A Biological Synopsis of Walleye (*Sander vitreus*)

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A BIOLOGICAL SYNOPSIS OF WALLEYE
(*Sander vitreus*)

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ABSTRACT

Hartman, G.F. 2009. A biological synopsis of walleye (*Sander vitreus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2888: v + 48 p.

This synopsis reviews biological information on the walleye in support of a risk assessment evaluating the impacts of its expansion into non-native areas of Canada. Walleye is a fecund piscivore widely distributed in North America from about 32° to 68° north latitude. Large, shallow, turbid lakes are optimal. Walleye are top predators and will eat almost any living organism they can get into their mouths. Yellow perch are the main prey. While much sought by anglers, walleye also supports substantial commercial fisheries. Walleye have been heavily stocked across North America for 120 years, to establish new populations, supplement existing stocks, or for put-and-take fisheries. The ecosystem effects of these introductions have been wide-ranging and are difficult to predict or control. Introduction of walleye may affect other fish through competition, predation, or by altering species composition. In western reservoirs, such as in the Columbia, walleye predation may be a serious problem for salmonids.

RESUMÉ

Hartman, G.F. 2009. A biological synopsis of walleye (*Sander vitreus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2888: v + 48 p.

Le présent synopsis examine les données biologiques sur le doré jaune pour appuyer une évaluation des risques portant sur les effets de l’expansion de son aire de répartition vers des régions non indigènes au Canada. Le doré jaune est un poisson piscivore prolifique qui occupe en Amérique du Nord une vaste aire de répartition, du 32° au 68° de latitude nord. Il privilégie les eaux turbides des grands lacs de faible profondeur. Le doré jaune est un prédateur de niveau trophique supérieur et il consomme à peu près n’importe quel organisme vivant qu’il lui est possible d’avaler. Sa proie principale est la perchaude. Tout en étant très populaire auprès des adeptes de la pêche à la ligne, le doré jaune est également l’objet d’importantes pêches commerciales. Pendant 120 ans, on a fortement empoissonné les cours d’eau de doré jaune, partout en Amérique du Nord, en vue d’établir de nouvelles populations, d’alimenter les stocks existants ou encore d’approvisionner les pêcheries à peuplement organisé. Les conséquences de ces introductions sur l’écosystème ont eu une portée très large et sont difficiles à prédire ou à contrôler. L’introduction du doré jaune peut influer sur d’autres poissons par la concurrence et la prédation ou par une altération de la composition spécifique. Dans des réservoirs de l’Ouest comme le Columbia, la prédation par le doré jaune peut représenter un problème important pour les salmonidés.

1.0 INTRODUCTION

Walleye, *Sander vitreus*, is a fecund piscivore usually found in moderately productive lakes. Walleye is an effective predator, much sought by anglers; it also continues to support substantial commercial fisheries. The range of walleye in North America has expanded dramatically through transfers intended primarily to augment recreational fisheries. The ecosystem effects of these introductions have been wide-ranging and remain difficult to predict or control.

This paper provides information on the distribution, biology, and native range expansion of walleye in Canada, and describes documented risks to other biota.

1.1 NAME, CLASSIFICATION AND IDENTIFIERS

Kingdom: Animalia
Phylum: Chordata
Class: Actinopterygii
Order: Perciformes
Family: Percidae
Genus: *Sander*
Species: *vitreus*

Scientific name: *Sander vitreus* Mitchill (1818)

Common names (English): blue pike, dory, glass eye, gray pike, green pike, jack salmon, marble eye, pickerel, pike-perch, wall-eyed pickerel, wall-eyed pike, wall-eyed pike-perch, walleye, walleye pike, walleyed pike, yellow pickerel, yellow pike, yellow pike Perch, yellow pike -perch, yellow walleye

Common Names (French): doré

Integrated Taxonomic Information System Serial Number: 650173
Sources: Zip Code Zoo; Animal Diversity Web (all 2008).

1.2 DESCRIPTION

Young walleye are sub-cylindrical but becomes more compressed as they grow (Scott and Crossman 1973). In Canada, walleye have achieved lengths of 1,067 mm; specimens over 700 mm are considered large (Scott and Crossman 1973). The greatest body depth is under the anterior half of the first dorsal fin.

The head and teeth are well suited to predation. The head length, relatively greater in young fish, is 23.8 to 28.4% of body length. The head is armored with serrae on the preopercular bone and a spine on the opercle. The eye, relatively large in the young, is 16.1 to 26.7 % of the head length. The mouth is large and horizontal, with equal upper and lower jaws (Figure 1). The maxillary forming the outer margin of the upper jaw extends past the center of the eye. There are strong teeth on the maxillaries, premaxillaries, jaws, head of the vomer, and palatines. The canine teeth on the head of the vomer may be re-curved for effective predation. There are teeth on the inner and outer edges of the gill arches (Scott and Crossman 1973).

The fins are well developed and contain spiny and soft rays. The two dorsal fins are clearly separated, with the anterior fin supported by 12 to 16 strong spines. The second dorsal is supported by one spine and 18 to 22 soft rays. The pectoral fins are rounded and without spines. The pelvic fins are supported by one spine and five rays.

Ctenoid scales are extensive and well developed. They cover the back, sides, under-belly, and pectoral area. The opercular and preopercular areas are lightly scaled or naked. Overall color of the walleye varies with habitat and may range from olive-green to golden-brown to yellow on the back. The belly is whitish and paler than the back and sides. The sides and back may have six to ten diffuse dark blotches.

Figure 1. Walleye *Sander vitreus*, Image courtesy of the New York State Department of Environmental Conservation, Albany NY.

1.2.1 Taxonomy and genetics

Walleye is a close relative of the perches and darters. There is a wide range of variability both within and between walleye populations. Walleye and sauger (*Sander canadense*) hybridize in nature (Scott and Crossman 1973; Billington and Koigi 2003). The value of such hybrids for aquaculture is dealt with in Garcia-Abiado et al. (2004).

The history and differentiation among species of Sander dates back at least ten million years. The separation of the North American and European species occurred 5-10 million years ago (Billington et al. 1990); sauger (now *Sander canadensis*) and walleye began divergence 3-4 million years ago. During Wisconsin and Pre-Wisconsin glaciations, the walleye was pushed to the south, with re-invasion of Canada occurring in the post-glacial period. Mitochondrial DNA studies indicate that a “type A” group predominates in the eastern Great lakes, and a “type B” group in the western Great Lakes (Billington and Hebert

1988). The presence of a third mtDNA group in South Indian Lake, Manitoba, western Lake Superior, Hay River, NWT, and South Dakota supports the possibility of a third refugium in the upper Missouri River (Ward et al. 1989).

2.0 DISTRIBUTION

2.1 GLOBAL NATIVE DISTRIBUTION

Walleye is widely distributed in North America (Figure 2).. It is usually confined to fresh water and occurs only rarely in brackish water. In the U.S., walleye occur naturally from New Hampshire, south to Pennsylvania and west of the Appalachians to the gulf coast in Alabama. Natural distribution includes the eastern parts of Nebraska, North and South Dakota (Lee et al. 1980).

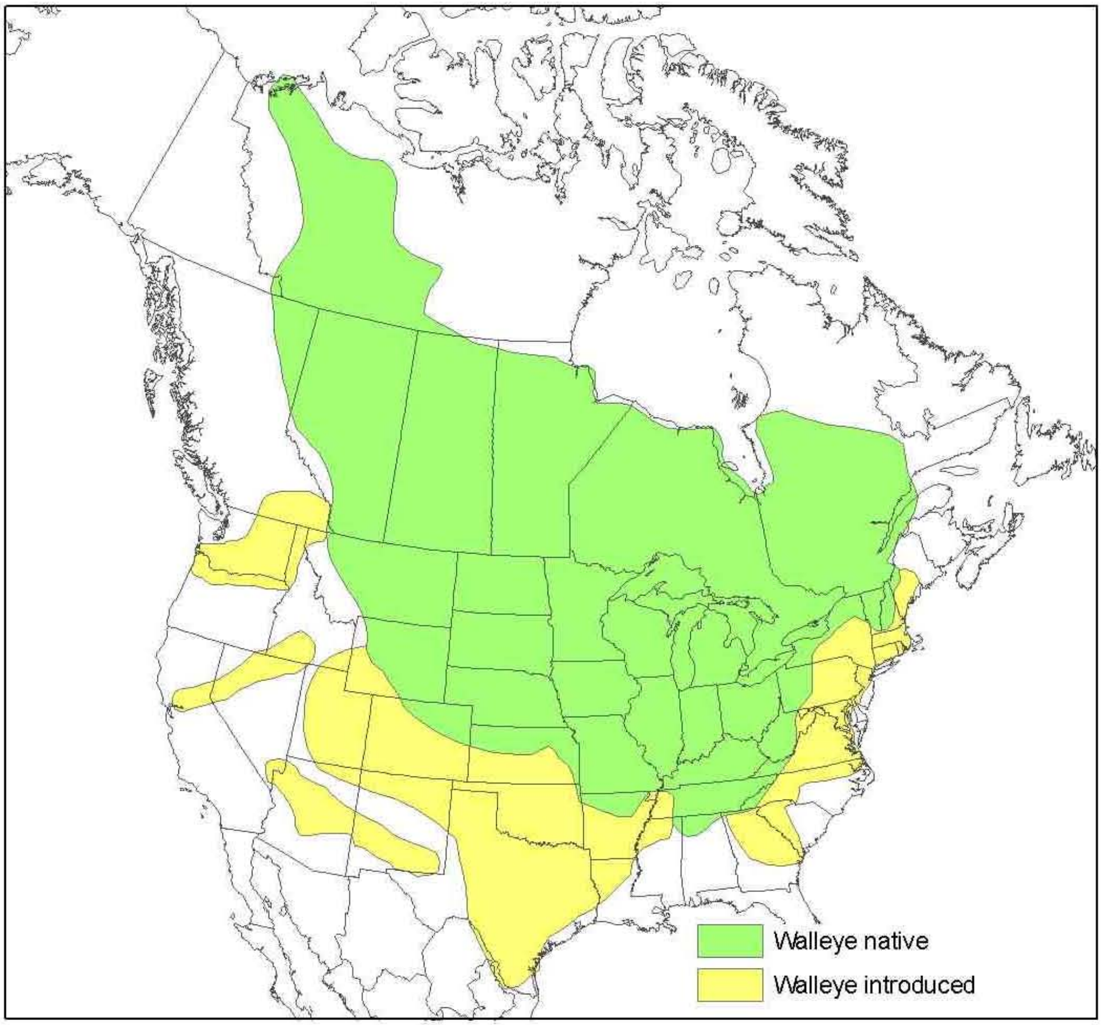

Figure 2. The North American distribution of walleye from Bradford et al. (2008)

2.2 NATIVE DISTRIBUTION IN CANADA

In Canada, walleye occurs from Quebec up to and including the Peace and Liard River systems in north-eastern B.C. Its northerly limits follow the boundaries of northern Saskatchewan and Manitoba, along the southern shores of Hudson Bay and James Bay eastward into Labrador. It occurs in the Mackenzie River drainage to the mouth of the river.

The most northerly large-lake population is in Great Bear Lake, where walleye are restricted to a small area at the south end of McVicar Arm. Walleye occurs further north in the delta of the Mackenzie River, where conditions may not be representative of the latitude (Johnson 1975).

In B.C., walleye occur naturally only in the north-eastern corner of the province. Native distribution includes the lower Peace, Liard, and Hay River drainages. They do not occur naturally in all water bodies within this region (McPhail 2007). In both the Peace and Liard drainages, walleye are found below major barriers formed by canyons and rapids (McPhail and Carveth 1994). Below Peace Canyon Dam, walleye occur in the Halfway, Pine, lower Moberly and Beatton rivers. A native lacustrine population may occur in Moberly Lake. However, Moberly Lake is a cold “lake trout system” which may not be favorable to walleye life history needs (Baccante 2007 pers. comm.). In the Liard River system, walleye are found below the Liard canyon in the main stem and in the Petitot River. Native lacustrine populations are found in Maxhamish and Klua Lakes (Anderson 2007 pers. comm.).

In Alberta, water temperature and elevation determine the limits of distribution. No native, reproducing populations of walleye occur at elevations higher than 1,000 m. The distribution of walleye in Alberta has not changed appreciably during the history of fisheries management (Sullivan 2007 pers. comm.)

2.3 NON-NATIVE DISTRIBUTION IN CANADA

The distribution of walleye has increased significantly in Canada and the U.S. In Canada, expansion in all provinces except B.C. has involved increases in range rather than invasion of entirely new drainages. In B.C., expansion has involved an entirely new watershed-the Columbia River system.

Aquatic species may invade new areas through as many as eight different pathways (Kerr et al. 2004). These include fish stocking programs, live bait industry, canals and diversions, all of which may be responsible for walleye invasions. Walleye were first introduced in the United States northwest in the 1940s and 1950s, and now occur throughout the upper Mississippi and Columbia River basins (McMahon and Bennett 1996). First stockings in Wyoming in 1936 were unsuccessful, but those in 1943 and 1946 established fisheries (White 1982). In 1960, walleye were introduced into Lake Roosevelt, about 200 km from the B.C.-Washington boundary. From there they spread though the lower Columbia River and upstream into B.C. In this region, several fisheries have developed in tail-waters and reservoirs (McMahon and Bennett 1996). Beginning in 1974, walleye were stocked in several reservoirs in southern Idaho. In Wyoming, walleye were first recorded in 1961 in a reservoir in the upper Platte River. During subsequent high water periods, they were flushed down the Platte River and now occupy reservoirs in 450 km of river (McMahon and Bennett 1996). Walleye currently occur in all states except Hawaii and Alaska.

2.3.1 Expansion of distribution in British Columbia

There is an introduced population of walleye in Charlie Lake, near Fort Saint John. They were introduced from Ontario in 1957, as an egg plant (Lyons 2007 pers. comm.). At the time of the introduction, Charlie Lake had a dense but un-quantified population of non-sport fish. Walleye now thrive there, primarily on zooplankton (Baccante 2007 pers. comm.). Walleye have been successfully introduced into Swan Lake. Efforts to introduce walleye from Charlie Lake into Cameron Lake have not been successful.

In south-central B.C., walleye ascended through the Columbia system through planting, invasion, and illegal transport following the 1960 introduction in Roosevelt Reservoir. McMahon and Bennett (1996) list thirty occurrences in the Columbia River: nineteen were from planting, nine from invasions, and two were from illegal introductions. McPhail (2007) describes walleye as “seasonally abundant” in the Columbia main stem from Keenleyside dam south to the U.S. border. At the confluence of the Columbia and Kootenay rivers, near Castlegar, walleye occupy the lowest 1.5 km of the Kootenay River below the Brilliant Dam (Golder and Associates Ltd. 2003). They occur in the Waneta and Seven Mile reservoirs in the Pend d’Oreille system and in the Kettle River just north of the international boundary (McPhail 2007). There is a small population of walleye in Christina Lake (Jantz 2007 pers. comm.).

Walleyes may be blocked from ascent far into B.C. in the Kettle River; however, further movement into the Arrow lakes (Columbia River) is possible. A barrier on the Kettle River, about 0.5 km upstream from the confluence with the outlet creek from Christina Lake, blocks upstream invasion farther into B.C. There are locks in the Keenleyside Dam though, built in 1969, which may permit movement of walleye. The lock can accommodate small boats but it is not clear to what degree conditions below the dam may impede upstream walleye movement.

2.4 MODES OF INVASION

Fish are moved by government agencies in response to changing demands of the angling public. Illegal introductions are also carried out by anglers or “bucket biologists” (McMahon and Bennett 1996). Such transfers are difficult to prevent.
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When walleye were proposed as a way to increase angling opportunities for the Ferry Canyon Reservoir, Montana Fish and Wildlife (MFW) hosted a workshop on trout-walleye interactions, carried out a survey (1,831 anglers) and did a pre-introduction risk assessment. On the basis of the results, MFW decided not to introduce walleye; unfortunately, walleye were nonetheless introduced illegally and have proliferated (McMahon and Bennett 1996).

3.0 BIOLOGY AND NATURAL HISTORY

3.1 AGE AND GROWTH

Growth rates in walleye are influenced by factors such as latitude, productivity of lakes, predator - prey relationships, population density and food quality. There are 150 records of 'length-at-age' for walleye in Colby et al. (1979).

Walleye occupy a range from about 32° to 68° north latitude, which influences growth rate. Baccante and Down (2003) and Colby et al. (1979) indicate that overall growth among populations at low latitudes is more rapid than it is at high latitudes. At five years, fish in Charlie Lake are about 35 cm, while those in Saginaw Bay and Claytor Reservoir are about 42 and 65 cm respectively. At 10 years, fish are about 40, 55 and 80 cm respectively in Charlie Lake (55° N.), Saginaw Bay (44º N.) and Claytor Reservoir (37º N.). Although only nine populations were reviewed in this study, the range of sizes that walleye may reach was 45 to 70 cm by age 14. Length increased more rapidly during the first six years.

While population density is a strong regulator of growth in adult walleye populations, its influence is moderated by other factors including pH, conductance, morphoedaphic index (MEI), and maximum depth (Sass and Kitchell 2005). Nate et al. (2000, 2001) reported that lake size, percentage of sand and muck bottom, and water conductivity all had a positive influence on walleye abundance.

As with adults, growth rates among young age-0 walleye are strongly affected by density, but are also influenced by density-independent factors. The growth rates of young walleye are highest in spring and early summer, when fish are most susceptible to physical and biotic factors. Most age-0 walleye growth in Lake Winnebago, Wisconsin occurred during July-August, and was over by October (Staggs and Otis 1996). In this study, water temperature had the greatest positive effect on growth. In studies in Illinois reservoirs, Hoxmeier et al. (2006) showed that increased benthic prey density had a positive effect on growth among age-0 walleye at all sizes from 6 mm and 100 mm. On the other hand, elevated temperature had a positive effect on only the 6 mm larval fish. In pond and tank experiments, growth rate of larval walleye increased with density of zooplankton. Consumption of zooplankton increased with food density up to 20-

30 plankton/l. However, when plankton was held at low levels, larval walleye switched to feeding on benthic invertebrates.

Density of fish, hence prey availability, affect the growth of young walleye. In a major stock rehabilitation program in Lake Erie, standing stock in 1983 was estimated to be three times greater than it was in 1976. Lengths of young-of-the-year walleye declined from about 212 mm to 190 mm during this period (Muth and Wolfert 1986).

Both competition and predation may affect survival and growth of young walleye. In a study in Lake Winnebago, Wisconsin, there was evidence of competition between young-of-the-year walleye and sauger *Sander canadensis* (Staggs and Otis 1996). Both species grew more rapidly when abundance of freshwater drum *Aplodinotus grunniens* and trout-perch *Percopsis omiscomaycus* were high. In centrarchid-dominated waters, survival of walleye larvae and fry (48 to 61 mm) was below 4%. Growth of larger stocked walleye (132 to 216) mm was slower in waters where bluegill *Lepomis macrochirus* densities were high (Santucci and Wahl 1993).

Growth rate in walleye is sexually dimorphic. Growth data from 1990 to 1999 for a sub-sample of 25 surveyed lakes indicated that females were about 4, 11, and 15 cm longer than males at 4, 10, and 15 years respectively (Sass and Kitchell 2005). Mathias et al. (1985) reported a similar relationship between walleye sex and growth rate. In their paper, 6-year-old males and females were the same length. However, females in the 16 to 20 year age classes were about 6 cm longer than males.

All of these observations indicate complex relationships among competition, predation, and abiotic factors that influence walleye growth and survival. These relationships affect recruitment, and may not readily be extrapolated from one geographic area to another. For example, in Oneida Lake, N.Y., rapid growth among age-0 walleye moved the cohort quickly past a critical 175 mm size, so that growth and recruitment were positively related. In Lake Erie, however, density and predation among young walleye were low. Rapid warming of the lake during spring, coupled with the size of the parent stock, increased recruitment of age-1 fish to the age-2 group (Madenjian et al. 1996).

3.2 PHYSIOLOGICAL TOLERANCES

Normal function among fishes occurs within species-specific ranges of oxygen concentration, pH, temperature and other factors. The physiological tolerance of a species determines the levels at which stress or functional limitations occur. Some levels of tolerance can be raised or lowered by acclimation (Brett 1958).

3.2.1 Temperature

Published temperature tolerances vary. For example, upper limits for adult walleye are given as 29 to 31ºC (Hokanson 1977), and 34 to 36ºC (Momot et al. 1977 cited in McMahon et al. 1984). Adult walleye avoid temperatures >24ºC (McMahon et al. 1984). Lower lethal temperatures for walleye are not well defined; however, pre-spawning behavior may begin at 1.1ºC (Colby et al. 1979), so the lower lethal temperature must be near zero.

Lower temperature limits for spawning are near 1.1ºC; upper temperatures were 11.1 °C (Scott and Crossman 1973). The upper temperatures limiting successful spawning and egg viability may, however, vary among populations (Colby et al. 1979). Schneider et al. (2003) concluded that the normal temperature fluctuations in hatcheries or natural spawning grounds are not great enough to affect walleye egg incubation.

Different age groups of young walleye vary in their tolerance to abrupt temperature change. In laboratory and field tests, walleye of total length 9.3 mm and acclimated to 14 ºC experienced higher mortality than did 44 mm fish when transferred to 31 ºC water (Clapp et al. 1997).

Walleye fry are sensitive to light (McMahon et al. 1984). The demersal fry actively seek shelter and prefer turbid water. Optimum temperature for fry is 22°C; no growth occurs below 12°C, or above 29°C. Temperatures of 31°C to 33°C are lethal. Optimum oxygen concentration is ≥5 mg/l (McMahon et al. 1984).

3.2.2 Oxygen

Oxygen enters water through diffusion, aeration (rapid water movement) and .photosynthesis. Oxygen can be removed from water by decomposition of organics, and its concentration falls with increasing temperature; low oxygen can readily become a stress factor. Walleye are not stressed by the highest concentrations that may occur, but can tolerate low oxygen concentrations for a short time only. Levels below 1 mg/l are lethal (McMahon et al. 1984). At 1.0 to 1.5 mg/l, walleye may rise to the surface, and at 0.6 mg/l they become uncoordinated and expire (Colby et al. 1979, McMahon et al. 1984). Incubating eggs may tolerate oxygen concentrations as low as 3.4 mg/l, although delayed hatching and reduction in fry size occur at these levels (McMahon et al. 1984).

3.2.3 pH

A range of pH from 6.0 to 9.0 is considered to have no stressful effects on walleye. pH levels below 6.0 may cause reproductive failure and loss of recruitment (McMahon et al. 1984). In this case, the pH value is beyond the tolerance level for one activity, but may be tolerable in terms of survival as shown in Brett's model (Brett 1958).

pH tolerance may be affected by other water quality parameters. Populations of roach and perch are unaffected in some Finnish lakes at pH 5.5 to 6.5, even though values below pH 6.0 are considered too low for fish. The amounts of aluminum or calcium affect biological responses to low pH (Mannio 2001). In some situations, low pH may reduce reproductive success, resulting in low fish densities and higher growth rates (Raitaniemi 1999).

Bioassay experiments indicated that pH levels from 9.8 to 10.3 were lethal to 3 to 12-day old walleye. In 3-day old walleye, no 6 hr. mortality occurred at pH 8.01 to 9.8. At pH 10.5, 100% mortality occurred within two hours. Eight-day fry were less tolerant to pH 10 than were 3-day old fry (Bergerhouse 1992).

3.2.4 Pollution

Walleye may be stressed by a wide range of pollutants. Sources in Canadian waters include sediment from forestry operations, run-off from agricultural lands, sewage from urban areas, chemicals from pulp mills, waste from mining and oil operations, and fiber from pulp mills. In a study of the Peace, Athabasca and Slave River systems, Cash et al. (2000) found dioxins, furans and other organic contaminants at levels comparable to those in other Canadian rivers, although the amounts of mercury, PCBs, dioxin and furans exceeded guidelines at certain times and locations. Although walleye were not dealt with in the study, it was found that sex hormones were depressed in burbot and long-nose suckers, and external abnormalities were common (Cash et al. 2000).

In Canada, there are about 6,000 abandoned mine sites. Few are being monitored for impacts of acid mine discharge or metal contamination (Leis and Fox 1996). In one study, young walleye were smaller and had smaller stomach contents after a gold mine tailings spill than those in a control area. Densities were lower due to higher mortality or out-migration (Leis and Fox 1996). Historically, pulp mills produced fiber that consumed oxygen, smothered walleye eggs, and limited the survival of young-of-the-year walleye (Smith and Kramer 1963, 1965, Smith et al. 1966, Colby and Smith 1967). Pulp mills in Canada still produce cumulative environmental stresses. Fish such as walleye are still subject to contaminants in systems like the Athabasca River in Alberta. However, levels of fiber are lower, and the environmental concentrations of furans, dioxins, chlorinated resin acids and chlorophylls have declined since 1980. Nevertheless, the compounds are still found in fish, and their cumulative effects still cause stress (Alberta Environment 2002).

3.3 REPRODUCTION

Reproduction in fishes involves development of reproductive structures, maturation of eggs and sperm, movement to a spawning site and spawning behavior; all are underlain by physiological processes and endocrine control. The topic is dealt with by Hoar (1969).

3.3.1 Maturation

The size and age at which walleye reach sexual maturation is dependant on water temperature and lake fertility. The latter influences food availability (Colby et al.1979) and the amount of energy available for gonad development (Henderson and Nepszy 1994).

Walleye are sexually dimorphic. Females have a higher growth rate than males before and after maturation; by age 6, immature females averaged 390 mm, while males averaged 325 mm. Among mature fish age-6 to 16, females were about 90 mm longer than males (Henderson et al. 2003).

Females mature at 3 to 6 years and 356 to 432 mm (Scott and Crossman 1973). Males mature earlier (2 to 4 years) and as small as 270 mm. There is a trend to earlier maturation among faster growing fish. There is also a trend for later maturation in colder waters in which walleyes have a longer life span. In Lake Oneida, N.Y., the proportion of non-ripening walleye was highest during years of poorest growth (Colby et al. 1979).

Maturation of walleye eggs requires winter temperatures below 10ºC. Walleye failed to reproduce in a reservoir in which the winter temperatures were 10 to 12.5ºC (McMahon et al. 1984). During winter, cold water may enhance ovarian development by increasing the likelihood that certain amino acids are incorporated into the egg membranes (Zweifel 2006).

3.3.2 Fecundity

There is correlation between body size and relative size of the gonad. Ovaries in mature females may be from 16.3 to 27.8% of the body weight depending on location and female size. Walleyes have high fecundity (Carlander 1950; Wolfert 1969; Baccante and Reid 1988; Baccante and Colby 1996). Fecundity in walleye may vary with a number of factors such as fish size, population, geographic area, exploitation rate and latitude. Depending on size, walleye may produce from 40,000 to 612,000 eggs (Scott and Crossman 1973).

There may be discrete population differences in fecundity. Walleye in the western basin of Lake Erie produce about 75,000 eggs at 445 mm (Wolfert 1969), while those in the eastern basin produce about 60,000. Wolfert (1969) found that the fecundity rises to about 600,000 for a fish 775 mm long in the western basin, whereas a fish 775 mm long in the eastern basin contained 400,000 eggs. Females in the western basin matured at a shorter length and younger age than those in the eastern basin, and the two groups may constitute discrete populations with different length/fecundity relationships (Wolfert 1969).

Exploitation rate can change fecundity in walleye. Reduction of populations from 1,336 to 375 in Henderson Lake, and from 5,596 to 4,206 in Savanne Lake, resulted in fecundity increases of 27% and 35.8% respectively (Baccante and Reid 1988).

3.3.3 Spawning habitat

Walleye spawn in lakes and rivers. Walleye do not normally choose mud bottom areas, sludge, fiber deposits, steep slope shore areas or shallows that were not under wave action (Colby et al. 1979). In lakes, they spawn in relatively shallow water, from a few centimeters to several meters deep. In rivers, spawning depths were 0.6 m in the Provo River, Utah, and 0.2 to 0.9 m in the Talbot River, Ontario (Colby et al. 1979).

Eschmeyer (1950) cited in Colby et al. (1979) reviewed the spawning ground conditions described by several workers. Walleye have spawned in mouths of rivers and creeks, along shorelines, on sandy bars, on shallow bars and flats bordering deep water, on stick and stone in running water at the base of water falls, in lakes over broken rocks, in streams on sandy bars, in near-shore sites in shallow bays, on hard bottom in running water, in riffles in tributary streams and, in some cases, over vegetation (Colby et al. 1979).

Cobble and gravel reefs are optimum spawning habitat. Preferred stream velocities ranged for 0.0 to 1.0 m/sec. with a mode at 0.8 m/sec. Preferred depth was 1.3 m (McMahon et al. 1984). These data are based on information from the Missouri River and sites in Michigan and may not apply to situations further north. Spawning does not always take place on rubble and gravel areas. In the upper Mississippi River, six out of seven radio-telemetry tracked walleye spawned in a back-channel with flooded timber, bulrushes, and reed-canary grass (Ickes et al. 1999).

The lower reach of the Pushkwakau River is one of the best known stream spawning habitats in Saskatchewan. Spawning and egg incubation depths there ranged from 7 to 94 cm. Preferred water velocity in the spawning area ranged from 30 to 100 cm/sec. The substrate in the area of most spawning was gravel and cobble (Liaw 1991).

3.3.4 Pre-spawning movements and spawning behavior

Lake and reservoir populations of walleye make moderate migrations to spawning areas. Walleye from Lac La Ronge migrated 10 to 15 km through an adjacent lake to tributaries. Over the six-year study, runs occurred at different intervals depending on temperature. Migration periods were as early as April 8 to May 11 in 1951, and as late as May 6 to May 22 in 1956 (Rawson 1957). The majority of walleye were recovered within 25 km of the site where they were marked as spawners. Of 18 walleye recovered, 8 had traveled between 2 and 4 km.

One fish tagged in the Spokane River traveled 139 km up the reservoir and was recovered at Kettle Falls (McLellan and Scholz 2002). Tag recovery data does not provide precise timing of spawning migrations but they do provide evidence of the mobility of the fish.

3.3.5 Spawning time and behavior

Spawning occurs later in more northerly populations. In northern Canada, spawning may occur as late as the end of June, or it may fail to take place at all if water temperatures are too low (Scott and Crossman 1973). Walleye spawning occurs at night and the fish leave the shallow spawning areas as morning approaches.

Some homing behavior occurs among walleye populations. Tag and release studies indicated that walleye in the Muskegon River Michigan, returned to the same spawning area year after year (Crowe 1962). Olson and Scidmore (1962) found that some walleye homed in a study at Many Point Lake, northern Minnesota. Homing did not occur among the majority of fish, and the pattern of homing was irregular (Olson and Scidmore 1962).

Walleye are broadcast spawners. Males, who move onto the spawning areas first, are not territorial. In a stream environment, courtship begins with both sexes approaching from behind and pushing against the other fish. Approached fish either hold position or withdraw. As the behavior progresses, a group of several males and one female moves up from the bottom. Spawning occurs in open water (Ellis and Giles 1965). Females release eggs 200 to 300 at a time, as often as every five minutes. They may complete spawning in one night and leave, but males remain longer in the spawning area (Colby et al. 1979). The eggs fall to the bottom, where they adhere to the gravel and later may sink into crevices as they become water-hardened and lose their stickiness (Scott and Crossman 1973).

3.3.6 Hatching and larval growth

Walleye eggs require from 4 to 10 days to hatch, depending on water temperature (Scott and Crossman 1973). Walleye larvae are believed to do best if they grow on clean, firm gravel substrates with adequate oxygen. At oxygen concentrations below 3.4 mg/l, larval development was retarded, size was smaller and, the surviving fry were weaker swimmers (Colby et al. 1979). In Lake

Erie, year-class success was highest during years when the rate of water warming in the incubation period was highest (Busch et al. 1975; Roseman et al. 1996). Mortality of eggs may range from 100% to as low as 3.4% (Baker and Scholl 1969, cited in Colby et al. 1979). Wind action, current, low oxygen levels (in muddy areas), stranding and predation may cause mortality. High mortalities at this stage are a major cause of year strength fluctuation.

Egg size influences the early life history of walleyes. Larvae from eggs with the most yolk were largest (Moodie et al. 1989). The fragile, newly hatched larvae are 6 to 8.6 mm long. Once the yolk sac is used up, fry move into water 3.05 to 8.6 m deep (Scott and Crossman 1973). Walleye that hatch out in streams are carried downstream to lakes. In Apsley Creek, Ontario, newly hatched walleye larvae drifted passively downstream to Jack Lake (Corbett and Powles 1986). Optimum temperatures for fry survival are from 15 to 2 ºC. In the lower Wisconsin River, abundance of age-0 walleye was best predicted by average water temperature during April, the month of spawning (Lyons 2003).

3.4 FEEDING AND DIET

There are ontogenetic shifts in walleye diet, from zooplankton to benthic invertebrates to fish (Hoxmeier et al. 2004). Adult walleye are essentially full-time piscivores.

3.4.1 First diets and feeding ontogeny

Food of larval walleye in Oneida Lake consisted mainly of copepods, cladocerans, and fish. However, the fish were selective in their choice of plankton species (Houde 1967). Stocked walleye fry in Clear Lake, Iowa began feeding on zooplankton at 9 mm. The size of the zooplankton they ate increased as they grew and moved inshore. There was evidence that early season walleye diet reflected the composition of zooplankton in Clear Lake.

The food of walleye shifts quickly from plankton to invertebrates and then to fish (Scott and Crossman 1973; Colby et al. 1979; Mathias and Li 1982). Colby et al. (1979) listed the plankton and invertebrates eaten by walleye 5 to 9 mm long: rotifers, copepod nauplii and adults and cladocerans. Zooplankton concentrations of 49 per liter were enough to support successful growth at first feeding in ponds (Johnston and Mathias 1993). As fry grew they ate more of the large zooplankton (Houde 1967) and, at the same time, began to concentrate on mayfly nymphs. By 30 mm, walleye fry shifted to fish (Colby et al. 1979).

Year-class strength can be strongly influenced by conditions during the first year of life. In Lake Erie, young walleye 7 -8 mm long fed primarily on phytoplankton, rather than their usual food, zooplankton (Paulus 1972; cited in Colby et al. 1979).

3.4.2 Cannibalism

Cannibalism is a significant part of walleye feeding behavior and may affect population structure. It has been recorded in a number of lakes (Rawson 1957; Chevalier 1973; Colby et al. 1979) and is common among young walleye in pond environments (Loadman et al. 1986). Cannibalism in Oneida Lake was considered high enough to affect year-class strength (Chevalier 1973).

Cannibalism is influenced by the availability of other fish prey species. Cannibalism by adults on young-of-the-year walleye was low in Oneida Lake during years when perch were abundant. Forney (1974) suggested that perch might act as a buffer controlling the intensity of predation. In Lake of the Woods, Minnesota, young-of-the-year and 1+ walleye preyed on nine species of fish, including their own. However, the amount of cannibalism was low, and predation on sauger was negligible (Swenson and Smith 1976).

3.4.3 Diet in a natural habitat

Walleye consume a wide range of fish. Colby et al. (1979) list the following species or groups of species that are preyed upon by walleye: sucker *Catostomus* sp., crappie *Pomoxis* sp., alewife *Alosa pseudoharengus,* gizzard shad *Dorosoma cepedianum,* sculpin *Cottus* sp., peamouth *Mylocheilus caurinus,* emerald shiner *Notropis atherinoides,* spottail shiner *Notropis hudsonius,* northern pikeminnow *Ptychocheilus oregonensis,* redside shiner *Richardsonius balteatus,* white perch *Morone americana,* white bass *Morone chrysops,* rainbow smelt *Osmerus mordax,* yellow perch *Perca flavescens,* darters *Percina* sp., trout perch *Percopsis omiscomaycus,* coho salmon *Oncorhynchus kisutch,* rainbow trout *Oncorhynchus mykiss,* sockeye salmon *Oncorhynchus nerka,* chinook salmon *Oncorhynchus tshawytscha*, and freshwater drum *Aplodinotus grunniens*. Additional species taken are bluegill *Lepomis macrochirus* (Kolar et al. 2002); tessellated darter *Etheostoma olmstedi,* burbot *Lota lota,* pumpkinseed *Lepomis gibbosus* and cisco *Coregonus artedii* (Forney 1974); bluntnose minnow *Pimephales notatus,* golden shiner *Notropus volucellus,* johnny darter, *Etheostoma nigrum,* and logperch *Percina caprodes* (Lyons 1987).

This enormous variety clearly suggests that walleyes will eat any species of fish they can; however, perch is the most common. Walleye can have a large impact of the prey species in a lake. In Lake Erie in 1986 and 1987, walleye consumed 94,300 and 83,700 tons of prey respectively (Hartman and Margraf 1992).

Prey body size and abundance may influence its use by walleye. Body depth may be a determining factor in the size of fish eaten. Prey body depth, relative to walleye length, was similar for three common food species tested in laboratory experiments: bluegill *Lepomis macrochirus*, gizzard shad *Dorosoma cepedianum* and golden shiner *Notemigonus chrysoleucas*. Prey species length was less critical (Einfalt and Wahl 1997). Prey species abundance may influence the rate of predation. Before alewives arrived in the spring in Lake Michigan, rainbow smelt were the most important item in the diet of walleye. After spawning alewives moved inshore and become abundant, they formed 71% of the diet of the walleyes. Once alewives left in the fall, no single prey species predominated in the diet (Wagner 1972).

When rainbow smelt *Osmerus mordax* were stocked in Horsetooth Reservoir, CO, consumption of crayfish, salmonids, and bass species by walleye declined to near zero (Jones et al. 1994). These results might suggest introduction of a buffer prey species when walleye enter salmonid waters. However, there may be serious risks in introducing a second exotic species into salmonid habitat. Magnuson (1976) described such bio-manipulation as “a game of chance”.

3.4.4 Special attributes-sight and feeding

The retinal layer of the walleye eye contains a highly developed layer of sensitive epithelial pigment and guanine (Ali and Anctil 1968). The latter gives the eye its characteristic reflective appearance. This feature adapts the walleye to turbid water and crepuscular feeding (Ali and Anctil 1968). Large, shallow mesotrophic lakes with turbid environments (Secchi disc 1–2 m) are optimal habitats for the walleye (Scott and Crossman 1973). Although walleye can thrive in clear water, a special layer in the retina, the tapetum lucidum, is extremely sensitive to light.

The teeth and jaws undergo seasonal changes that enable walleye to prey upon different fish. The average lengths of dentary, premaxillary, vomer, and palatine teeth increased during spring, summer and fall, the maximum feeding period of walleye in Lac Ste. Anne, Alberta. Mouth indentation (the distance from tip of nose to the posterior end of the maxillary) increased from spring to fall and then through the winter period (Langer 1974). The mouth width did not follow a clear seasonal pattern. The data do, however, indicate that changes in walleye mouth features coincide with periods of maximum predation.

3.5 HABITAT

Walleye occur naturally from northern Canada to the Gulf of Mexico and are tolerant of a wide range of conditions. Large, shallow turbid lakes provide optimal conditions (Scott and Crossman 1973, Hoff 2002).

Populations are more persistent in rivers with mean June flows greater than $60 m^3$/sec, and that have not been degraded by logging (Eshenroder 2003). Habitat requirements for walleye have been described in Colby et al. (1979), and Kendall (1978). Walleye require different habitats during different stages of their lives.

3.5.1 Adult habitat

Adult habitat is defined by lake size, bottom type, depth, temperature, oxygen concentration, pH, light and turbidity (Colby et al. 1979). Suitable lakes are usually ≥ 400 ha, with large littoral zones. Walleye prefer shallow areas over rock and gravel shoals, and occur at depths from 1 to 15 m. They are usually found above the thermocline, but may drop through it during feeding. Walleye survive in a wide range of light and turbidity, but reach highest abundance in turbid waters with moderate light intensities. Physiological differences among different walleye races may reflect the habitat in which they evolved.

Walleye abundance varies with a number of limnological variables. Nate et al. (2001) found that abundance increased with lake area, but was negatively related to the following: area of the watershed, percentage of sand and or muck bottom, and conductivity. In the upper Bay of Quinte, increased light intensity and oligotrophication as a result of water clarification have coincided with the dreissenid mussel invasion. This has resulted in the bay becoming less habitable for walleye (Chu et al. 2004). A study of 49 lakes in Ontario showed that productivity of walleye was correlated with the amount of habitat providing optimum conditions of light transmission and temperature (Lester et al. 2004).

In the Columbia River in British Columbia, most walleye were caught in three types of bank habitat: (1) habitats in which banks were generally stable and at repose, with “cobble/small” or “boulder/gravel” substrates; (2) where shoreline was uniform and water velocities adjacent to the bank were low; (3) where instream cover was limited to roughness and overhead cover was provided by turbidity (Golder Associates Ltd. 2003);

3.5.2 Young-of-the-year (YOY) habitat

In lakes, young walleye occupy different habitats as they develop. Newly hatched fry, 6 to 8 mm long, have heavy yolk sacs which affect their mobility and thus, they are not able to swim. They remain on the bottom for about five days and as the yolk is used up, at about 9.5 mm, they move up and into open water. They may be carried about in the currents of the lake and they do not actively migrate to the shore area (Colby et al. 1979). At about 25 mm they make a transition from a pelagic to a demersal mode of life and take up residence in shallow, sheltered bays (Ryder 1977). In Oneida Lake, 9.5 mm fry, which have a sustained swimming ability of <3cm/sec (Houde 1969), drift with the current until captured in eddies in bays. They remain concentrated there until, at about 25 mm, they make the transition to bottom dwelling (Houde and Forney 1970).

Habitat of YOY fish changed during the course of the summer in Big Clear Lake, Ontario. In the early demersal period (mid-June to mid-July), YOY walleye used habitat 2 to 5 m deep with high macrophyte cover. During the late demersal period, (mid-July to mid-August) they shifted to low-cover shallow areas. There was also a positive relationship between prey abundance and habitat (Pratt and Fox 2001). In river systems, the distance from spawning to nursery areas and the temperature when fry drift to the nursery habitat both affect survival. At greater distances and longer drifting times, mortality risk increased because of starvation, which may be further increased at high temperatures (Jones et al. 2003).

Habitat requirements for juvenile walleye are similar to those of the adults once they leave the shallows (Colby et al. 1979).

3.6 BEHAVIOR AND MOVEMENTS

Fish movements include diel movements of various degree and direction, as well as regular seasonal movements for feeding or escape. Fish may also make migrations to spawning areas, which may be followed by passive or active downstream return of the young. In one part of their distribution or another, walleye exhibit some of these movements.

3.6.1 Movement of fry and juveniles

Young-of-the-year walleye leave shallow bays and move to deeper water from mid-summer to early autumn. They may make this movement to avoid high temperatures in the shallow areas (Colby et al. 1979). Young walleye migrate passively downstream to nursery areas. In the Valley River system, near Dauphin Lake, Manitoba, adult walleye may migrate upstream 70 km or more, making necessary a long movement of fry back to Dauphin Lake. The duration of drifting can influence mortality (Jones et al. 2003).

The time of day during which fry drift varies from one location to another. In Apsey Creek, southeastern Ontario, walleye larvae began drifting 19 days after peak spawning. Over 90% of the walleye larvae moved between 21:00 and 24:00, and were captured mid-depth in the creek (Corbett and Powles 1986).

3.6.2 Diel movements

Walleye may exhibit diel vertical movements associated with changing light intensities. They may come into shallow water to feed at night. Walleye residing between two dams in the in the Au Sable River, Michigan, were routinely active from dusk until dawn. They foraged one to two km from the resting site and congregated near sites where juvenile brown trout were stocked (DePhilip 2001).

Laboratory experiments showed that walleye 10 to 14 cm long would assume progressively higher vertical positions in a tank as light intensity was reduced from 200 to 2 lx. As the light intensity was increased the fish moved downward (Scherer 1976). Walleye move into shallow water or upper pelagic levels at night or during dawn or dusk to find optimum illumination for feeding (Colby et al.

1979), although this pattern of diel behavior is not recorded in all studies. Radio-tagged walleye moving parallel to shore in Lake Bemidji showed no diel movement onto and from shore (Holt et al. 1977).

3.6.3 Non-spawning movements

During late summer, autumn and winter, adult fish may move into deeper water. During periods of high flow, they seek out large rivers and move into tributaries of Lake Huron. Adult walleye in Little Cutfoot Sue Lake, Minnesota, move from depths of 1.2-3.0 m into depths of 3.7-4.3 m. during summer. However, juvenile fish did not make the same movement (Colby et al. 1979).

Extension of seasonal movements for feeding or spawning, coupled with changes in watershed conditions, may result in a species extending its range. Feeding movements upstream or passive displacement of fish downstream have accounted for much of the dispersal of walleyes throughout the Columbia River system.

Walleye may move large distances. In a five-year study in Great Slave Lake, distances between release and recapture were usually small, but one walleye was recovered 378 km from the tagging location (Keleher 1963).

3.6.4 Spawning movements

Mature walleye migrate from their over-wintering areas to spawning locations during late winter and early spring. This basic pattern occurs in both lakes and rivers. Pre-spawning fish make complex movements within systems of interconnected lakes and rivers (Rawson 1957; Ferguson and Derksen 1971; Rasmussen et al. 2002). Pre-spawning walleye in Nipigon and Black Bay migrated into local tributary rivers in late April and early May. Even though the bays are within about 45 km of each other the stocks were discrete.

After spawning, fish tagged in the Nipigon River dispersed in both directions. Some went to upstream lakes, some went back into Nipigon Bay (Ryder 1968). Fish tagged in the upper Mississippi River at Guttenberg, Iowa, also moved in two directions (Schoumacher 1965). Thirty-one walleye in the Cedar River, Iowa were fitted with radio transmitters during the autumn and tracked for two years. During a flood, the fish were displaced downstream and used backwaters and flooded timber for cover. In spring they moved back upstream to spawn, then dropped downstream and remained in pools (Paragamian 1989).

Spawning migrations may involve downstream movement to the spawning sites. In the Missouri River, near Fort Benton, Montana, walleyes, tracked by radio, moved downstream 240 km, spawned and returned, in some cases, to the same pool (Montana Fish, Wildlife and Parks 2004). Walleyes in the Columbia River made movements in two directions from the tagging sites. Four fish, marked in the Kettle River, were recovered after downstream movement to the spawning site in the Spokane River section of Lake Roosevelt. After spawning in the Spokane River, some fish remain the reservoir and others remain in the river. "*The majority of the walleye that leave tend to move north towards Kettle Falls*" (McLellan and Scholz 2002). Twenty-six marked walleyes were recovered between 1997 and 2001 in British Columbia from locations such as Trail (4), Hugh Keenleyside Dam (6), Waneta Dam (7), the U.S.-Canada border (6) and Castelgar (2) and one other. These data, although based on an array of tagging and recovery sites, indicate that walleye in the Columbia River system move actively (McLellan and Scholz 2002). Most fish marked in the spawning run were recovered within 25 km of the tagging site. One fish tagged in the Spokane River traveled 139 km up the reservoir and was recovered at Kettle Falls about 30 km south of the US-Canada border (McLellan and Scholz 2002).

Homing behavior was exhibited by several walleye populations. Walleye tagged on the spawning grounds tended to return to the same area in successive years (Eschmeyer and Crowe 1955; Rawson 1957; Crowe 1962; Olson and Scidmore 1962). In Oneida Lake, New York, marked walleye returned to the same location in successive years. Spawning populations from three tributaries partially intermingled in summer; however, there were differences in summer distribution of the three spawning populations (Forney 1963).

3.6.5 Swimming speed and capacity to pass barriers

Swimming performance, particularly the capacity for short bursts of speed, is an important measure of a species' ability to invade new habitat. The review of Beamish (1978) covers a great deal that is critical in understanding issues of fish swimming performance. Much of the research has been on design of fish passage structures.

Beamish (1978) defined sustained swimming performance as the speed that could be maintained for 200 minutes or more. Prolonged swimming was the speed possible for 20 to 200 minutes, and ended in fatigue. Critical swimming velocity is the maximum that a fish can attain for a specific time period. It is usually determined in a laboratory. The highest speed of which a fish was capable is the burst speed which can maintained for up to 20 seconds. The various capacities may influence whether a fish can pass a confronted barrier on one hand or, sustain swimming in some particular habitat on the other. Each of these will influence where the fish may be found. Each is relevant in the determination of where an invasive species may go and, survive when it gets there.

Publications on walleye deal with walleye swimming capacity using some of the foregoing criteria, and include sustained swimming of larvae (Houde 1969); sustained swimming speed for adults (Peake et al. 2000); critical speeds of adults (Jones et al. 1974); and burst speeds for adults (Castro-Santos and Haro

2000; Peake et al. 2000; Haro et al. 2004;). VanderKooy and Peterson (1998) compared the critical swimming speeds of young walleye with the current speeds in their environments, and Tarby (1981) studied rates of oxygen consumption and metabolic expenditure for resting and swimming walleye.

The likelihood of a fish passing a barrier involves both the capacity of the fish to perform in experimental situations and, the behavioral inclination to do so in nature.

The sustained swimming speed (*sustained swimming performance in Beamish 1978*) for small walleyes increases with fish length. Swimming speed, i.e., the velocity that is sustained for one hour by 50% of the fish, increased from 0.5 cm/sec to 5 cm/sec for fish from 7.5 cm to those near 16 cm long. In these experiments, Houde (1969) found great variation in responses among the fish and showed that the swimming speed reaches an asymptote at about three body lengths/sec.

Jones et al. (1974) carried out experiments to determine the prolonged swimming speed of Mackenzie River walleyes. They carried put experiments to determine the transit time for the smallest size of fish that could be expected to pass upstream through a 100m culvert at various water velocities. A condensed version of the results showed that the maximum water velocity at which a 40 cm long fish could make the 100m transit in 10 minutes is about 70 cm/sec. Correspondingly, the maximum water velocity through which an 11 cm fish could make the 100m transit in 10 minutes, is 30 cm/sec. The results from Jones et al. (1974) are calculated statistically and the authors recommend "*some caution*" in interpreting them.

Haro et al. (2004) measured and expressed swimming performance in a different fashion. They measured the maximum distance of ascent of fish, 314 to 317 cm long, at three water velocities. The distance decreased with increase in water velocity. Haro et al. (2004) modeled the percentage of fish that would pass various distances across a velocity barrier. Their model shows that, at a water velocity of 4 m/sec, a fish can not pass further than 5 m. At water velocity of one m/sec, 70% of the fish can pass upstream for 20 m.

Peake et al. (2000) determined the highest speeds that could be maintained aerobically by fish, 18 to 67 cm, for 60 and 10 minutes. These time criteria are not the same as those of Beamish (1978), but rather are about half of his values for sustained, and prolonged swimming performance. Differences between sustained swimming speed (Ucrit60 in Peake et al. 2000) and prolonged swimming speed (Ucrit10), is about 0.3 m/sec for small fish and, 0.2 m/sec for largest fish. Results show that the burst speed, that of a startled fish darting for one or two seconds, is high relative to that of sustained and prolonged swimming speeds. The data on prolonged swimming speed may be the most applicable to understanding of fish passage limitations in rapids >50 m.

The kind of data presented above provides some measure of the limitations on movement of walleye past barriers. The chance of a fish passing a barrier may be influenced by several things. These include water temperature and migration or movement state, i.e., is the fish returning to a spawning area. Some of the experimental data vary. In these cases, are fish upset by the test experience itself, and hence all are likely to perform less?

3.7 DISEASES AND PARASITES

Walleyes may be infected with a wide range of diseases and parasites. The major groups of organisms or afflictions that walleye may have are listed and, at best, are indicative of the range of the topic. It is not complete enough to provide any good indication of the number of diseases and parasites that may affect walleyes across their continental distribution. Walleyes may be infected with the following major groups of diseases or parasites:

3.7.1 Viral disease

Viruses cause the occurrence of diseases that produce tumors. Lymphocistis, a common viral disease among walleye, causes lumps on the skin and fins. Dermal sarcoma is caused by a retrovirus and results in tumors of the skin. Lymphosarcoma is a malignant form of tumor growth (Anonymous 2002).

3.7.2 Fungal disease

Saprolegniasis, caused by a variety of fungi, affects the skin, gills and eggs of walleye. It is related to a group of warm-water fungi. The disease is common in Saskatchewan (Anonymous 2002) and presumably occurs elsewhere. Various forms of trauma such as handling, cold and bacterial infection can pre-dispose a fish to fungal infection.

3.7.3 Bacterial disease

Walleye are susceptible to several bacterial diseases, four of which are commented on here. Columnaris disease is caused by *Flexibacter columnaris* and is stress-related in culture situations. It can occur internally or externally. It appears as dark grey or yellow lesions or ulcers. Bacterial diseases caused by Aeromonas and Pseudomonas are common infections that may be sub-acute or chronic. They may affect the liver, kidneys and, other internal organs. *Aeromonas salmoncida* causes furunculosis, which can be carried in the wild but affects cultured fish in particular.

3.7.4 Parasites

A wide variety of protozoan parasites infect walleye. One of them, *Ichthyoptirius multillis*, can be seen with the naked eye. It is a ciliated protozoan that causes white spots on the gills, fins, and skin. Myxosporidia are spore forming protozoans. They cause hemorrhaging of the gills and skin.

Copepod parasites include the many species of fish lice. *Ergasilus centrachidarum* is a species specifically identified as a walleye parasite.

Three genera of nematode and one of acanthocephala parasitize walleyes. The nematodes *Contracaecum* sp. *Eustrongylides* sp. and *Rhaphidascaris* sp., and the acanthocephalan species *Neoechinorhynchus tenellum* were listed by Dechtiar (1972) as newly discovered walleye parasites. This suggests that there are more previously recorded nematodes. Four genera of cestodes were identified as walleye parasites: *Bothriocephalus* sp., *Proteocephalus* sp., *Triaenophorus* sp. and *Diphyllobothrium* sp. (Poole and Dick 1985). Adult tapeworm *Diphyllobothrium latum* can grow to several meters and, infect humans.

Walleye may be infected by two kinds of flukes or trematoda. The order Digenea includes about 6,000 species. The monogenean flukes *Cleidodiscus aculeatus* and *Urocleidus aculeatus* are external parasites. *U. aculeatus* attaches to the gills of the host fish. The digenean flukes are represented in a huge array of different and complex life cycles. The larval stages of some *Diplostomum* sp. occur in the eye of the host. The infection commonly known as ‘Black spot’ *Apophallus brevis* is caused by skin pigment accumulation around the larval as it develops in the skin of a fish.

4.0 USE BY HUMANS

The walleye is is probably the most economically important sport and commercial species in Ontario and the prairie provinces. It is a major species in Quebec’s recreational fishery (Fisheries and Oceans Canada 2005). When caught, it is not as lively a fish as a trout or salmon, but it is strong and tends to go to the bottom. Although not a commercial species in the U.S., it is highly esteemed there. To maintain stocks in Canada and the U.S., over one billion fry are raised for stocking.

4.1 RECREATIONAL FISHERY

Walleye is an important recreational species in all parts of Canada except Newfoundland, the Maritimes and Yukon. From 1975 to 1985, 20-25 million walleye were caught each year (Fisheries and Oceans Canada 2005). Annual sport catches of 1.06 to 4.28 million occurred in Lake Erie alone but, from 1985 to 2004, the catch numbers indicate a decline in Lake Erie stock strength (Thomas et al. 2005). Where walleye occurs, it is a preferred species. In Saskatchewan, 72.3% of resident anglers preferred walleye, as did 69.1% of non-resident anglers (Derek Murray Consulting Associates 2006).

Since 1985, walleye has been a significant recreational species in B.C. Catches of 13,000 to 107,000 fish from a small area in the northeastern part of the province and about 50 km of the upper Columbia River indicate its importance. Walleye have been recorded in fishery catch data in six of the nine management regions of B.C. (Levey and Williams 2003). In the Peace and Omineca regions, catch numbers were relatively high in 1985, dropped in 1990, rose again by 1995, and dropped again in 2000. In the Kootenays the pattern was different, with numbers rising until 1995 and then falling by 2000. It is unclear whether theses changes reflect year-class strength or changes in angling pressure (Levey and Williams 2003).

4.2 STOCKING

Walleyes have been stocked in very large numbers across North America and in some jurisdictions stocking has gone on for over 120 years. There are a large numbers of papers on the topic. Addison and Ryder (1970) list 2,053 publications on walleye stocking prior to 1970. Most of these are old and in un-referred U.S. state publications that are not easily accessible.

Stocking walleyes is a widespread and large activity. In U.S.A. and Canada over one billion walleyes are stocked annually (Burden 2007) as there is a great deal of interest in the species. This interest, and the degree to which it is manifested, influences the amount of pressure put on government agencies to bring walleye in. It is also a factor that affects the likelihood of illegal introduction.

4.2.1 Stocking in Canada

In British Columbia, no walleye are currently stocked. The species was introduced into Swan Lake, south east of Dawson Creek, and to Charlie Lake near Fort St. John in 1957.

Walleye are not stocked regularly in Alberta. Stocking is carried out there to establish walleye populations, but not to sustain them (Alberta Government, Sustainable Resources Development 2006). There were no stockings in 2004 and 2005. In 2006, introductions to establish walleye populations were made in Lac La Biche, Primrose Lake and Sylvan Lake.

Stocking and transfer records from Saskatchewan show that from 1923 to 2004 an average of 22,105,550 walleye were stocked each year. Three recent years of data show a high rate of walleye stocking in Manitoba. Approximately 90.9 and

27.6 million fry were stocked in 2003 and 2006 respectively (Manitoba Water Stewardship 2008).

Walleye have been stocked in Ontario since 1884. Both eggs and fry have been stocked in large numbers with as many as 113 million eggs planted in 1944, and 393 million fry let loose in 1940 (Kerr 2006). In some years, eggs, fry and fingerlings were all stocked. Between 1990 and 2004, there has been an emphasis on fingerlings.

4.2.2 Evaluation of stocking

Walleye stocking is done to establish new self-sustaining populations, to supplement existing stocks, or to operate a put-and-take fishery. Maintenance stocking (planting in lakes where there is no natural reproduction) has provided angling in many lakes. More usually, supplemental stocking is done in lakes that already have walleye in them. Effectiveness varies, and only in some lakes is there a positive correlation between stocking and year class abundance (Colby et al. 1979). Stocking walleyes smaller than 76mm, in waters where there is an established walleye population, meets with low success in most cases.

Among the different types of program, there is great variability in the levels of success (Madenjian et al. 1991). Among other things, it is evident that geographic area can influence success. Understanding the nature of conditions that permit successful introductions is important because successful introduction conditions reflect the situations where invasions may be most likely to succeed.

Only 23 of 97 introductions to reservoirs in Ohio were successful in establishing self-sustaining populations. Introductions in five California reservoirs have failed to establish reproducing populations (Colby et al. 1979). However, more successful introductions have been made in many other water-bodies. Fishable and reproducing populations have, for example, been established in reservoirs in Washington, in the Columbia system, in Colorado, Kansas, South Dakota, and the southeastern states.

In 1992, The North American Journal of Fisheries Management devoted an issue to walleye stocks and stocking. Subjects include studies on survival of different sized stocked fish (Koppelman et al. 1992); evaluation of stocking to enhance a commercial fishery (Mathias et al. 1992); and assessments of fry or fry and fingerling stocking in different lake or river situations in the U.S. (Paragamian and Kingery 1992; Mitzner 1992; Fielder 1992; Jennings and Philipp 1992). An overriding message was that the success of any stocking practice remains largely unpredictable. The factors that governed the success of walleye plantings were food availability, temperature, weather, and predation (Ellison and Franzin 1992). Other factors that affected success were handling time, condition of fish, and closeness of match between conditions where fish came from and where they were planted.

Kampa and Jennings (1998) and Li et al. (1996) also evaluated factors influencing stocking success of walleye. These included fish condition at the time of stocking, time and method of handling fish before introduction, stocking density, predation, lake area, maximum depth, pH, food supply and the genetic characteristics of the stocked fish. Pond-reared walleye fry survived better than pellet-fed fry. Fry condition and the degree of pre-release stress influenced survival. In several of the studies they reviewed, Kampa and Jennings (1998) found that larger fish, i.e. >150mm, survived better than smaller ones. Cannibalism is a source of mortality among released fish and may reduce stocking success.

A model has been developed to predict the probability of successful introductions (Bennett and McArthur 1990). In the analysis they found that four physical variables - area, maximum depth, pH, and date the impoundment was formed - were significant in determining stocking success.

Colby et al. (1979) found that walleye did prefer lakes with large area, but also preferred moderately shallow water and turbid conditions. In contrast, the analysis of Bennett and McArthur showed that 72.7% of the manager-classifications for reservoirs, and 68.8% of those for lakes were correct. Laarman (1978) stated that success or failure of stocking appeared to depend heavily on both biological and physical environmental conditions. Madenjain et al. (1991) showed that success of stocking was strongly dependant on growth during the first summer and autumn after stocking. Over-winter survival was strongly dependant on size of fish during the autumn.

4.3 COMMERCIAL FISHERIES

The Canadian commercial walleye fishery is centered primarily in Ontario, Manitoba, and Saskatchewan. A total of 264,244,193 kg of fish has been caught from 1955 to 1999, but catches have been unstable. The annual catch fell from 9,090,909 kg in 1955 to about 2,954,500 kg in 1971. From 1955 to 1999 it rose to about 8,409,090 kg (Lemm 2002). From 1980 through 1999, three provinces - Ontario, Manitoba, and Saskatchewan - accounted for 98.4% of the commercial catch. The remaining 1.6% came from Alberta, Northwest Territories, and Quebec.

Fluctuation and instability have characterized commercial walleye fisheries across Canada. The causes vary from region to region. In Lake Erie, pollution in spawning streams, silting of lake spawning and nursery areas, over-fishing, changes in limnological conditions and increasing populations of rainbow smelt may all have contributed to fluctuations (Lemm 2002). Changes in access, increased fishing pressure, and changes in gear and fishing boats may all have caused changes in Manitoba’s walleye yields.

Ontario production was dominated by the catches from the Great Lakes, and most of the Great Lakes catch comes from Lake Erie. In 1956, the Lake Erie fishery collapsed and catches fell back to a range of 455,00 to 1,363,600 kg in the mid-sixties (Regier et al. 1969). Wolfert (1981) showed how the interaction of environmental conditions and over-zealous fishing damaged walleye stocks in eastern Lake Erie. From 1950 to 1978, year-class strength peaked four times in association with a rapid rise in water temperature during incubation. Each time a strong year class appeared, small-meshed gill net fishing rose sharply and removed about 50% of the fish before they could reach maturity. Lemm (2002) provides an instructive discussion of the history and causes of changes in walleye populations in the three sub-populations of Lake Erie as well as for those of Lakes Huron and Ontario.

Manitoba's walleye production is the second highest in Canada. The average annual catch from 1980 to 1999 was 3,282,273 kg, 44.3% of the Canadian total (Lemm 2002). About 60% of the walleye harvest in Manitoba comes from Lakes Winnipeg, Winnipegosis, and Manitoba. Walleye are not present in large numbers north of the 12°C isotherm, and the 16.5°C represents the northern limit for “reasonably successful” populations of walleye (Lemm 2002).

Saskatchewan is the third largest producer in Canada. The average annual harvest from 1980 to 1999 was 581,364 kg. Most commercial walleye fishing occurs north of 54°N. Over time, walleye catches have fluctuated as much as threefold.

Alberta, N.W.T., and Quebec account for only 1.6% of the Canadian catch. The fishing areas in these parts of Canada lie at the northern or north-western limits of walleye distribution. There are no commercial walleye fisheries in B.C.

4.4 AQUACULTURE

In stocking programs, walleyes are reared to a range of sizes from fry to large fingerlings to be stocked in ponds, lakes or streams. This section deals with the process and problems of culturing fish to these different release sizes. Relatively few walleye are reared in to market size facilities. However, information about aquaculture, for example egg fertilization and early rearing, provides further understanding of aspects of walleye biology that may be critical in dealing with it as an invasive species.

Culture begins with stripping eggs and sperm, usually from wild fish. The best spawn-taking temperature is from 7.2 to 10°C. Fertilization is most often carried out at field sites where the eggs are taken. Eggs are delicate until water-hardened at 1 to 2 hours after fertilization. Larger and/or older females produce eggs with higher fertility rates. Eggs taken late in a spawning run have higher fertility than those taken earlier. This may simply be due to better temperature conditions (Colby et al. 1979).

Walleye may be cultured in extensive or intensive systems. Extensive culture involves pond rearing with natural food. In intensive culture, fish eat artificial food. There is no single pond culture system that has proven best (Harding et al. 1992). Four critical elements affect success of walleye culture: non-inflation of swim-bladder, clinging behavior, non-feeding, and cannibalism. Non-feeding and cannibalism are the most serious.

5.0 IMPACTS ASSOCIATED WITH INTRODUCTIONS

The potential impacts from invasion by a top predator may occur in all parts of the biological system in question. While it may be possible to observe the most dramatic and immediate effects of invasion by a species like walleye, it is much more difficult to predict the long term consequences.

Rutherford et al. (1999) developed models to predict effects of zebra mussel invasion on perch and walleye; the results showed the complexity of processes initiated by a new species in the environment. Zebra mussels clarified the water, changed the zooplankton community, affected the growth of macrophytes and, in doing so, changed the habitat for walleye and other fish species.

The introduction of walleye, while at a different position in the trophic scale, may produce changes of the same order. The effects of change over time and the interactions of multiple species make predictions difficult. Pothoff (2003) stated that high population densities of fathead minnow *Pimephales promelas* can reduce zooplankton densities, which results in increased phytoplankton, which in turn reduces water clarity and macrophyte abundance. This may affect waterfowl. The introduction of walleye fry resulted in reduction of fathead minnow fry and then adults. This allowed an increase in cladocerans, which reduced phytoplankton and allowed the pond to become clear.

5.1 IMPACTS ON ZOOPLANKTON AND BENTHIC MACROINVERTEBRATES

The present review did not turn up published reports of clear impacts on zooplankton or benthic macroinvertebrates. Young walleye initially feed on small zooplankton, but the literature did not demonstrate an impact on this plankton form. There are cases in which zooplankton densities fell and walleye starved. Houde (1967) cited cases of starvation among zander *Stizostedion lucioperca* when zooplankton became scarce. It was not clear, however, that the fish caused the depletion. The duration of the limnetic stage of walleye suggests that they should not have a depleting effect on the plankton community. Fox (1989) showed that weekly increase in walleye length was positively related to chironomid biomass, but did not show that the fish reduced the biomass.

Under-yearling walleye may spend only a month or two inshore before they move to open water. If they are to have a significant impact on benthos, they have limited time to do so. Reed and Parsons (1999) examined the effects of walleye on macroinvertebrate numbers in a series of six ponds in Minnesota, where there was concern that stocked walleye were negatively affecting mallard production by consuming invertebrates. Young walleye reduced macroinvertebrate numbers in one of five ponds. Fathead minnows were considered to have had as much effect on macroinvertebrate numbers as had walleye. Walleye in these ponds did not exert heavy predation pressure on the fathead minnows, or the minnows would not have had the effects they did.

It may be difficult to demonstrate that walleye have a particular effect on zooplankton in a body of water unless it is the only species present. Bulkley et al. (1976) found that in Clear Lake, Iowa, six species of fish consumed an array of zooplankton species. Different kinds of fish were heavy consumers of the same zooplankton species; however, the time at which a species of zooplankton was heavily used differed. In these complex faunal situations, it may be problematic to demonstrate a “walleye impact” even if some zooplankton species are depleted.

5.2 IMPACTS ON FISH

The introduction of walleye may negatively affect other fish through competition, predation, or altering species composition and hence relationships among the other species. If walleye of the right size are available they may also serve as forage for other species of fish.

5.2.1 Competition

Through the course of a fish’s life it may face either in intra- or inter-specific competition. Publications deal with both types and evidence for competition was, in most publications, based on the walleye and some other species both using the same resource at the same time (usual examples were food). It is, however, necessary to be cautious in interpreting similarity in use patterns as an indication of competition (Nilsson 1958; 1963; Hartman 1965).

Nilsson (1958, 1963) demonstrated that when competition for food occurred between species, interactive segregation of use patterns also occurred. Hartman (1965) found the same principle applied to competition for space. In these cases of competitive interactive segregation, resources were partitioned, with each species focusing on the type of resource it was behaviorally or physically best suited to exploit.

Walleye fry may coexist with the young of a number of other fish species. Bulkley et al. (1976) showed that different species of young fish may utilize the same food resources concurrently, or at different times. Young perch and walleye ate a different spectrum of food organisms. This may indicate that little inter-specific competition occurs, or that interactive segregation occurs. McMahon (1992) suggested that competition would occur between walleye, perch and trout fry in the Canyon Ferry Reservoir where no thermal stratification would separate them.

At adult or near-adult size, walleye may compete with largemouth bass, northern pike, and sauger. In oligotrophic lakes they may compete with lake trout. However, these two species are spatially separated. In the Great Lakes, lake trout are a top native predator in Lakes Ontario, Michigan, Huron, and Superior, while walleye are the top predator in Lake Erie (Anonymous 2005).

In a study of interactions between walleye and four other species of potential competitors or predators, Fayram et al. (2005) identified muskellunge, smallmouth bass, largemouth bass, and northern pike as species with which walleye may interact either through competition or predation. Based on their analysis, using four selected criteria of fish relationships in Wisconsin lakes, they concluded that largemouth bass was the only competitor. They suggest, however, that competition may occur with other species in other lakes. The exclusion of competition with northern pike was notable because Craig and Smiley (1986), Lysak (2004), Minnesota DNR (2007) and Minnesota Pollution Control Agency (1999) all identify northern pike as a competitor for walleyes.

If walleye and sauger occur sympatrically, they may compete. Turbid water may favor sauger because its eye is even better suited to dim light (Ryder 1977). McMahon (1992) reported evidence for competitive interaction between brown trout and walleye. In the Seminole Reservoir, numbers and condition of brown trout decreased markedly after expansion of the walleye population.

Walleye and pikeminnow both consumed salmonids in Lake Roosevelt. Modeled predation impact of an estimated 273,524 walleye and 39,075 pikeminnow in the reservoir indicated losses of 41,220 kg of kokanee and rainbow trout through walleye consumption and 18,640 kg by pikeminnow consumption (Baldwin et al. 1999). If competition is indicated by similarity of food items used, then the two species were competing in Lake Roosevelt.

There was a partial overlap in diet between walleye and yellow perch in western Lake Erie. Age-1 walleye and age-2 perch both consumed clupeids from June onward. However, the diets of the two species were separated by heavy, year-round consumption of invertebrates by perch. Knight et al. (1984) concluded that, while there was diet overlap, there was no evidence that walleye-perch competition for food was a limiting factor for either species.

5.2.2 Predation

Walleye are top predators and will eat almost any living organism they can get into their mouths. Yellow perch are the main prey. They were the major food item in 16 studies reviewed by Colby et al. (1979). Pierce et al. (2006) showed strong interdependence between walleye stocking and perch abundance. When walleye stocking was terminated, perch numbers rose, and their growth rates fell. When walleye were restocked, predation increased, perch numbers declined and their growth rate increased. Lyons and Magnuson (1987) found that when young perch were scarce in a northern Wisconsin lake, walleye predation accounted for 100% of the mortality for darters and 75% of the mortality for minnows. When perch were abundant, walleye switched to preying on them and predation on minnows and darters was reduced. In western Lake Erie, walleye predation, which was preferential for soft rayed fish, changed the community structure. Perch were not indicated as a major prey species.

Predator-prey relationships involving walleye are complex (Li and Moyle 1981; Lyons and Magnuson 1987; Knight and Vondracek 1993; Findlay et al. 2000; Liao et al. 2002). They are difficult to manage once this top predator has been introduced. In small temperate lakes, piscivorous species may alter communities significantly. In a study of 506 small temperate lakes in the Adirondacks, top predators decreased species richness in native minnow communities by as much as two thirds (Findlay et al. 2000).

McMahon and Bennett (1996) provided a valuable understanding of the sequence of events following walleye introduction and efforts to manage fisheries afterwards. Walleye were introduced into Seminole Reservoir, which already had a “put-grow-and-take” rainbow and brown trout fishery. Initially the walleye consumed darters, suckers, and minnows. As these species declined under predation, walleye shifted to planted salmonids. Most of the 500,000 planted salmonids fingerlings were eaten by walleye within a few weeks. Scattering the plantings of the salmonids did not prevent predation. As the walleye population grew, it over-exploited food resources. Cannibalism increased and walleye growth and condition decreased. Managers then planted an alternate forage base of gizzard shad and emerald shiner. This improved walleye size and condition. However, to avoid predation on the salmonids, managers had to plant trout 200 to 340 mm long. McMahon and Bennett (1996) stated that managers have repeatedly observed the creation of a “predator trap,” which has led them to stock large trout to avoid predation losses.

In some cases, walleye introductions have produced stable fisheries. If flushing rates are high, walleye recruitment may remain low and they may establish stable populations. Walleye stocked into Cooney Reservoir to control sucker populations, and into Dailey Reservoir to control stunted yellow perch, have remained stable (McMahon and Bennett 1996).

In western reservoirs, such as those in the Columbia system, walleye predation may be a serious problem for salmonids. Reservoir level fluctuations cause wide changes in prey numbers in species such as yellow perch. Walleye deplete their main prey and turn to other species. The lack of cover during summer draw-down in reservoirs makes prey vulnerable. When numbers of one prey species are low, walleye shift to alternate species (McMahon and Bennett 1996).

While the heaviest predator on salmonids in the lower Columbia is pikeminnow (Beamesderfer et al. 1996), losses from walleye are large. The highest losses of salmonids to piscivores occur in the lower Columbia; highest densities of walleye occur in the reservoir above the Dalles dam, followed by Bonneville, John Day, and McNary. Beamesderfer and Nigro (1989) estimated that walleye consumed 400,000 salmonids per year from 1983 through 1986. In the mid-1980s, salmonids made up 14%, by weight, of the diet of walleye in the lower Columbia River (Temple et al. 1998). These authors estimated that loss of salmonids in the three lowermost reservoirs could be up to two million. Most of this predation is by walleye smaller than 300mm, so sport fishery-based control would not have much effect (Temple et al. 1998).

In the region of the Rocky Reach dam, approximately 70% of the way from the Bonneville dam to Grand Coulee dam, walleye are relatively rare. Short reservoir retention times limit their abundance, particularly if high flushing rates occur at time of larval abundance (BioAnalysts Inc. 2000). In Lake Roosevelt, above Grand Coulee dam, kokanee and rainbow trout are the main salmonid prey of walleye. In 1999 and 2000, walleye represented 89 and 94% of the piscivore community and pikeminnows made up only 3 and 5% on those years. Salmonids were an important part of their diet. In 1999, kokanee constituted 75 to 100%, by weight, of the diet of walleye >300mm. They were present in 81% of the non-empty walleye stomachs. In 2000, kokanee and rainbow trout made up 25 to 79%, by weight, of the large walleye (300 to 644mm) diet, and 8% of the small walleye (275 to 299mm) diet (Baldwin et al. 2003). These authors estimated that walleye consumed 9.4% of the hatchery-produced kokanee and 7.3% of the hatchery trout within 41 days of release.

Large numbers of hatchery salmonids are released into Lake Roosevelt. Baldwin et al. (2003) concluded that these releases swamped the predators in Lake Roosevelt. Appropriate release strategies may thus be important in reducing predation levels on hatchery salmonids. Walleye densities are relatively high at kokanee release sites, particularly during spring (McLellan et al. 2004).

5.2.3 Food for other fish

The literature on walleye as prey is far sparser than on walleye as predator. Walleye are eaten by northern pike, muskellunge, adult perch, sauger and lamprey (Scott and Crossman 1973). Colby et al. (1979) list northern pike, sauger, bullhead, burbot, yellow bass, yellow perch, white bass, rainbow smelt and alewife as walleye predators. Benike (2006) found that walleye abundance declined concurrent with an increase in largemouth bass. In the Bay of Quinte, Lake Ontario, a resurgence of walleye coincided with the collapse of alewife and white perch in the late 1970s (Stewart et al. 2000). White perch and white crappie were indicated as walleye predators in South Bay, Lake Champlain (U.S. Fish and Wildlife Service 2004).

Many fish eat walleye eggs. Colby et al. (1979) listed carp, yellow perch, sucker, and minnow as potential egg-eaters. Bullhead and yellow bass consumed walleye eggs in Clear Lake, Iowa. In Lake Erie, yellow perch, spottail shiner, stone cat and sucker were all found to contain walleye eggs (Colby et al. 1979). Egg predation may be increased by low temperature during incubation, when eggs take longer to hatch.

Walleye fry may be subject to predation by yellow perch *Perca flavescens*, white bass *Morone chrysops*, yellow bass *Morone mississippiensis*, smallmouth bass *Micropterus dolomieui*, rainbow smelt *Osmerus mordax*, sauger *Sander canadense*, burbot *Lota lota* and northern pike *Esox lucius*. Roseman et al. (1996) concluded that a combination of strong winds, predation, and low incubation temperature was largely responsible for reduced survival among age-0 walleyes spawned on reefs in western Lake Erie.

6.0 IMPACT SUMMARY

The potential impacts from invasion by a top predator may occur in all parts of a biological system. The introduction of walleye may negatively affect other fish through competition, predation, or altering species composition and relationships among the other species. Predator-prey relationships involving walleye are complex and difficult to manage once this top predator has been introduced.

Walleye will eat almost any living organism that they can get into their mouths. Among all species preyed upon by walleye, yellow perch were dominant. In western reservoirs, such as those in the Columbia system, walleye predation may be a serious problem for salmonids. Appropriate release strategies may thus be important in reducing predation levels on hatchery salmonids. In some cases, walleye introductions have produced stable fisheries.
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Walleye may also serve as forage for other fish, although much less is known about this aspect of their ecosystem role. Walleye are preyed upon by northern pike, muskellunge, adult perch, sauger, lamprey, bullhead, burbot, yellow bass, rainbow smelt and alewife. Many species of fish eat walleye eggs.

There are key elements that determine where walleyes will flourish if introduced. Walleye are distributed over very wide range from the lower Mississippi to the mouth of the Mackenzie River. They occur and survive under diverse conditions, but some conditions are far better than others for them. The critical habitats are listed below:

1) Large mesotrophic lakes or low-flushing-rate reservoirs.
2) Moderately turbid water.
3) Oxygen, >3mg/l.
4) pH 6 to 9.
5) Clean gravel or cobble spawning beds.
6) Temperatures above 8°C, and rising during incubation.
7) Appropriate species of zooplankton in a bloom that coincide with hatching and early feeding of larvae.
8) A diverse forage fish fauna.

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