Biological Synopsis of Smallmouth Bass (*Micropterus dolomieu*)

T.G. Brown, B. Runciman, S. Pollard, A.D.A. Grant, and
M.J. Bradford

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, B.C.   V9T 6N7 CANADA

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BIOLOGICAL SYNOPSIS OF SMALLMOUTH BASS (*Micropterus dolomieu)*

by

T. G. Brown, B. Runciman, S. Pollard, A. D. A. Grant, and M.J. Bradford

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, B.C.   V9T 6N7 CANADA

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ABSTRACT

Brown, T. G., Runciman, B., Pollard, S, Grant A.D.A. and Bradford, M.J. 2009. Biological synopsis of smallmouth bass (*Micropterus dolomieu)*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2887: v + 50 p.

This synopsis reviews biological information on the smallmouth bass in support of a risk assessment evaluating the impacts of its expansion into non-native areas of Canada. Smallmouth bass is native to the fresh waters of eastern-central North America. Its North American expansion started in the late 1800s and it is now one of the most widely distributed fishes in the world, mainly because of its popularity among anglers. Smallmouth bass usually reside in the littoral zone of clear lakes and slower moving rivers. Juvenile bass > 50mm TL are piscivorous, as are adult fish, and their diet is comprised of crayfish, minnows and other fish and amphibians. Introduced bass can have significant impacts on native fish communities through predation, especially for small-bodied fish such as minnows and salmonids and can cause the extirpation of some populations.

RESUME

Brown, T. G., Runciman, B., Pollard, S, Grant A.D.A. and Bradford, M.J. 2009. Biological synopsis of smallmouth bass (*Micropterus dolomieu)*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2887: v + 50 p.

Le présent synopsis examine les données biologiques sur l’achigan à petite bouche 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. L’achigan à petite bouche est un poisson d’eau douce indigène du centre-est de l’Amérique du Nord. L’expansion de son aire de répartition en Amérique du Nord a débuté à la fin des années 1800 et il est aujourd’hui l’un des poissons les plus répandus dans le monde, principalement en raison de sa popularité auprès des pêcheurs à la ligne. L’achigan à petite bouche fréquente généralement la zone littorale de lacs à eau claire et les cours d’eau à courant faible. Les juvéniles de >50 mm de longueur totale sont piscivores, tout comme les adultes, et leur régime alimentaire se compose d’écrevisses, de ménés et d’autres poissons et amphibiens. À cause de la prédation, les achigans introduits peuvent avoir d’importantes répercussions sur les communautés de poissons indigènes, particulièrement sur les poissons de petite taille comme les ménés et les salmonidés, et ils peuvent causer la disparition de certaines populations.

1.0 INTRODUCTION

Smallmouth bass are highly prized as a recreational sports fish. Their value as a sports fish has led to their many global and North American introductions. They are considered to be capable invaders, strong competitors, and known predators on native fish species. Factors favoring invasive smallmouth bass include their small size at the onset of piscivory, juvenile use of cover, low overlap with other predators (Gard 2004), and high fecundity combined with parental care. It is also likely that smallmouth bass will increase their range north in response to climatic trends associated with global warming (Jackson and Mandrak 2002). Their invasive spread into new water bodies is considered a threat to freshwater biodiversity and to the species currently supporting commercial, recreational, and native food fisheries. The recent, apparently deliberate and clearly illegal spread of bass into new water bodies has created considerable concern.

A qualitative and quantitative risk assessment is required by DFO to determine the level of risk that bass species pose to freshwater lakes, rivers and existing fisheries. This report provides the basic biological information required for this risk assessment.

1.1 NAME, CLASSIFICATION AND IDENTIFIERS

Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Actinopterygii
Order: Perciformes
Suborder: Percoidei
Family: Centrarchidae
Genus: *Micropterus*
Species: *dolomieu*

Scientific Name: *Micropterus dolomieu* Lacepède (1802)

Common name (English): smallmouth bass

Common name (French): achigan à petite bouche

Integrated Taxonomic Information System Serial Number: 550562
Sources: Zip Code Zoo; Animal Diversity Web (all 2008).

The genus name *Micropterus* means "small fin"; the species name honours the French mineralogist Dieudonne de Dolomieu. "Small fin" is actually a misnomer; the specimen in question had a damaged fin, which gave the appearance of a small fin behind the dorsal. Numerous other regional common names for smallmouth bass can been found in Scott and Crossman (1973).

1.2 DESCRIPTION

Members of the sunfish family have two dorsal fins which appear joined. The anterior fin has spines and the posterior one has soft rays (Scott and Crossman 1973). Although members of the sunfish family are usually laterally flattened (compressiform), basses tend to be slightly more fusiform (streamlined), with an emarginated tail. This implies that they can swim faster in open water and have excellent acceleration. Smallmouth bass has the general body shape of a slender, streamlined perch (Figure 1). Most smallmouth bass caught in Canada range from 20-38 cm in length (Scott and Crossman 1973).

Smallmouth and largemouth bass can be easily told apart. While the maxilla of the smallmouth is roughly even with the pupil of the eye and the upper jaw reaches to near the rear margin of the eye, the largemouth bass upper and lower jaws extend past the back edge of the eye. The largemouth has a more pronounced notch between the spiny and soft parts of the dorsal fin, while this notch is more broadly connected in the smallmouth. The smallmouth has irregular dark brown dorsal vertical bars or shading, while the largemouth bass has irregular bars forming a strip along the side and is often dark green on the dorsal surface. The eye of largemouth is gold, while the smallmouth bass eye is often red.

The dorsal colouring of adult smallmouth bass tends to match its environment, and can vary from dark-brown to dark-olive-green to bronze. Smallmouth taken from weedy areas are often greenish, while those found near rocky lake shoals may be shades of brown and light gold (Scott and Crossman 1973). The sides are lighter than the dorsal surface and the underside is cream to white. Olive-green bars radiate dorsally from the eye and one bar radiates from the eye to the snout. The sides can have 8-15 pronounced or vague, vertical bars that are sometimes broken (Scott and Crossman 1973).

Juvenile smallmouth bass have similar colours, but the vertical bars or rows of spots are more pronounced. The caudal fin is also unmistakably orange.

Figure 1. Smallmouth bass *Micropterus dolomieu*. Image courtesy of the New York State Department of Environmental Conservation, Albany, NY.

1.2.1 Taxonomy

The perciformes (perch-like fishes) make up one of the more numerous orders of vertebrates. The suborder Percoidei includes the bass, crappies, bluegill and pumpkinseed fish. The genus *Micropterus* contains eight species of bass (Near et al. 2003). Although *Micropterus dolomieu* is commonly referred to as a bass, it is actually in the sunfish family. The Centrarchidae or sunfish family is native to North America and is the second largest fish family in North America, comprising 30 species (Scott and Crossman 1973). The sunfish family is characterized by a generally compressiform shape, with 3 anal and 6-13 dorsal spines.

2.0 DISTRIBUTION

2.1 GLOBAL NATIVE DISTRIBUTION

Smallmouth bass were originally restricted to the fresh waters of eastern-central North America. The species occupied the Ohio, Tennessee, upper Mississippi basin, Saint-Lawrence River and Great Lakes systems (Scott and Crossman 1973; Figure 2).

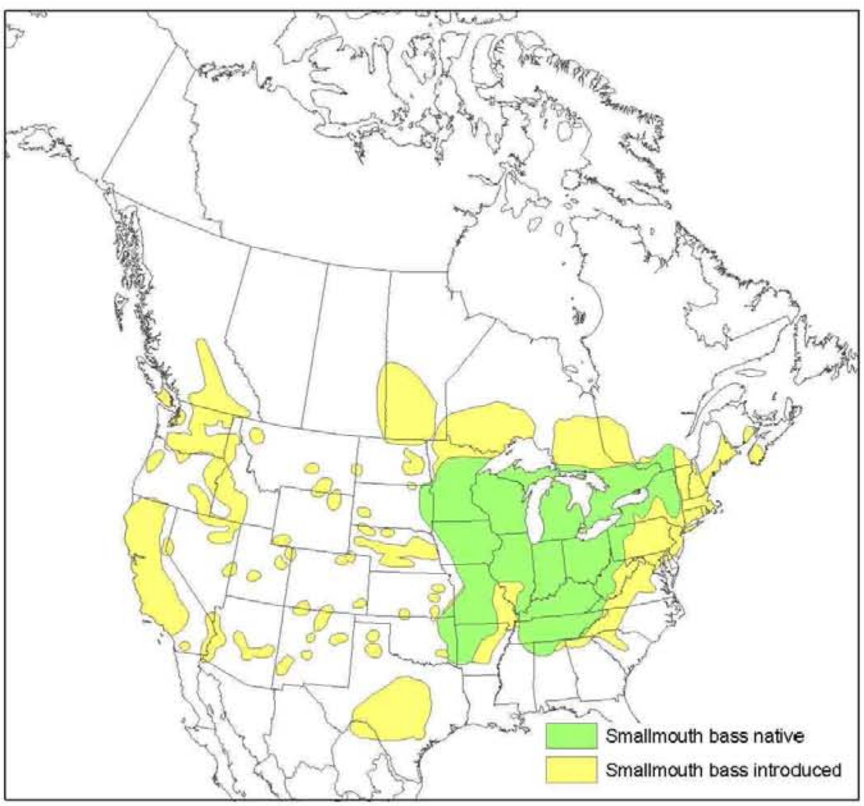

Figure 2. Native and non-native distribution of smallmouth bass in North America from Tovey et al. (2008).

2.2 NATIVE DISTRIBUTION IN CANADA

Two of the black basses, the large and smallmouth bass, were native to Canada. The original Canadian distribution of smallmouth bass was restricted to the Great Lakes - St Lawrence system (Scott and Crossman 1973) with the exception of Lake Superior (McPhail 2007a).

2.3 NON-NATIVE DISTRIBUTION

Smallmouth bass have been introduced to Africa, Europe and Russia, as well as both east and west across Canada and almost everywhere in the U.S. (Scott and Crossman 1973). The initial expansion of smallmouth bass range took place in the mid-1800s, to central New York State through the Erie Canal, then across the United States as far as California. They were introduced into California in 1874 (Moyle 2002) and transplanted into the New England states in the late 1800s. Smallmouth bass is now found in all states except Florida, Louisiana and Alaska.

Smallmouth bass are still numerous in southern Ontario, especially in tributaries and streams flowing into Lake Ontario. The native populations in southern Ontario and Quebec have expanded northwards to Timmins in Ontario and Hull in Quebec. Smallmouth bass have been successfully stocked in both eastern and western Canada. The Ontario Department of Game and Fisheries planted a considerable number of Ontario lakes with bass in the early 1900s (MacKay 1963). In 1987, it was estimated that 2,421 Ontario Lakes contained populations of smallmouth bass (Kerr and Grant 1999).

Although smallmouth bass are not native in the Maritime Provinces, they currently inhabit a number of water bodies there. Through legal (1967, 1968, 1971, and 1984) and illegal transfers, as well as natural migration, smallmouth have become established in over 71 lakes and 23 watersheds in Nova Scotia (McNeill 1995). Smallmouth bass were introduced into New Brunswick from Maine in about 1869 and have become well established throughout a number of southwestern drainages (Scott and Crossman 1973; McNeill 1995). They were legally introduced into Nova Scotia from New Brunswick sources between 1942 and 1953 (McNeill 1995). In Canada, smallmouth bass have not been introduced into P.E.I. or Newfoundland.

Smallmouth bass introduced into the prairie-provinces are considered to be near their environmental limit. In Manitoba, smallmouth are found upstream of Lake Winnipeg in the Winnipeg River, and are occasionally caught in Lake Winnipeg, the Red River and Lake of the Woods. Smallmouth bass were intentionally introduced into Lake Winnipeg (Franzin et al. 2003) in the early 1900s but have not dominated anywhere in Manitoba.

Smallmouth bass were introduced into Alberta in the early to mid 20th century by individuals or managers acting on their own initiative; these fish did not survive (Scott and Crossman 1973; Nelson and Paetz 1992). Some reproduction of a small population introduced between 1977 and 1984 into Island Lake, north of the town of

Smoky Lake in south-eastern Alberta, has been observed. Remnants of this population may still exist (Nelson and Paetz 1992).

Smallmouth bass were introduced into a number of small ponds and lakes in south-eastern Saskatchewan (Langhorne et al. 2001). They are found primarily in the southern lakes region.

In British Columbia, smallmouth bass now occur in most of the lowland Okanagan lakes, many lakes on Vancouver Island (including the Gulf Islands) and in the Kootenays (McPhail 2007a), as well as a small number of systems in the Shuswap and Quesnel systems of the mid-Fraser drainage.

2.4 MODES OF INVASION

Invasive fish species have been introduced into North American water-bodies by a variety of methods, including authorized or government stocking programs. Once established, invasive species may disperse to adjacent connected water bodies. Seven key non-authorized pathways for introduction and spread of aquatic invasive species have been identified (CCFAM 2007). These include shipping, recreational and commercial boating, use of live bait, releases from the aquarium and water garden trade, releases from live food fish markets, illegal introductions to create fisheries, and through construction of canals and water diversions (new connections).

2.4.1 Authorized introductions

Introductions in British Columbia are discussed by McPhail (2007a). Smallmouth bass fry were reported introduced to Christina Lake in the Kootenays and Florence and Langford lakes on Vancouver Island by the Dominion Fisheries Department in 1901, using original Ontario stock. In 1908, bass were moved into Moyie Lake from Christina Lake; in 1920, St. Mary Lake on Saltspring Island was stocked with Langford Lake smallmouth. Three authorized stockings of smallmouth bass took place between 1982 and 1987. Smallmouth bass were transferred from Osoyoos Lake to Johnson Lake, an artificial landlocked lake, in 1982. Vaseaux and Skaha Lakes received Christina Lake smallmouth in 1987 in an authorized transfer by provincial fisheries staff. No transfers of smallmouth bass have since been authorized.

2.4.2 Live bait

A common avenue of introductions in eastern Canada and the U.S. has been through use as live bait for larger sport fish such as walleye, pike, and adult bass (Litvak and Mandrak 1993). Smallmouth bass juveniles could be introduced when live bait escapes or bait buckets are emptied, despite prohibitions against this (CCFAM 2007). Live bait release is also a possible vector for the spread of aquatic diseases (Ontario Ministry of Natural Resources 2007).

2.4.3 Illegal introductions

An important method by which bass and other invasive fish have spread outside their native range is through illegal introductions into new waterbodies. This type of introduction has been termed the “bucket brigade”.

2.4.4 Natural dispersal

Once established, populations of non-native fish can disperse through connected waters into adjacent habitats. Occurrence records for smallmouth bass match up with international trans-boundary waterways (Runciman and Leaf 2009) where they have been introduced earlier. In North America, introductions often have trans-boundary implications. An excellent example of this is in the Okanagan and Columbia river systems, where non-native fish including centrachids, ictalurids, percids, and salmonids were introduced by the U.S. Fish Commission during the late 19th and early 20th centuries (Bonar et al. 2005), and subsequent movements have been widespread. Introduced fish now utlilize similar habitat upstream from the international border (Scott and Crossman 1973; Wydoski and Whitney 2003; McPhail 2007a). In 1960, smallmouth bass were found in Osoyoos Lake in southern British Columbia, presumably having moved through connected trans-boundary waters.

3.0 BIOLOGY AND NATURAL HISTORY

3.1 AGE AND GROWTH

The development of smallmouth bass from fertilized egg to free-swimming fish is fairly rapid. Growth in the first year appears to be critical. Growth of young-of-the-year bass in a Wisconsin lake was independent of density but was positively related to water and air temperature during June-August (Serns 1982). Mean length of these Wisconsin age-0 smallmouth bass ranged from 68.7 to 81.3 mm for the period 1974-1981. Length of the growing season determined the size of bass fry entering winter, and size of young-of-the-year in autumn is correlated with over-winter survival (Jackson and Mandrak 2002).

Shuter et al. (1980) noted that growth ceased and the “winter starvation period” began when temperatures dropped below 7-10^{O}C. The critical size required at the end of the growing season was dependent upon the length of the starvation period. For example, if the starvation period was 60 days, 20-40 mm fish experienced some mortality; if the starvation period was 260 days, fish 60-100 mm experienced some mortality while fish less than 60 m experienced complete loss (Shuter et al. 1980).

In cooler areas, bass fry must reach an adequate size by the end of the first growing season if they are to survive the first winter. In Maine, when spawning occurs at the normal time, smallmouth bass age-0 typically reach average lengths of 56-74 mm, although some individuals may reach 100 mm by the end of their first growing season (Maine Department of Inland Fisheries and Wildlife 2002). Feeding stopped at water temperatures below 4°C (McPhail 2007a), followed by the period of survival on stored energy (Keast 1968). Curry et al. (2005) noted that there was size-dependent survival as young-of-the-year bass < 50mm died under the ice in New Brunswick. The distribution of smallmouth bass in northern Ontario appeared related to summer water temperature and growth period relative to the length of the starvation period (Jackson and Mandrak 2002).

Growth is temperature-dependent. Maximum growth rate of lab-held smallmouth bass fry was at 26-29°C (Horning and Pearson 1973) or 25-26°C (Coutant and DeAngelis 1983). The young fish grew 1.23 mm/day. When fish were held above 29°C, maintenance requirements increased faster than food intake, resulting in decreased growth. Under ideal water temperatures for age 0 and 1 fish, maximum growth rates were 2.85 mm or 0.99% per day (Anderson et al. 1981). In Idaho, growth can continue into October, and year-0 bass can reach 50-120 mm (Keating 1970). In the Columbia River, most growth occurred from July to October (Henderson and Foster 1956). Coble (1967) found a relationship between growth and water temperature in South Bay, Lake Huron, but only for bass aged 3 to 5; growth was associated with warmer surface waters from July-Sept. There is a relationship between growth (age at length 280 mm) and environmental factors such as mean air temperature and degree-days above 10°C (Beamsderfer and North 1996). Dunlop and Shuter (2006) found relationships between four growth variables (mean length for ages 1-4) and eight climatic variables. They noted a significant positive relationship between air temperature and early growth.

A variety of factors other than temperature can also influence growth. Native and introduced bass populations exhibit differences in growth rates. It is possible that introduced populations have not fully adapted to their new environments, and growth rates may be atypical (Dunlop and Shuter 2006). Factors such as parasite load and food supply may influence growth of older fish more than does water temperature (Coble 1971). Keast (1985) felt that the morphology of a lake was a major factor in growth and dominance in finfish. Growth was poorest in oligotrophic, cold, deep, lakes and there may be a relationship between littoral area and growth. Annual increases in mean calculated growth increments were greater for impounded smallmouth bass (King et al. 1991). The impounded waters had higher temperatures, maintained minimum flow, and had lower turbidity. Keating (1970) noted that the warmer waters of the upper Snake River did not generate greater or faster growth than the colder waters of other neighboring systems. He concluded that other factors such as type of available prey and inter or intra-specific competition may override any benefits from warmer waters. Fish community interactions may influence growth through increased activity and decreased food conversion efficiency (Purchase et al. 2005).

Keating (1970) provided tables of incremental growth for the first 7 years of life based on number of scale annuli. Mueller et al. (1999) examined growth rate of smallmouth bass in Lake Whatcom, Washington. They reported that growth rates were consistent with 25 other western warm-water lakes and provided tables on mean lengths by age for Washington State. Length and weight per number of annuli (3-11) were compared and illustrated by Henderson and Foster (1956). Growth of adults appeared to be reasonably steady with 3-annuli fish measuring approximately 300 mm and 11-annuli fish reaching 480 mm. Bennett et al. (1991) provided tables of length by age (1 to 13 years) for selected populations of smallmouth bass in the Pacific Northwest. Average young-of-the-year ranged from 71 to 101 mm, while age 2 fish ranged from 132 to 185. The smaller fish were from Brownlee Reservoir, Idaho, and Little Goose Reservoir, Washington. Bass from Lake Sammamish were the largest.

In Lake Sammamish, Washington, growth rates of smallmouth bass (first noted in early 1970s) were exceptional (Pflug 1981; Pflug and Pauley 1984). One-year-old fish averaged 10.1 cm growth, two-year-olds averaged 18.5 cm, three-year-olds averaged 26.0 cm, and at 6 years of age fish length was over 40 cm. Growth was attributed to an excellent food supply, abundance of habitat, warm water and lack of competitive species. The majority of the bass population (63%) was composed of 2-year-old (39%) and 3-year-old (24%) fish (Pflug and Pauley 1984).

Nova Scotia lakes can be classified as relatively unproductive (Alexander et al. 1986). Because of the short growing season and unproductive environmental conditions, smallmouth bass grow slowly in Nova Scotia, mature later and at a smaller size (McNeill 1995). The maximum age in Canada would appear to be around 15 years (Scott and Crossman 1973). In general, smallmouth bass do not grow as fast or get as big as largemouth bass. The world record smallmouth bass was caught in Kentucky in 1955 and weighed 5.4 kg. The Canadian record was caught in Ontario in 1954 and weighed 4.46 kg (Scott and Crossman 1973).

Smallmouth bass are sexually mature in the 2nd to 4th year in more northern areas, where maturity may be delayed if food is scarce or water is relatively cool. Smallmouth bass males and females of similar age appear to exhibit no sexual dimorphism, perhaps because of an equal expenditure of energy on somatic growth (Dunlop et al 2005); females invest a large amount of energy into gonad development while males invest an equal amount into nest construction, courting, and parental care. However, Henderson and Foster (1956), who examined sport-caught smallmouth bass from the Columbia River, Washington, found females were larger and made up a greater portion of the catch than males. Male behaviour may have required a slightly greater expenditure of resources.

3.2 PHYSIOLOGICAL TOLERANCES

3.2.1 Temperature

Water temperature is one of the most important environmental variables affecting smallmouth bass (Armour 1993), and influences range and distribution, migration, spawning date, nest guarding behaviour, success of incubation, growth rate, period of growth and winter responses such as feeding curtailment (Shuter et al. 1980,1983,1985; Shuter and Post 1990). Smallmouth bass are often considered to be a cool-water fish even though they are relatively tolerant of high water temperatures (Armour 1993).

Edwards et al. (1983) gave the upper temperature limit for adult smallmouth bass as 32^{O}C, the optimum range for adult rearing as 21-27^{O}C, and the optimum range for spawning as 12.8-21^{O}C. Smallmouth bass remained in warm (>28^{O}C) waters even though cooler water was available (Bevelhimer and Adams 1991). In that experiment, bass selected 31^{O}C waters when choices of cover and food availability were added. Laboratory preference was estimated to be approximately 28^{O}C (Ferguson 1958). In Virginia, smallmouth bass tolerated ambient stream temperatures up to 35^{O}C (Stauffer et al. 1976). Smallmouth bass exposed to 35^{O}C for 9 days were not significantly affected, and the estimated upper ultimate incipient lethal temperature was 37^{O}C (Wrenn 1980).

Adult smallmouth bass can survive in regions with extreme winter conditions but they do not actively feed at < 10^{O}C (Keating 1970). Smallmouth bass have been observed to reproduce in Saskatchewan (Marshall and Johnson 1971). Keast (1968) noted that smallmouth bass do not actively feed until temperature reaches 8.5^{O}C, and cessation of feeding has been noted when water temperature dropped below 7-10^{O}C (Shuter et al. 1980). Sudden drops in temperature may also cause mortality. Although fish acclimated to 22.2-26.4^{O}C survived a temperature drop of approximately 16^{O}C, they succumbed to fungal infections within 7 days (Horning and Pearson 1973). In an Illinois study, smallmouth bass became lethargic at 4.4^{O}C and settled into interstitial spaces on the river bottom, where they were susceptible to abrasion and displacement during flood events (Sallee et al. 1991). Keating (1970) speculated that, for Idaho River, lowering maximum summer water temperature to improve conditions for salmon and steelhead would reduce bass productivity.

Spring and summer water temperatures are important factors in successful reproduction and the survival of fry. A correlation between higher water temperature during the first growing season and bass year-class survival was noted for Oneida Lake, New York (Forney 1972). Forney (1972) speculated that a strong year-class of smallmouth bass was related to above normal June temperatures, while Clady (1975) noted a similar relationship between temperature (June through October) and year- class size. There was a positive correlation between autumn 1st year fish length and winter survival rate (Oliver et al. 1979). Wismer et al. (1985) found that smallmouth bass <60mm long rarely survived the first winter. The abundance of bass in autumn was positively correlated with spring and summer water temperature (Serns 1982).

Shuter et al. (1980) reported a relationship between mean July air temperature and survival of young-of-the-year bass. He noted that, based on known smallmouth bass distribution, the likelihood of winter survival is essentially zero in lakes where the mean July air temperature is 16.6^{O}C or less. When mean July air temperature dropped below 18^{O}C, there was a corresponding decrease in winter survival and an increase in the relative number of lakes where average winter survival was too low to support reproducing populations. By combining equations developed to estimate the time of egg deposition, hatching, and fry nest emigration (Shuter et al. 1980, 1983), estimates of total mortality for alternative temperature regimes can be developed (Armour 1993).

The weight of evidence indicates that northern distribution of smallmouth bass is limited by temperature (Shuter and Post 1990; Jackson and Mandrak 2002). Length of the growing season determines the size of juveniles entering their first winter. The size of young-of-the year bass in autumn is correlated with their over-winter survival as size dependent over-winter survival is dependent upon the length of the starvation period. Jackson and Mandrak (2002) used the July mean air temperature threshold of 18^{O}C to delineate the limit of bass range. However, they felt that with global climate change the northern range limit may increase.

3.2.2 Water discharge, velocity and clarity

Riverine populations of smallmouth bass have been adversely influenced by high flow conditions during the nesting period, and also by high winter discharge (Swenson et al. 2002). Survival of smallmouth bass is negatively correlated with the preceding winter's river discharge (Sallee et al. 1991). The timing of flooding and the size of the fish during the period of high water are important considerations (Filipek et al. 1991). Floods did not seem to have an impact on larger fish; flooding prior to spawning seemed to improve reproductive success. There was a higher rate of nest success when stream flows were relatively stable through the spawning and nursery seasons. Fry acclimated to warmer waters exhibited higher mortalities to cold flood waters than fry acclimated to cooler waters (Larimore 2000). Analyses in warm water streams indicated that discharge during the spawning/rearing period had a greater effect on future adult density and fishing yield than did spawning/rearing temperature or winter discharge (Larimore 2000).

Smallmouth can be found in streams with moderate gradients (0.75-4.7 m/km) that provide alternating pools and riffles (Edwards et al. 1983). Fry can be displaced from nests in lab experiments by water moving greater than 8 mm/s (Simonson and Swenson 1990). Optimal water velocity for yearling bass is 10 mm/s (Paragamian and Wiley 1987).

High levels of sediment and turbidity are major threats to the viability of smallmouth bass populations. The best smallmouth bass habitat is non-turbid water (Armour 1993). Smallmouth bass are highly visual predators and they require clear waters to be effective (Sweka and Hartman 2003). Increasing turbidity decreases reactive distance, ultimately reducing overall prey consumption. However, once a prey item has been reacted to, turbidity does not have an impact on capture success (Sweka and Hartman 2003). An increase in turbidity can cause displacement of bass (Larimore 1975). The smallmouth bass is considered to be intolerant of high silt and turbidity and has been eliminated for some distance below these sources (Femmer 2002; Bunt et al. 2004). Paragamian (1991) found that smallmouth bass were absent from silt-laden reaches of poor habitat in Iowa. He felt that sediment was a major habitat factor in the viability of smallmouth bass populations.

3.2.3 pH

Smallmouth bass can exist only within certain limits of water acidity (Kane and Rabeni 1987). Nearly 20% of the Adirondack lakes have lost one or more fish populations due to acidification (Baker et al. 1993). Brook trout and acid-sensitive minnow species suffer more than bass species.

Smallmouth bass were highly sensitive to elevated aluminum concentrations at low pH (Baker et al. 1993). Such conditions are common in low-alkalinity waters receiving acid precipitation, for example Hamilton Harbour. The most toxic forms of aluminum are inorganic monometric forms, and aluminum toxicity to fish has shown to be highest at pH of 5.0-5.5 where these forms predominate. Kane and Rabeni (1987) concluded that a pH of 5.1 adversely affects young smallmouth bass, and the addition of aluminum makes a low pH (5.5) much more toxic.

3.2.4 Oxygen

Smallmouth are less tolerant of low dissolved oxygen (> 6 mgl-1), low pH (tolerates 5.7 to 9.0, prefers 7.9 to 8.1), and high turbidity (< 25 JTU) than are largemouth bass (Lasenby and Kerr 2000). Optimal dissolved oxygen levels for smallmouth bass vary by life stage. Although normal activities require > 6 mgl^{-1}, spawning requires > 7 mgl^{-1}, and embryo/larvae development requires > 6.5 mgl^{-1} (Davis 1975).

3.3 REPRODUCTION

The high reproductive potential of smallmouth bass reflects high fecundity and egg/fry protection by males (Scott and Crossman 1973). Variation in annual recruitment in Ontario Lakes was dependent upon water temperature and adult abundance (Shuter and Ridgway 2002). Shuter and Ridgway (2002) noted a decline in the ratio of recruits to adults as the number of adults increased (density dependence).

Not all mature bass spawn each year in the spring. The decision as to which fish will breed is predetermined the year before through some poorly understood but complex natural process (Raffetto et al. 1990). It has also been found that if any of the relatively few male protectors are removed from their nest or abandon it due to energetic condition, no other males replace them that spring, and the brood will not survive (Ridgway and Friesen 1992).

In northern areas, smallmouth bass spawn as late as June or July, and the eggs hatch 4-10 days later at the temperatures common in Canadian situations (Scott and Crossman 1973). The unfertilized eggs measured in eastern systems ranged from 1.2-2.5 mm in diameter (Scott and Crossman 1973; Hardy 1978). At hatching, the larvae range from 4.0 mm (McPhail 2007a) to 5.9 mm (Scott and Crossman 1973). Fry are transparent at the time of hatching and they remain in the nest for 10-12 days until the yolk is absorbed (McPhail 2007a), at which time they are 8.7-9.9 mm in length (Scott and Crossman 1973) and their colour will change. McPhail (2007a) notes that the fry are black after their yolk is absorbed and gradually turn green over the next month.

3.3.1 Water conditions

Spawning times and success of smallmouth bass spawning vary annually and geographically. In lentic environments, spawning time is associated with water temperature and its rate of increase (Shuter et al. 1980; Graham and Orth 1986; Ridgway and Shuter 1991; Ridgeway et al. 1991a). A drop in temperature of as little as 2°C can result in abandonment of the nest, especially when the water temperature drops below 15°C (Rawson 1945). In lotic environments, hydrologic factors (discharge) may also influence timing (Surber 1943; Graham and Orth 1986). Flooding (Cleary 1956) or a drop in temperature (Rawson 1945) can disrupt spawning and divide spawning seasons into two periods. In northern latitudes, bass spawn later than they do in southern environments.

Male bass are sensitive to water level and drops in temperature. A reservoir draw-down may cause abandonment of nests (Clark et al. 1998). Reynolds and O'Bara (1991) examined the reproductive ecology of smallmouth bass in two small streams of the Tennessee River system for two years. They attributed differences in nest site selection and spawning success to heavy rainfall and high discharge in late May and June. They noted that nest success decreased as substrate coarseness increased, because fanning by males was less effective in removing silt. They found that larger males were more successful, possibly due to their ability to remove more silt.

In Virginia, spawning is initiated when water temperature approaches 15^{O}C, and continues at temperatures ranging from 12.5 to 23.5^{O}C (Graham and Orth 1986). Spawning in Virginia may extend from late-April through to mid-July. In Idaho, nests with eggs were observed from late May to early July, while most of the spawning activity was between June 15 and July 1 (Keating 1970). Spawning takes place in the Clearwater and Salmon Rivers, Idaho, when temperature reaches 15-16^{O}C. In the Columbia River, unsuccessful spawning was noted as early as April, and successful spawning was observed in July and August when temperature was 15.5-23.8^{O}C (Henderson and Foster 1956).

In Ontario, the male smallmouth bass (3-5 years of age) starts nest-building at 12.5^{O}C, and mating commences when water warms to 16^{O}C (Scott and Crossman 1973). This is usually from May to early July. Shuter et al. (1980) noted that spawning typically occurs between March and May but, in the extreme northern extent of its distribution, smallmouth spawning may be delayed a month. The onset of spawning is based mainly on degree-days, when temperatures exceed 10°C. In Quebec, smallmouth bass spawn in May and June when temperature reaches 18-20^{0}C and daylight photoperiod is 14 hrs and increasing (Cantin and Bromage 1991). Earlier or later spawning may be initiated if water temperature and photoperiod are manipulated. In Saskatchewan, smallmouth bass spawning was initiated at approximately 18^{O}C; nest abandonment occurred with a drop to 14^{O}C (Rawson 1945). A second spawning period took place when temperature rose above 15^{O}C.

3.3.2 Spawning behaviour

The male smallmouth bass excavates a small, saucer-shaped nest in firm sand, mud, or gravel < 2.5 cm in diameter, at a depth of 0.6-1.8m (Moyle 2002; McPhail 2007a). The nest is concave, in the center of which there is a cluster of large stones; it is anywhere from 30 to 183 cm in diameter (Scott and Crossman 1973).

Mating takes place when a female bass enter the male's territory. A complex dance occurs, with the two fish rubbing and biting (Scott and Crossman 1973). The male will drive the female to the nest to spawn, and after spawning may drive her away (Moyle 2002). Several females may spawn in the nest of one male, and individual females may spawn in the nests of several males (Scott and Crossman 1973) but, for the most part, each is monogamous (Moyle 2002). The act of egg deposition takes about 5 seconds, but may be repeated for up to 2 hours with periods of nest-circling lasting 25-45 seconds (Scott and Crossman 1973). Total spawning may last for 6 to 60 days (Scott and Crossman 1973; Shuter et al. 1980; Graham and Orth 1986).

Females lay approximately 2,000 eggs at each spawning, and a female can produce 2,000 to 21,000 eggs (Moyle 2002). The norm is usually around 5,000 to 14,000 (Scott and Crossman 1973). Females have been found to lay a maximum of approximately 7,000 eggs per pound of fish (Scott and Crossman 1973). Eggs are enclosed in a tough skein and are adhesive. Bass eggs have been described as difficult and time-consuming to handle under hatchery conditions (Sparrow and Barkoh 2002).

Parental care is the sole responsibility of the male (Scott and Crossman 1973; Philipp et al. 1997; Cooke et al. 2002), who guards the eggs for 4-6 days, then the fry for approximately two weeks before they disperse (Scott and Crossman 1973; Neves 1975). The guarding period until dispersal may last from 19 to 28 days in an Ontario lake (Turner and MacCrimmon 1970).

3.3.3 Survival and predation

Survival of larval bass is linked to predation (Shroyer and McComish 2000) and to prey community structure (Siefert 1972; Bonar et al. 2005; Fulford et al. 2006). High levels of predation are related to nest failure (Lukas and Orth 1995). A male guarding a nest is effective against a single intruder, but not against a number of determined predators. The male will leave the nest to chase one fish, thus providing an opportunity for other predators (Thomas 1995). Up to 40% of all smallmouth bass nests fail; a successful nest may ultimately produce about 2,000 fry (Scott and Crossman 1973).

For lake-spawning smallmouth bass, nest survival along lake margins appears to be influenced by storms (Steinhart 2004). Boats and motors passing too closely overhead can also destroy eggs and nests (Wydoski and Whitney 2003). This may in part be due to higher levels of siltation. Pflug (1981) speculated that the slightly deeper spawning depths noted for Lake Sammamish 1.2-3.7 m may be to avoid wave action from heavy boat traffic in May and June. Parental care seems necessary to prevent egg predation

(Cleary 1956), and removal of guarding males leaves the nests open to predators. Fishing for nesting smallmouth in Ontario reduces the number of fingerlings that survive (Lewin et al. 2006).

3.4 FEEDING AND DIET

3.4.1 Juvenile diet

Larval smallmouth bass feed on their yolk sac until it is depleted, which corresponds to a body length of approximately 8.7 to 9.9 mm (Scott and Crossman 1973). The primary prey items of larval smallmouth bass are copepods, water fleas and other small zooplankton. Fry approximately 6 mm in length, rise from the nest in a shoal and feed on zooplankton while still protected by the male (Moyle 2002).

There is a shift from zooplankton to aquatic insects as the fish increase in size. First foods of 9 mm bass were chironomidae and copepoda, but they shifted to ephemeroptera at approximately 15 mm when fins have developed and mouth size increased (Easton and Orth 1992). In culture ponds, adult copepods and cladocerans were eaten by young bass (less than 19 mm in length), and were still an important item in bass from 36-49 mm, but a shift towards more insects was noted as size increased (Farquhar and Guest 1991).

Crayfish and fish start becoming important in a smallmouth's diet when it grows to > 50 mm in total length; once the fish has reached 100-150 mm, these dominate (Moyle 2002). The summer diet of 27.7-107.7 mm bass below a dam in Virginia was dominated by ephemeroptera (Baetidae) nymphs (Easton et al. 1996). Ephemeropteran nymphs represented 59.7% of the diet of smallmouth bass in Pennsylvania (Johnson and Dropkin 1995). Young–of-the-year bass avoided tricoptera and selection for chironomidae, amphipoda and isopoda were variably used. Aquatic dipterans (mainly chironomid larvae and pupae) dominated age 0 smallmouth bass diet in a California reservoir (Okeye and Hassler 1985). Keating (1970) noted that the occurrence of insects in age-0 smallmouth bass stomachs was 84%. Chironomids and mayfly dominated, but 36% were terrestrial (ants, grasshoppers) and flying aquatics (adult mayflies). Applegate and Mullan (1967) felt that chironomid larvae were important to bridge the gap from an entomostracan diet to a diet of fish. They noted that, in one Arkansas reservoir, chironomids dominated the diet of bass approximately 36 mm long, but the diet shifted to gizzard shad at 40 mm.

The importance of other prey items such as fish and crustaceans increases as the fish grow. Lachner (1950) reported that smallmouth bass in East Koy Creek, New York, that were less than 40 mm in length did not eat fish, while those over 60 mm rarely ate insects. Under-yearling bass consumed both fish (cyprinidae) and invertebrates (primarily ephemeroptera and chironomidae); although fish were 20% of the diet numerically, they represented about 80% of the total caloric intake. Livingstone and Rabeni (1991) felt that adequate growth could only be maintained if smallmouth bass diet shifted to a sufficiently abundant supply of small fish.

3.4.2 Adult diet

From age-1 on, smallmouth bass eat mostly fish, insects and crayfish (Scott and Crossman 1973). In New York water bodies, forage species included northern shiner, bluntnose minnow, central stoneroller, northern creek chub and fantail darter (Lachner 1950). The bulk of diet consisted of crayfish, fantail darters, and aquatic insects (Lachner 1950). All basses are cannibalistic. In Tennessee, juvenile bass were the only piscivores consumed and they were eaten only by other bass (Raborn et al. 2003). This cannibalism was considered to have a density-dependent effect on survival (Raborn et al. 2003).

In the Snake River, 86% of the diet by weight consisted of crayfish, 11% fish (no salmonids, some smallmouth bass young, shiner and sucker), 2% insect, and 1% terrestrial (Keating 1970). Crayfish were considered to be an important diet item in Lake Whatcom, and the crayfish fishery was considered to result in substantial declines in production of smallmouth bass (Mueller et al. 1999). Bass can consume frogs, tadpoles, fish eggs, and plant material (Scott and Crossman 1973).

Bass do consume salmonids. In Lake Sammamish, Washington, crayfish and sculpin were a major portion of annual diet except for May, when migratory salmon juveniles were the most important (Pflug and Pauley 1984). Fish represented 73% and 54% of the diet in 1979 and 1980. Salmonids were numerically the primary fish prey and represented 34% of it in 1979. Bass of different sizes preyed upon different sizes of salmonids (Pflug and Pauley 1984). Salmonids taken by age-1 bass averaged 44 mm, by age-2 bass averaged 74 mm, by age-3 bass averaged 78 mm, and by age-3-6 bass averaged 66 mm.

Salmonids > 100 mm long were rarely consumed by smallmouth bass. A negative relationship was noted between salmonid consumption and smallmouth bass size. Fritts and Pearsons (2006) discovered that the smallest studied bass size class (150-190 mm) was the greatest consumer of salmonids. They suggested that smallmouth bass of 100 mm could easily consume fish 30-35 mm long, the size of newly emerged salmonid fry.

In the Columbia River, crayfish were the main food item (72% of total volume), although ten species of fish were consumed. The fish species that dominated the diet were sculpin *Cottus* sp., white crappie *Pomoxis annularis*, redside shiner *Richardsonius balteatus* and northern pikeminnow *Ptychocheilus oregonenisis* (Bennett et al. 1991). Chironomidae were the dominate prey item of bass >150 mm in spring (50% by number) but represented only 2% by weight, compared to fish and crayfish. The dominant fish prey species by weight in spring were; migrating salmonids and catostomids, followed by chiselmouth *Acrocheilus alutaceus* and northern pikeminnow (Bennett et al. 1991).

A population of smallmouth bass in an Idaho reservoir has been described as planktivorous (Dunsmoor et al. 1991). In spring, the smaller bass (< 100mm) numerically consumed 91% cyclopodia and 7% *Daphnia*, while in summer they consumed 75% *Daphnia*, 17% cyclopodia and 6% *Leptodora*. The next size class (101-200 mm) in the spring fed on *Daphnia* 77%, 12% *Leptodora* and plumatellidae 9%) and in summer fed on *Daphnia* 82% and *Leptodora* 17%. Bass > 200 mm consumed 78% plumatellidae in spring and in summer ate *Daphnia* 69% and *Leptodora* 39%. The most important zooplankton were *Daphnia* and *Leptodora*, for all size classes. The older size classes of smallmouth bass grew rapidly on a zooplankton diet despite their lack of planktivorous adaptations (Dunsmoor et al. 1991).

Pflug (1981) examined bass diet in Lake Sammamish, Washington, and noted considerable overlap between largemouth and smallmouth bass, although he felt there was very little competition between these two basses because they were spatially separated in very different habitats. Possibly the greatest dietary overlap occurs between juvenile smallmouth bass, yellow perch and pumpkinseed (Johnson 1983).

3.5 HABITAT REQUIREMENTS

3.5.1 General habitat

Although bass is primarily a lake fish (Scott and Crossman 1973), it also inhabits rivers. Bass require large lakes (> 40.5 ha) and wide rivers or streams (> 10.5m wide) (reviewed by Edwards et al. 1983). The best smallmouth bass lakes are mesotrophic, clean and clear, with an average depth of >9m, and rocky shoals (reviewed by Edwards et al. 1983). Pflug (1981) observed that smallmouth were often associated with a littoral drop-off and that lake substrates tended to be gravel and cobble. The littoral zones are important because both spawning and rearing occur there.

The best rivers for smallmouth bass have been described as mid-order, cool and clear, with moderate current, a gradient between 0.75 m/km and 4.7 m/km, and over 50% pool (Lasenby and Kerr 2000). Abundant shade and cover, substrates of gravel and larger materials, and deep pools are also important (Edwards et al. 1983; Armour 1993).

Although smallmouth bass are generally confined to fresh water, they may move into low salinity areas of tidal rivers for short periods of time (Schmidt and Stillman 1998). In their native range, smallmouth bass can be found in the upper reaches of estuaries of larger rivers (Moyle 2002).

Smallmouth bass seek out structures such as logs, rocky outcroppings, or pier posts (Etnier and Starnes 1993). In Lake Sammamish, smallmouth bass, unlike largemouth bass, were rarely associated with aquatic vegetation (Pflug 1981). Residence areas were devoid of vegetation, but had cover such as docks, submerged logs and overhanging shoreline vegetation.

Smallmouth bass habitat changes with season and fish size. Keating (1970) described some of these differences for the Snake, Clearwater and Salmon rivers in Idaho. Fingerling bass were abundant in isolated pools, sloughs, and shallow still-water areas along the banks. Juvenile bass (25-100 mm) found refuge under rubble even in shallow water. Adults preferred cover such as angular bedrock crevices and deep pools. In winter, smallmouth bass hibernate within rock fissures, crevices, rock ledges, and even in hollow logs. In summer they occupy the warm epilimnetic waters of shallow lakes and shallow bays of larger, deeper lakes (Baker et al. 1993). Bass move to deeper waters in winter. If lakes are to support over-wintering bass they should be at least 3-15 m deep (Stuber et al. 1982).

Paragamian (1991) recorded the highest densities of smallmouth bass downstream of dams; channelized sites were poor habitat, and smallmouth bass were never found in silt-laden sections. Bass density decreased with increased stream drainage area and with decreased stream gradient.

3.5.2 Spawning habitat

The best sites for nest-building have been described as between 1-2.5 m in depth, with the substrate particle size near 30 mm (Clark et al. 1998). Smallmouth bass spawn in protected coves, bays, and shorelines where the water warms the earliest. Nest sites are usually associated with some form of cover like fallen trees, boulders and dense vegetation (Moyle 2002). Nests are usually in less than 3 m deep, but have been noted at depths of 6.1m (Scott and Crossman 1973). Forney (1972) observed spawning at 4.3-5.5 m in Lake Oneida, New York and attributed the deeper depth to wave action.

3.6 INTERSPECIFIC INTERACTIONS

In Wisconsin streams, smallmouth bass were closely associated with one particular fish community (Lyons et al. 1988). This fish assemblage included rosyface shiner, stonecat, hornyhead chub, shiner, and golden redhorse. The authors felt this assemblage was a good indicator of potential smallmouth bass habitat.

In Eastern Canadian water-bodies, walleye (*Serranidae*) and smallmouth bass can often be found in the same waters. A review of almost 1,000 Ontario lakes reported that northern pike, walleye, and smallmouth bass were a common fish association found together in 17.8% of the lakes (Johnson et al. 1977; Kerr et al. 2004). Smallmouth bass do better than walleye in water bodies with a low abundance of forage fish, a high degree of shoreline irregularity, rocky-boulder substrates, and high transparency (Kerr and Grant 1999). The two species appear to co-exist well in larger lakes with a diversity of different habitats.

3.7 BEHAVIOUR AND MOVEMENTS

3.7.1 Spawning migrations

Smallmouth bass populations have been described as seasonally migratory or non-migratory. Newbrey et al. (2001) considered them to be clearly migratory, and many lake populations undergo short spawning migrations (Cuerrier 1943). Langhurst and Schoenike (1990) observed smallmouth bass greater than 200 mm migrating 69-87 km down the Embarrass River to the Wolf River when the autumn water temperature fell below 16°C. These smallmouth bass returned to the Embarrass River to spawn in April and May. An upstream movement during the spawning period has been reported in the Red Cedar River, Wisconsin (Paragamian 1973). An upriver movement of smallmouth bass from Lake Simcoe into the Pefferlaw River in Canada was documented, with 34% of river spawners returning in subsequent years (Robbins and MacCrimmon 1977). Most adults moved downriver in late June and July, when temperatures approached 25°C. In Ontario, individual males tended to nest close to the previous year's site (Ridgway et al. 1991b). In Lake Ontario, smallmouth bass were considered to be non-migratory (Gerber and Haynes 1988).

Some bass repeatedly home to the same nesting site each year, and over 85% of these return to within 130 m of where they nested in previous years (Scott and Crossman 1973). In Lake Sammamish, Washington, smallmouth bass returned to a specific residence (41%) after displacement distances ranging from 1 to 10 km (Pflug 1981). In Elkhorn Creek and Kentucky River, Kentucky, the movement pattern of 305-406 mm smallmouth bass was examined by radio telemetry (Van Arnum et al. 2004). The population of bass was considered to be 69% migratory and 31% sedentary. When fish were displaced following spawning, the majority (60%) returned to their home creek.

3.7.2 Home range

Smallmouth bass exhibit considerable fidelity to a given location. Usually they stay within 8 km of the place of original capture, but longer movements have been recorded (Scott and Crossman 1973). Larimore (1952) found that bass transferred to other sections of streams showed an amazing ability to return to home pools either upstream or downstream. Langhurst and Schoenike (1990) noted that when the bass returned to the Embarrass River to spawn, most bass returned to the same 5 km section of river. In Lake Huron, 72% of tagged smallmouth bass were recovered within 3 km of their release site; only 5% were recovered more than 8 km away (Fraser 1955).

In rivers, movements may be more restricted. Smallmouth bass appear to respect stream riffles as boundaries, and movement may be limited to 50-150 m (Gerking 1953). A few bass moved upstream to a different pool. In Ozark streams, smallmouth bass movement was limited to a few sections of stream, and individuals often remained in one pool (Otto 1962). Movement, when it occurred, ranged from 30 m to one kilometer; return movement to home pools was noted. Todd and Rabeni (1989) noted that another Missouri stream-based smallmouth population demonstrated a strong home pool attachment but they did move, predominantly in the spring and fall. Bass were found to have moved as far as 7.5 km upstream and 5.7 km downstream in movements non-correlated with high water events. Twenty-five percent of the study population did not return (Todd and Rabeni 1989).

3.7.3 Diel movements and schooling

Smallmouth bass exhibit considerable diel activity. Feeding can be observed at any time of day or night depending upon the conditions, but smallmouth bass are usually most active in the early morning and evening (Moyle 2002). In the northeast, smallmouth bass food consumption was reported to increase throughout the day and peak consumption occurred at 20:00 (Johnson and Dropkin 1993).

Bass seek protection from light during all stages of life (Edwards et al. 1983) and will refuge under banks in rivers or in deeper water in lakes. They will move to deeper water in winter and will move into bays that have warmer water in spring (Scott and Crossman 1973).

Smallmouth bass of different ages have a slight schooling tendency in some seasons. Young bass have a schooling tendency (Becker 1983), while older bass are often caught by recreational fishers in what are considered shoals (Moyle 2002). In an eastern Ontario lake in late November, an aggregation of smallmouth bass was detected by radio transmitters in approximately 10 m of water (Bunt et al. 2003).

3.7.4 Swimming speed

The swimming speed of bass is size-dependent (Peake and Farrell 2004). The speed of smallmouth bass (24-38 cm) was measured on a 25 m raceway with water velocities ranging from 40 to 120 cm/s. The maximum sustained speed was 97.3 cm/s, with a peak of 81.4 to 122.9 cm/s (Peake and Farrell 2004). Smallmouth bass preferred water velocities less than 0.2 m/s in all seasons (Todd and Rabeni 1989). Smallmouth bass need to accelerate quickly but, based on their general body shape it is likely they are poor at ascending barriers. In a detailed bibliography on the effects of stream barriers on fish movement, Newbrey et al. (2001) reported that no information was found on the leaping ability of smallmouth bass.

3.7 DISEASES AND PARASITES

Eastern smallmouth bass host a number of bacterial, viral, and parasitic diseases. Among these the most well known in Eastern Canada are bass tapeworm *Proteocephalus sp*. and the grubs *Posthodiplostomum* sp., *Clinostomum* sp., and *Uvulifer* sp. (Hoffman 1967). Egg masses can be infected and killed by fungus (Scott and Crossman 1973).

In Eastern North America, smallmouth bass populations may be controlled in part by the degree of parasitic infections. Becker et al. (1966) counted 21 different parasites on 489 bass from a reservoir in Arkansas. They speculated that the high level of parasitism had contributed to a decline in the bass sport fishery. In Gull Lake, Michigan, it was felt that parasitic infections may regulate the bass population (Esch and Huffines 1973). The extent of organ damage was directly dependant on the number of parasites present.

3.7.1 Infection rates for introduced fish

Although a wide variety of parasites and diseases affect smallmouth bass, most of these have not spread to Western North America. In general, rates of parasitism for introduced fish are lower than in their native range. Smallmouth bass from Christina Lake (Kettle River Drainage), B.C. were examined for parasites, and infection rates compared to smallmouth bass from Wisconsin and Ontario (Bangham and Adams 1954). Eighty per cent were infected with four different species of parasites (Bangham and Adams 1954). This compares to 24 different parasite species on smallmouth bass in Wisconsin and 30 in Lake Huron. The major parasites for smallmouth bass in British Columbia are: *Proteocephalus* sp., *Rhabdochona* sp., *Ergasilus caeruleus (*Margolis and Arthur 1979; McDonald and Margolis 1995) and an unnamed cestode (Bangham and Adams 1954).

Smallmouth bass introduced to California had few parasites relative to fish in their native range (Bangham and Adams 1954). In California (Lake Oroville) it was indicated that "There is little information on the warm water diseases present and their impacts on the fishery" (Keefe 2003). However, it was speculated that few parasites were present; of the potentially significant warm water diseases, only *Epistylis* sp. was observed in bass.

3.7.2 Worms

Specific parasites may infect an introduced species at very high levels. In the Snake River, introduced bass were heavily infested with the nematode *Contracaecum* sp. One tapeworm was also found in the 10 stomachs examined, and fingerling bass in shallow pools were infected with *Ichthyophthirius* sp. (Keating 1970). Bass from the Okanagan system (i.e. Vaseux Lake) have been rumored to be full of "worms" and some fishermen do not consider them edible (Schwanky 2006). The exact species of parasite has not been identified in this case, but the broad tapeworm *Diphyllobothrium latum*, bass tapeworm *Proteocephalus ambloplites* and nematodes are possibilities.

The bass tapeworm is considered a problem for trout and salmon management in the Pacific Northwest as the worm can develop after ingestion of copepoda (Becker and Brunson 1968). Cyclopoid copepods (first host of bass tapeworm) are an important food item for rainbow trout, cutthroat trout and coho salmon (Antipa 1974). The bass tapeworm *Proteocephalus ambloplites* attacks reproductive organs and can cause sterility (Scott and Crossman 1973). Largemouth bass in British Columbia can carry *Proteocephalus amploplites* (Bangham and Adams 1954; Margolis and Arthur 1979; McDonald and Margolis 1995), although a different species of tapeworm (*Proteocephalus* sp and not *amploplites*) has been found in smallmouth bass in British Columbia. Bengeyfield (1990) felt that the accidental introduction of bass tapeworm into Lower Mainland waters could be avoided by obtaining certified bass stocks. Although legal bass transfers are unlikely to occur in B.C. in the near future, the spread of bass tapeworm might continue through stockings by persons unaware of the dangers.

3.7.3 Viral hemorrhagic septicemia

Viral hemorrhagic septicemia (VHS) is a serious systemic disease of fish and is an emerging disease in the Great Lakes (Fisheries and Oceans Canada 2008). Fisheries and Oceans Canada (DFO) determined that the VHS virus detected in the Great Lakes is a North American strain, closely related to the strain found on the east coast. In 2005, mortalities appeared in the Bay of Quinte, Lake Ontario and Lake St. Clair. Over 50 species of marine and freshwater fish can carry the virus (Iowa State University 2007), and it has been found in 12 species in the Great Lakes, with freshwater drum, smallmouth bass, crappie, muskellunge and bluegill the most affected (Fisheries and Oceans Canada 2008). The pathogen cannot infect humans who eat infected fish (Whelan 2007).

It was originally believed that Atlantic salmon infected with VHS and stocked in Puget Sound were responsible for introducing this new disease to west coast waters (Fuller et al. 1999). However, strains of VHS have been reported in wild populations of herring and pilchard along the Pacific coast (Iowa State University 2007), and the disease is currently thought to be endemic in some Pacific marine species (Dorthee Kieser, pers. comm., undated). The eastern VHS isolate may cause mortality in salmonid species such as chinook salmon and rainbow trout that have not have been affected by other isolates (Iowa State University 2007).

4.0 USE BY HUMANS

4.1 RECREATIONAL FISHING

Smallmouth bass is a prized sport fish, one of the most popular in North America (Lasenby and Kerr 2000). Huge recreational fisheries feature tournaments and derbies where large prizes are offered. In 2001, a survey produced by the US Fish and Wildlife Service indicated that there were 34.1 million anglers who generated $35.6 billion for the US economy, of which 11.3 million (or 33% of the freshwater anglers) fished for bass (United States Department of the Interior 2002). Smallmouth is one of the mainstays of the sport fishery and associated tourist industries in eastern Canada (Scott and Crossman 1973). Fisheries management throughout North America supports these bass fisheries through regulation, habitat enhancement, and hatchery augmentation. There is a movement toward catch-and-release fishing in many places.

In British Columbia, the 2000 freshwater sport fishery involved 400,000 licensed anglers (Levey and Williams 2003). In 2002, sport fishing (tidal and non-tidal) was estimated to contribute $233 million to BC’s GDP and support 8,900 jobs (Ministry of Agriculture and Lands 2007). At that time, very little of this could be attributed to bass fishing, but bass appears to be gaining in popularity. In B.C., smallmouth and largemouth bass have created recreational opportunities in four regions (Lower Mainland, Vancouver Island, Okanagan, and Kootenays; Figure 2). Bass have existed in a few B.C. lakes for approximately 100 years and some (i.e. Vaseaux Lake and Duck Lake) currently support a trophy bass fishery.

4.2 COMMERCIAL FISHING

There is presently no commercial fishery in Canada that targets smallmouth bass. A commercial fishery did exist for them until 1936, when the fish was restricted to sport use (Scott and Crossman 1973). Although commercial freshwater fishermen target species such as lake whitefish and yellow perch, the gill-nets used are not species specific. Non-target species such as smallmouth bass are by-catch in Lake Ontario at certain times of year (Smith and Edwards 2002).

4.3 AQUACULTURE

In Ontario, hatcheries produce bass fingerlings for stocking into waters where populations need to be replenished or augmented. The first artificial propagation of smallmouth bass took place in Ontario in 1880, when a supply of fry was produced to stock regional lakes for recreational purposes (Lasenby and Kerr 2000). As of 1999, propagation of smallmouth bass still occurs at 25 private hatcheries in south-central Ontario (Lasenby and Kerr 2000). Smallmouth bass fingerlings planted into test ponds experience poorer survival than those placed in a stream environment. In Ontario, stocking densities of 100 fry/ha are utilized (Lasenby and Kerr 2000).

5.0 IMPACTS ASSOCIATED WITH INTRODUCTIONS

5.1 IMPACTS ON PLANKTON, ZOOPLANKTON, BENTHOS, AND ALGAE

Most river and lake-rearing littoral fish consume similar zooplankton (i.e. copepods and cladocerans) and insects (chironomids and ephemeroptera) for at least the early portion of their life. Smallmouth bass shift to fish and crayfish at a relatively small size (<80 mm), so the majority of direct competition for non-fish prey is from young-of-the-year. Although smallmouth bass is considered to be a top predator, it may also take a large proportion of macroinvertebrate production (MacRae and Jackson 2001). It has been suggested that bass can change chironomid and odonata abundance (Morin 1984).

The introduction of smallmouth bass may indirectly reduce crayfish abundance (Stein and Magnuson 1976; Mather and Stein 1993; Somers and Green 1993). Crayfish are omnivores, grazing on periphyton and macrophytes and consuming invertebrates (Hill and Lodge 1995; Nystrom et al. 1996; Bondar et al. 2005). A reduction in crayfish numbers might modify macrophyte and algae abundance as well as disrupt detrital pathways. This may indirectly contribute to differences in habitat complexity and to differences in the benthic invertebrate community (Jackson and Harvey 1993; Kerr and Grant 1999).

The introduction of non-indigenous fish species can be accompanied by a shift in prey community structure and food web dynamics (Pazzia et al. 2002). The presence of bass can indirectly change the flora and fauna of a system through the alteration of fish community structure and the behaviour of other fish species. Algae-grazing minnows such as *Campostoma anomalum* can markedly alter the algal primary productivity and the invertebrate community composition of streams (Gelwick and Matthews 1992). While largemouth bass introduction has been demonstrated to change algae-grazing minnow behaviour and increase the standing crop of algae in Oklahoma streams, (Power et al. 1985), smallmouth bass introductions had less influence (Harvey et al. 1988). Smallmouth bass do, however, appear to have reduced the abundance, altered habitat use, and possibly extirpated smaller minnows and dace from Ontario and northern systems (Crossman 1991; MacRae and Jackson 2001).

5.2 IMPACTS ON FISH

The reduction and/or elimination of small-bodied fish following smallmouth bass introduction has been well documented in North America (Robinson and Tonn 1989; Findlay et al. 2000; Weidel et al. 2000; MacRae and Jackson, 2001; Jackson and Mandrak 2002) and other parts of the world (Impson 1998; Iguchi et al. 2004).

Smallmouth bass pose a threat to native fish faunas through competition for food and predation (MacRae and Jackson 2000; Weidel et al. 2000). Factors favoring invasive smallmouth bass include their small size at the onset of piscivory, juvenile use of cover, low overlap with other predators (Gard 2004), and high fecundity combined with parental care. Their value as a sports fish has led to their many global and North American introductions. It is also likely that smallmouth bass will increase their range north in response to climatic trends associated with global warming (Jackson and Mandrak 2002).

Once established in new ecosystems, smallmouth bass rapidly dominate, reducing the abundance and diversity of local species. In South Africa, smallmouth bass predation is considered to be the critical mechanism for the loss of indigenous fishes (Impson 1998) especially in the Rodegat River (Woodford et al. 2005). Black basses are characterized as an invasive alien fish in Japan, and smallmouth bass has been described as the “world’s most disastrous invasive species” by Iguchi et al. (2004). Numerous methods to remove them have been considered, as their introduction is a major concern for the conservation of native biodiversity. Invasive bass constitute a “serious biohazard,” and the bibliography written by Hosoya and Nishi (2003) promotes their eradication in Japan.

A model was developed to identify Ontario lakes most vulnerable to invasion by smallmouth bass and most likely to be impacted by their introduction (Vander Zanden et al. 2004). This model used environmental variables including mean annual temperature, mean annual precipitation, and community composition to predict bass viability. The model also examined the potential for impact using fish species distribution data and through consideration of lake food webs.

5.2.1 Hybridization

Smallmouth bass interbreed with at least four other basses including largemouth, redeye, spotted, and Guadalupe bass (Kerr and Grant 1999; Moyle 2002), of which only the largemouth bass co-exists in British Columbia. Although in vitro laboratory mating supports the potential for interspecific hybridization, evidence for natural hybridization is sparse (Whitmore and Hellier 1988). Smallmouth-spotted bass hybrids have been found in Missouri, Arizona, California, Kansas, and Oklahoma; smallmouth-Guadalupe bass and smallmouth-largemouth hybrids have been noted in Texas (Whitmore and Hellier 1988; Fuller 2007).

Guadalupe bass is seriously threatened by introgression with introduced smallmouth bass within its native range and the hybrid is fertile and capable of backcrossing to the parent species (Whitmore 1983). There was more backcrossing to smallmouth bass than to Guadalupe bass, and introgressive hybridization represented a threat to the already depleted Guadalupe bass.

5.2.2 Predation and competition

Smallmouth bass are believed to have an impact on walleye year-class strength (Johnson and Hale 1977). In some Northern Wisconsin lakes, the introduction of either smallmouth bass or walleye into the same system resulted in reduction or elimination of the other species (Frey et al. 2002). Frey et al. (2002) reported that predation by adult walleye on smallmouth bass was low from June to October, while predation by young-of-the-year walleye on young-of-the-year smallmouth bass was substantial during July and August. They also noted that dietary overlap between young of the two species was significant during July and September. They predicted that the high abundance of walleye young-of-the-year could eliminate whole year-classes of bass. However, in a Wisconsin multi-lake study, Fayram et al. (2005) found that largemouth bass had a detrimental impact on the survival of stocked walleye, while northern pike and smallmouth bass did not have strong predatory or competitive interactions with walleye populations.

Lamprey were found in the stomachs of 10% of the smallmouth bass examined from the Umpqua River (Close et al. 2002). This result differs from the findings of Summers and Daily (2001) who examined the stomachs of 186 smallmouth bass from the Willamette River and found lamprey in only one. It is possible that occurrence of western brook lamprey in diets is underestimated because they lack diagnostic bones that can remain intact during digestion.

Smallmouth bass and yellow perch commonly coexist in eastern North American lakes. Potential competitive interactions (diet overlap) have been reported for young smallmouth bass and juvenile yellow perch (Serns and Hoff 1984). These include dietary overlap of aquatic insects. Slow growth of smallmouth bass in the St. Lawrence River (Stone et al. 1954) was attributed to competition by rock bass and yellow perch. Yellow perch are considered a forage fish in lakes containing predators such as bass, pike and walleye (Scott and Crossman 1973). In four New Brunswick lakes, minnows were considered to be the most important forage prey for adult smallmouth bass, although yellow perch and pumpkinseed were also consumed (Curry et al. 2004). Curry et al. (2004) noted that yellow perch were reduced in size when bass were large, and the smaller yellow perch represented a greater proportion of the lake biomass when bass biomass increased in a lake. However, direct competition between lake fish species was not readily apparent.

5.2.2.1 Interactions with northern pikeminnow

Studies at Dalles Dam tailrace (Petersen 1991) indicated a recent, relatively high number of smallmouth bass compared to the native northern pikeminnow *Ptychocheilus oregonensis*. In the Yakima River, Washington, smallmouth bass have replaced northern pikeminnow as the major piscivore on salmonids (Fritts and Pearsons 2006). Ward et al. (1995) reported that direct and indirect competitive interactions between various fish predators may affect northern pikeminnow habitat use, prey availability and juvenile survival. They felt that these interactions may contribute to differences in growth, mortality, and recruitment of northern pikeminnow. Fletcher (1991) speculated that smallmouth bass feed on other piscivorous fish such as northern pikeminnow, and this might offset or more than offset the impacts of smallmouth bass predation on salmonids. Gard (2004) described smallmouth bass as ecologically similar to the closely related Sacramento pikeminnow *Ptyhcocheilus grandi*, and noted that smallmouth bass had replaced other native fishes in California streams. In the Colorado and Green Rivers, competition and predation from introduced smallmouth bass and northern pike are considered to be the major reason for the decline in Colorado pikeminnow and other fish species (Burdick 2007). Following introduction of smallmouth bass in three Idaho reservoirs, the catch of pikeminnow declined, and kokanee populations and returns of hatchery rainbow appeared to have increased (Fletcher 1991).

5.2.2.2 Interactions with forage fish and minnows

Small-bodied fish is a prime forage item for smallmouth bass, and young smallmouth are a major source of larval fish mortality (MacRae and Jackson 2001). Minnows appear to be the most important fish forage item in lakes, followed by pumpkinseed and yellow perch (Curry et al. 2004). In Dworshak Lake, Idaho, smallmouth bass feed on redside shiner (Fletcher 1991).

There is a relationship between the number of small fish taken and the availability of crayfish. Where crayfish are numerous, a smaller percentage of the diet consists of fish (Keating 1970; Shively et al. 1991). The examination of 72 Snake River smallmouth bass stomachs, from fish larger than 100 mm, indicated a diet of 86% crayfish and 11% fish by weight. An examination of 45 bass stomachs sampled from the Clearwater River yielded 84% fish and 2% crayfish, by weight. The fish found in the bass stomachs were identified as dace, shiner, and small sucker (Keating 1970).

The reduction or elimination of small-bodied fish (i.e. minnows) by smallmouth bass and other predators is a consistent theme in the scientific literature. Introduced smallmouth bass in Ontario appear to have reduced abundance, altered habitat use, and locally extirpated many small-bodied species such as brook stickleback *Culaea inconstans*, fathead minnow *Pimephales promelas*, pearl dace *Margariscus margarita* and *Phoxinus* sp. (MacRae and Jackson 2001). In Alberta, piscivory is a major factor in structuring lake fish assemblages, and lakes with piscivores have reduced minnow diversity (Robinson and Tonn 1989). Following introduction of smallmouth bass and northern pike in a small lake in Gatineau Park Quebec, minnow richness was reduced (Chapleau et al. 1997). Fuller (2007) speculated that the introduction of smallmouth bass may have contributed to the demise of an isolated population of trout-perch *Percopsis omiscomaycus* in the Potomac River. The expansion of the introduced smallmouth bass has been associated with the decline in native hardhead, and predation by bass may have been a major factor in the extinction of the thicktail chub in California (Cohen and Carlton 1995). Prior to smallmouth bass introduction, peamouth chub represented 60.5% of Lake Whatcom's fish population (Mueller et al. 1999); fifteen years later, peamouth chub represented 22.2% of the populations.

In Adirondack lakes, native minnow richness was dramatically reduced when northern pike, largemouth bass and smallmouth bass were present (Findlay et al. 2000). Five different minnow species were affected by the piscivores. Fish community response was monitored in one oligotrophic Adirondack Lake (Weidel 2002). Following a 90% reduction in smallmouth bass abundance, the relative abundance of six native littoral species increased from 4 to 90 times their pre-removal abundance. Increased abundance was noted for pumpkinseed, creek chub, common shiner, white sucker, brook trout, and central mudminnow.

Jackson and Mandrak (2002) indicated bass introductions will likely lead to the extirpation of an estimated 25,000 cyprinid populations and the possible loss of four cyprinid species in Ontario. They predicted that the northern expansion of smallmouth bass will substantially change ecosystems and fish biodiversity, and cause reductions in growth and yield of recreational species (i.e. lake trout). Species considered vulnerable to smallmouth bass predation included fathead minnow, pearl dace, northern redbelly dace and finescale dace (Jackson 2002). It was noted that lakes with trout contained significantly more species of cyprinids, whereas lakes with bass showed fewer species (Jackson and Mandrak 2002; Jackson 2002).

5.2.2.3 Interactions with salmonids

Smallmouth bass have been introduced into many coldwater environments containing lake trout. Although Evans et al. (1991) concluded that smallmouth bass were segregated from lake trout on a spatial and functional basis and thereby did not have a detrimental impact on them, the mechanism of interaction was not clear. Catch rates of lake trout and growth rates of juvenile lake trout tended to be higher in Minnesota lakes that had no smallmouth bass (Eiler and Sak 1993). Following the introduction of smallmouth bass in a number of North American Lakes, an abrupt and drastic reduction in maximum size, maximum age, and size at maturity of lake trout was noted (Pazzia et al. 2002). The mechanism for this change was related to the consumption of littoral prey and reduction in littoral prey densities by the introduced bass species, to the point where lake trout were forced to feed almost entirely on zooplankton and benthic invertebrates (Casselman and Grant 1998; Vander Zanden et al. 1999). Lake trout typically consume minnows and other small fish in the littoral zone during spring and winter when lake trout and cyprinids spatially overlap. Vander Zanden et al. (1999) found that the presence of bass altered the diet of lake trout. Bass eliminated some cyprinid species or reduced their abundance via both direct and indirect effects and thus reduced the availability of small fish as food for trout. Lake trout either experienced reduced resource availability or were forced to switch to less optimal prey. Thus, the lower growth rate observed in lake trout was associated with the forced consumption of smaller and less digestible prey through competition with bass (Pazzia et al. 2002).

In North America, smallmouth bass have greatly expanded their range, and numerous case studies of bass interactions with sports fish such as brook trout or (speckled trout), exist (Ryder and Johnson 1972, Martin and Fry 1973). Smallmouth bass were not originally present in the Adirondacks, where their introduction into many lakes has had a strong negative impact on native brook trout (Whittier and Kincaid 1999). In the 1920s, bass were introduced to Lake Opeongo, New York, and the decline in brook trout that followed was attributed to the dietary overlap between the two species and to predation on young-of-the year trout in spring (Olver et al. 1991). In Maine, numerous unauthorized introductions of smallmouth bass have altered fish populations and ecosystems with some deleterious effects. It is likely bass will eventually out-compete and eliminate the fishery for brook trout (Land and Water Resources Council 2002).

Following removal of smallmouth bass from a northeastern lake, an increase in brook trout catch rates suggested that the prior high density of smallmouth bass had limited brook trout abundance (Whittier and Kincaid 1999). This result supports previous observations that brook trout are found less frequently in fish communities in northeastern lakes containing smallmouth bass (Whittier and Kincaid 1999). In Arkansas, pools were dominated by smallmouth bass and riffles by rainbow trout; competition for food may have occurred as juvenile smallmouth base used riffle areas extensively for feeding (Ebert and Filipek 1991).

Bull trout and Dolly Varden are considered to be cold-water fishes, while smallmouth bass is a cool-warm water fish. There are physiological differences between the native chars and smallmouth bass that might limit their spatial overlap, thus reducing the potential for interaction. Bull trout, brook trout and bass do overlap in the Kootenay River. At the southern margins of their range bull trout are considered to be in serious decline (McPhail 2007b).

Smallmouth bass clearly prey on juvenile migrating salmonids (Warner 1972; Weidel et al. 2000; Fritts and Pearsons 2006) and trout (Tabor and Wurtsbaugh 1991). However, the degree to which this affects salmonid abundance is not so clear. Scientific literature for the lower, un-impounded Columbia and Willamette Rivers supports the conclusion that juvenile salmonids are typically not a major part of adult smallmouth bass diet (Zimmerman 1999, Summers and Daily 2001). However, predation on migrating salmonids by smallmouth bass is apparently high during spring and early summer, when fry and sub-yearling chinook salmon of suitable size are abundant and when their habitat overlaps with that of smallmouth bass (Tabor et al. 1993).

Fletcher (1991) examined ten case studies of smallmouth bass and salmonid interaction in the northwestern U.S. He concluded that in five cases after smallmouth bass became established there was an indication of increased survival rates of salmonid species and in no cases were there clear indications of reduced salmonid survival. It must be noted that two of these case studies involved a series of upper Columbia River reservoirs where the release of large hatchery-reared trout juveniles dominated.

John Day Reservoir, mid-Columbia River, hosts large populations of smallmouth bass, and predation on salmonids is well documented (Rieman et al. 1991; Beamsderfer and Rieman 1991). Fletcher (1991) questioned what portion of the salmon smolts noted in predator fish stomachs were ingested live, and which were dam-injured. He also noted that smallmouth bass were not the main consumer of salmon smolts. He indicated that smallmouth bass consumed 6.95 smolts/yr compared to 23.14 smolts/yr by walleye and 24.68 smolts/yr by northern pikeminnow.

Smallmouth bass predation was also examined on three rivers. Fletcher (1991) questioned the sources of information that reported the reductions in sucker, pikeminnow, and chiselmouth populations by smallmouth bass in Owyhee River, Oregon. He felt that consumption of anadromous salmonids was not an issue on the John Day River, Oregon, as no juvenile salmon were found in bass stomachs. Fletcher noted that steelhead, spring chinook salmon and coho salmon returns have remained fairly constant since smallmouth bass were introduced into the Umpqua River, Oregon. However, these salmonid populations are supplemented with hatchery fish.

Two case studies of bass predation in lakes were examined by the same author. Fall chinook salmon and coho salmon smolts are annually released into Lake Sammamish, Washington. Fletcher (1991) felt that survival rates of chinook increased following bass introduction, and the slight reduction in coho survival was not significant. Lake Osoyoos, in British Columbia and Washington, contains a population of smallmouth bass and supports a sockeye salmon run. Fletcher (1991) compared sockeye productivity in Lake Osoyoos to neighbouring Lake Wenatchee (sockeye but no smallmouth bass) and felt that if bass predation were a significant problem, Lake Osoyoos should have lower survival rates.

A study by Bennett et al. (1991) examined bass predation on out-migrating salmonids in Lake Sammamish, Washington. Chinook and coho salmon smolts migrate through the littoral areas in April and May and are preyed upon by both large and smallmouth bass (Pflug 1981; Pflug and Pauley 1984). In Lake Sammamish, largemouth bass consumed more salmonids than did smallmouth bass (Pflug 1981). Bennett et al. (1991) speculated that bass predation on juvenile salmonids was generally low.

In the Columbia River, the dominant fish prey species for smallmouth bass in spring were migrating salmon juveniles (Bennett et al. 1991). No salmonids were observed in bass diet during the summer and autumn. Bass prey on salmon and steelhead smolts immediately downstream of dams and throughout the reservoirs, which makes bass a less desirable sport fish. Salmonids contributed the most to overall total weight of food items observed in bass stomachs (28.2%), although their contribution to total numbers was less than 1%.

Smallmouth bass are considered to be the least important of four major salmonid predators in the Columbia River system (Poe et al. 1987, 1991; Rieman et al. 1991; Vigg et al. 1991), although they were estimated to account for 9% of the total fish mortality of chinook salmon in John Day Reservoir (Beamesderfer and Rieman 1991). Studies conducted throughout the lower Columbia and Snake Rivers by Zimmerman (1999) support the earlier diet information. Salmonids comprised about 6% of smallmouth bass diet, 11% of walleye diet, and 41% of northern pike-minnow diet.

However, in 2006, Fritts and Pearson found that the length of the predator seemed to influence diet. They found that smallmouth bass salmonid predation was negatively correlated to the length of the bass. In that study, Fritts and Pearson showed that most of the smallmouth bass that were eating salmonids had a fork length (FL) of less than 250 mm. Smallmouth bass of this size were the most abundant in the Yakima River and were more likely to prey on salmonids. This is in contrast to the Northern pikeminnow diet of salmonids in the Columbia River, which was positively correlated to an increase in length; northern pikeminnow were not found to be highly predaceous on salmonids until they reached a fork length of 250 mm (Poe et al. 1991; Vigg et al. 1991).

Studies by Tabor et al. (1993) indicated seasonally higher rates of consumption of migrating salmonids than indicated in earlier studies. In the Columbia River, piscivorous fish were sampled over a 6-km stretch of river from May to mid-June. Juvenile salmonids represented 59% of the smallmouth bass diet by weight and were present in 65% of the stomachs. Northern pikeminnow consumed from 0.34 to 0.55 salmonids per predator daily. Smallmouth bass were estimated to consume from 1.0 to 1.4 salmonids daily; they consumed mostly sub-yearling chinook salmon (Tabor et al. 1993). Bennett et al. (1991) concluded that predation on sub-yearling chinook salmon is known to be significant in the Columbia River and the size of juvenile salmonid may influence predation. He suggested that predation on Snake River fall chinook was potentially deleterious. Rieman et al. (1991) felt that sub-yearling chinook salmon may be more susceptible to predation because of their small size and later out-migration. Fayram and Sibley (2000) reported that 28% to 38% of the smallmouth bass diet in Lake Washington consisted of out-migrating juvenile sockeye. They concluded that smallmouth bass predation was likely not the reason for the observed decline in sockeye salmon survival in recent years.

The timing of juvenile salmon runs as well as spatial habitat overlap are important in establishing the rate of salmonid consumption by bass. For bass and salmonids in Lake Washington, overlap was minimal because sockeye and coho salmon juveniles had passed through Lake Washington prior to warming of the littoral zone (Eggers et al. 1978; Fayram 1996; Fayram and Sibley 2000; Kurt et al. 2003). Bass remain inactive until temperature rises in spring. If migrating salmon can move through water bodies containing smallmouth bass when water temperatures are still low, they may avoid heavy predation. This argument is well presented in the literature. Fletcher (1991) reported that 23% of the smallmouth bass stomachs taken from the John Day River in Oregon when water temperatures were below 15°C were empty. Predation on sub-yearling salmon that remain to rear rather than migrate through bass-dominated areas may be much higher (Fishman Environmental Services 2001).

5.3 WILDLIFE

Bass predation is not limited to purely aquatic groups (Semlitsch 2000). Smallmouth bass (usually considered in combination with other bass species) also consume a variety of amphibians and reptiles including juvenile snakes and turtles (Fuller 2007). Introduced centrarchids were suggested as the reason for the decline of native ranid frogs in California (Kiesecker and Blaustein 1998) and for reduced California tiger salamander *Ambystoma californiense* populations (Dill and Cordone 1997). Invasive smallmouth bass that have become established in the Mersey River, Nova Scotia, are reported to prey on hatchling turtles (Blanding's Turtle Recovery Team 2002).

5.4 IMPACT SUMMARY

Although a top predator, smallmouth bass may also take a large proportion of macro-invertebrate production, and can change the flora and fauna of a system through the alteration of fish community structure and the behaviour of other fish species. Once established in new ecosystems, smallmouth bass rapidly dominate. In addition to fish, smallmouth bass also consume a variety of amphibians and reptiles including juvenile snakes and turtles. They are capable of hybridizing with at least four other bass species, although the effects in nature are not well understood.

Smallmouth bass pose a threat to native fish faunas, especially small-bodied fish, through competition and predation. Small-bodied fish like minnows, pumpkinseed and yellow perch are prime forage items for smallmouth bass, and their reduction or elimination is a consistent theme in the literature. Smallmouth bass also compete with northern pikeminnow and lake trout.

There is considerable literature that clearly demonstrates that smallmouth bass prey on salmonids. However, the ultimate effect on salmonid abundance is not so clear. Timing of juvenile salmon runs and spatial habitat overlap with bass are important considerations. Heavy predation may be avoided if migrating salmon can move through water bodies containing smallmouth bass when water temperatures are still low and bass are less active.

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