood of catching lake sturgeon in foraging areas as opposed to migrating from habitat to another and to minimize lethal bycatch.
UTM coordinates, water depth, and a description of the substrate were obtained at each site, which allowed HSIs to be calculated for each net site. In 2004, sites were selected based on interpolated HSIs from the HSM; if on-site measurements indicated that the interpolated HSI was incorrect (e.g. a poor habitat quality set in habitat with an observed HSI > 0.3 when the HSM gave a predicted HSI <0.3), these nets were removed from the analysis. In 2006, all candidate net sites were first evaluated to ensure that predicted (interpolated) and observed HSI classifications matched.

Captured lake sturgeon were extricated, sampled, tagged and released. Individuals less than 80 cm TL were considered juveniles, individuals greater than 80 cm TL and less than 115 cm TL were considered subadults, and individuals greater than 115 cm TL were considered adults (Haxton, unpublished data).

An important question arises as to the ability of short-net sets to provide reasonable estimates of abundance along a habitat quality gradient. To address this issue, two standard index netting techniques (Nearshore Community Index Netting (NSCIN) and Fall Walleye Index Netting (FWIN)) were used to assess fish communities in Ottawa River Reaches. NSCIN requires the use of 1.8 and 2.4 m trapnets randomly set for 24 hours from mid-August until water temperatures recede to 13°C; FWIN require the use of 2.5 – 15.2 cm stretched mesh gillnets randomly set for 24 hours in two depth strata (2 – 5 m; 5 – 15 m) during the fall when water temperatures are between 10 – 15°C. Both techniques sampled lake sturgeon (Haxton 2002). Habitat was not described at each location during the netting, however, due to the number of habitat substrate sampling
stations conducted in the three reaches (whether from initial habitat mapping or habitat validation), habitat could be determined for 55 netting sites (12 FWIN and 43 NSCIN) with the criterion that the habitat sample station was within 100 m of the netting location (gill nets were 76 m; trapnets had 67 m leads). An HSI value was calculated for each netting site.

To test the predictive power of the HSM, we fitted Poisson regression models to sturgeon abundance in (a) adult and (b) juvenile per net set using habitat suitability (good, poor) based on observed site characteristics as the predictor (i.e., we used a generalized linear model in S-Plus with a Poisson family and a log link function). Poisson regression was first fitted to paired nets correctly placed based on observed HSI values and then to all nets correctly placed based on observed HSI values without regard to paired placements. In addition, logistic regressions were conducted for nets with and without sturgeon in adult and foraging habitat. And finally, Poisson regression was fitted to standard index netting where habitat characteristics could be determined; lake sturgeon CUE was the dependent variable and observed HSI, netting technique (FWIN or NSCIN) and the interaction between netting technique and HSI as predictors. $R^2$ values were determined for Poisson regressions by dividing the deviance explained by a variable of interest by the total deviance of the model. Over-dispersion (i.e., larger variance than would be expected from a Poisson assumption) was examined by dividing the deviance by the degrees of freedom; if greater than 1, then over-dispersion is possible. None of the Poisson regressions provided evidence of over-dispersion and therefore further analysis was conducted. To test whether the predictive ability of the HSM at larger spatial scales
(between reaches), we examined the relationship between lake sturgeon CUE in standard index netting projects (Haxton and Findlay, unpublished data) to the overall \( C_f \) for each river reach.

**Model modification**

In a separate analysis, we used Discriminant Function Analysis (DFA) to assess the ability of habitat measures at validation sites to correctly classify sites into those for which (a) no; or (b) one or more sturgeon was captured during the sampling period; therefore, catch or no catch of lake sturgeon was the grouping variable and all habitat measures (e.g., depth, sand, silt etc.,) were used as the predictors. We also fitted generalized additive models (GAM – a method for fitting smoother curves to data with single or multiple predictors and a response variable) using Poisson families with a log-link function using habitat variables (e.g., sand, silt etc.), water depth and distance from the closest shore as predictors and number of lake sturgeon caught as the dependent variable. In these analyses, lake sturgeon were categorized by maturity (juveniles, subadults/adults and combined). Finally, Poisson regression model was fitted to lake sturgeon catch and habitat variables.

**Statistical analysis**

Poisson regression and generalized additive modeling were conducted using S-Plus 6.2 (Insightful Corporation Seattle, Washington). All other statistical analysis was conducted
using SYSTAT v 11 (SYSTAT Software Inc., Richmond, CA). Significance was determined at $P = 0.05$.

**Results**

Predicted adult and juvenile foraging habitat suitability maps for Lower Allumette Lake, Upper Allumette Lake and Lac des Chats based on interpolated site characteristics are shown in Figures V - 3 through V - 6. Comparison of observed versus predicted (on the basis of spatial interpolation) substrate compositions at the 156 validation sites indicate that with the exception of water depth, habitat interpolations are very poor (Figure V - 7) as was the correlation between scalars of observed and predicted habitat types at sample sites ($R^2 = 0.01$).

**Model validation**

Model assessment involved 82 paired net sets (164 net sets) in predicted good and poor habitat, 43 and 39 paired sets in adult and juvenile habitat respectively (Table V - 2) with 73 lake sturgeon were sampled from all sites. Lake sturgeon CUE was significantly greater in good habitat for both adults (Poisson regression; d.f. = 30, $P = 0.024$; $R^2 = 0.158$) and juveniles (Figure V - 8; Poisson regression; d.f. = 20, $P = 0.005$; $R^2 = 0.226$) using correctly placed, paired nets. Using all correctly placed nets (i.e., not necessarily paired net placements), adult lake sturgeon CUE was significantly greater in good adult habitat than in poor adult habitat (Figure V - 8; Poisson regression; d.f. = 64, $P<0.001$)
but fitted models have low predictive power ($R^2 = 0.175$). Conversely, juvenile sturgeon CUE in good juvenile habitat was not significantly greater than poor juvenile habitat (Poisson regression; d.f. = 60, $P = 0.12; R^2 = 0.03$). The proportion of nets with lake sturgeon catches in observed versus predicted good and poor habitat were similar (Figure V - 9). Habitat was a good predictor of adult and juvenile catches (Logistic regression; $G = 5.85$ d.f. = 1 $P = 0.016$ and $G = 6.30$ d.f. = 1, $P = 0.012$ respectively). Lake sturgeon catch in comparison to HSI value was significant in adult habitat (Poisson regression d.f. = 83, $P = 0.002$) but the predictive power was very low ($R^2 = 0.089$) and only marginally insignificant in juvenile habitat (Poisson regression; d.f. = 74, $P = 0.052$) although the predictive power was very low ($R^2 = 0.045$). Catch-per-unit-effort (sturgeon caught per net set) was greater in the 24 hour sets in comparison to the short set nets (Figure V - 10). Lake sturgeon catch from standard index netting (i.e., 24 hour sets) was significant in relationship to HSI (Poisson regression, d.f. = 53, $P < 0.001; R^2 = 0.06$) but this relationship was negative (i.e., lake sturgeon CUE decreased with increasing HSI score; Figure V - 11).

With respect to the predictive value of the HSM at larger scales, Lower Allumette Lake, which had the higher lake sturgeon CUE from both standard index netting techniques, also had greater estimated mean $C_F$ (Figure V - 12).
Model modification

Discriminant function analysis did not distinguish between nets that caught lake sturgeon versus those that did not based on habitat variables (Figure V - 13).

Based on GAM, juvenile lake sturgeon showed: a depth preference of 5 m, diminishing with increasing depth; a positive relationship with increasing detritus, clay, silt, sand, gravel, and rubble composition; and were not as abundant with increasing distance from shore (Figure V - 14). Adult/subadult lake sturgeon demonstrated: a depth preference up to 13 m and then declined; a negative relationship with increasing composition of detritus, clay, silt, sand, gravel and rubble; and were less abundant with increasing distance from shore (Figure V - 15). For all life stages combined, there was a depth preference of 5 m; sturgeon numbers declined after the composition of detritus reached 50%, silt reach 20%, sand reached 70% and rubble reached 50%. Sturgeon demonstrated an affinity to shore (Figure V - 16). There were significant relationships between: lake sturgeon caught in adult nets and depth (Poisson regression; d.f. = 83, \( P = 0.008; \) \( R^2 = 0.067 \)), detritus (Poisson regression; d.f. = 82, \( P = 0.007; \) \( R^2 = 0.068 \)), gravel (Poisson regression; d.f. = 78, \( P = 0.035; \) \( R^2 = 0.041 \)) and rubble (Poisson regression; d.f. = 77, \( P = 0.105; \) \( R^2 = 0.062 \)); sturgeon caught in juvenile nets and depth (Poisson regression; d.f. = 74, \( P < 0.001; \) \( R^2 = 0.14 \)) and gravel (Poisson regression; d.f. = 69, \( P = 0.005; \) \( R^2 = 0.009 \)); and sturgeon caught in all nets combined and depth (Poisson regression; d.f. = 159, \( P = 0.005; \) \( R^2 = 0.041 \)), detritus (Poisson regression; d.f. = 158, \( P < 0.001; \) \( R^2 = 0.082 \)), clay (Poisson regression; d.f. = 157, \( P = 0.007; \) \( R^2 = 0.038 \)) and gravel (Poisson regression; d.f. = 154, \( P = 0.007; \) \( R^2 = 0.067 \)).
Discussion

The HSM showed some promise – generally more lake sturgeon were caught in good versus poor in the short set nets (fine scale) and lake sturgeon CUE in standard index netting programs was proportional to the overall foraging component in different reaches (large scale). However, the HSM generally had low predictive power and variation at the larger scale was high. Several other key issues were identified in this study when applying an HSM. Although a spatial application was developed from an aspatial lake sturgeon HSM, the means of populating the model is problematic. Interpolation from original sample sites proved inaccurate and therefore cast doubt on model products (i.e., Figures V - 3 to V - 6). To ameliorate these concerns, suitability of locations (i.e., good or poor habitat) were determined prior to netting – Poisson and logistic regressions suggests there is some predictability however the predictive power of the model was still low. This did not improve when assessed by short net sets or long net sets. Habitat characteristics at netting locations where lake sturgeon were sampled could not be discriminated from where they were not sampled. Generalized additive models identified differences in habitat preference between adult/subadults and juveniles, supported by Poisson regressions albeit with low predictive power. Discriminant function analysis indicated there was overlap and habitat characteristics could not be confidently discriminated therefore, modifications to the model specific to the Ottawa River to improve the predictive power could not be applied.
The lake sturgeon HSM was initially developed for medium sized, slow flowing rivers in northern Ontario (Moose River basin; Threader et al. 1998). Differences in populations or variations in habitat among geographical areas (Pajak and Neves 1987; O'Neil et al. 1988; Glozier et al. 1997; Vismara et al. 2001; Strakosh et al. 2003) may account for the low predictive power of adult and juvenile foraging in the Ottawa River. The lake sturgeon HSM however, was not empirically developed and therefore should have general application. Adult and juvenile foraging habitats are based primarily on substrate which is used as a surrogate for prey (i.e., macroinvertebrates). Abundance and distribution of sturgeon has been related to availability of preferred prey (Chiasson et al. 1997; Hayes and Werner 2004) although other studies have suggested juvenile lake sturgeon presence could not be explained by food habits (Nilo et al. 2006). This model demonstrated some ability to predict good habitat both at the small scale and larger scale. The low predictive power (i.e., \( R^2 \)) observed with each test may in fact be due to measurement error in both the dependent variable (i.e., habitat variables used in calculating the HSI) and predictors (i.e., netting results).

The use of short set gillnets (90 -120 minutes) in this study may be subject to criticism however, the intent was to target lake sturgeon actively feeding in those locations and avoid the capture of migrating lake sturgeon in non-suitable habitat. This may still be a bias in the validation technique as gillnets are a passive means of assessment. Another bias may be diel movements of lake sturgeon. They purportedly inhabit deeper waters during the day move to shallower water at night to feed (Holgren and Auer 2004) therefore lake sturgeon movement may be greater at night than day (Chiasson et al. 2019).
Morse et al. (1997), however, did not observe differences in diel and nocturnal habitat selection. Despite this, we sampled 72 lake sturgeon in short set nets for a overall CUE of 0.44 lake sturgeon per net suggesting short sets were not problematic. More lake sturgeon were sampled (i.e., lake sturgeon CUE was greater) with overnight nets sets however, there was a negative relationship between HSI and lake sturgeon CUE suggesting i) the habitat model as it exists is not valid; ii) overnights sets sampled a preponderance of migrating lake sturgeon; or iii) our assumption that lake sturgeon would be sampled more frequently in areas of good foraging habitat is incorrect. Different techniques such as baited set lines (e.g., Thomas and Haas 1999) or trawls may be a better technique to use as it targets lake sturgeon actively feeding in the area and may reduce the biases introduced by the techniques used.

Variation in habitat selectivity exists among lake sturgeon populations. For example, juvenile lake sturgeon preferred clay in Moose River (Chiasson et al. 1997) whereas silt was the predominant substrate utilized by juveniles in the St. Lawrence River (Hayes and Werner 2004). Adult lake sturgeon in the St. Lawrence River used areas dominated by boulders followed by silt (Hayes and Werner 2004) whereas lake sturgeon in the Groundhog River preferred substrates with organic or coarse material (sand/organic, sand/gravel, gravel, rubble; Seyler 1997). In the Sturgeon River, lake sturgeon were found over mud during the day and over mud/sand during the night (Holtgren and Auer 2004) whereas sand was the preferred habitat in the Kettle River except during low water periods when sand, muck and detritus were equally used (Morse et al. 1997). Given this, a general HSM for lake sturgeon would be expected to provide low predictability.
Conversely, in order to be an effective ‘predictor’, the HSM would have to be modified specific to each river to accommodate for differences in habitat selectivity. Models that have been developed empirically for specific waterbodies have been tested on other systems. Transferability of HSI values from one system to another is generally low (Glozier et al. 1997; Guay et al. 2003; Strakosh et al. 2003; Hedger et al. 2004; Moir et al. 2005) although it has been shown to be effective when used on systems in close proximity (Rubec et al. 1999).

While a lot of time and effort was expended, especially in the 1980s, to develop HSMs for a variety of species, limited use and application has been made of them, especially in published literature. A citation review was conducted on the 53 fish HSMs posted on the USGS website (Haxton, unpublished data). These HSMs were referenced 169 times in scientific literature; the majority were used as general references (e.g., stating an HSM was developed or using some general information from the model). Two attempts at validating one of these HSMs have been published: in one instance, the model was refuted (Lowie et al. 2001); and in the other, while reliability of suitability indices appeared high, there was little correlation between HSI and species biomass (Layher and Maughan 1985). Some studies applied portions of HSMs (i.e., only used certain HSI; e.g., Bray 1996); some studies corroborated portions of HSMs but refuted other portions (e.g., Kocik and Taylor 1996). Some considered the models too simple (e.g., Minns et al. 1996). Pajak and Neves (1987) attempted to correlate HSI with standing stocks of rock bass (Ambleplites rupestris) and determined the correlation to be poor or spurious.
Despite the lack of use of the aforementioned models and the development of alternate techniques such as habitat probabilistic index—determined by logistic regressions—HSI’s are still the most commonly used index of habitat (Ahmadi-Nedushan et al. 2006). They form the basis of other habitat models such as Instream Flow Incremental Model or Physical Habitat Simulation Model (Guay et al. 2000). Several issues remain with HSMs:

1) they assume that variables affect fish independently, whereas variables may interact and therefore affect fish distribution (Guay et al. 2000);

2) variability is not often taken into account with HSMs (Bender et al. 1996; Roloff and Kernohan 1999) and therefore it is difficult to ascertain whether differences in HSI scores are actually different (Bender et al. 1996) or how this variability affects the final HSI output (Roloff and Kernohan 1999).

Large differences in HSI scores (e.g. 0.38 – 0.81) have been found not to be significantly different (Bender et al. 1996); and 3) assumptions that accompany habitat models affect their validity (Boisclair 2001). These assumptions should be tested along with validation of the models (Brooks 1997; Boisclair 2001) to assess their reliability and applicability before use (O’Neil et al. 1998).

Conclusions

Habitat suitability index models in general appear to be unreliable or largely untested; at least validation results have not been published in literature. With this in mind, we developed a spatially explicit form of an existing lake sturgeon HSM and tested its predictive power. Problems occurred with populating the model’s parameters: substrate interpolations proved inaccurate therefore the output of the model could not be used at a
fine scale (i.e., for setting nets in good versus poor habitat). Model outputs should be validated (i.e., assess their accuracy) before they are accepted carte blanche. The HSM demonstrated some predictability of lake sturgeon abundance at multiple scales suggesting there is some applicability of this model. However, the predictive power of the model was generally low. Further research should be conducted for improving the predictive power of HSMs to improve their reliability.

Acknowledgements
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References


Table V - 1. Suitability indices for adult and juvenile substrate types (Threader et al. 1998).

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Adult foraging SI</th>
<th>Juvenile foraging SI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clay</td>
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<td>0.2</td>
</tr>
<tr>
<td>Silt</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Sand</td>
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<td>Gravel</td>
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<td>0.5</td>
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<td>Bedrock</td>
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<td>0.2</td>
</tr>
<tr>
<td>Detritus</td>
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<td>0</td>
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</table>
Table V - 2. Number of nets set in good and poor habitat for each life stage based on predicted habitat type and observed habitat using paired net sets correctly placed and all net sets correctly placed.

<table>
<thead>
<tr>
<th></th>
<th>Adult habitat</th>
<th></th>
<th>Juvenile habitat</th>
<th></th>
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</thead>
<tbody>
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<td>good</td>
<td>poor</td>
<td>Good</td>
<td>Poor</td>
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<tr>
<td>Predicted</td>
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<td>39</td>
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<td>Observed (paired net sets)</td>
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<td>Observed (all nets sets)</td>
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<td>33</td>
<td>50</td>
<td>12</td>
</tr>
</tbody>
</table>
Figure V - 1. Ottawa River reaches used for habitat suitability modeling; location of
Ottawa River in relationship to Lake Ontario and the St. Lawrence River (insert).
Figure V - 2. Juvenile habitat suitability in relation to foraging depth and water velocity (Threader et al. 1998); water depth is on the $x_1$ axis and water velocity on the $x_2$ axis.
Figure V - 3. Predicted habitat suitability for juvenile lake sturgeon on Lower and Upper Allumette Lakes, Ottawa River, based on the aspatial habitat suitability model (Threader et al. 1998) and interpolation of habitat characteristics derived from 380 sampling locations.
Figure V - 4. Predicted habitat suitability for adult lake sturgeon on Lower and Upper Allumette Lakes, Ottawa River, based on the aspatial habitat suitability model (Threader et al. 1998) and interpolation of habitat characteristics derived from 380 sampling locations.
Figure V - 5. Predicted habitat suitability for juvenile lake sturgeon on Lac des Chats, Ottawa River, based on the aspatial habitat suitability model (Threader et al. 1998) and interpolation of habitat characteristics derived from 680 sampling locations.
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Figure V - 8. Average (+/- 1 SE) lake sturgeon CUE (sturgeon per net) based on paired nets sets and nets set in good or poor observed habitat.
Figure V - 9. The proportion of nets with CUE > 0 in locations with observed (based on measured site characteristics) poor and good quality habitat based on the Threadder et al. (1998) habitat suitability model; and predicted (i.e. based on interpolated site characteristics) poor and good quality habitat.
Figure V - 10. Average (+/- 1 SE) lake sturgeon CUE (sturgeon per net) in validation nets (90 – 120 minute sets), Fall Walleye Index Netting (FWIN) and Nearshore Community Index Netting (NSCIN) nets (24 hour sets).
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Figure V - 13. Plot of nets with and without sturgeon catches against their values for two discriminant functions.
Figure V - 14. Generalized additive model graphs and estimated 95% confidence intervals of juveniles caught in relationship to habitat variables.
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Figure V - 16. Generalized additive model graphs and estimated 95% confidence intervals of sturgeon caught (all life stages) in relationship to habitat variables.
Chapter VI. Summary and Conclusions
Waterpower management affects the aquatic community. This thesis conducted a qualitative and a systematic review of effects. The main conclusions derived in the manuscript entitled *Meta-analysis of the ecological impacts of freshwater power management* were i) macroinvertebrates are adversely affected in areas frequently dewatered; ii) the aquatic communities downstream from hydro-electric facilities are adversely affected by a hypolimnetic draw; iii) fluvial specialists are adversely affected in terms of abundance by deviations from natural flows whereas abundance of habitat generalists does not significantly change. Further research that could be conducted on each conclusion that could not be discerned by meta-analysis on existing published literature includes: i) What effect does the impoverished macroinvertebrates have on benthivores within that waterbody? ii) What aspect of hypolimnetic draws (e.g., oxygen saturation, changes in thermal regime etc.) affects the downstream community the greatest? iii) What fills the niche of fluvial specialists in a river if habitat generalists abundance does not increase after flows are modified?

The next manuscript, *Variation in lake sturgeon abundance and growth among river reaches in a large regulated*, assessed which anthropogenic stressors affected lake sturgeon abundance among reach types. Commercial harvest, water power management and contaminants were the stressors that were assessed. Commercial harvest while at one time probably limited populations, did not explain the variation in lake abundance among river reaches. An array of organic pesticides and industrial pollutants were assessed in lake sturgeon sample, only mercury was elevated in the sturgeon samples whereas many other contaminants were not detected. Neither growth nor condition was affected by
increasing mercury burden suggesting that it was not limiting populations. In addition, mercury burden in Ottawa River lake sturgeon was within the range of other North American population although populations that intuitively should have greater mercury burden (e.g. St. Lawrence River), were lower. Further research could be conducted on why the differences among populations were observed, whether due to chemical composition of water (e.g., dissolved organic carbon or calcium levels) or differences in growth. In addition, the effects of mercury burden on reproductive condition should be assessed by assessing gonadosomatic index in relation to mercury burden. The variation in lake sturgeon abundance was explained by water power management; lake sturgeon were significantly lower in abundance in managed reaches in comparison to unimpounded river reaches. Growth was significantly greater in managed reaches suggesting: i) density dependent compensation; and ii) food was not limiting sturgeon populations within managed reaches. And, size structure was skewed to larger sturgeon in managed reaches suggesting recruitment is limited within these reaches. More powerful tests to assess if water management is limiting lake sturgeon populations would be i) rehabilitate or create spawning shoals downstream of dams and ensure adequate flows during the spawning and incubation period; or ii) stock managed reaches with juvenile lake sturgeon. Recruitment would be identified as the limiting factor to population recovery if lake sturgeon abundance increased in either of the proposed studies.

The third manuscript entitled *Variation in large-bodied fish community structure and abundance among river reaches subject to different management regimes in a large river* assessed 11 large-bodied fish species with differing life history traits among three water
management regimes, winter reservoirs, run-of-the-river and unimpounded reaches. The premise of this study was if water power management is affecting fish abundance and life history characteristics, then all fish with similar life history traits should be affect the same way. Our conclusions were that water management regimes affect large bodied community structure. Discriminant function analysis and neural network classified (> 70% classification rates) water management regime based on fish sampled in nets (both trapnet and gillnet separately). Littoral zone benthivores were significantly lower in winter reservoirs than unimpounded reaches which was predicted due to the level of drawdown in these reaches during the winter month and the subsequent affects on benthos production. Conversely, other benthivores (common white sucker and Moxostoma sp.) increased in abundance which suggest food requirements can be fulfilled below level of drawdown (i.e., do not rely on feeding in the littoral zone). Planktivores or species that are planktivorous at early life stages, significantly increased in winter reservoirs suggesting conditions were favourable. Growth, condition and mortality did not vary among reach types except smallmouth bass were in better condition in winter reservoirs than unimpounded reaches. And finally, lake sturgeon were the only fast water spawning species whose recruitment was affected in run-of-the-river reaches suggesting spawning requirements are more stringent for lake sturgeon, a fluvial dependent species, than other fast water spawning species. Potential further research could be on other regulated river systems to determine if similar effects are observed under similar water management regime.
The final manuscript entitled *Evaluation of the predictive power of a lake sturgeon habitat suitability model at multiple scales* developed a spatially explicit application of an existing habitat suitability model for lake sturgeon, applied the model to several Ottawa River reaches and evaluated the predictive power of the model. It was determined that model outputs were unreliable (i.e., they were not accurate). This was related back to interpolation of substrate layers. Attempts to improved (e.g. used a different interpolation technique, change the resolution) were ineffective. As such, habitat suitability index was determined for each netting location. Significantly more lake sturgeon were sampled in good (HSI > 0.6) habitat in comparison to poor habitat (HSI < 0.3) in both juvenile foraging and adult foraging habitat. In addition, lake sturgeon CUE from standard index netting projects increased in proportion to the overall foraging component (C_F) suggesting the model has some predictability at multiple scales. However, the predictive power of the model was generally poor ($R^2 < 0.18$) leading to the question on how predictive is this HSM? More research is required on if and how predictive power HSMs can be improved.

**Management Implications**

This study pertained to a large river bordering eastern Ontario, western Quebec. Water management regimes appear influence fish community structure, particularly affect lake sturgeon populations. Water management in the Ottawa River is primarily for hydro-electric purposes although it does fill a vital flood control component. Drastic changes to operating regimes are unlikely which means if the winter drawdown is limiting
benthivore population, lake sturgeon and other littoral zone benthivores will probably become locally extirpated in these reaches. A fate that will have to be accepted!

Run-of-the-river reaches appear to have recruitment issues probably relating to spawning habitat. In a large river such as the Ottawa River, lake sturgeon appear to be able to survive in fragmented reaches; there appears to be adequate foraging areas as suggested by growth analysis. Protection of mature females through harvest control and rehabilitation of spawning shoals could be a step towards assisting recovery of this species although it would be a long process strictly due to lake sturgeon life history traits.

There is a cost to our actions - hydroelectric production affects fisheries. A species such as lake sturgeon unfortunately are the cost, especially in winter reservoirs, and in terms of recruitment, in run-of-the-river reaches. One solution would be to remove all dams and eliminate all harvest (since dams are not the sole cause of lake sturgeon decline). Removal of dams is not a cost that the hydro producers would be willing to bear, nor would it be politically acceptable. The quagmire we are we face is trying to balance the use of the resource (water) for hydro-productions with a world wide decline of sturgeon. Providing water during critical times instead of utilizing it for profit may be the cost hydro-electricity producers may have bear. Lake sturgeon populations not recovering to historical levels may be a cost they have to bear if we want to balance hydro production and sturgeon populations.
We can learn for our experiences and utilize this knowledge for future hydro-electric projects, especially on rivers with sturgeon populations. Large reservoirs with a winter drawdown should be avoided. River reaches should be as large and diverse as possible to provide habitat for different life stages. Areas should be constructed at the base of dams for spawning and adequate flows during the spawning period should be requirement of any site lease. Hydrologic manipulation of rivers should be planned to minimize the risk of entrainment and seasonal disruptions in habitat or food availability (McKinley et al. 1998). Fish ladders should be incorporated within dam designs to prevent the isolation of fish populations. Natural reaches should be maintained in all rivers as a refuge for riverine species. A barrier free 250 -300 km combined river and lake range is recommended to sustain self reproducing lake sturgeon populations (Auer 1996); which essentially means some rivers should not be developed. A portion of unregulated rivers should be maintained on the landscape to ensure biological integrity of the ecosystem is sustained (Pringle et al. 2000). We may not be able to protect all lake sturgeon populations, but with careful management and planning, we may be able to prevent the extirpation of a prehistoric fish.
General References


Chao, B.F. 1991. Man, water and global sea levels. EOS, Transactions of the American Geophysical Union 72: 492


Statement of Contributions of Collaborators and/or Co-Authors

Results and manuscripts presented in this thesis were produced by Tim Haxton under the auspices of thesis supervisor Scott Findlay. Scott’s involvement was that of a thesis supervisor aiding in study design, statistical analysis, reviewing and commenting on all manuscripts. Ron Threader, Ontario Power Generation, is a co-author on one manuscript. Ron was the author of the original habitat suitability index model and provided advice on interpretations of his model, financial assistance and reviewed a draft of the Assessing the predictive value of a lake sturgeon habitat suitability model manuscript.
Appendix A. Studies incorporated into the meta-analyses
Appendix A – 1. Studies, endpoints, design and means of experiment and control groups included in effects of dewatering meta-analysis.

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Appendix A – 2. Studies, endpoints, design and means of experiment and control groups included in effects of hypolimnetic draw meta-analysis.

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Appendix A – 3. Studies, endpoints, design, habitat guild and means of experiment and control groups included in effects of flow deviation meta-analysis.

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