Feeding and Habitat Preferences of Non-Native Smallmouth Bass (*Micropterus dolomieui*) in Lakes Throughout British Columbia

by

Martina Beck
BSc, University of Victoria, 2008

A Masters of Science Submitted in Partial Fulfillment
of the Requirements for the Degree of

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in the School of Environmental Studies

Supervisory Committee

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Abstract

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Characterization of smallmouth bass (*Micropterus dolomieu*) interaction with native species assemblages, especially salmonids, in lakes throughout BC is prerequisite to identification of high-risk systems warranting on-going monitoring. Therefore this project addresses the following issues:

How does smallmouth bass (SMB) trophic profile overlap with native species and does it vary across time and space? Schoener's index of dietary overlap was not significant between SMB and rainbow trout (*Oncorhynchus mykiss;* α=0.406, 0.257), or cutthroat trout (*Oncorhynchus clarkia;* α=0.145, 0.29). Prey fish levels (E_i =35.4%) and the total energetic density (14.91±4.74J/g) of the cutthroat trout diet from Weston Lake (SMB free) were significantly higher compared to the diet of cutthroat trout from Cusheon Lake (E_i =3.3% and 7.69±1.93J/g) where non-native SMB have been introduced. Within the Vancouver Island study lakes, gut-content analysis revealed available signal crayfish serve as an important prey resource in the SMB diet (E_i =34%). What capacity do SMB have to take advantage of seasonal pulses of forage? SMB displayed the ability to rapidly (within 24hrs.) alter their diet and consumption levels (4.7 times higher) to maximize on pulses of rainbow trout fry following a stocking event. SMB did not spatially overlap with spring peaks in salmonid fry runs in the Okanagan lakes, as water temperature remained around the 10°C threshold when SMB are not yet active. Kokanee (*Oncorhynchus nerka*) fry did however make up E_i =83% of the yellow perch (*Perca flavescens*) diet.

SMB are thriving in locations suspected to be on the limit for their environmental suitability through increased size at age for SMB in the Cariboo region in order to adapt to a longer (by 62 days) winter starvation period. SMB are a generalist predator able to adapt and thrive in very different systems; high vs. low productivity, few or many fish species, crayfish or no crayfish. The likely impacts of this in BC could include shifts in the diet of other fish species and increased costs associated with only stocking larger catchable sized trout in lakes containing non-native SMB. Policy recommendations based on our findings are that SMB introductions into systems that have rainbow/cutthroat trout are likely to cause the highest impacts on our native fisheries in BC if the systems are; highly productive, contain a high diversity of small bodied fish and invertebrate species, lack signal crayfish and large lakes with predominant littoral zones and complex shorelines.

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Acknowledgments

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Introduction

Distribution and habitat

Smallmouth bass (*Micropterus dolomieu*) belong to the Centrarchidae or sunfish family and are native to eastern-central North America from the Great Lakes south to northern Georgia and Alabama, east to the Appalachian range, and west to eastern Oklahoma (Figure 1; Scott and Crossman 1973, MacCrimmon and Robbins 1975). The range of smallmouth bass (SMB herein) began to expand in the late 1800's, primarily due to human introductions (Scott and Crossman 1973). SMB are now a prized recreational sport-fish throughout North America providing significant cultural and economic incentive to enhance recreational fishing opportunities through unauthorized stocking (Litvak and Mandrak 1993, CCFAM 2007, McPhail 2007a, Brown et al. 2009). SMB have been introduced into over 20 countries including Japan, Australia, South Africa and in parts of Europe (Scott and Crossman 1973). The range of countries with successful introductions highlights the overall capacity for SMB to successfully establish across a very broad range of environments outside their native distribution. Despite continued eradication efforts SMB have established in highland lakes in Japan, and pose threats to the native biodiversity associated with feeding pressures exerted by this non-native species (Iguchi et al. 2004).

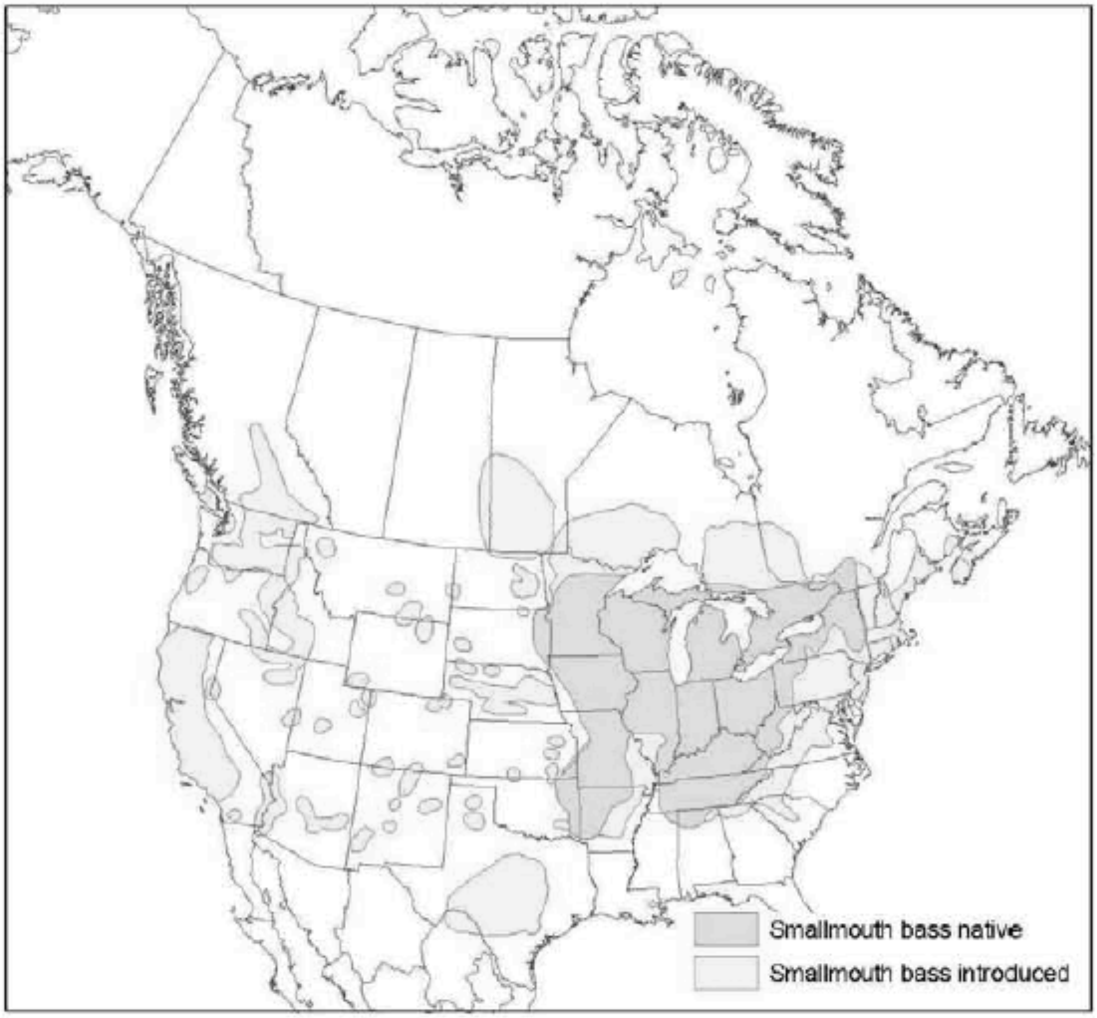

Figure 1. The native (dark gray) and introduced (light gray) distribution of smallmouth bass (*Micropterus dolomieu*) throughout North America (Tovey et al. 2008).

SMB primarily reside in the littoral zones of lakes during the summer months seeking out areas of cover such as submerged logs, docks and rock outcroppings (Pflug and Pauley 1984, Mueller 2002). Unlike largemouth bass (*Micropterus salmoides*), SMB are rarely associated with aquatic vegetation (Mueller 2002), and while SMB primarily reside in lakes they do also inhabit streams. SMB ideally require large mesotrophic lakes (>40.5 ha), with an average depth of >9m and rocky shoal habitats (reviewed by Edwards et al.

1983). Habitats with low turbidity are ideal for SMB, as they are highly visual predators (Armour 1993).

Growth and reproduction

SMB are a warm-water species (preferred adult temperate range 21-27°C in the summer) and water temperature is an important abiotic variable affecting growth (Armour 1993). The shallower warmer waters of the littoral zone are where both spawning and rearing of SMB occurs (Pflug 1981). Eastern Canadian SMB populations typically spawn between May and early July, when water temperatures are a minimum of 16°C. SMB grow exceptionally fast during the first years of life, and young of the year SMB on average range from 70-101mm in size, while two year old SMB range from 132-185mm in size (Bennett et al. 1991). Age at maturity of SMB differs within its native and introduced ranges. Sexual maturity may not be achieved until age six or seven in northern latitudes; age three or four in central regions; and age two or three in southern latitudes (Robbins and MacCrimmon 1974, Pflieger 1975, Edwards et al. 1983). The maximum recorded age of SMB in Canada is 15 years, but they do not grow as fast or as large as the closely related largemouth bass species (Scott and Crossman 1973).

The northern distribution boundary of SMB is likely temperature limited as when surface water temperatures drop below 7-10°C they cease feeding, and move to deeper warmer waters until temperatures rise in the spring (Shuter et al. 1980). Total degree-days above 10°C is an important correlate of growth in SMB and is related to the length of the SMB growing season (Beamsderfer and North 1996). Feeding and growth during the summer months (approximately June to October) is critical for the overwinter survival of SMB (Shuter et al. 1980). Young of the year SMB exhibit size dependent variations in winter mortality, with smaller fish being less tolerant of starvation conditions (Shuter et al. 1980, Shuter and Post 1990). Mean annual air temperature (°C), duration of starvation period (days), size after first year (mm) and food availability are important variables related to winter-starvation of SMB (Shuter et al. 1980, Shuter and Post 1990, Beamsderfer and North 1996).

SMB Trophic profile and impacts

SMB are a voracious top-level predator in freshwater systems. As visual feeders their prey selection is influenced by water clarity, prey size and prey availability and they feed at any time of day or night, but typically are most active in the early morning and evening (Moyle 2002, Sweka and Hartman 2003). Young of the year SMB typically consume smaller prey species such as aquatic insects and plankton. When SMB reach 40-100mm in size their diet shifts towards larger prey items such as: fish; crayfish; larger macroinvertebrates; and even terrestrial vertebrates (e.g. birds, turtles and frogs; Keating 1970, Rabeni 1992, Moyle 2002). Crayfish are an important part of the diet of SMB (Stein 1977, Rabeni 1992, Downen 1999); in the Columbia River 72% of SMB diet (by volume) is crayfish (Bennett et al. 1991). Further in systems where crayfish abundances are high fish make up a smaller percentage of the SMB diet (86% crayfish and 11% fish) (Keating 1970, Shively et al. 1991).

SMB become piscivorous two to three years younger than many other predatory fish, and this shift gives them a competitive advantage over other fish species (Mittelback and Persson 1998). SMB can consume juvenile salmonids up to 56% of their own size (Fritts and Pearsons 2006). The overall impacts of SMB predation on salmonids vary from one system to another; depending on both the spatial and temporal overlap between the two species (Eggers et al. 1978, Fayman 1996, Fayram and Sibley 2000, Kurt et al. 2003). In Lake Washington (WA, USA) SMB predation rates on juvenile salmonids were the highest in June, when the two species overlapped in space and time. A synthesis of the studies from the Pacific Northwest, suggests that when SMB are present up to 35% of sympatric wild out-migrating salmon are consumed by SMB (Carey et al. 2011).

The impacts of introducing a top-level piscivore, such as SMB into freshwater ecosystems can cause cascading effects across the entire food web, and alter trophic interactions (Carpenter et al. 1985). In Northern Ontario, there is evidence of pelagic lake trout and littoral non-native SMB sharing habitat in lakes that don't contain pelagic prey fish (Figure 2: Vander Zanden et al. 1999b). The lack of pelagic prey fish causes the normally pelagic lake trout to move into littoral habitats where SMB reside in the summer months. The sharing of littoral habitats by these two piscivorous species results in competition for littoral food resources, having large impacts on food web linkages, and trophic structure of the native community (Figure 2: Vander Zanden et al. 1999b). In MacDonald Lake (Ontario, CA), SMB became the dominant piscivore in the littoral zone within four years of their introduction; forcing lake trout to shift from a primarily piscivorous diet to a zooplankton-dominated diet (Figure 2; Vander Zanden et al. 1999b).

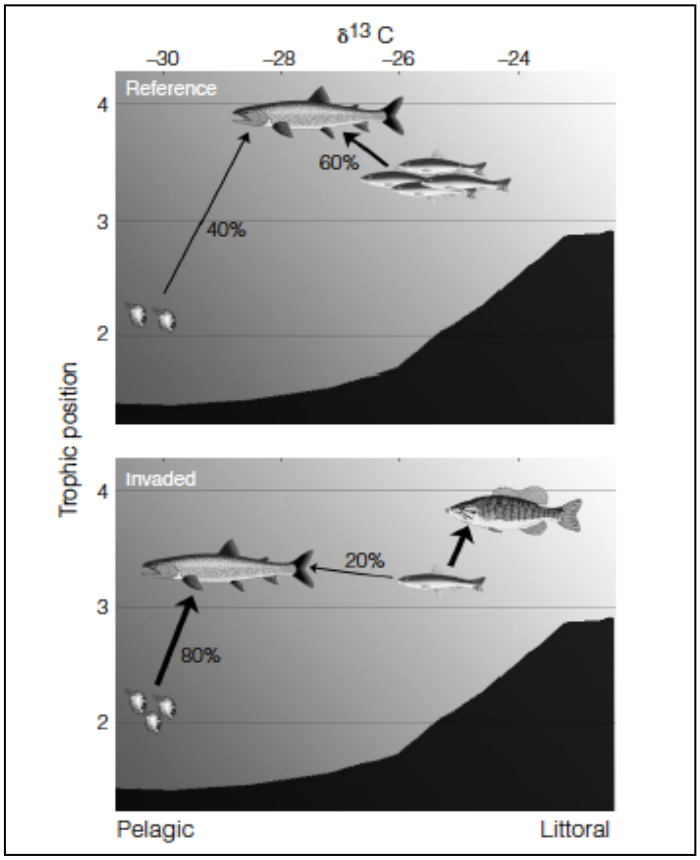

Figure 2. The pathways of energy flow through food webs of reference lakes containing lake trout and smaller prey fish (top) and invaded lakes (bottom) containing lake trout, prey fish and SMB, in northern Ontario. Changes in trophic position of lake trout are based on $\delta^{15}N$ and $\delta^{13}C$ data (Vander Zanden et al. 1999b).

The success of SMB introductions has been attributed to their small size at onset of piscivory; low overlap/competition with other predators; and high fecundity combined with parental care yielding high recruitment (Vander Zanden et al. 1999b, Gard 2004, Brown et al. 2009). SMB could potentially have very significant impacts on out-migrating salmonids and trout in BC however, the extent of SMB predation remains unknown (Brown et al. 2009). Data pertaining to when and where SMB occur within BC lakes would provide important information regarding if and when SMB may spatially and temporally overlap with salmonids and trout within BC.

Optimal foraging theory

Predators may consume many different prey species, and important questions arise regarding why predators actively choose to feed on certain prey over others (Mittelback 2012). The optimal foraging theory addresses the question of what rules of prey choice result in the greatest energy gain per unit time spent foraging (i.e. optimal diet; Schoener 1971, Emlen 1973, Maynard Smith 1974, Werner and Hall 1974). The two primary predictions from the optimal diet model are that (1) foragers should prefer the most profitable prey (i.e. yield the most energy per unit handling time) and that (2) an efficient forager should expand its diet to include more low-value prey as the abundance of higher value prey decreases (Stephens and Krebs 1986, Sih and Christensen 2001, Mittelback 2012). The optimal foraging theory highlights that feeding efficiency and maximization of energy gain have an important role in determining the predator diet choice and is closely linked to the overall density of prey in the environment (Sih and Christensen 2001, Mittelback 2012).

Quantifying the diet and trophic overlap

Piscivorous fish in aquatic ecosystems reduce abundance of their immediate prey and alter the entire aquatic food web (Carpenter and Kitchell 1993, Brown et al. 2009). Piscivorous diets frequently exhibit seasonal, annual and ontogenetic variability (Ridenhour 1960, Keast 1977, Colby et al. 1979, Keast 1985, Keast and Eadie 1985), and prey species composition, abundance and availability are important factors reflected in the diet (Forney 1974, Knight et al. 1984, Hartman and Margraf 1992, Cobb and Watzin 1998). Quantifying the diet of piscivorous fish is essential towards understanding the trophic relationships within aquatic food webs (Gerking 1994). At present, a detailed description of the diet of non-native SMB in lakes throughout BC is limited (Sharma et al. 2009). A comprehensive diet analysis is the critical first step in assessing the degree of trophic overlap between SMB and other predator fish species in lakes throughout BC.

Stomach content analysis is a commonly used method to quantify the diet of fish (Hyslop 1980, Bowen 1983, Smith 1985). The prey items present in a fish stomach can be quantified using several approaches (Hyslop 1980, Wallace 1981, Smith 1985, Peterson and Fry 1987, Cortes 1997, Tirasen and Jørgensen 1999) and most commonly are expressed in percent contribution by frequency of occurrence, number count or the gravimetric method. Frequency of occurrence (%FO) is the percent of fish stomachs that contain a specific prey item, relative to the total number of fish with food in their stomachs (Bowen 1983). Trends in the diet at the population level can be expressed using %FO however, more specific information pertaining to an individual stomach, such as the amount of a given prey item is lost using the %FO method (Hyslop 1980).

Alternatively, the quantity of a given prey item can be expressed as the percent contribution by number counts (%N) using:

$$\%N = (N_{ij}/\Sigma_{ni}N_{ij} \; * 100) \qquad 1$$

where N_i is the number of prey item i in the stomach contents of the individual fish j, and $\Sigma_{ni}N_{ij}$ is the sum of the total number of all prey items in the stomach of individual fish j (Bowen 1983). This is a commonly used method however %N has the tendency to over estimate the importance of smaller prey items, such as plankton and insect larva that occur in very high numbers, but contribute relatively little energetic value to the overall diet (Hyslop 1980). While larger, more energetically valuable prey items such as fish and crayfish are frequently underestimated using %N, therefore, one must be cautious when only expressing the diet of fish as %N (Hyslop 1980).

The most widely used method for expressing the diet is the gravimetric method, which can be expressed as either percent volume (%V), or percent weight (%W) using

$$\%W = (W_{ij} / \Sigma_{ni} W_{ij}) * 100 \qquad 2$$

where W_i is the weight of prey item i in the stomach contents of the individual fish j, and $\Sigma_{ni} W_{ij}$ is the sum of the total weight of all prey items in the stomach of individual fish j (Bowen 1983). This method provides a more accurate assessment of the percent contribution of larger prey items, however this comes at the cost of being considerably more time consuming over the %N and %FO approaches (Hyslop 1980).

Each of the methods described above come with their own disadvantages and certain approaches are better than others depending on the objectives of a study (Bowen 1983). A detailed diet analysis at the individual fish level requires the %N and/or %W methods (Hyslop 1980) and the %W method has regularly been used as the preferred method for quantifying the diet of piscivores such as SMB (Pelham et al. 2001, Contente et al. 2012, Creque and Czesny 2012).

Several different indices have also been developed in order to quantify the dietary overlap between putative competitor species, or between inter-specific age and size classes. Such indices include MacArthur and Levins's measure (MacArthur and Levins 1967), Schoener's Index (Schoener 1970), Morista's Measure (Morisita 1959a), Simplified Morista Index (Horn 1966) and Horn's Index (Horn 1966); with Schoener's Index being the most popular amongst the literature (Krebs 1999). Each index comes with it's own individual biases associated with changes to the number of resources, sample size and resource evenness (Krebs 1999). Indices such as these should be interpreted with caution, as they are not direct measures of competition between two predator species, therefore, competition cannot be inferred (Bowen 1983). Provided these indices are interpreted appropriately they can provide powerful tools for assessing the trophic overlap between species (Krebs 1999). In aquatic ecosystems containing non-native predator fish species such as SMB overlap indices serve as important tools for quantifying the degree of trophic overlap with other predator fish species and prey items such as juvenile salmonids (Vander Zanden et al. 1999b, Brown et al. 2009).

Management

Managing the introduction, establishment and spread on non-native fish in nature is highly complex, due to conflicting socio-economic drivers, conservation efforts, and diverse academic perspectives (Brown et al. 2009, Gozlan et al. 2010). Despite the increasing evidence of adverse effects of non-native fish on receiving environments, economic incentives continue to drive further introductions. Illegal introductions are spreading non-native SMB across southern and central BC. As a top-level predator, SMB consume a broad array of resources (Scott and Crossman 1973), creating the opportunity for numerous competitive interactions between SMB, and many other fish species, including salmonids. However, further complicating this situation is the growth of SMB as a popular BC sport fish, with several lakes in BC supporting “trophy” bass fisheries (Brown et al. 2009). Managing the competing interests of stakeholders in other jurisdictions, has proven to be a complex exercise (Carey et al. 2011).

Concern is currently escalating in the Pacific Northwest (PNW), regarding the lack of basic information on system-wide abundances and ecology of SMB (Carey et al. 2011).

These data are critical to making informed management decisions that will help minimize SMB impacts on salmon (Carey et al. 2011). There is a need for improved understanding of how SMB interact with native BC species assemblages in lakes throughout the province, in order to properly manage this non-native species (Sharma et al. 2009).

Non-native SMB in British Columbia

From 1901 to 1923, “bass/sunfish” were legally introduced into four lakes on Vancouver Island, and one lake in the Okanagan region (Runciman and Leaf 2009). As of 2008, SMB presence have been confirmed in 70 water bodies in BC (Figure 3) of which as many as 66 were illegal introductions (Runciman and Leaf 2009). SMB populations within BC are primarily found in individual lakes or small lake groups, that are isolated either geographically, physically, and/or hydrologically (Runciman and Leaf 2009). Exceptions to this include large lakes and rivers, such as Osoyoos Lake and the Okanagan River which both provide favourable habitat for SMB (Runicman and Leaf 2009).

Global temperature patterns are predicted to change in the future and the subsequent changes to thermal habitat may alter boundaries that currently limit the distribution of many species (Jackson and Mandrak 2002). Under a situation of increasing average temperatures, it is expected that the current range of smallmouth bass will expand beyond its present northern distribution (Shuter et al. 1980, Jackson and Mandrak 2002). Based on several model parameters, including lake surface area and proximity to human populations Sharma et al. (2009) identified 138 BC lakes appropriate for future colonization by SMB. Of these 138 lakes, 20 of them support at least one salmon species, 122 lakes support at least one trout species, and 29 lakes support at least one cyprinid species (Sharma et al. 2009).

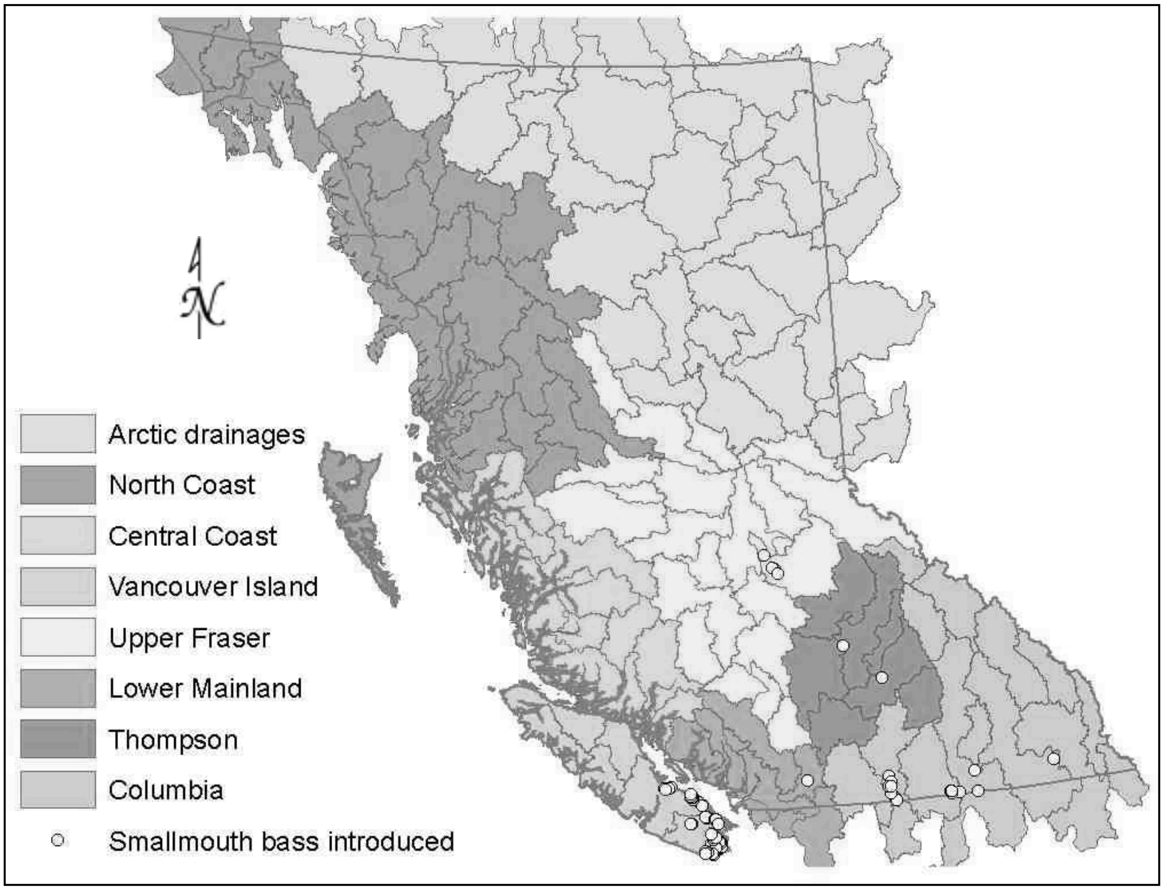

Figure 3. The distribution of confirmed (white circles) smallmouth bass occurrences in British Columbia. Coloured areas represent Ministry of Environment provincial management regions (Runicman and Leaf 2009).

Vancouver Island:

SMB populations have been confirmed in 36 lakes and 14 streams on Vancouver and the Gulf Islands (Runicman and Leaf 2009). From 1901 to 1923, four lakes including St. Mary, Spider, Langford and Florence Lakes were stocked with "bass/sunfish" (Runicman and Leaf 2009). The fact that only four lakes were stocked by government agencies, while current records show SMB distributions across 20 separate drainages, suggests that most SMB populations on Vancouver and the Gulf Islands established from independent, illegal introductions (Runicman and Leaf 2009).

Vancouver and Gulf Islands lakes and streams containing SMB populations, support a variety of native and non-native species including: bull trout (*Salvelinus confluentus*)*;* cutthroat trout (*Oncorhynchus clarkii*); Atlantic salmon (*Salmo salar*)*;* burbot (*Lota lota*)*;* western brook lamprey (*Lampetra planeri*)*;* brown catfish (*Ameiurus nebulosus*)*;* prickly sculpin (*Cottus asper*)*;* Chinook (*O. tshawytscha*)*;* chum (*O. keta*)*,* coho (*O. kisutch*) and pink salmon (*O. gorbuscha*)*;* Dolly Varden (*Salvelinus malma malma*)*;* kokanee (*O. nerka*)*;* pumpkinseed sunfish (*Lepomis gibbosus*)*;* rainbow trout (*Oncorhynchus mykiss*)*;* threespine stickleback (*Gasterosteus aculeatus*) and yellow perch (*Perca flavescens*). However, only three of the 53 water bodies containing SMB populations currently support anadromous salmon species. All water bodies containing SMB include native sport fish many of that are stocked; 27 of the lakes and streams contain other non-native fish species (Runicman and Leaf 2009).

Cariboo Region:

SMB were initially reported in the northern Cariboo Region in 2006, and they are believed to be the first non-native fish species to be introduced into the Beaver Creek watershed (Gomez and Wilkinson 2008). SMB currently inhabit 55km of the Beaver Creek watershed including a chain of six lakes (Figure 4); in June 2010 SMB were reported in the nearby Big Lake, further expanding their range (Gomez and Wilkinson 2008). The Beaver Creek watershed is located 38.3km from the Fraser River (Google Earth Inc 2013) one of the largest and arguably most culturally and ecologically important salmon rivers in the world. There is considerable concern that the range of

SMB could expand into the nearby Fraser River introducing an as yet unknown level of threat to native salmonids (Gomez and Wilkinson 2008).

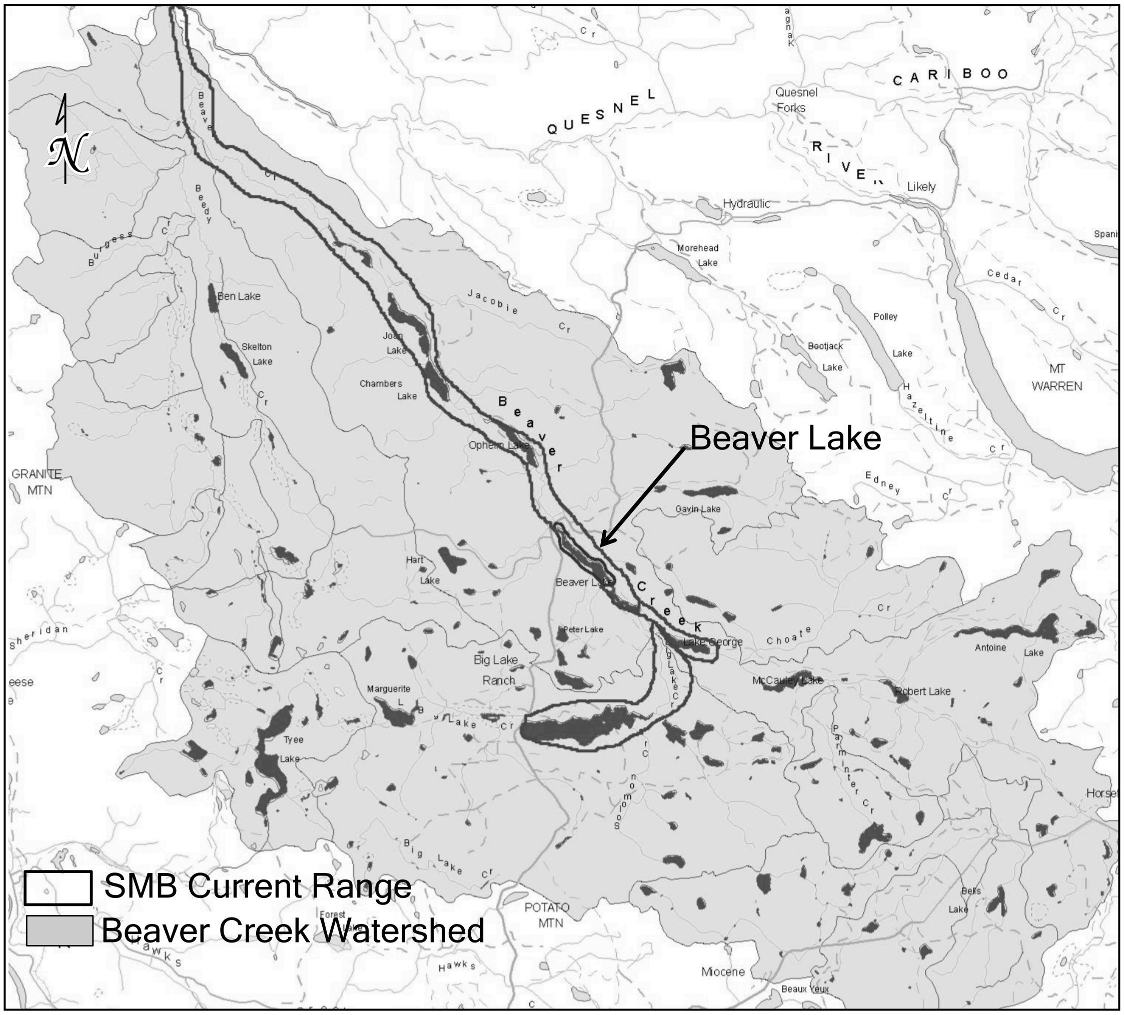

Figure 4. Map of the Beaver Creek watershed (gray area) in the northern Cariboo region of BC, the black line shows the known range (2007) where SMB have been introduced into the watershed (Gomez and Wilkinson 2008).

Okanagan Region:

SMB populations have been confirmed in seven lakes and three streams in the Okanagan Lake watershed. In 1901, Christina Lake was reportedly stocked by the federal Department of Fisheries with 500 “bass/sunfish”. In 1987 and 1988, provincial government agencies authorized transfers of SMB from Christina Lake into Vaseux Lake and Skaha Lake, to supplement pre-existing SMB populations (MOELP 1995b, 1995c). Of the ten water bodies in the Okanagan Lake watershed containing SMB, Osoyoos Lake and the Okanagan River are the only two that support anadromous salmon (Runicman and Leaf 2009). However, hatchery programs are now releasing sockeye salmon fry (*Oncorhynchus nerka*) into the Okanagan River upstream of Skaha Lake providing this species with access to Skaha and Vaseux Lakes, both of which contain SMB (Runicman and Leaf 2009).

Signal crayfish

Signal crayfish (*Pacifastacus leniusculus*) are native to BC, and their distribution ranges from Vancouver Island to the Kootenays (49°N, 118°W) (Bondar et al. 2005, Larson et al. 2012). Signal crayfish are present in numerous lakes containing SMB on Vancouver and the Gulf Islands (Bondar et al. 2005). Pro-bass lobbyists on Vancouver and the Gulf Islands have long argued that the presence of signal crayfish in lakes containing SMB mitigates the risk of predation by SMB on other prey species, such as juvenile fish. At present, these hypotheses remain untested, and there is a need to further investigate how the presence of crayfish might affect SMB predation rates on other native prey species, such as juvenile salmonid species. The Cariboo region (52°N, 121°W) is beyond the northern limit of signal crayfish in BC (Bondar et al. 2005), providing the opportunity to assess the diet of SMB in lakes without signal crayfish.

SMB and BC stocking programs

Direct spatial and temporal overlap between SMB and salmonids are particularly worrisome in BC, as native salmonids are an extremely valuable species, both culturally and economically throughout the province. Within BC, trout hatchery programs provide enhanced fishing opportunities for recreational anglers throughout the province. Close to 900 lakes and streams throughout BC are stocked with salmonids and significant economic investments ($8.57 million in 2010) are put into hatchery programs annually (Bailey and Sumaila 2013). In 2010, the direct economic benefit of freshwater fishing in BC was $545.7 million; contributing $164 million in value added GDP and $93.6million in wages and benefits (Bailey and Sumaila 2013). In 2005, the SMB recreational fishery accounted for 8.18% of total freshwater fish catch with an approximate projected value of $13.38 million in 2010 (National Sportfish Survey 2005; Bailey and Sumaila 2013). The economic benefits from the BC stocking programs in 2010 returned $24 in angler expenditures for every $1 invested (Bailey and Sumaila 2013). However, a growing number of the stocked systems are being exposed to and potentially threatened by non-native fish, such as SMB.

Reduced survival of fry and fingerling-sized trout, stocked in lakes on southern Vancouver and the Gulf Islands containing non-native fish, such as SMB have been reported (Silvestri and Fosker 2003). In an effort to counter suspected predation and competition pressures exerted by non-native SMB, hatchery programs have switched to primarily stocking these lakes with larger “catchable” sized trout (> ~150 mm) (Silvestri and Fosker 2003). At present very little is known about how SMB may be impacting stocked trout populations and what the long-term economic implications may be for BC’s hatchery programs.

Research objectives

The overall objectives of this MSc. thesis, are to gain a better understanding of the feeding preferences of non-native SMB and the potential trophic overlap with native/stocked fish species in BC lakes to inform provincial fisheries policy and management. Specifically:

1. *Identify the abiotic variables and habitat characteristics associated with SMB populations in lakes throughout British Columbia*

Ho: SMB length at age (length/age) does not differ significantly ($P \geq 0.05$) *between the northern and southern SMB study lakes.*

2. Does SMB trophic profile overlap with trout species and does it vary across temporal and spatial gradients?

Ho: SMB trophic profile does not significantly overlap ($\alpha \leq 0.6$) *with trout species.*

Ho: SMB trophic profile does not differ significantly (ANOSIM $P \geq 0.05$*) within and between lakes.*

A subset of objectives seek to address the role of signal crayfish in the diet of SMB with the following questions

3. Do SMB selectively forage for signal crayfish? And if so, does the presence of signal crayfish alter trophic mediated impacts of SMB on other species?

Ho: Crayfish levels in the SMB diet is not significantly correlated ($P \leq 0.05$) *with crayfish relative abundance levels across the Vancouver Island study lakes.*

The final objectives of this study is to assess the ability of SMB to maximize predation during peaks in food availability, specifically:

4. What capacity do SMB have to take advantage of pulses of forage, such as stocking *events?*

Ho: SMB do not spatially and temporally overlap (SMB CPUE=0) with spring kokanee and sockeye fry and smolts in the Okanagan study lakes.

Ho: SMB predation levels on hatchery trout fry (consumed trout fry/SMB) does not differ significantly ($P \geq 0.05$) across a temporal gradient following a stocking event.

The results from this study will provide critical baseline data for provincial fisheries management, regarding the diet and ecology of SMB populations in lakes throughout BC including those at the northern limit of their geographic range in Canada. SMB have the ability to adapt and thrive in very different systems. Results from this research will provide fine scale data regarding lake characteristics most likely to support non-native SMB. The findings from this research will be used to inform policy management regarding what types of lakes are likely to experience the highest impacts on our native fisheries in BC following an SMB introduction.

Methods

Study lakes

The physical, chemical and biological (fish species composition) characteristics of all lakes in BC containing smallmouth bass (SMB) were obtained using BC Ministry of Environment's (MOE) Fisheries Inventory Summary Systems (FISS) online database (FISS 2013). Sample lakes were selected based on surface area (small vs. large), depth (deep vs. shallow), fish species composition, trophic access, and public road access. All data were collected and recorded following the standards and procedures set out by the BC Ministry of Environment (Resource Inventory Committee 1997). All necessary fish collection permits were obtained through the BC Ministry of Environment, and the University of Victoria (UVic) Animal Care Unit.

Three sample lakes on southern Vancouver and the Gulf Islands (48°N, 123°W) were selected for SMB data collection in 2011 and 2012; Cusheon, Shawnigan and Spider Lakes. In 2012, these three lakes were sampled in addition to two lakes in the Cariboo region (52°N, 121°W; Beaver and Chambers Lakes), and three lakes in the Okanagan region (49°N, 119°W; Skaha, Vaseux and Osoyoos Lakes; Figure 5). The Cariboo region is beyond the northern limit of signal crayfish (*Pacifastacus leniusculus*) (Bondar et al. 2005), and as such provided the opportunity to assess the diet of SMB in lakes without crayfish. The Okanagan sample lakes provided the opportunity to assess the diet of SMB in systems containing higher diversity of both prey and predator fish species relative to the study lakes on Vancouver Island (Table 1). In order to assess for differences in the diet of trout in the presence and absence of SMB, three reference lakes on Vancouver Island containing trout and no SMB were selected for sampling in 2012

(Table 1). The three reference lakes (Weston, Maple and Reginald Lakes) reflect similar fish species composition, and/or lake characteristics of the three SMB study lakes on Vancouver Island.

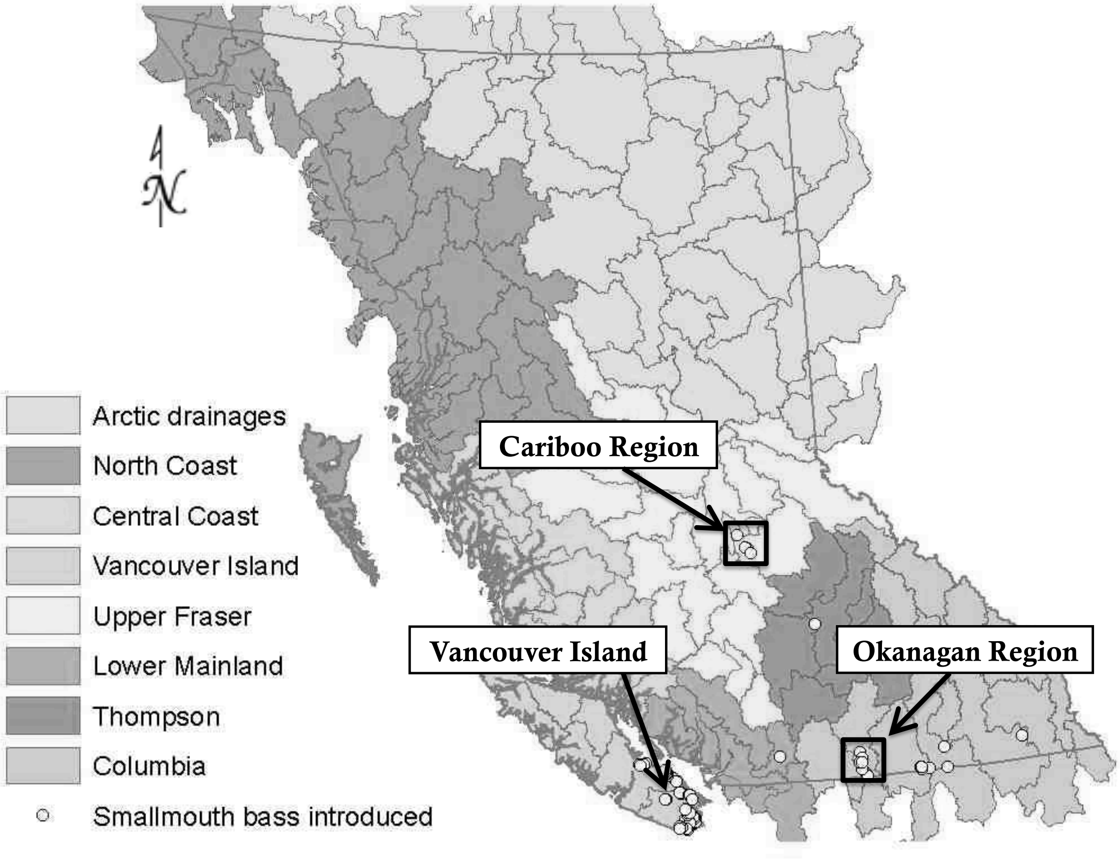

Figure 5. Regional study lakes located on Vancouver Island, Cariboo, and Okanagan regions, for the 2011 and 2012 field seasons. White symbols indicate release records of SMB in British Columbia (Hatfield and Pollard 2006).

For the 2011 field season, monthly gillnet sampling in Shawnigan, Cusheon and Spider Lakes ran from June to November, and in 2012 from late May to late September. Environmental parameters were recorded during monthly gillnet sampling events for the Vancouver Island study lakes. In September 2011, field-stocking experiments were conducted in Spider and Shawnigan Lakes, in order to assess the temporal gradient of SMB predation on hatchery rainbow trout fry (Table 1). Gillnet sampling in the

Okanagan lakes took place in late April, and again in early September 2012, while gillnet sampling in the Cariboo lakes took place in early July and September 2012. Differences in the timing of lake sampling for the two regions resulted in variations in the surface water temperatures during gillnet sampling.

Table 1. Research objectives assessed in each of the study lakes from the Okanagan, Vancouver Island and Cariboo regions during the 2011 and 2012 field seasons.

Regions	Study lakes	SMB trophic profile	Trophic overlap	No SMB lakes	Crayfish Relative abundance	SMB salmonid predation	Field stocking experiment	Habitat data
Okanagan	Skaha	X	-	-	-	X	-	X
	Vaseux	X	-	-	-	X	-	X
	Osoyoos	X	X	-	-	X	-	X
Vancouver and Gulf Islands	Shawnigan	X	X	-	X	-	X	X
	Spider	X	X	-	X	-	X	X
	Cusheon	X	X	-	X	-	-	X
	Reginald	-	-	X	-	-	-	-
	Weston	-	-	X	-	-	-	-
	Maple	-	-	X	-	-	-	-
Cariboo	Beaver	X	-	-	-	-	-	X
	Chambers	X	-	-	-	-	-	X

In July, September and November 2012 gillnet sampling for rainbow and cutthroat trout took place in the three reference lakes (SMB free) on Vancouver Island (Weston, Maple and Reginald Lakes). Snorkel surveys to quantify the relative abundance of signal crayfish were conducted in Shawnigan, Cusheon and Spider Lakes from mid July to late September 2012. See the appendices for lake characteristics of all study lakes.

Fish collection

Fish were sampled using sinking gillnets 91.2 m long, 2.4 m deep, with six, 15.2 m long panels of varying mesh sizes (25, 76, 51, 89, 38 and 64 mm stretch mesh), in order to target fish ranging from approximately 114mm to 380mm in total fork length

(Resource Inventory Committee 1997). It is important to take into account the biases associated with gillnets, as it is a passive sampling technique and relies on fish to swim into the nets and does not target less active fish (Resource Inventory Committee 1997). SMB are crepuscular and sampling effort was focused accordingly. Size bias of the gillnets could not be avoided and SMB <100mm in length were underestimated in the catch data.

Nets were set across sites of varying habitat types, including woody debris, bare substrate, rocks, and vegetation in the littoral zone (<6 m). Gillnets were set before sunrise and/or after sunset, during peak SMB feeding activity (Moyle 2002), in addition to overnight sets to capture night-time feeding activity by trout species. For each net, the start and end depths, substrate type, GPS coordinates, weather conditions and soak time were recorded. The average SMB catch per unit effort (CPUE) was calculated for each of the study lakes by habitat type. CPUE was calculated by taking the total number of SMB caught, divided by the total soak time for each individual net, then averaged across all nets set in each habitat type.

Fork length (mm) and wet weight (g) were recorded for all catch from gillnets. The condition factor was calculated for all retained fish using the coefficient of condition (K) (Carlander 1950);

$$K = \frac{W}{L^3} \times 100{,}000 \tag{3}$$

where W= wet weight (g) and L=fork length (mm). All SMB and a maximum sub-sample of 30 fish per species from each gillnet were lethally sampled for stomach/intestine samples, muscle tissue, and scales/otoliths using the methods described below. Stomach samples were preserved in the field for subsequent laboratory analysis. Stomachs were removed by making an incision along the ventral side of the fish starting at the anal cavity and ending just above the pectoral fins. A second incision was made dorsally along the pectoral fin in order to access the stomach at the start of the esophagus. Any regurgitated stomach contents present in the mouth were removed with forceps and preserved with the stomach sample. Stomachs were injected with 95% ethanol and stored in Whirl-Pak® bags containing 95% ethanol with an ethanol; tissue ratio of no less than 70:1. All fish carcasses were immediately transported to the University of Victoria and frozen for preservation.

The sagittal otoliths are located under the posterior part of the brain in two fluid filled cavities (sagittal wells) on either side of the brain (Thermal Mark Lab 2005). Otoliths were removed by cutting into the top of the head, just above the eye socket, and towards the back of the head and the false operculum. The cut portions of tissue and brain matter were removed to expose the left and right sagittal wells (Thermal Mark Lab 2005). The sagittal otoliths were located and removed using forceps and immediately placed in water for cleaning. Otoliths were left to dry for approximately one hour and then put into labeled glass vials (Sclerochronology Lab 2012).

Subsamples of fifteen otoliths per lake were selected from Cusheon, Shawnigan, Spider and Beaver Lakes for age analysis. The subsamples were randomly selected across a full size range of SMB, with an emphasis towards larger sized bass, in order to ensure otoliths were large enough for age analysis (See Appendix E for complete list of SMB otoliths sampled). The Department of Fisheries (DFO) Sclerochronology Lab, at the Pacific Biological Station (PBS), in Nanaimo B.C, conducted the otolith reading. For long-term storage at the Sclerochronology Lab, otoliths were placed in a 50:50 solution of glycerine and water, with thymol added to prevent fungal growth. The break and burn method (Christensen 1964) was used by the Sclerochronology Lab in order to read and age the otoliths.

Modified gee minnow traps with enlarged openings of three to five inches were set during the 2011 gillnet sampling in the three Vancouver Island sites, to establish presence/absence of species not captured within the gillnets and included young of the year SMB, threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*) and signal crayfish (*Pacifastacus leniusculus*). Eight minnow traps were set per gillnet sampling event in each lake for ~12-18 hrs. across varying habitat types (woody debris, vegetation, bare and rock) in depths less than five meters. Depths, substrate type, soak time, weather conditions and GPS coordinates were recorded for each minnow trap (Larson and Tait 2011). Weight (g) and carapace length (mm) (for crayfish) and/or fork length (mm) (for fish) were recorded and specimens were photographed and labeled (Larson and Tait 2011). Crayfish were taken to the University of Victoria, and frozen for preservation and future analysis.

SMB habitat

1. *Identify the abiotic variables and habitat characteristics associated with SMB populations in lakes throughout British Columbia*

Qualitative snorkel surveys were carried out in each of the Vancouver Island sample lakes from May to August 2011, in order to assess habitat types associated with SMB presence. Snorkel transects of varying length were conducted across all habitat types; categorized as aquatic vegetation, bare substrate, rock/boulders or woody debris.

Habitat monitoring was also conducted during snorkel transect surveys assessing signal crayfish abundance estimates from July to September 2012. Substrates were recorded as; rocky (pebbles or boulders), vegetation, woody debris (submerged logs) or bare substrate (mud/sand). The ratio of lake perimeter (m) to lake surface area (ha) was used as a proxy for shoreline complexity.

The environmental parameters of the lakes were measured by way of secchi depth (m), temperature (°C) and dissolved oxygen (DO; mg/L). Secchi depth (m), and temperature and DO water profiles were taken between 12:00 and 14:00 hrs. at the deepest point of the lake, during each gillnet sampling event. Temperature and DO profiles were measured using an YSI Model 57 Dissolved Oxygen Meter (YSI Inc and Xylem Inc 2011), and 14 m cable. HOBO Water Temperature Pro v2 Data loggers (Onset Computer Corporation 2012) were placed in Shawnigan, Cusheon and Spider Lakes from June 2011 to March 2013, to record daily surface temperature. Three temperature loggers were placed in each of the lakes, in approximately one to two meter depths, and dispersed throughout the lake. Temperature recordings were taken hourly, and loggers were checked every three to four months.

Hourly water temperature recordings from Beaver Lake (using Onset Tidbit temperature loggers in approximately one-meter depths) were obtained for June to November of both 2011 and 2012. Due to ice cover in the Cariboo region temperature loggers were removed for the winter months and re-installed after a short delay following ice off. Therefore temperature data was not available from November 2011 to June 2012 for Beaver Lake (Figure 2). Hourly temperature data were averaged to obtain the mean daily temperature. The number of degree-days with mean daily surface water temperature above 10°C was calculated for the three Vancouver Island sample sites and Beaver Lake. The winter starvation period was calculated by subtracting the total days in one year (365) by the degree-days >10°C in each lake. Mean annual air temperature (°C) was obtained from the Environment Canada National Climate Data and Information Archive (Environment Canada 2013). Mean annual air temperature data was only available for 2010 in Williams Lake (52°10'59.0"N; 122°03'15.0"W) for the Cariboo region and mean annual air temperature from the Victoria station (48°38'50.01"N; 123°25'33.0"W) for 2010 was used for the Vancouver Island region.

SMB growth

Age data from the subsample of otoliths were used to establish growth curves for the remaining SMB catch from Beaver, Shawnigan, Cusheon and Spider Lakes. In order to estimate growth curves for each of the SMB populations the inverse of the von Bertalanffy growth equation (Bertalanffy 1934) with length as a function of age was used:

$$t(L) = t_0 - \frac{1}{K} * \ln\left(1 - {}^{L}/_{L_\infty}\right) \qquad 4$$

Where the age, t, is the independent variable (x), the slope $b = k$ and the intercept a = -k*t_0 . L_∞ is interpreted as "*the mean length of infinitely old fish*" or "*asymptotic length*" (Sparre and Venema 1998), and due to small sample size the largest fish in each study lake was used (see Table 13A). k is a "*curvature parameter*" which determines how fast the fish approaches its L_∞, and is equal to the slope b of the curve. The third parameter, t_0= -a/b, is the point in time when the fish has zero length (Sparre and Venema 1998) and was calculated from intercept over slope. Fork length (mm) over age was estimated for

SMB catch data from Beaver Lake and the three Vancouver Island study lakes as a measure of SMB length at age (Dunlop and Shuter 2006).

Trophic profile

2. Does SMB trophic profile overlap with trout species and does it vary across temporal and spatial gradients?

The total number of each prey item present in a stomach was counted and summed across all prey to yield a grand total in the stomach (Bowen 1983). The total by prey provides the representative percentage by numbers, of each prey item consumed by the predator. Aquatic insects and crayfish were enumerated using head counts, as the heads remain intact the longest following ingestion (Bowen 1983). Ingested prey fish in SMB stomachs frequently lack heads; therefore, intact vertebrate spines were used to count individual prey fish. Length was recorded for fish (fork length) and crayfish (carapace length) when specimens were still intact. All prey items were identified to the lowest taxonomic level possible using a dissecting microscope (x10). In the case of smaller taxonomic groups, such as larval and pupae stages of macro-invertebrates, identification was made to the order level. All specimens enumerated from stomachs were kept and preserved in 95% ethanol.

In order to quantify the biomass of prey items in the stomachs, wet weight estimates were taken separately for prey fish, crayfish and macroinvertebrates. Prey items were blotted dry for 10 seconds with paper towel and weighed to the nearest 0.001g. For stomach samples containing smaller microinvertebrates, such as cladocera (*Daphnia spp*.) and copepods (*Leptodiaptomus spp.*) in advanced stages of digestion, pooled weights were taken for these prey items. The wet weights provided the representative percentage, by weight, of each prey item consumed by the predator. Stomach samples with only one individual and a total wet weight < 0.01g were removed from further analysis. Rare prey items contributing <3% (biomass) to the overall diet, with the exception of prey fish and crayfish, were combined into a single prey category and referred to as "other". Biomass was also expressed as the percent contribution by energetic density (%E_i) of each prey item, calculated from the measured wet weights, and energetic density (J/g) values obtained from the literature (Cummins and Wuycheck 1971, Probst et al. 1984, Tabor et al. 2007; Table 2).

Table 2. Energetic density values (Joules/g wet weight) used for calculating the percent contribution of various prey items in the predator's diet. Values were taken from the references cited below.

Prey Category	Prey Items	J/g (wet weight)	Reference
Fish	fish general	4185	Winberg (1956)
	rainbow trout	6069	Yule and Luecke (1993)
	yellow perch	2512	Hanson et al. (1997)
	sculpin	5413	Cummins and Wuycheck (1971)
Invertebrates	general	5648	Cummins and Wuycheck (1971)
	crayfish	3766	Cummins and Wuycheck (1971)
	odonata	2775	Cummins and Wuycheck (1971)
	diptera	2742	Cummins and Wuycheck (1971)
	ephemeroptera	3675	Hanson et al. (1997)
	daphnia	3344	Cummins and Wuycheck (1971)
	copepods	3344	Cummins and Wuycheck (1971)
	gammarids	3389	Cummins and Wuycheck (1971)
	gastropods	2130	Driver et al. (1974)
	chaoborus	1836	Cummins and Wuycheck (1971)
Other	terrestrial insects/rodents	4000	Bonar et al. (2005)
	leeches (annelids general)	2698	Cummins and Wuycheck (1971)

The total energetic density value (J) for all enumerated prey within each individual stomach sample was calculated and corrected for the size of the predator (J/g). The mean was then taken across all stomach samples for a given predator fish species to determine the average total energetic density value per stomach (J/g) for each predator fish species from a given study lake.

Signal crayfish

3. Do SMB selectively forage for signal crayfish? And if so, does the presence of signal crayfish alter trophic mediated impacts of SMB on other species?

The relative abundance of signal crayfish in Cusheon, Shawnigan and Spider Lakes was compared to the SMB catch per unit effort data across the various habitat types present in each lake. Crayfish abundance sampling took place between July and September 2012, when crayfish behaviour is not affected by mating, female crayfish are not bearing eggs, and crayfish are most active (Larson 2012 Pers. comm). Signal crayfish are a burrowing species and their distributions are not uniform and vary with depth and substrate type, with peak densities occurring near rocky areas and submerged logs (Davies 1989, Somers and Green 1993, Mueller 2002, Bondar et al. 2005). Signal crayfish and SMB are both positively correlated with boulder/rock substrate, and negatively associated with silt/sand substrate, and aquatic vegetation (Mueller 2002). Timed snorkel surveys were carried out at the locations of the SMB gillnet sampling and across all habitat/substrate types present in each lake to ensure that transects traversed all habitat types, including less favourable crayfish habitat types, such as aquatic vegetation.

Snorkel surveys were conducted along 50 m transect lines, and randomly set either perpendicular or parallel to the shoreline, in depths ranging from one to three meters (see appendix for location of transect sample sites within the study lakes). Compass bearings were taken in order to follow a straight line from the starting point. Two snorkelers swam on either side of the transect line, and recorded all crayfish present within 1m of either side of the transect line. A total area of $100m^2$ was surveyed per transect line, across a total of ten to twelve transects per lake. Any rocks or submerged logs that could be moved by the snorkeler were flipped and observed for signs of crayfish. For each transect habitat type was recorded as rocks (small, medium or large), vegetation, woody debris/submerged logs or bare/sand substrate.

Crayfish relative abundance estimates were calculated for each of the lakes using the data collected from the snorkel transect surveys. The total lake surface area (m^2) of the littoral zone (< 6m) was obtained from bathymetric maps, downloaded from the BC MOE Fisheries Inventory Summary Systems (FISS) online database (FISS 2013). The proportion of transects sampled across each habitat type, was used to estimate the total surface area of each habitat type in the lake. Mean crayfish abundance levels (crayfish/m^2) per habitat type was then multiplied by the total surface area calculated for each of the habitat types. This data provided preliminary crayfish relative abundance estimates for each lake.

SMB salmonid predation in BC

4. What capacity do SMB have to take advantage of pulses of forage, such as stocking events?

Salmonid fry and smolts; a potential prey resource for SMB, migrate through the Skaha and Osoyoos Lake systems, with peak runs occurring from mid-April to early May. In order to assess if SMB are targeting the migrating juvenile salmonids, gillnet sampling took place in late April 2012 in Skaha and Osoyoos Lakes. Gillnet sample sites within each lake were selected in ideal SMB habitat (logs, rocky substrates and overhangs).

SMB and BC stocking program

4. What capacity do SMB have to take advantage of pulses of forage, such as stocking events?

This work was conducted in collaboration with the Freshwater Fisheries Society of BC (FFSBC), in September 2011. Rainbow trout fry (referred to as trout fry from this point forward) were stocked into Shawnigan and Spider Lakes located on Southern Vancouver Island. Both lakes are annually stocked in the spring and early summer with yearling (> ~100 mm) and catchable size (> ~150 mm) rainbow trout by FFSBC (FFSBC 2011). On September 12th, 2011 approximately 13,000 trout fry (subsample mean fork length =83.66mm±12.63, n=124) were released into Shawnigan Lake (Table 3) at a public boat launch located on the northeast side of the lake (see appendices). This location was selected based on the optimal surface water temperatures (<21°C), and a depth profile allowing the trout fry to reach deeper colder waters in close proximity (~ 80m) to the release site. On September 20th, 2011 approximately 4,423 surplus hatchery trout fry (subsample mean fork length =85.04mm±13.63, n=156) were released into Spider Lake (Table 3), at the only public road access available (see appendices). The release site is located at the head of a shallow bay, and the trout fry must travel approximately 450m to the central basin before reaching deeper colder waters.

Prior to the release of the trout fry a sub-sample of 124 trout fry for Shawnigan Lake, and 156 trout fry for Spider Lake were haphazardly selected from the holding tanks of the

FFSBC truck (using a dip net) and measured for length. Fork lengths (mm) were taken in order to establish the size distribution of the trout fry being released into each of the lakes. The trout fry were anaesthetized and immediately following length measurements were placed in freshwater, and monitored for normal activity levels prior to their release. Following the release of all hatchery trout fry the sites were closely monitored from shore for two hours, to observe for any signs of mortality in the trout fry (e.g. fish floating belly up on the surface).

Sampling effort

In order to establish a baseline of the SMB diet in the two lakes, SMB stomach samples were collected from both lakes within one week prior to the release of the trout fry. Sample sites were selected based on the most appropriate substrate for setting sinking gillnets (clear of branches/logs that may snag/tear gillnets), across all habitat types present (woody debris, bare, rock/cobble and vegetation) in the littoral zone (depths < 10m). During the pre-stocking sampling two gillnets were set in both lakes before sunrise when SMB primarily feed (Moyle 2002), and a third gillnet was set overnight to capture nocturnally feeding SMB (Table 3, Appendix D). On September 9th/10th 2011, three gillnets were set in Shawnigan Lake, and an additional three gillnets were set in Spider Lake on September 10th-11th. Due to low sample sizes obtained during September 10th-11th sampling in Spider Lake two additional sinking gillnets were set; one before sunrise and one overnight on September 18th -19th (Table 3).

Table 3. Dates and number of gillnets set for each time interval during the field stocking experiment in September 2011. The total number and average fork length (mm) of hatchery rainbow trout fry released into Shawnigan and Spider Lakes.

Time Interval	**Shawnigan Lake**		**Spider Lake**	
	Date	**# of Nets**	**Date**	**# of Nets**
Pre-Stocking	Sept. 9th/10th	3	Sept.10th/11th and 18th	5
12hrs	Sept.12th	4	Sept.20th	4
24hrs	Sept.13th	2	Sept.21st	2
36hrs	Sept.15th	2	Sept.24th	2
Pre-Stocking	Sept.18th	2	Sept.27th	2
Number of Trout Fry Stocked	13,000		4,423	
Avg. Size Of Trout Fry Subsample	83.6mm±12.6 (n=124)		85.0mm±13.6 (n=156)	

Largemouth bass in the Kootenay region of BC, exerted significant predation pressure on newly stocked trout fry within twelve hours and one week of their release (Lee et al. 2006). Thus to assess the temporal gradient across which the SMB predation on trout fry reaches a maximum, the post-stocking sampling was conducted within twelve hours, twenty-four hours, thirty-six hours, one week and one month post-release. Due to low sample sizes obtained at the one-week sampling interval, data was pooled with the data collected at the one-month post-stocking sampling interval (referred to as "post-stocking" herein).

Sample sites were selected to be in close proximity (<450m) to the release site in prime SMB habitat, based on appropriate depth (<10m) and substrate for setting sinking gillnets (rocks, submerged logs and overhangs). Sample sites were kept constant throughout the post-stocking sampling period to control for spatial variability. A total of twenty nets were set across both lakes during the one-month period of post-stocking sampling (Table 3). During post-stocking sampling two gillnets were set before sunrise and one or two set prior to dusk, to capture daytime and night-time feeding activity, respectively (Table 3).

Consumption levels

Stomach content analysis was used to assess the predation levels of SMB on trout fry. Any fish present in SMB stomachs that could not be identified as trout fry were counted as unknown fish and placed in a separate prey category. All prey items enumerated from stomachs were kept and preserved in 95% ethanol. The total (theoretical) number of SMB necessary to consume all 20,000 trout fry stocked into both lakes was calculated.

The evacuation rate (E90) is the time required for SMB to digest 90% of the prey in their stomach and varies with water temperature, predator and prey size (Rogers and Burley 1991). The time (hours) required for one SMB to digest one trout fry was determined by calculating the E90 values, using the equation below (Rogers and Burley 1991);

$$\mathrm{E} = \mathrm{S}\,(1 - e^{-0.005t\, s^{(-0.29)} e^{(0.15T)} W^{(0.23)}})^{1.95} \qquad 5$$

where S = meal weight (g), t = time (hrs.), T = water temperature (°C), and W = predator weight (g). Separate E90 rates were calculated for each of the three primary size classes of SMB consuming try fry. The predator (SMB) weight was an average taken across all samples within each of the three size classes.

Statistical analysis

The frequency of occurrence (%FO_i), percent by numbers (%N_i), and percent by biomass (%E_i) were used as the quantitative diet indices (Tirasen and Jørgensen 1999). In order to estimate the variability associated with these diet indices non-parametric 95%

confidence intervals (CI) were calculated by bootstrapping 5000 pseudo-replicates (10,000 pseudo replicates showed no significant difference), using each stomach as a separate sampling unit (Tirasen and Jørgensen 1999). Bootstrapping was carried out using the statistical software package R version 0.97.248 (R Core Development Team 2011). The breadth of prey items making up the diet of SMB and other predator fish species was calculated, for each sampling unit, using the Shannon-Weiner diversity index, Pielou's evenness' index and total species richness. Prey species diversity, feeding evenness and species richness indices were calculated using PRIMER–E software (Clarke and Gorley 2006).

Diet data for SMB and the other fish species was heavily zero inflated and did not meet normality after data transformation (Shapiro-Wilk < 0.05), therefore to assess for significant differences in the percent contribution of prey in the diet the non-parametric Kruskal-Wallace test was used. Non-parametric Mann-Whitney U-test was used to test for differences between the means of the total energetic density value (J/g) of the predator's stomach contents. Statistical analysis was carried out using the statistical software package R version 0.97.248 (R Core Development Team 2011).

Habitat data

Data for climate and other abiotic variables did not meet normality (Shapiro-Wilk < 0.05) therefore the non-parametric Spearman Rank correlation was used to assess the relationship between abiotic variables (i.e. lake surface area) and SMB condition factor and SMB catch per unit effort (CPUE). The non-parametric Kruskal-Wallace test was used to assess for any significant differences in abiotic variables and SMB condition factor and CPUE across all seven-study lakes. Statistical analysis was carried out using the statistical software package R version 0.97.248 (R Core Development Team 2011).

Trophic profile

The diet of SMB and other fish species typically includes multiple prey items; therefore, a multivariate approach was used to assess the diet of SMB and other fish in lakes throughout BC. Diet data (expressed as $\%E_i$) for each stomach sample containing prey was imported into PRIMER-E software (Clarke and Gorley 2006) and square root transformed, standardized and converted into a Bray-Curtis similarity matrix. The Bray-Curtis similarity matrix was used as input for non-metric multi-dimensional scaling (NMDS) ordinations. Principal component analysis (PCA) was used to assess the amount of variance explained by lake for the field stocking experiment in order to determine if data from the two lakes could be pooled together.

Trophic overlap

In order to assess for similarities within the SMB and among the other predatory fish species, multivariate analysis of similarities (ANOSIM) was used (Clarke and Warwick 2001). Analysis of similarities (ANOSIM) is similar to a univariate two-way ANOVA, except, a non-parametric randomization procedure is used (Clarke and Warwick 2001). Analysis of similarities (ANOSIM) is based on random permutations of rank similarities among and within sampling units from the Bray-Curtis similarity matrix. A global test statistic (R) is then calculated, which reflects the observed differences between sampling units compared to differences between replicates within sampling units (Clarke 1993). Sampling units (groups) for this study included study lakes, predator fish species (SMB, RB, CT and YP), months and SMB size classes. The replicates within each sampling unit were the individual stomach samples. All ANOSIM and NMDS ordinations were run in PRIMER-E, and 2-D representation of NMDS results was considered meaningful when stress was <0.2 (Clarke 1993).

Results from ANOSIM were presented in the text with a capital “R”, and values can range from -1 to 1. A value of +1 indicates that all the most similar samples are within the same groups, values of 0 indicate completely random grouping, i.e. very similar between groups. A value of -1 indicates that the most similar samples are all outside of the groups i.e. more similar between groups then would be expected (PISCES 2013). Global R-values <0.2 were not considered biologically meaningful and could not be accepted as a reliable test statistic (Clarke and Gorley 2006). Schoener’s overlap index (Schoener 1970) was calculated as a complementary analysis to ANOSIM using;

$$\alpha = 1 - 0.5\ \left(\sum_{x=i}^{n} \left| p_{xi} - p_{yi} \right|\right) \tag{6}$$

where n=number of prey species, p_{xi}=proportion by energetic density of prey category *i* in the diet of species *x*, and p_{yi}= proportion by energetic density of prey category *i* in the diet of species *y*. Values range from 0 to 1, with 0 being no overlap and 1 being total overlap, biologically meaningful overlap was considered > 0.6 (Zaret and Rand 1971). Mean proportions (by energetic density) of each prey item in the predator diet were used in the calculations.

Results

Fish collection

A total of 400 SMB were collected during the 2011 and 2012 field seasons from the three Vancouver Island (VI) lakes (82-505mm, mean ± SD = 221.2 ±102.76), and 78 SMB were collected from Beaver Lake in the Cariboo in July and September 2012 (Table 4; 87-427mm, mean ± SD=198±115mm). Due to small sample size, SMB samples from Skaha (n=5), Osoyoos (n=6) and Vaseux Lakes (n=15) in the Okanagan were pooled together for a total of 26 SMB (Table 4).

Table 4. Summary of SMB catch and other native and stocked fish species captured during the 2011 and 2012 field seasons for the seven SMB study lakes and the three trout reference lakes (SMB free). K=mean condition factor, n=sample size, SMB=smallmouth bass, RB=rainbow trout, CCT=cutthroat trout, YP=yellow perch, KO=kokanee. **Fork length and condition factor is for all catch data (n).*

Study Lake	**Species**	**Year**	**n**	**# with full stomachs**	**Fork Length (mm)***				**K***	
					Mean	**SD**	**Min**	**Max**	**Mean**	**SD**
Spider	**SMB**	**2011**	62	50	190	76	90	444	1.57	0.24
Cusheon			85	63	164	86	82	458	1.52	0.11
Shawnigan			90	59	311	99	105	483	1.43	0.21
Spider	**SMB**	**2012**	63	48	222	90	106	453	1.68	0.14
Cusheon			50	39	161	44	93	505	1.55	0.10
Shawnigan			50	43	269	68	171	469	1.53	0.16
Cariboo			78	57	198	115	87	427	1.48	0.25
Skaha			5	3	257	91	108	455	1.63	0.24
Osoyoos			6	5	339	126	110	495	1.52	0.18
Vaseux			15	13	236	49	100	309	1.38	0.08
Spider	**RB**	**2011/ 2012**	133	104	318	58	109	412	1.07	0.10
Maple		**2012**	24	23	333	39	270	445	1.03	0.13
Reginald		**2012**	30	28	328	21	281	371	1.17	0.08
Cusheon	**CCT**	**2011/ 2012**	84	75	277	87	129	427	1.01	0.11
Weston		**2012**	15	15	307	47	221	380	0.99	0.08
Shawigan	**YP**	**2011**	130	109	140	32	14.5	224	1.16	0.16
Osoyoos		**2012**	34	22	161	30	131	245	1.20	0.11
Shawnigan	**KO**	**2012**	21	21	249	13	220	271	1.30	0.13

SMB habitat

1. Identify the abiotic variables and habitat characteristics associated with SMB populations in lakes throughout British Columbia

Vancouver Island lakes

Within each of the three Vancouver Island study lakes SMB were most frequently caught in rocky or bare habitats and less in vegetation (Figure 6). Within each study lake sampling efforts were not equally distributed across all habitat types (Table 5), which likely created a biased toward the more abundant habitats within each study lake. SMB catch per unit effort (CPUE) was negatively correlated with sampling depth (m) across both Spider and Cusheon Lakes (Spearman; ρ= -0.329, P=0.037; ρ= -0.4754, P=0.012) but was not significantly correlated in Shawnigan Lake (Spearman; ρ= -0.256, P=0.157). As observed with SMB, crayfish abundance levels (crayfish/m^2) were highest in either rock, or bare substrates for Shawnigan and Spider Lakes, respectively (0.118 and 0.04 crayfish/m^2; Figure 6a and 6c). In Cusheon Lake however, crayfish abundance levels were highest in aquatic vegetation (0.0025 crayfish/m^2; Figure 6b).

Table 5. The proportion that each habitat type made up of the transect samples across the three Vancouver Island study lakes sampled from July to September 2012.

Habitat Type	Cusheon	Spider	Shawnigan
Vegetation	36%	25%	25%
Rocky	9%	17%	50%
Bare	45%	42%	17%
Woody debris	9%	17%	8%

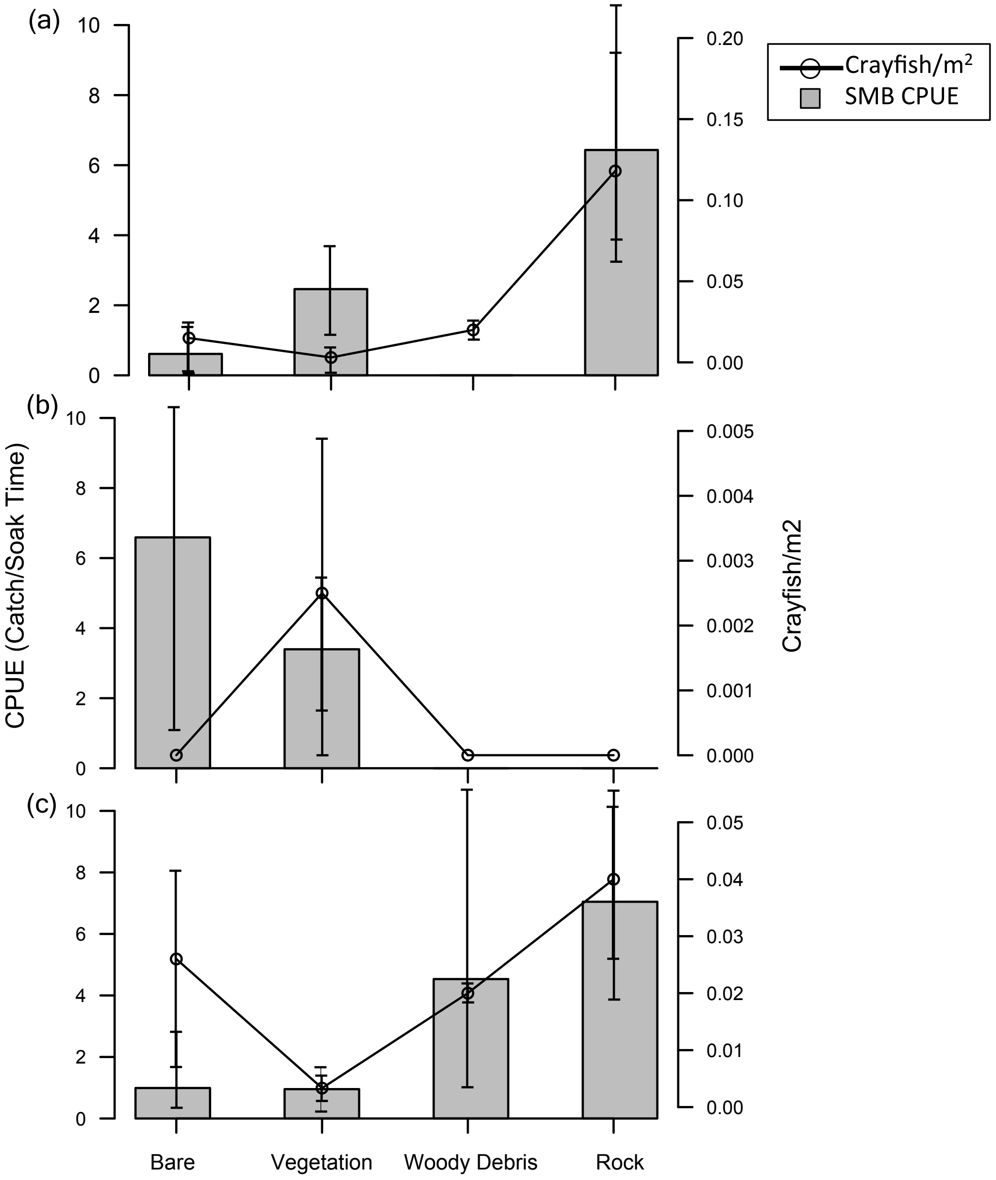

Figure 6. Catch per unit effort from SMB gillnet sampling for 2011 and 2012 field seasons across the four primary habitat types in (a) Shawnigan, (b) Cusheon and (c) Spider Lakes on Vancouver Island. Line plot displays the crayfish relative abundance levels (crayfish/m^2) by habitat type estimated from the snorkel transect surveys in 2012.

SMB CPUE did not increase until water temperatures approached 20°C in late-July to early August across both 2011 and 2012 (Figure 7) and no SMB were captured after mid-October 2011 across all three of the Vancouver Island study lakes. Temperature levels in 2011 and 2012 for Shawnigan and Cusheon Lakes were very similar to historical temperatures levels from approximately 40 years ago (FISS 2013), indicating that the timing of SMB CPUE from the two field seasons likely reflects previous years (Figure 8).

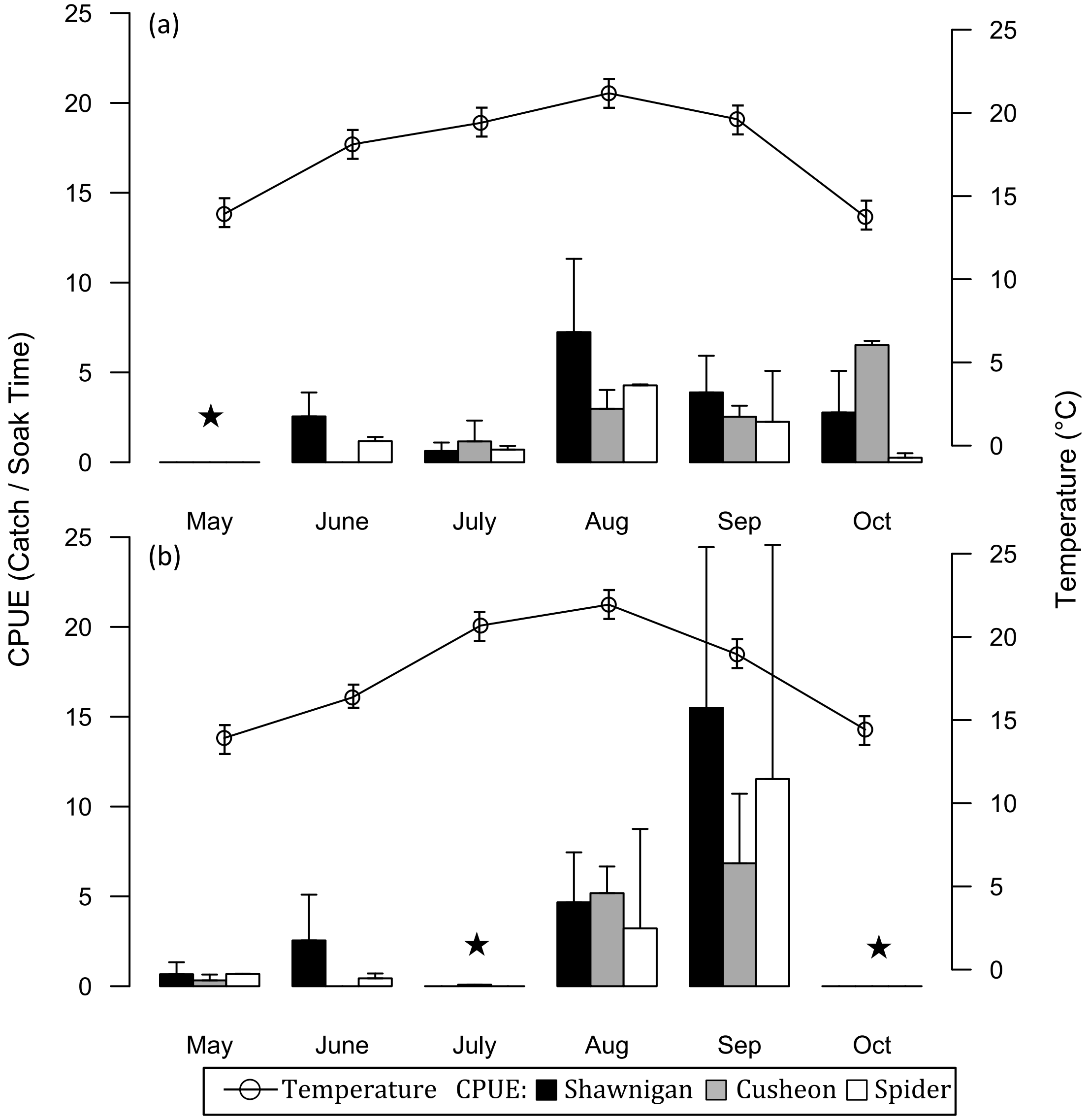

Figure 7. Temporal differences in SMB catch per unit effort (CPUE; # of SMB/soak time) and mean temperature (°C) by month for (a) 2011 and (b) 2012 sampling seasons across the three Vancouver Island study lakes. Error bars represent 95% CI using bootstrap method. *Gillnet sampling did not take place in May 2011 and October 2012, and only took place in Cusheon Lake in July 2012.

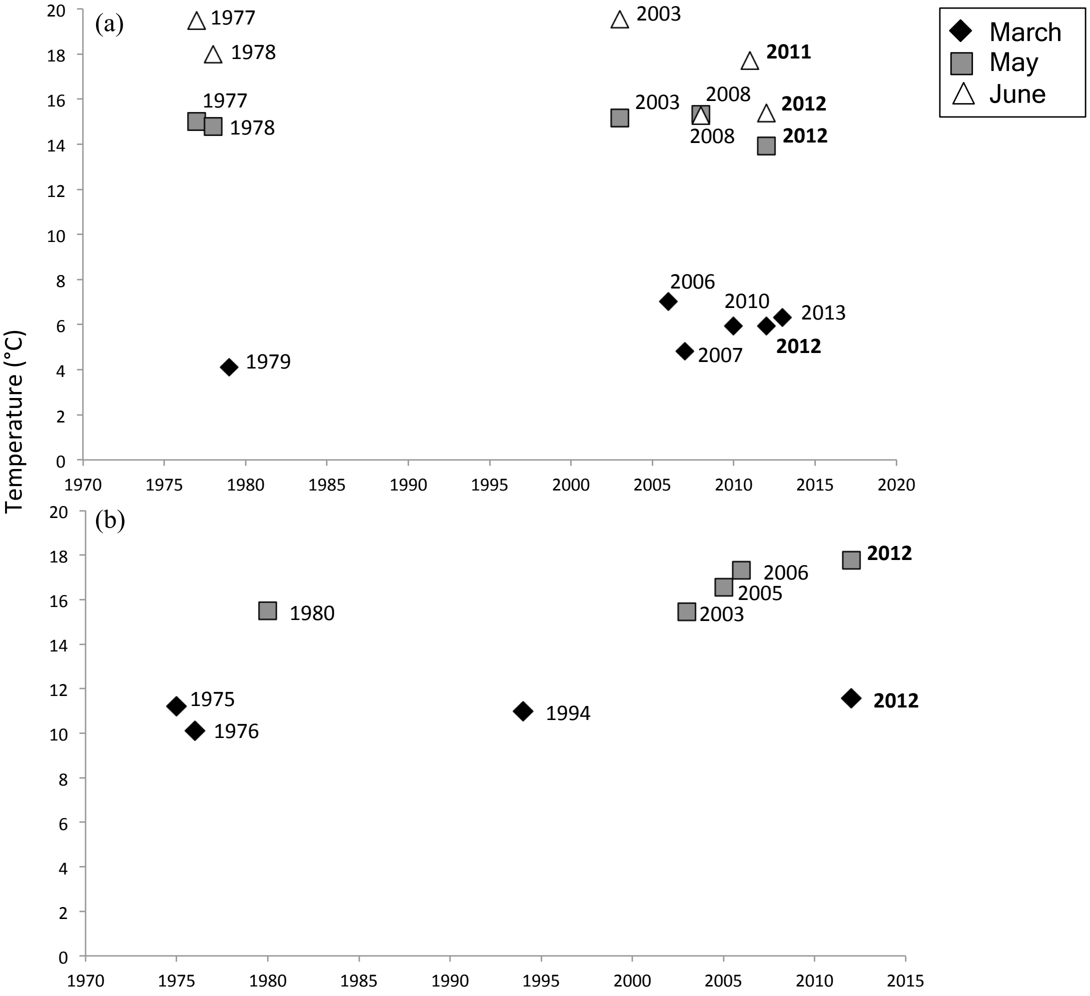

Figure 8. Historical records of mean annual surface temperature (°C) levels in (a) Shawnigan and (b) Cusheon Lakes for the months of March, May and June (FISS 2013). Bolded labels indicate the sampling years (2011 and 2012). *Temperature data was not available for the months of April and May of 2011 for Cusheon Lake.*

All BC study lakes

Secchi depth (m) and SMB CPUE were positively correlated when all seven study lakes were included (Table 6; n= 7, p = 0.389, P<0.01) and when only large study lakes (>20m max depth and >100ha in size) were included in the analysis (Table 6; n= 5, p= 0.687, P<0.01). The observed decrease in the relationship between lake surface area (ha) and SMB condition factor (K) when small study lakes were removed from the analysis (n=5, p= 0.186 P<0.01) indicates that the small study lakes are positively associated with SMB condition factor (Table 6). When only large study lakes were included in the analysis shoreline complexity (m/ha) was not positively correlated with SMB CPUE and condition factor (n=5, ρ=0.111, P=0.226; n=5, ρ=-0.026, P=0.780). This could be linked to shoreline complexity having a greater effect in smaller lakes (<100ha). The observed change in the relationship with shoreline complexity for large lakes may also be attributed to the removal of Spider Lake (<100ha), which contains a complex shoreline (numerous bays and islands) relative to the other study lakes.

Table 6. Results from Spearman's non-parametric rank correlation (ρ and P-values) for comparisons between lake characteristics and SMB catch per unit effort (CPUE) or SMB condition factor for 2011/2012 data from (1) all BC study lakes (n=7) and (2) large* BC study lakes only (n=5).

Variables		**All Study Lakes n=7**		**Large Study Lakes* n=5**	
Independent	Dependent	ρ	P-value	ρ	P-value
Max lake depth (m)	CPUE	-0.175	0.011	0.462	<0.01
Perimeter (m)	CPUE	-0.073	0.290	0.462	<0.01
Secchi Depth (m)	CPUE	0.389	<0.01	0.687	<0.01
Surface area (ha)	CPUE	-0.217	<0.01	0.237	<0.01
Shoreline Complexity (m/ha)	CPUE	0.365	<0.01	0.111	0.226
Max lake depth (m)	Condition Factor	-0.212	<0.01	0.272	0.002
Perimeter (m)	Condition Factor	0.117	0.090	0.272	0.002
Secchi Depth (m)	Condition Factor	-0.251	<0.01	0.168	0.064
Surface area (ha)	Condition Factor	0.374	<0.01	0.186	0.040
Shoreline Complexity (m/ha)	Condition Factor	0.413	<0.01	-0.026	0.780

**Large study lakes are those >20m max depth and >100ha in size*

SMB growth

In 2011, the number of degree-days > 10°C was 147 days in Beaver Lake (Cariboo region) and 62 days fewer than in Shawnigan Lake on Vancouver Island, with 209 degree-days >10°C (Figure 9). This indicates a shortened growing season by approximately two months for SMB populations in the northern Cariboo region and a correspondingly longer winter starvation period (degree days <10°C).

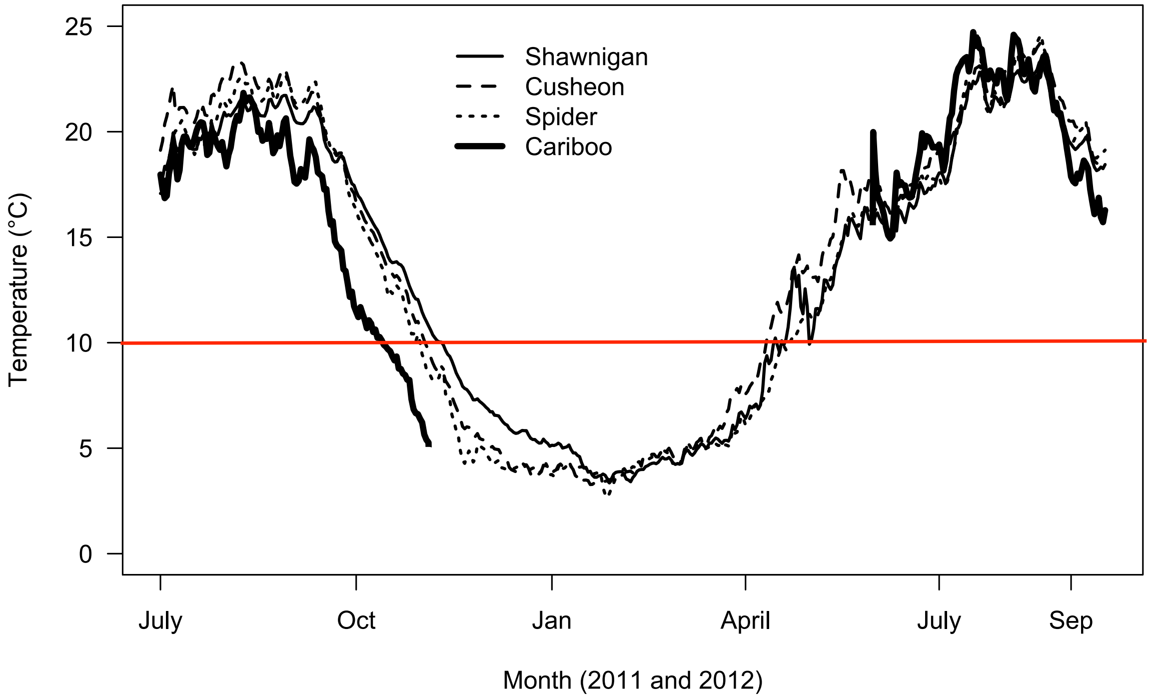

Figure 9. Comparisons of mean daily surface temperature from the southern Vancouver Island (Cusheon, Spider, Shawnigan) and the northern Cariboo (Beaver Lake) study lakes for both 2011 and 2012. Horizontal red line marks the 10°C temperature threshold. *Temperature data was collected from Tidbit temperature loggers at near shore depths (~1m) but was not available for Beaver Lake from November 2011 to June 2012 due to removal of loggers during winter ice cover.

Despite temperature data showing a shortened growing season for SMB in the Cariboo, the growth curve for SMB from Beaver Lake was higher than all three SMB growth curves from the southern Vancouver Island study lakes (Figure 10). The observed higher growth curve for SMB from Beaver Lake could be linked to primary productivity levels (chlorophyll a mg/L) being over two times higher in Beaver Lake (0.0056mg/L) relative to the Vancouver Island study lakes (0.0026, 0.0025 and 0.0015mg/L; Figure 11).

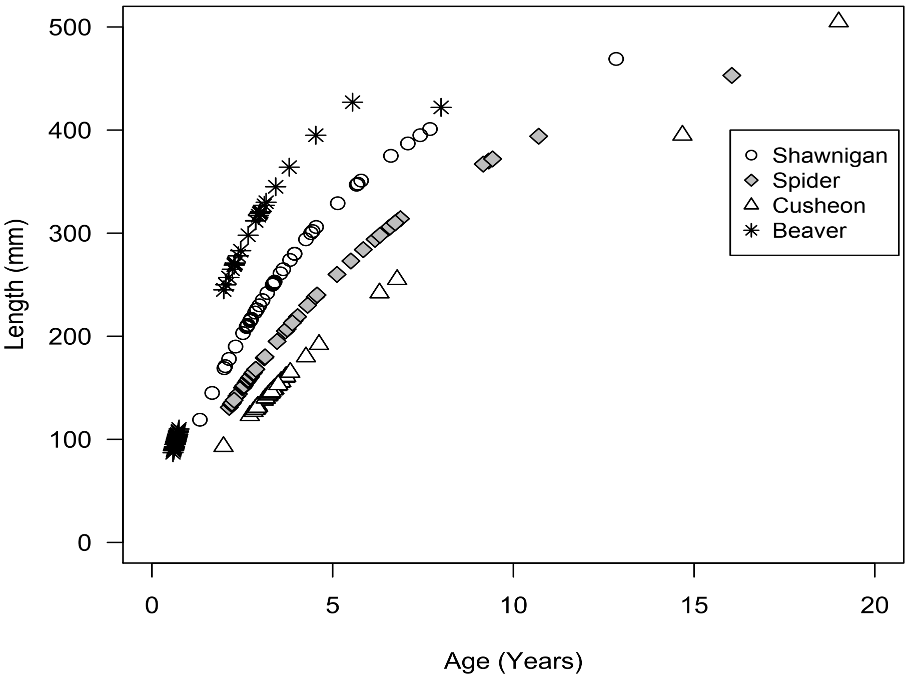

Figure 10. Growth curves illustrating age (years) versus fork length (mm) for SMB collected from all three of the southern Vancouver Island study lakes (Cusheon n= 102, Spider n=98, Shawnigan n=102) and Beaver Lake (n= 57) in the northern Cariboo region for 2011 and 2012.

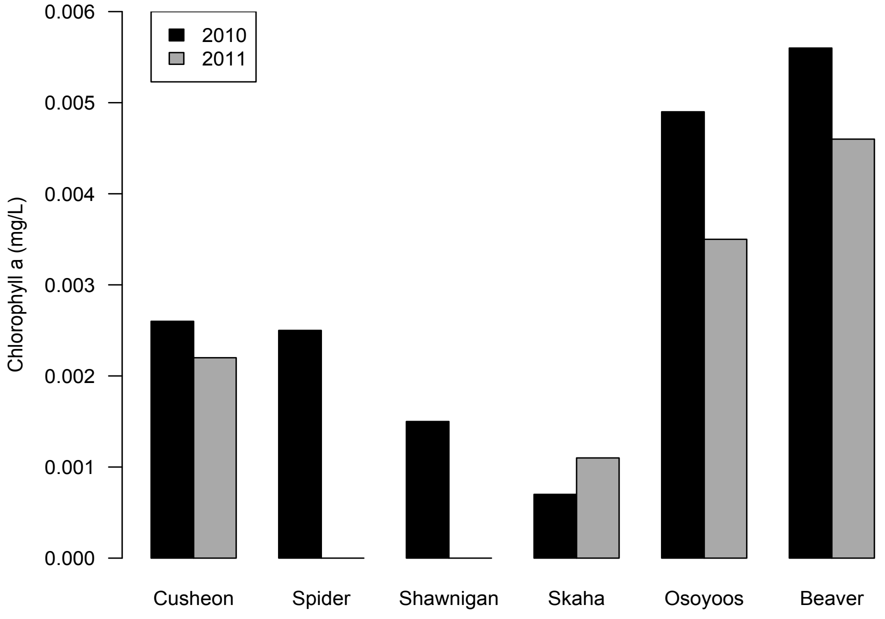

Figure 11. Primary productivity (chlorophyll a) levels for the Vancouver Island (Cusheon, Spider, Shawnigan), Okanagan (Skaha, Osoyoos) and Cariboo (Beaver) region study lakes for the month of September in 2010 and 2011 from the MOE database (FISS 2013).

Mean length at age (length/age) for SMB from Beaver Lake (n=57, 130.8±3.0) was significantly larger (Kruskal-Wallis; $\chi2$=112.5, df=1, P <0.01) compared to SMB from the three Vancouver Island study lakes (56.6±1.26; Table 7. SMB length at age was negatively correlated with degree-days >10°C (n=187, ρ=-0.646, P<0.01) and mean annual air temperature (n=187, ρ=-0.415, P<0.01) across the Cariboo and Vancouver Island study lakes. Mean annual air temperature for Williams Lake in the Cariboo region was 5.5°C for 2010, but southern Vancouver Island was nearly double that at 10.3°C in 2010 (Environment Canada 2013).

Table 7. Mean annual air temperature (°C) and primary productivity levels (mg/L) for 2010 and SMB fork length (mm)/age for SMB sampled in 2012 from Beaver Lake in the Cariboo and from 2011/2012 in the three Vancouver Island study lakes (Shawnigan, Spider and Cusheon Lakes).

Study Lake	Mean Air Temp (°C)	Degree Days >10°C	Starvation Period (days)	Productivity (chl a mg/L)	Length/ Age±SE
Shawnigan	10.3	209	156	0.0015	72.5±1.63
Spider	10.3	199	166	0.0025	53.4±1.10
Cusheon	10.3	205	160	0.0026	43.0±0.67
Beaver	5.5	147	218	0.0056	130.8±3.0

Trophic profile

2. Does SMB trophic profile overlap with trout species and does it vary across temporal and spatial gradients Vancouver Island study lakes

In order to accurately quantify the contributions of larger prey items such as fish and crayfish in the SMB diet the percent contribution by energetic value (%E_i) was used for analysis of all the diet data (Table 8). The overall SMB diet did not have a biologically meaningful difference across the three Vancouver Island study lakes due to an unreliable global R-value <0.2 (ANOSIM by lake; global R=0.135, P<0.01). The statistical significance of the global R-value (P<0.01) is likely driven by the large zero-inflated data set. The SMB diet data for the three Vancouver Island study lakes (n=302) was pooled for comparisons to the Cariboo and Okanagan study lakes.

Prey fish contribution levels did not differ significantly across all three study lakes (Kruskal-Wallis; $\chi 2$=5.02, df=2, P =0.08), making up E_i= 17.6%, E_i= 22% and E_i= 25% of the SMB diet in Spider, Cusheon and Shawnigan Lakes, respectively (Figure 12 and Table 8). Crayfish made up anywhere from E_i= 0.6% of the SMB diet in Cusheon Lake to E_i= 33.5% of the diet in Shawnigan Lake (Figure 12 and Table 8). Other prey items making up less than 10% of the SMB diet (such as dipterans, caddisflies and mayflies) did not differ significantly between the three study lakes (Figure 12; Kruskal-Wallis; $\chi 2$=0.11, df=2, P =0.947).

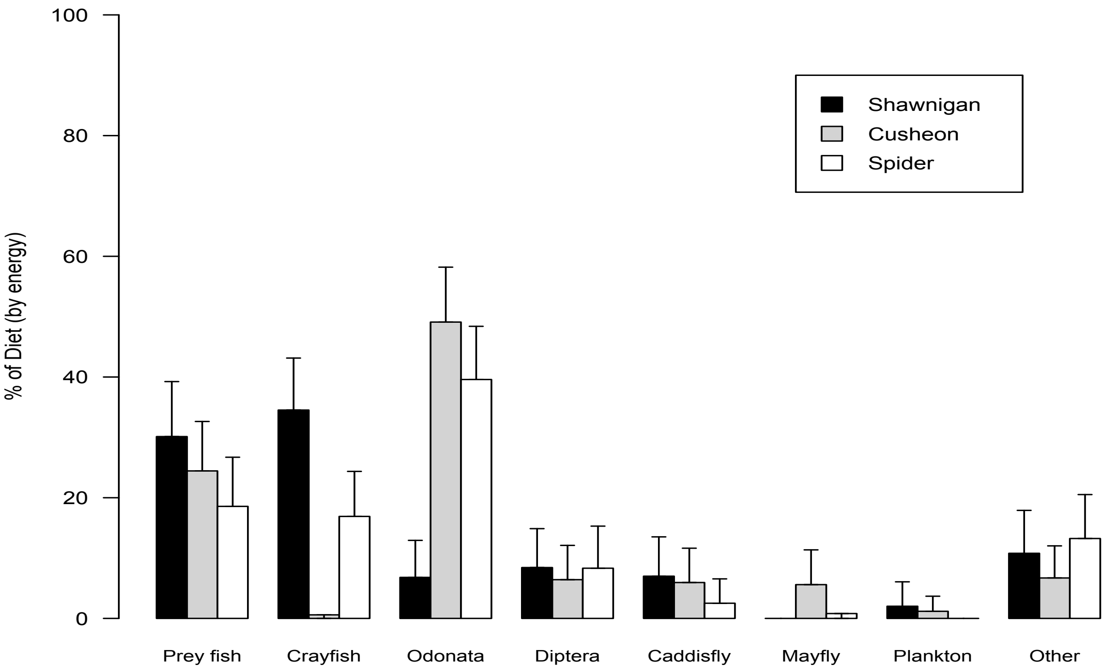

Figure 12. Trophic profile of the primary prey items (by %E_i) in the diet of SMB from Shawnigan (black), Cusheon (gray) and Spider (white) Lakes, during the 2011 and 2012 sampling seasons. Error bars represent 95% CI using bootstrap method. Prey items under the "Other" category, represent unidentified prey, or those prey items contributing <3% towards the overall diet. (ANOSIM by lake; global R=0.135, P<0.01).

Table 8. Percent occurrence (%FO), number of individuals (N), percent contribution by numbers (%N), energetic density E (J) and percent contribution by energetic density ($\%E_i$) for all prey items present in the diet of SMB from Shawnigan, Spider and Cusheon Lakes for the 2011 and 2012 field seasons pooled together.

Species	**Order**	**Category**	**Shawnigan n= 102**					**Cusheon n= 102**					**Spider n= 98**				
Fish			**FO**	**N**	**%N**	**E (J)**	**%E**	**FO**	**N**	**%N**	**E (J)**	**%E**	**FO**	**N**	**%N**	**E (J)**	**%E**
Threespine stickleback	*Gasterosteus aculeatus*	*Fish*	-	-	-	-	-	11.3	37	11.4	127597	16.4	-	-	-	-	-
Yellow perch	*Perca flavescens*	*Fish*	0.6	1	0.2	0.6	0.4	-	-	-	-	-	-	-	-	-	-
Unidentified fish		*Fish*	21.0	60	24.6	73142	28.8	6.8	15	6.8	150982	8.1	13.2	41	10.6	134386	18.6
Aquatic Invertebrates																	
Crayfish	*Pacifastacus leniusculus*	*Crayfish*	24.4	87	27.5	315118	33.5	1.1	3	0.7	76073	0.6	14.3	53	12.7	282788	16.9
Dragonflies/ Damselflies	*Anisoptera/ Zygoptera*	*Odonata*	8.1	19	5.1	7504	6.6	36.7	259	44.2	49425	49.1	28.6	604	43.0	230455	39.6
Mayflies	*Ephemeroptera*	*Mayfly*	2.3	9	0.4	131	0.1	6.8	34	5.4	524	5.6	3.3	12	1.6	163	0.8
Stoneflies	*Plecoptera*	*Other*	0.6	1	0.2	50.8	0.4	4.0	48	4.3	10940	5.0	-	-	-	-	-
Bees/wasps	*Hymenoptera*	*Other*	-	-	-	-	-	-	-	-	-	-	4.9	1048	8.8	21242	6.7
Ants	*Hymenoptera*	*Other*	10.5	621	12.5	4931	7.0	1.1	2	0.3	16.9	0.0	6.6	35	4.4	763	2.9
Leech	*Hirudinea*	*Other*	-	-	-	-	-	-	-	-	-	-	0.5	1	0.2	1657	0.3
Caddisfly	*Trichoptera*	*Caddisfly*	8.1	171	6.3	41087	7.1	5.6	17	4.8	4921	5.9	10.4	15	3.0	4163	2.5
Copepods	*Copepoda*	*Plankton*	-	1	-	3.6	-	-	-	-	-	-	-	-	-	-	-
Daphnia	*Cladocera*	*Plankton*	1.2	705	1.2	668	1.0	4.0	165	3.2	97.2	0.9	-	-	-	-	-
Gammarids	*Amphipoda*	*Plankton*	1.2	267	1.7	1423	1.8	1.1	3	0.3	13.6	0.1	1.1	6	0.8	28.0	0.1
Chaoborus	*Diptera*	*Plankton*	1.7	70	2.0	274	2.0	4.0	30	1.9	102	0.3	-	-	-	-	-
Worms	*Annelida*	*Other*	-	-	-	-	-	0.6	1	1.0	111	0.3	-	-	-	-	-
Chironomids	*Diptera*	*Diptera*	12.8	151	12.1	4259	8.2	12.4	208	11.9	4561	6.4	10.4	142	11.8	12710	8.3
Beetles	*Coleoptera*	*Other*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified insects		Other	5.8	74	5.8	9658	3.1	4.6	35	4.2	9373	1.7	6.5	13	2.8	4017	2.8
	Totals		**-**	**2237**	**-**	**458249**	**-**	**-**	**857**	**-**	**434737**	**-**	**-**	**1970**	**-**	**692370**	**-**

Temporal trends

The diet of SMB did not have a biologically meaningful difference by month for any of the three Vancouver Island study lakes due to an unreliable global R-value of <0.2 (Figure 13; ANOSIM global R=0.09, P=0.01). Sample size was very low in May (n=1) and June 2012 (n=1) in Cusheon Lake and this likely skewed the data to the dominance

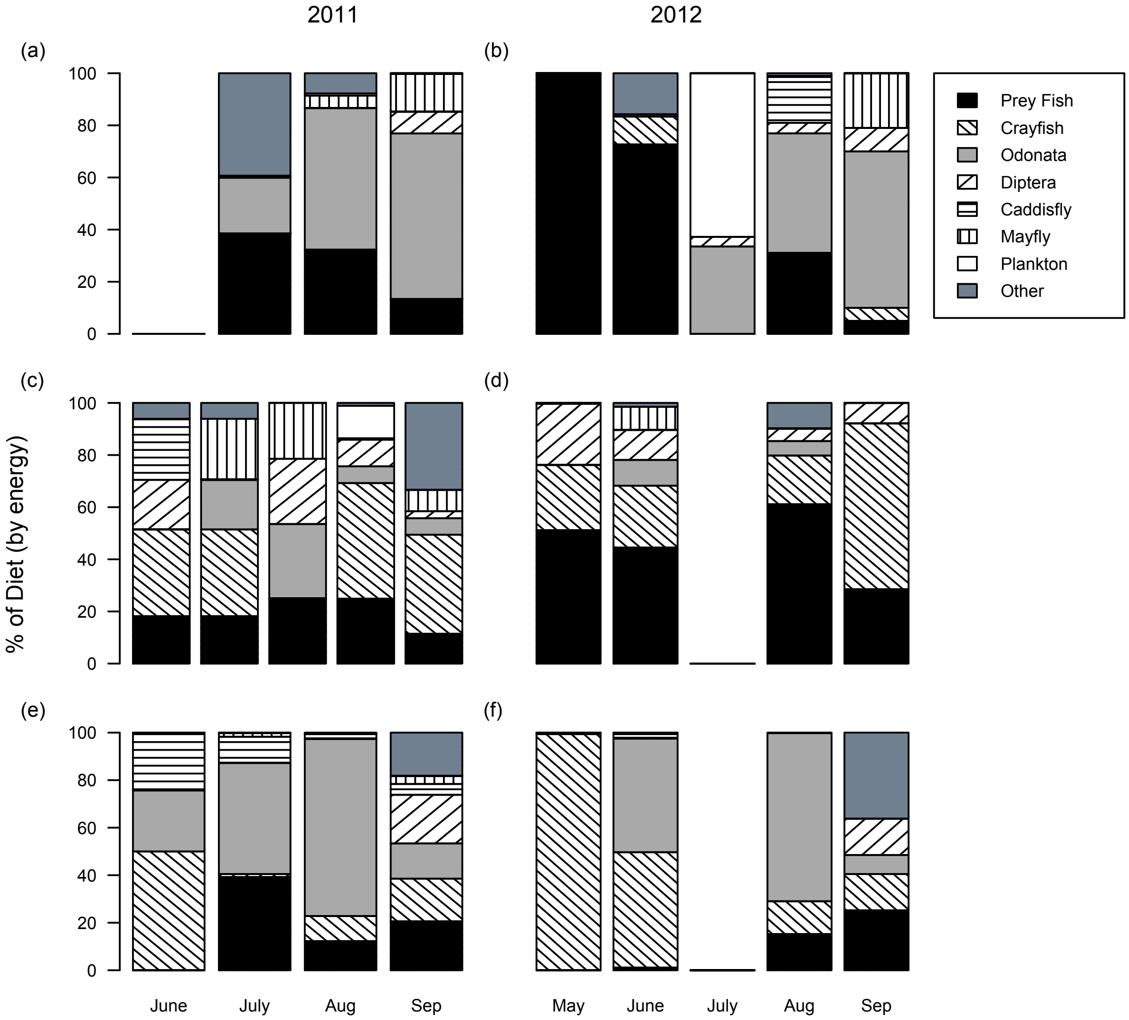

Figure 13. Temporal differences in the primary prey items contributing (%E_i) to the diet of SMB across the summer months for the 2011 (left column) and 2012 (right column) field seasons from Cusheon Lake (a,b), Shawnigan Lake (c,d) and Spider Lake (e,f) on Vancouver Island. ANOSIM by month; global R=0.09, P=0.01. *Data bars are absent for May 2011 and July 2012 because no sampling took place during those months. In June 2011, no SMB were caught during sampling in Cusheon Lake.*

of prey fish in the SMB diet (Figure 13a). The diet of SMB for each of the Vancouver Island study lakes was not significantly different by year (ANOSIM; global R=0.01, P=0.067), therefore, data from the 2011 and 2012 field seasons were pooled for statistical analysis, unless otherwise indicated.

All BC study lakes

The overall SMB diet did not have a biologically meaningful difference by region due to an unreliable global R-value of <0.2 (Figure 14; ANOSIM global R=0.134, P=0.01). The statistical significance of the global R-value (P=0.01) is likely driven by the large zero inflated data set. The SMB diet was more similar for study lakes within the same geographic region compared to lakes from other regions (Figure 14; Shawnigan vs. Cusheon Lakes global R=0.244, P=0.001; Cusheon vs. Osoyoos Lakes global R=0.341, P=0.004). Of the three Vancouver Island study lakes, the SMB diet from Shawnigan Lake was not significantly different from Osoyoos and Skaha Lakes in the Okanagan region (Figure 14; ANOSIM global R=0.121, P=0.152; global R=0.105, P=0.103, respectively). Conversely, the diet of SMB from Cusheon and Spider Lakes were significantly different from the Okanagan and Cariboo region study lakes (ANOSIM global R>0.2, P<0.05).

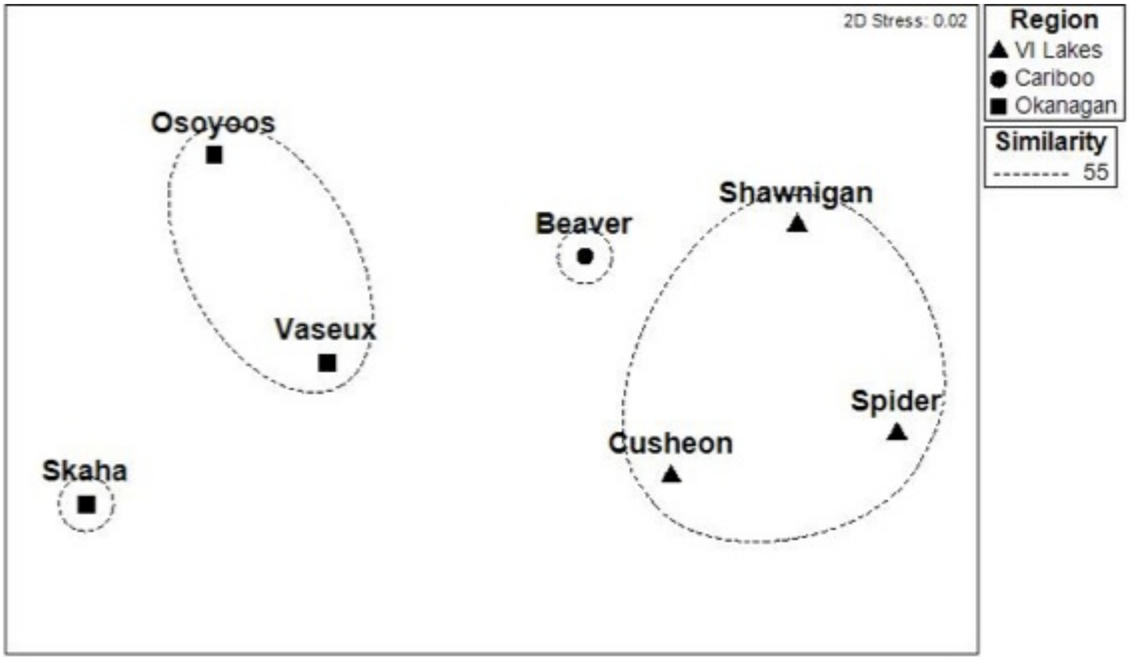

Figure 14. Overall SMB diet (%E_i) across all seven study lakes for the 2011 and 2012 field seasons depicted in a nonmetric multidimensional scaling (NMDS) plot. Symbols that are closer together have greater similarity than symbols that are further apart. Symbols within the dashed circles are 55% similar to one another (ANOSIM by lake; global R=0.134, P=0.01).

Prey fish were a dominant prey item in the diet of SMB across all three regions, contributing E_i=55%, E_i=32% and E_i=23% to the overall diet in the Okanagan, Cariboo and Vancouver Island (VI) study lakes, respectively (Figure 15 and Table 9). Interestingly, crayfish were only found in the diet of SMB from the Vancouver Island study lakes (E_i=16%) despite confirmed signal crayfish populations in the Okanagan study lakes (Bondar et al. 2005). Prey fish (E_i=32%) and smaller prey items such as copepods (E_i=22%) made up over 50% of the SMB diet in the Cariboo study lake (Figure 15 and Table 9) and prey species diversity (H'=0.30) and feeding evenness (J'=0.52) was significantly higher relative to the Vancouver Island and Okanagan study lakes (see appendices; Kruskal-Wallis; $\chi 2$=4.55, P=0.03). Other prey items such as: worms, leeches, and unidentified insects contributed between E_i=12% to E_i=19% to the SMB diet across all three geographic regions (Figure 15 and Table 9). It is important to take into consideration the differences in the temporal gradient of the when sampling took place across the three geographic regions. SMB were only captured in September 2012 from the Okanagan study lakes and in July and September 2012 from Beaver Lake in the Cariboo. The dominance of prey fish in the SMB diet from the Okanagan study lakes could be associated with seasonal pulses in prey fish availability. Similarly, the dominance of smaller prey items (e.g. copepods) in the diet of SMB from the Cariboo could also be associated with pulses in availability of smaller prey such as plankton.

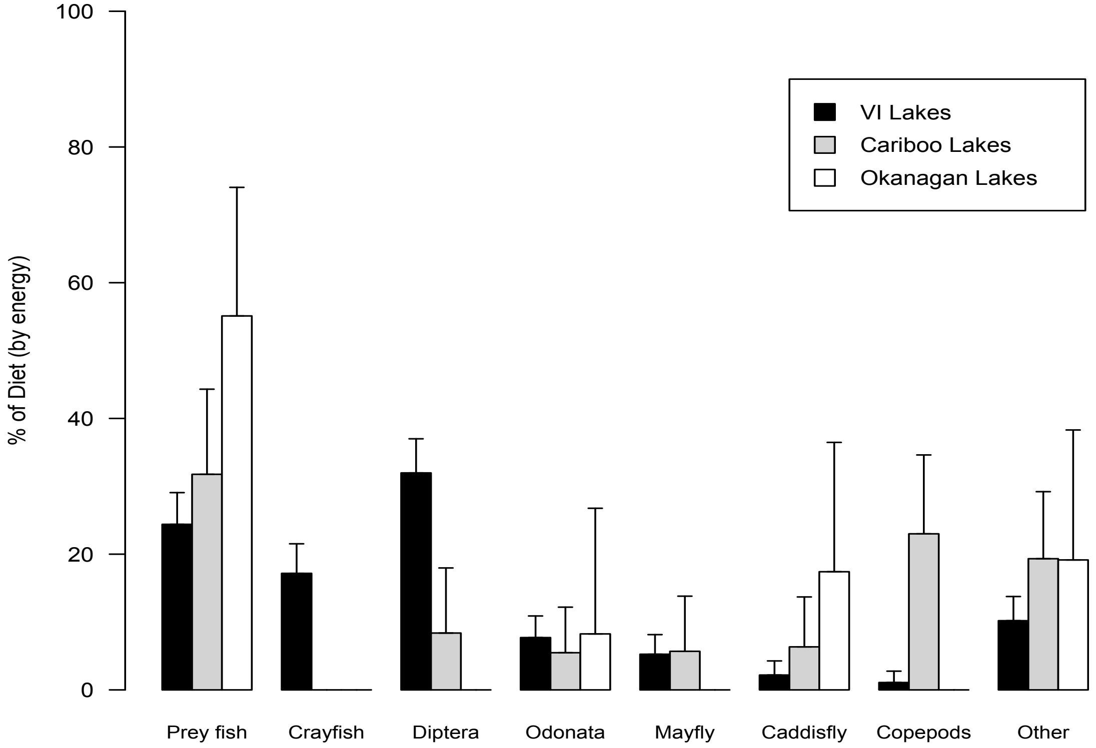

Figure 15. Trophic profile of the primary prey items (%E_i) making up the diet of SMB from the Vancouver Island (black), Cariboo (gray) and Okanagan (white) study lakes during the 2011 and 2012 sampling seasons. Error bars represent 95% CI using bootstrap method. ANOSIM by region; global R=0.13, P=0.01.

Table 9. Percent occurrence (%FO), number of individuals (N), percent contribution by numbers (%N), energetic density E (J) and percent contribution by energetic density (%E_i) for all prey items present in the diet of SMB from the Vancouver Island Lakes, Cariboo and Okanagan study lakes for the 2011 and 2012 field seasons pooled together.

Name	**Order**	**VI Lakes n= 302**					**Okanagan n= 21**					**Cariboo n= 57**				
		FO	**N**	**%N**	**E (J)**	**%E**	**FO**	**N**	**%N**	**E (J)**	**%E**	**FO**	**N**	**%N**	**E (J)**	**%E**
Yellow perch	*Perca flavescens*	0.2	1.0	0.1	131363	0.1	-	-	-	-	-	-	-	-	-	-
Unidentified fish	-	20.2	153.0	18.2	354735	24.0	48.1	20.0	43.5	77058	55	17	23.0	30.2	134924	31.8
Crayfish	*Pacifastacus leniusculus*	14.9	143	13.6	673979	17.0	-	-	-	-	-	-	-	-	-	-
Dragonflies/ Damselflies	*Anisoptera/ Zygoptera*	18.1	882	30.6	287385	31.7	3.7	4	3.2	397	0.1	6.0	16	8.2	8247	8.4
Mayflies	*Ephemeroptera*	4.6	55	2.5	818	2.2	7.4	229	22.6	5105	17.4	11.1	110	7.1	305	6.3
Stoneflies	*Plecoptera*	1.7	49	1.5	10991	1.8	7.4	9	5.7	808	5.5	-	-	-	-	-
Bees/wasps	*Hymenoptera*	6.5	1048	2.9	21242	2.2	-	-	-	-	-	-	-	-	-	-
Ants	*Hymenoptera*	1.9	658	5.8	5710	3.3	-	-	-	-	-	-	-	-	-	-
Snails/Clams	*Gastropoda*	0.4	1	0.0	433	0.3	-	-	-	-	-	-	-	-	-	-
Leech	*Hirudinea*	0.2	1	0.1	0.6	0.1	-	-	-	-	-	-	-	-	-	-
Caddisfly	*Trichoptera*	6.7	203	4.7	50171	5.2	-	-	-	-	-	6.0	7	2.2	427	5.7
Copepods	*Copepoda*	-	1	-	3.6	-	-	-	-	-	-	15.4	2829	21.1	1757	23.0
Daphnia	*Cladocera*	1.9	870	1.5	765	0.6	7.4	31	7.1	29	9.1	16.2	662	10.6	279	5.6
Gammarids	*Amphipoda*	1.3	276	0.9	1465	0.6	-	-	-	-	-	4.3	40	5.1	417	6.2
Chaoborus	*Diptera*	2.1	100	1.3	376	0.8	-	-	-	-	-	6.8	606	7.6	260	5.6
Worms	*Annelida*	0.6	2	0.4	1657	0.2	-	-	-	-	-	1.7	1	0.4	186	0.2
Chironomids	*Diptera*	13.7	501	12.0	21530	7.7	18.5	8	11.6	80	8.2	12.8	61	4.8	289	5.5
Beetles	*Coleoptera*	0.4	1	0.0	929	0.2	-	-	-	-	-	-	-	-	-	-
Unidentified insects	-	5.0	120	4.2	21686	2.1	7.4	2	6.3	64387	4.5	1.7	3	2.7	158	1.8
Totals		**-**	**5065**	**100**	**1585240**	**100**	**-**	**303**	**100**	**147864**	**100**	**-**	**4358**	**100**	**147250**	**100**

Ontogenetic trends

Juvenile SMB start feeding on prey fish at 91mm in fork length (Figure 16a) in Cusheon Lake, illustrating an early onset of piscivory in SMB from the Vancouver Island study lakes. SMB from the Vancouver Island study lakes showed no signs of an ontogenetic shift between the diet of juvenile and adult SMB and the overall prey composition did not differ significantly by size class (Figure 16 and 17c; ANOSIM; Global R=0.042, P=0.05). SMB from Beaver Lake show a prominent ontogenetic shift in their diet (ANOSIM by size class; Global R=0.494, P=0.01), with juveniles primarily feeding on smaller prey items such as copepods, dipterans, caddisflies and mayflies (Figure 17a). Conversely the diet of adult SMB was over E_i = 70% prey fish. The lack of prey fish in the diet of juvenile SMB (<200mm fork length) from Beaver Lake indicates a later onset of piscivory relative to the SMB from the VI lakes. The diet of SMB from the Okanagan study lakes did not show any signs of an ontogenetic shift (Figure 17b). Prey fish percent contribution was positively correlated with SMB fork length (mm), but was not statistically significant (Spearmann; ρ=0.318, P=0.159). The onset of piscivory could not be assessed for SMB from the Okanagan study lakes as SMB <100mm were not captured during sampling (Figure 17b).

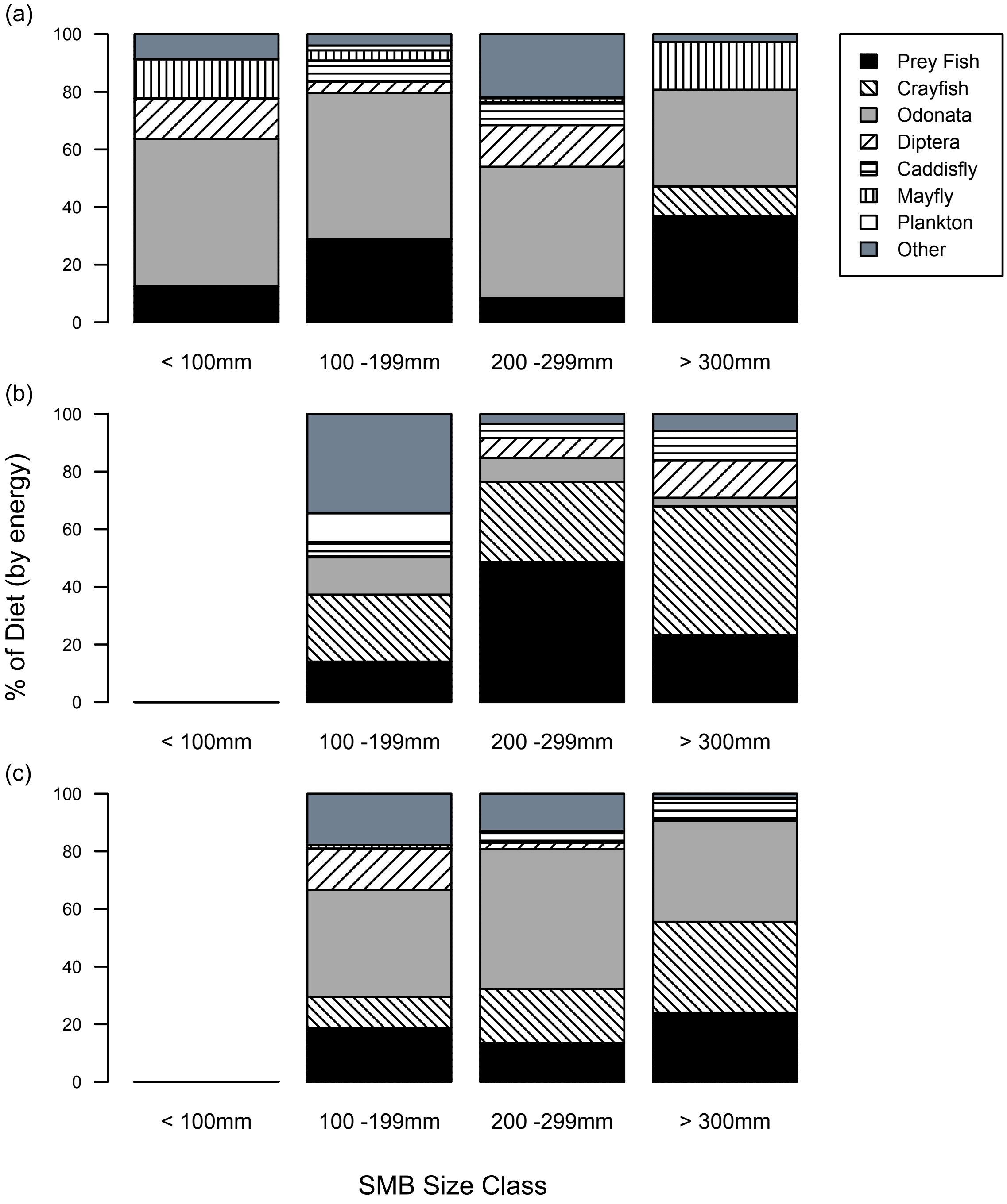

Figure 16. Ontogenetic trends of the primary prey items making up the diet of SMB (%E_i) by size class (<100, 100-199, 200-299 and >300mm) for the Vancouver Island study lakes. Includes data from both 2011 and 2012 field seasons for (A) Cusheon, (B) Shawnigan and (C) Spider Lakes.

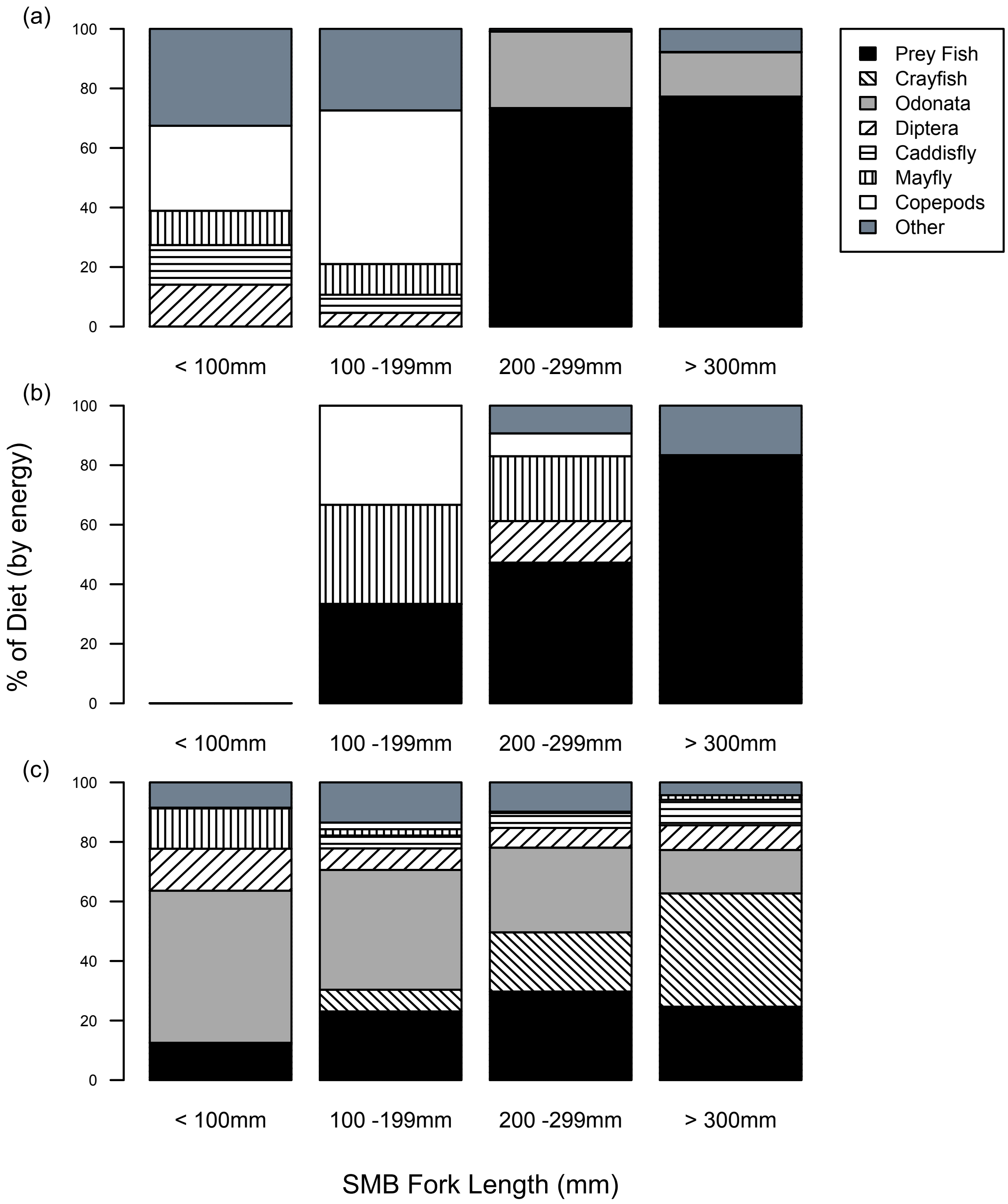

Figure 17. Ontogenetic trends of the primary prey items making up the diet of SMB (%E_i) by size class (<100, 100-199, 200-299 and >300mm). Includes data from the 2012 field season for the (A) Cariboo, (B) Okanagan study lakes and 2011/2012 data for the (C) Vancouver Island study lakes.

Trophic overlap

Does SMB trophic profile overlap with trout species and does it vary across temporal and spatial gradients?

None of the interspecific comparisons showed an ecologically significant (Schoener's overlap α > 0.6) trophic overlap with the diet of SMB across the Vancouver Island study lakes (Table 10 and Figure 18). Schoener's index of dietary overlap was greatest for small (<200mm) SMB and RB from Spider Lake (α=0.406; Table 10), however these results must be interpreted with caution due to the very small sample size (n=2, ANOSIM P>0.05) for the RB. Comparisons between the diet of RB from Spider Lake (SMB present) and Maple Lake (SMB free) show no signs of a significant shift in the trout diet (Figure 19; ANOSIM global R=0.06, P>0.05; α=0.53).

Table 10. Global R-values calculated from analysis of similarities (ANOSIM) and Schoener's Index of dietary overlap (α) for interspecific comparisons between the diets of SMB and other predator fish species present in the Vancouver Island study lakes.
** Denotes significant global R-values (P<0.05).*

Species	**Size Grouping (small=<200mm, Large=>200mm)**	**Sample size (n)**	**ANOSIM (global R)**	**Schoener's Index (α)**
SMB vs. RB	Small	56	-0.138	0.406
	Large	166	0.450*	0.257
SMB vs. CCT	Small	98	0.453*	0.145
	Large	80	0.528*	0.29
SMB vs. YP	Small	127	0.679*	0.245
	Large	186	0.638*	0.237
SMB vs. KO	All sizes	119	0.350*	0.01

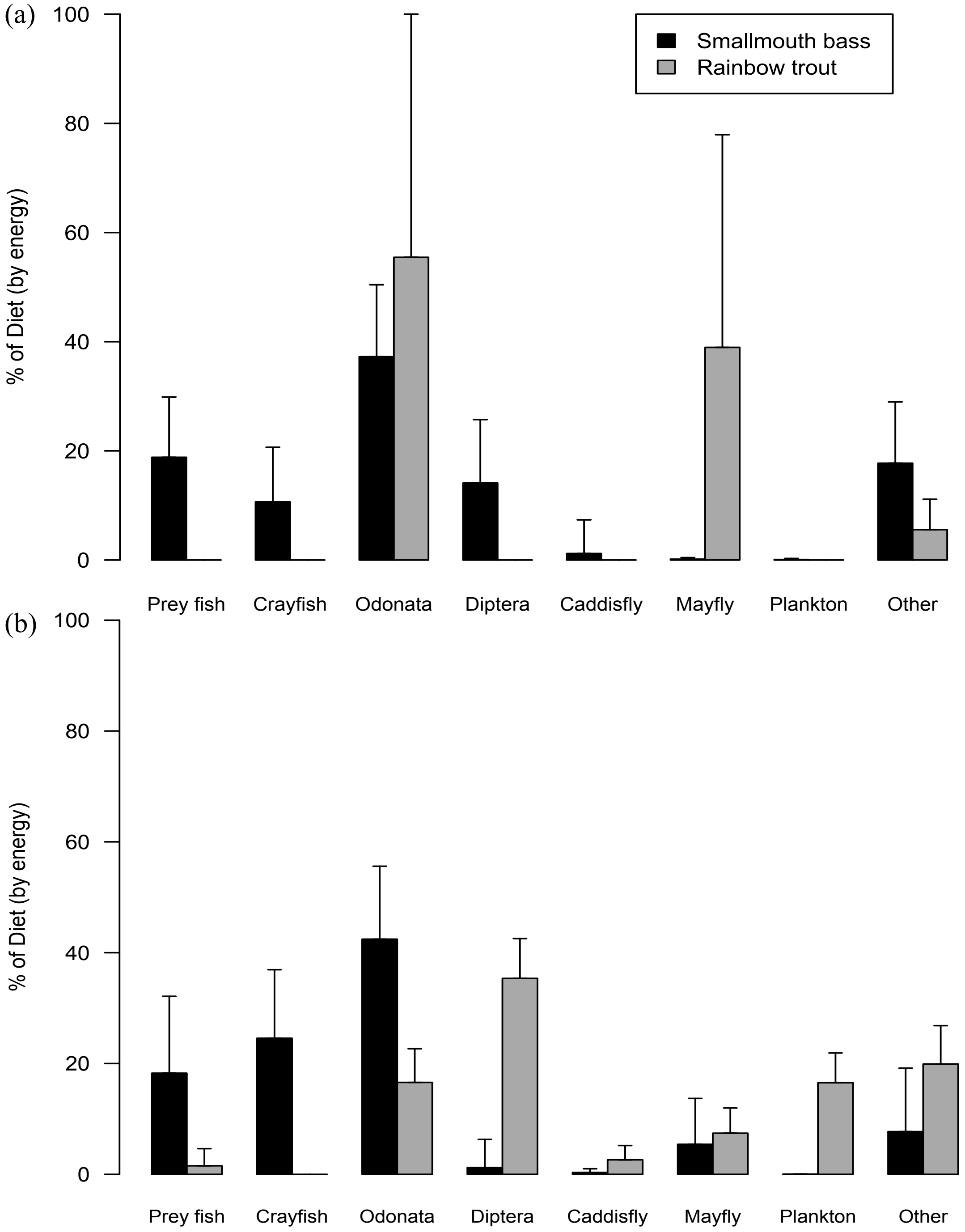

Figure 18. Trophic profile comparisons of the primary prey items making up the diet (%E_i) of SMB (black) and rainbow trout (gray) from Spider Lake during the 2011 and 2012 sampling seasons for (a) small fish (<200mm) and (b) large fish (>200mm). Error bars represent 95% CI using bootstrap method. Schoener's index of dietary overlap was $\alpha=0.406$ and $\alpha=0.257$, for (a,b) respectively.

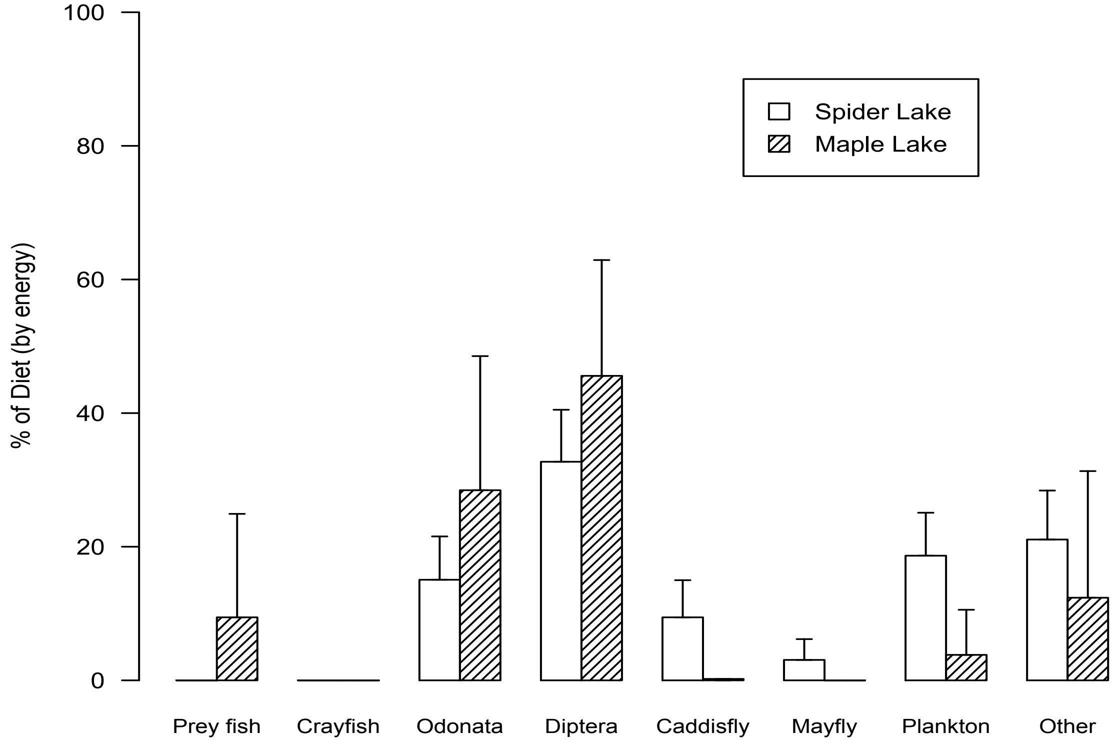

Figure 19. Trophic profile comparison of the primary prey items (%E_i) making up the diet of rainbow trout across all size classes from Spider (white) and Maple (striped) Lakes on Vancouver Island. Error bars represent 95% CI using bootstrap method. Schoener's index of dietary overlap was α=0.53 and ANOSIM global R=0.06, P>0.05.

Interspecific comparisons between CCT and SMB showed little trophic overlap across both the small (α=0.145) and large sized fish (α=0.290), with slightly greater overlap for the diet of larger sized fish (Table 10). The slightly higher trophic overlap between larger SMB and CCT is likely driven by greater overlap between odonates, dipterans and other macroinvertebrates in the diet (Figure 20b). The total energetic density value for the stomach contents of the average SMB from Cusheon Lake was three times higher than the stomach contents of the average CCT in Cusheon Lake (25.98±3.43J/g vs. 7.69±1.93J/g). This is likely due to the dominance of plankton (*Daphnia sp.*) in the diet of CCT (Figure 20; E_i=58.3%), which has a lower energetic value relative to prey fish and odonates that dominated the diet of SMB in Cusheon Lake (E_i=24.5% and E_i=49.1%, respectively).

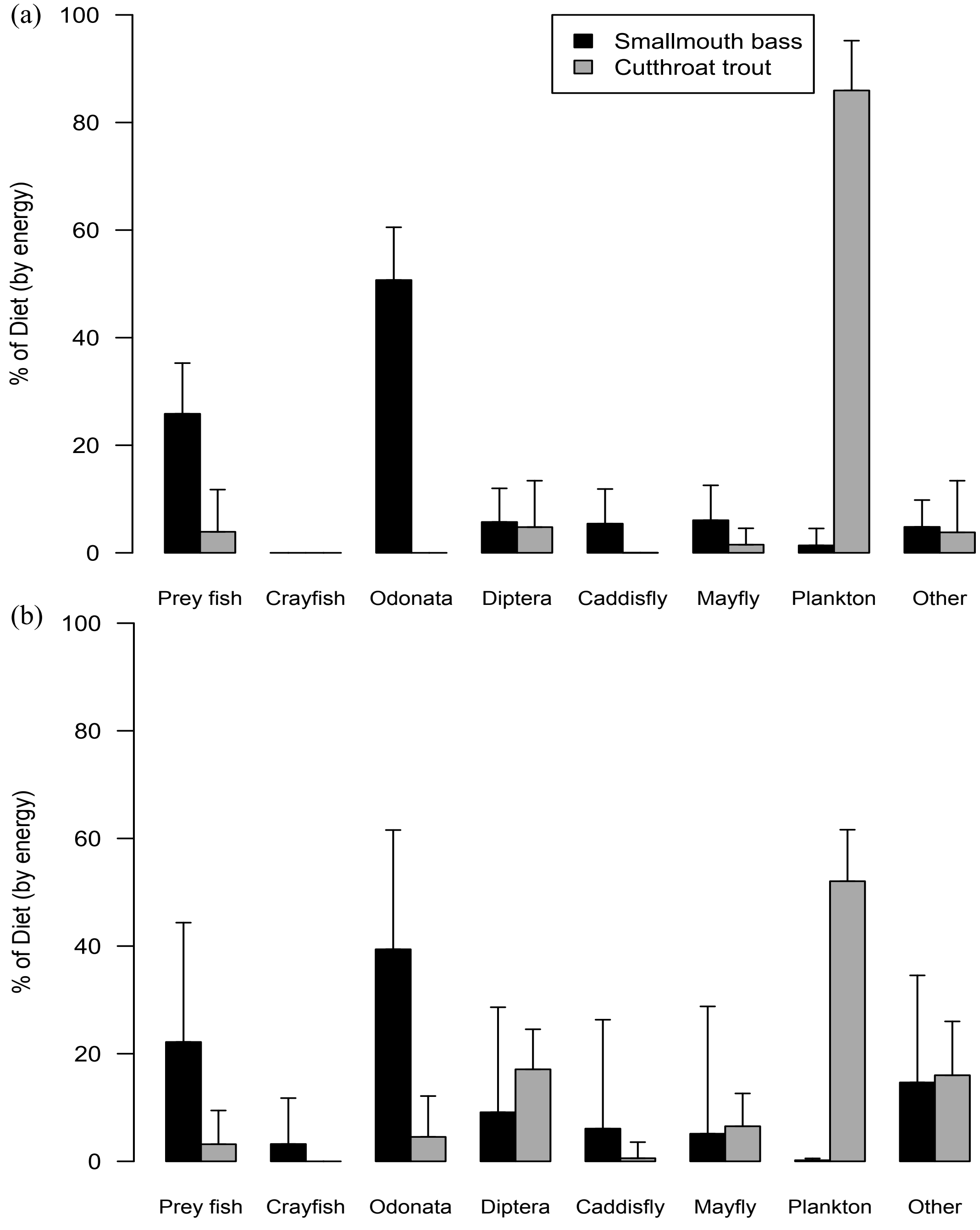

Figure 20. Trophic profile comparisons of the primary prey items in the diet (%E_i) of SMB (black) and cutthroat trout (gray) from Cusheon Lake during the 2011 and 2012 sampling seasons for (a) small fish (<200mm) and (b) large fish (>200mm). Error bars represent 95% CI using bootstrap method. Schoener's index of dietary overlap was α=0.145 and α=0.290, for (a,b) respectively.

The total energetic density value for the stomach contents of the average CCT from Weston Lake (SMB free) was twice that of the average CCT stomach contents from Cusheon Lake (Figure 21; 14.91±4.74J/g vs. 7.69±1.93J/g). This is likely due to the significantly higher levels of threespine stickleback (Figure 21; Kruskal-Wallis; $\chi2=19.29$, df=1, $P<0.01$) in the diet of CCT ($E_i=35.4\%$) from Weston Lake (SMB free) compared to the diet of CCT ($E_i=3.3\%$) from Cusheon Lake (SMB present).

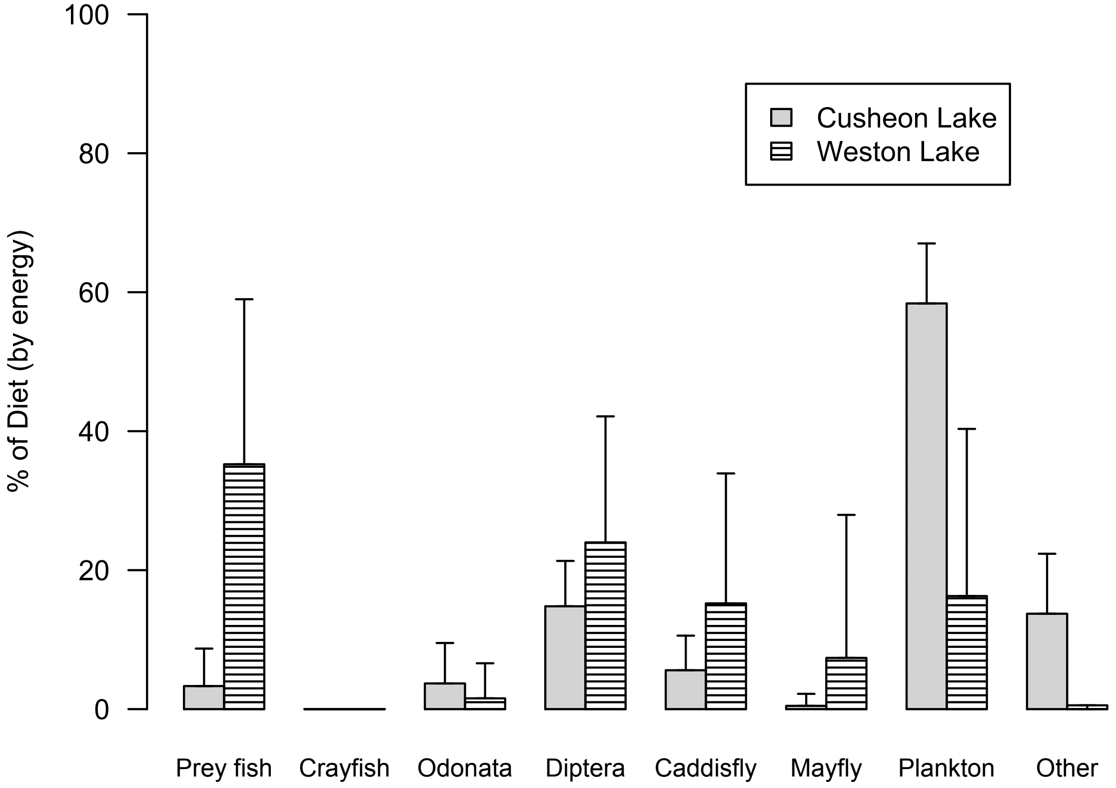

Figure 21. Trophic profile comparisons of the primary prey items in the diet ($\%E_i$) of cutthroat trout from Cusheon (gray) and Weston (striped) Lakes on Vancouver Island. Error bars represent 95% CI using bootstrap method. Schoener's index of dietary overlap $\alpha=0.43$ and ANOSIM global $R=0.206$, $P<0.05$.

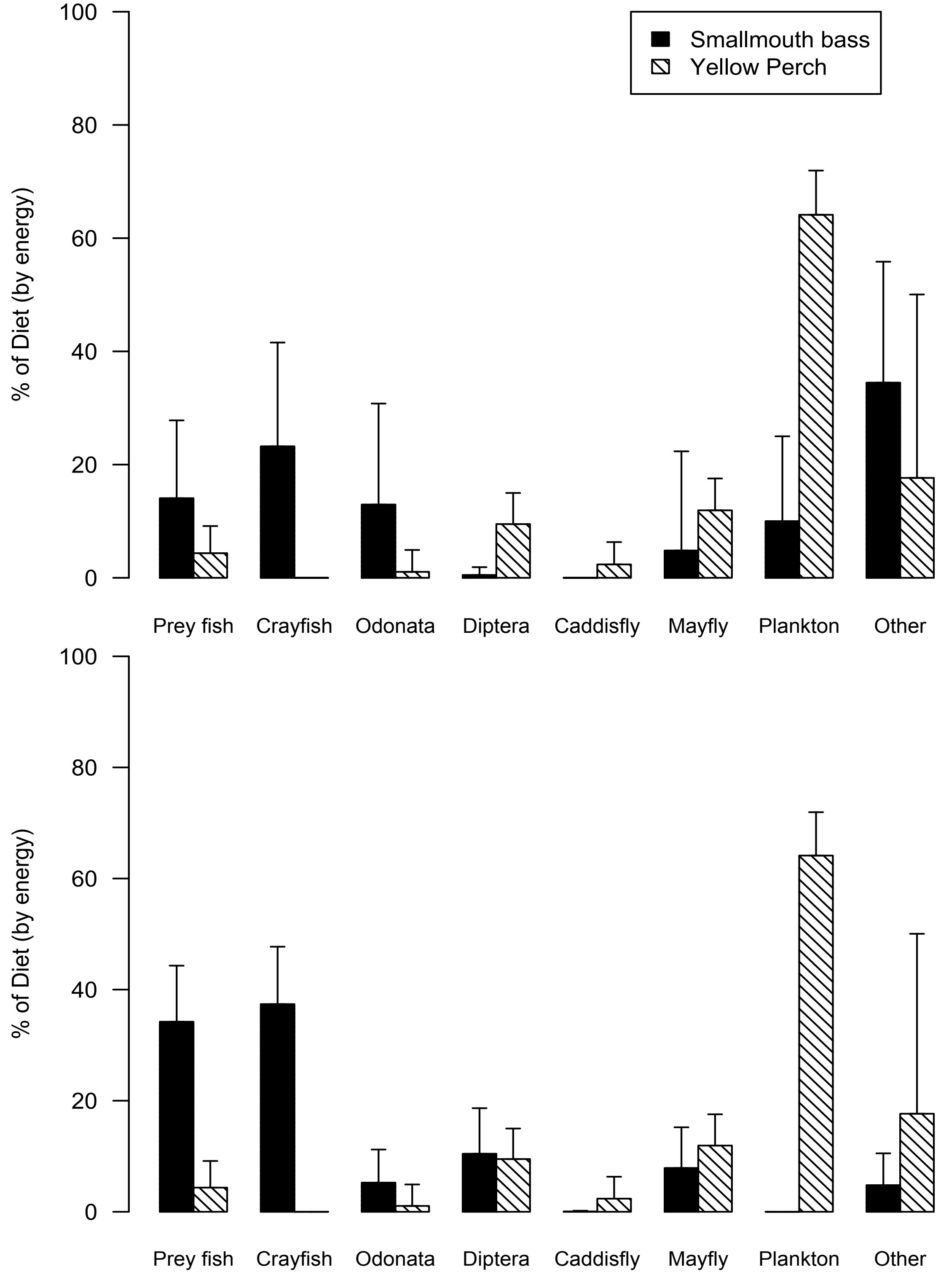

Figure 22. Percent contribution (%E_i) of the primary prey items found in the diet of SMB (grey) and yellow perch (black) for (a) small fish (<200mm) and (b) large fish (>200mm) from Shawnigan Lake during the 2011 and 2012 sampling seasons. Error bars represent 95% CI using bootstrap method. Schoener's index of dietary overlap was α=0.245 and α=0.237, for (a,b) respectively.

Smaller SMB and YP (<200mm) showed slightly higher trophic overlap (α=0.245) compared to the diet of large SMB (α=0.237) due to greater overlap between smaller prey items such as mayflies and plankton found in the diet of juvenile SMB (Table 10 and Figure 22). Prey species in the "other" category included aquatic ants (*formicidae*) in the SMB diet and snail/clams (*gastropoda*) in the YP diet (Figure 22). Across all size classes of SMB and KO from Shawnigan Lake there was no trophic overlap, with an overlap index of α=0.01 (Table 10). Plankton, specifically *daphnia sp.* made up E_i =99% of the KO diet but was not present in the diet of SMB from Shawnigan Lake.

Signal crayfish

Do SMB selectively forage for signal crayfish? And if so, does the presence of signal crayfish alter trophic mediated impacts of SMB on other species?

The signal crayfish relative abundance levels (crayfish/m^2) across the three Vancouver Island study lakes parallels the crayfish percent contribution levels (%E_i) in the SMB diet (Figure 23); with the highest levels observed in Shawnigan Lake (E_i=33.5% and 0.066 crayfish/m^2) and the lowest levels observed in Cusheon Lake (E_i=0.6% and 0.001 crayfish/m^2). Crayfish percent contribution in the SMB diet was positively correlated with crayfish relative abundance estimates but was not statistically significant (Spearman rank correlation; P=0.333). Crayfish provide greater energetic value per individual consumed (5336J) than prey fish did (3278J) towards the overall SMB diet (Table 8). In Cusheon Lake, when crayfish relative abundance levels were very low (E_i=0.6%), dragonfly (odonate) larvae and threespine stickleback percent contribution levels in the SMB diet were significantly higher (Figure 23; E_i=49.1% and E_i=16.4%, respectively).

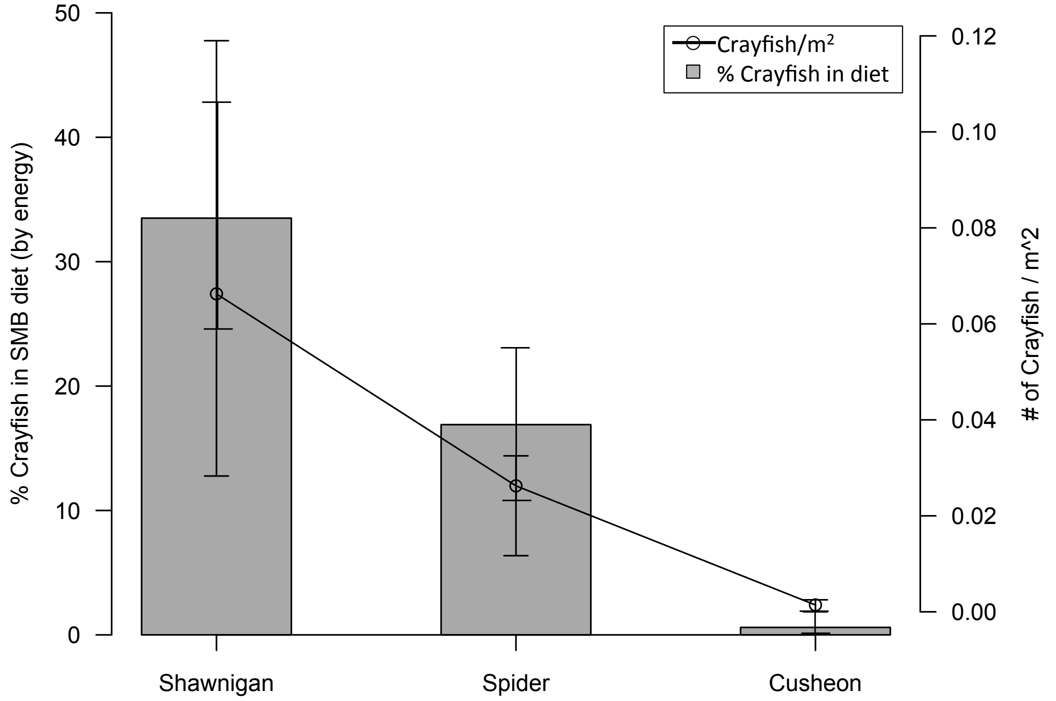

Figure 23. Signal crayfish percent contribution (%E_i) levels in the SMB diet for 2011 and 2012 (bar plot and primary y-axis) compared to signal crayfish relative abundance estimates (line plot and secondary y-axis) for (a) Shawnigan, (b) Cusheon and (c) Spider Lakes on Vancouver Island from July to September 2012. Error bars represent 95% CI using bootstrap method

SMB salmonid predation in BC

What capacity do SMB have to take advantage of seasonal pulses of forage?

Temperature levels (7.6±0.32°C) and CPUE (0 SMB/net) from late April 2012 sampling in the Okanagan lakes (Osoyoos and Skaha Lakes) revealed that SMB were not active in the littoral zone (<6m) at that time. Yellow perch captured (n=34) during gillnet sampling at the river mouth into Osoyoos Lake were however predating on Kokanee fry, which made up E_i=82% of the yellow perch's diet (Figure 24).

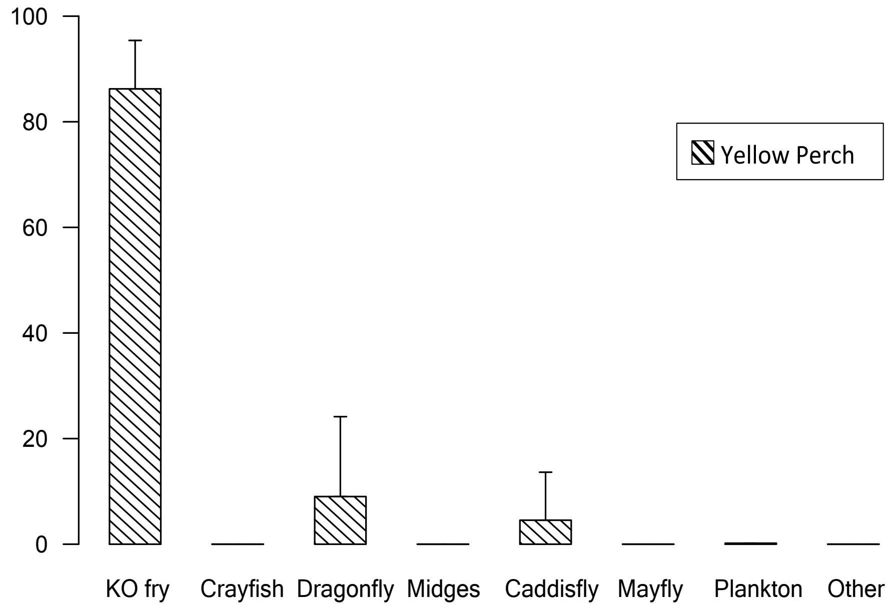

Figure 24. Trophic profile of the primary prey items (%E_i) in the diet of yellow perch (n=34) from Osoyoos Lake in the Okanagan during April 2012 sampling. Error bars represent 95% CI using bootstrap method.

SMB and BC stocking program

What capacity do SMB have to take advantage of pulses of forage, such as stocking events?

During the field stocking experiment in September 2011, a total of 175 (mean L=184mm±67.27mm) and 109 SMB (mean L=275mm±89.93mm) were captured from Spider and Shawnigan Lakes, respectively (Table 11 and Figure 25). Across all time intervals a total of 144 SMB from Spider Lake and 79 SMB from Shawnigan Lake had food in their stomachs, of which 32 and 17 SMB stomachs contained trout fry in them (Table 11). A total of 77 trout fry were found in the 32 SMB stomachs from Spider Lake and 48 trout fry from the 17 SMB stomachs from Shawnigan Lake for a total of 125 trout fry consumed across all the SMB sampled during the post-stocking time intervals (Table 11). Principal component analysis (PCA) revealed that study lake did not contribute significantly to the overall variance in the data (<%1 cumulative variance) therefore data from Spider and Shawnigan Lakes were pooled for the remainder of the analysis.

Table 11. Sample size of SMB captured during the field stocking experiment including the total number of SMB with full stomachs, the number of SMB stomachs that contained trout fry, and total number of trout fry present in the SMB stomachs.

Lake	Time Interval	SMB sample size	SMB with full stomachs	SMB with trout fry	# of trout fry in SMB stomachs
Spider	**Pre-stocking**	25	21	0	0
	12hrs	75	62	25	67
	24hrs	12	7	4	6
	36hrs	58	49	3	4
	Post-stocking	5	5	0	0
	Total	**175**	**144**	**32**	**77**
Shawnigan	**Pre-stocking**	27	23	0	0
	12hrs	12	9	7	19
	24hrs	25	16	6	24
	36hrs	27	15	4	5
	Post-stocking	18	16	0	0
	Total	**109**	**79**	**17**	**48**

There was a strong positive correlation (ρ=0.651, P<0.01) between the amount (g) of trout fry consumed and the size of SMB (g) (Figure 25), which is likely attributed to larger adult SMB being capable of consuming a greater quantity of prey relative to smaller juvenile SMB. The total number of trout fry consumed was greatest at the 12hr. time interval (n=86 trout fry), however individual SMB were actually consuming more trout fry (3 trout fry/SMB) during the 24hr. sampling interval (Figure 26b). The observed peak in trout fry per SMB at the 24hr sampling interval is likely an indication that the SMB had reached their satiation point.

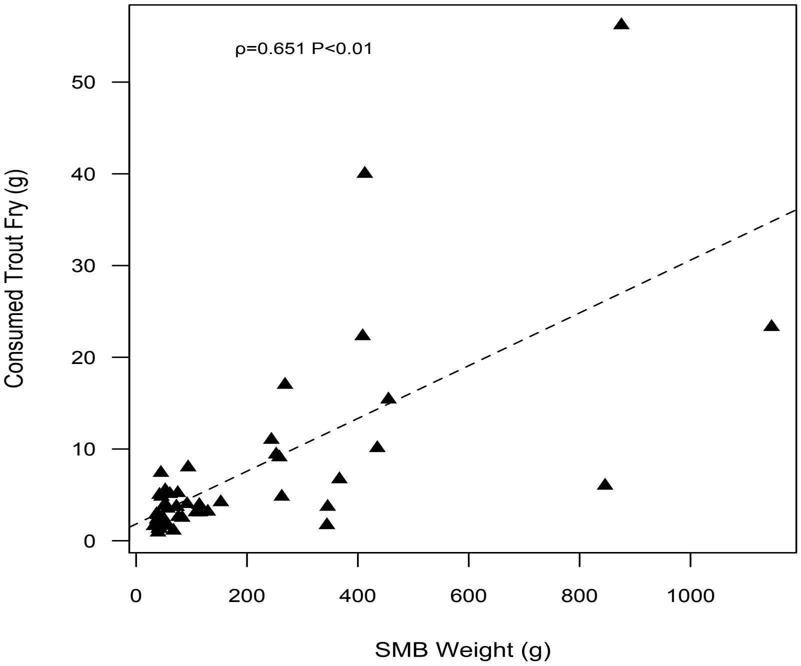

Figure 25. Weight (g) of SMB (predator) and weight of the trout fry (prey) consumed across all the post-stocking time intervals (12, 24 and 36hrs.) for both Shawnigan and Spider Lakes in September 2011.

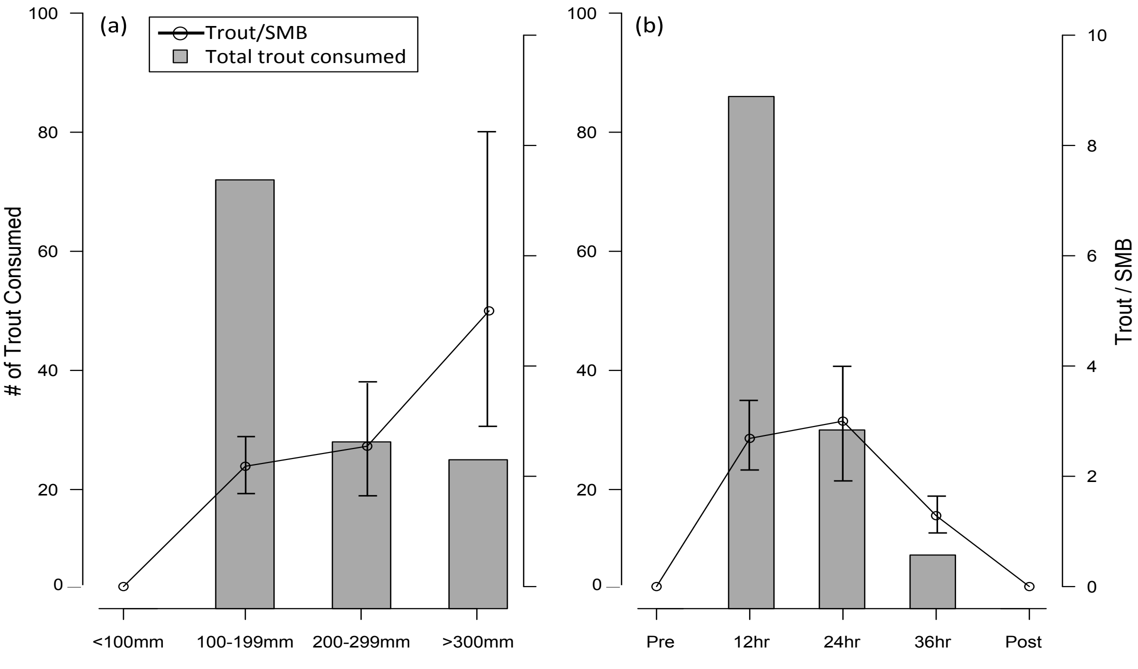

Figure 26. Total number of trout fry consumed (primary y-axis) by SMB and the total number of trout consumed per SMB (secondary y-axis) by (a) size classes of SMB and (b) time intervals for both Spider and Shawnigan Lakes combined. Error bars represent 95% CI using bootstrap method.

When trout consumption levels peaked at the 24hr. time interval crayfish percent contribution levels in the SMB diet were lowest across all the time intervals (Figure 27c; E_i =11.4%). As trout fry levels in the SMB diet decreased at the 36hr. time interval, crayfish levels began to increase and return to pre-stocking levels (E_i =28.4%) by the post-stocking time interval (E_i = 28.1%).

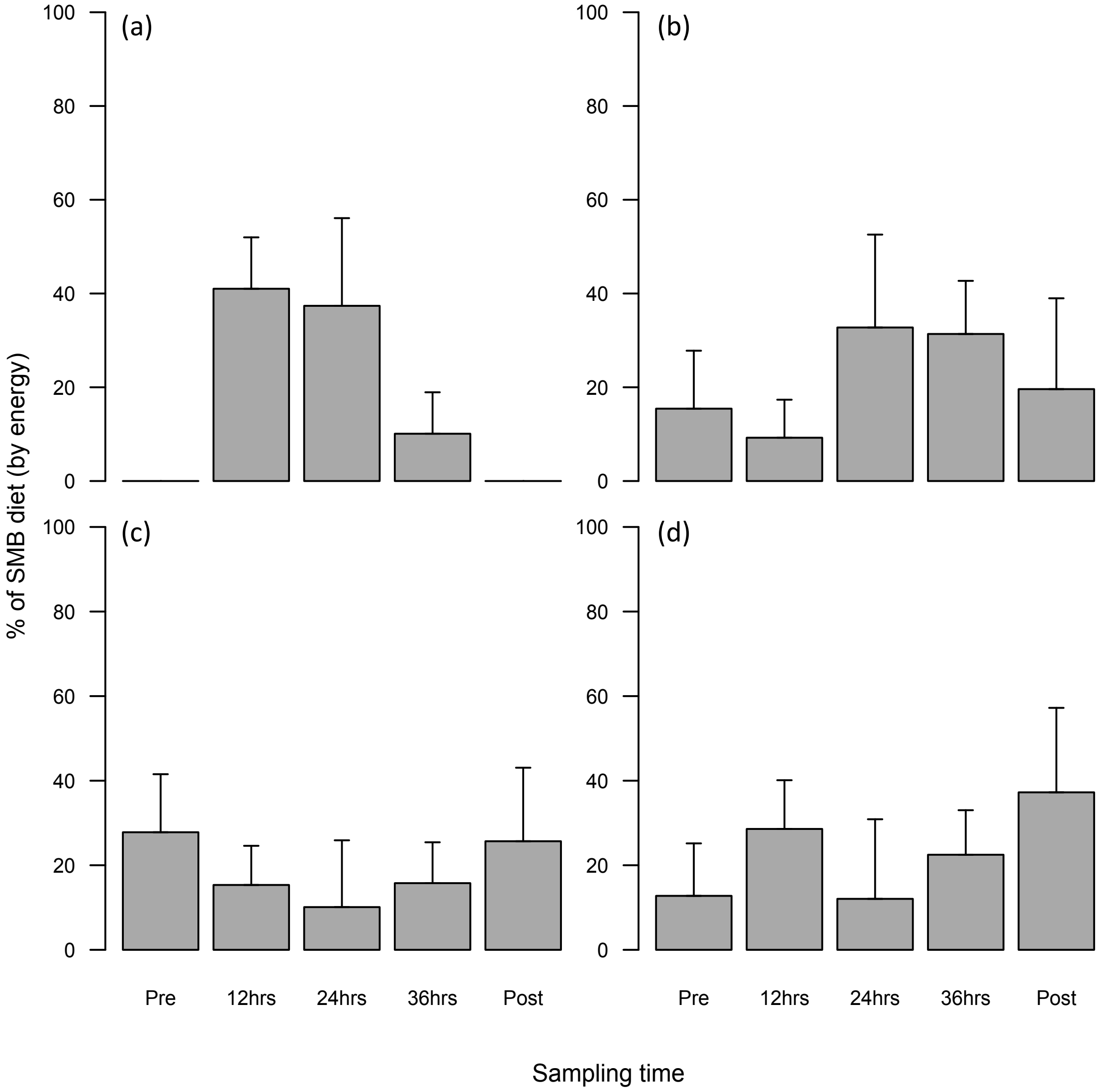

Figure 27. Trophic profile of the percent contribution (%E_i) of (a) hatchery trout fry (b) prey fish (c) crayfish and (d) dipterans in the diet of SMB across each time interval during the field stocking experiment. Error bars represent 95% CI using bootstrap method.

The total energetic value of the average SMB stomach was significantly higher (Figure 28; 183.8±27.34(J/g) vs. 17.58±3.91(J/g)) at the 12hr. time interval compared to the pre-stocking baseline levels (Mann Whitney; W=2567, P<0.01). The total energetic value of prey in the SMB stomachs from the pre and post-stocking time intervals (17.58±3.91(J/g) and 7.99±2.75(J/g)) were on the order of ten times lower than for the 12hr. and 24hr. time intervals (183.8±27.34(J/g) and 121.2±23.14(J/g)). This data illustrates that SMB have adapted by significantly increasing their consumption levels to maximize on pulses of forage (hatchery trout fry) following a stocking event (Figure 28).

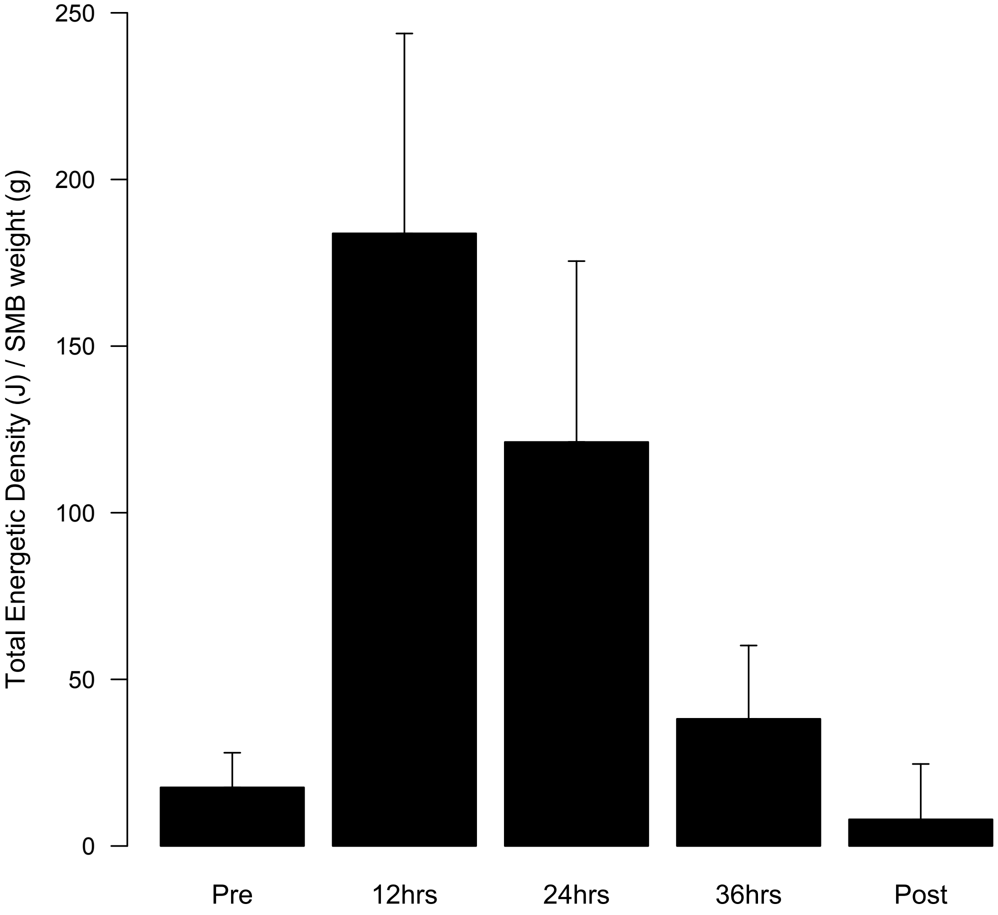

Figure 28. Mean total energetic density of stomach contents in each individual SMB (J/g) for each sampling interval during the field stocking experiment. Error bars represent 95% CI using bootstrap method.

The theoretical total number of SMB required to consume 20,000 trout fry within a 36 hr. period was calculated for each of the three size classes of SMB consuming trout fry (Table 12). It would take a total of 5906 SMB between 100-199mm in fork length, 4548 SMB between 200-299mm in fork length and 2833 SMB >300mm in fork length to consume 20,000 trout fry within a 36hr period. Due to differences in the consumption capacity of juvenile and adult SMB, it would require twice as many juvenile SMB as it would adult SMB to consume 20,000 trout fry within a 36hr. time period (Table 12).

Table 12. The theoretical total number of SMB in each size class (100-199mm, 200-299mm, and >300mm) required to consume a total of 20,000 hatchery trout fry within a 36hr. time period.

SMB size class	**Avg time (hrs) to digest 1 trout**	**# of trout stocked**	**# of trout consumed per SMB in 36 hrs**	**Total # of SMB**
100-199mm	10.63	20,000	3	5906
200-299mm	8.18	20,000	4	4548
>300mm	5.1	20,000	7	2833

Discussion

SMB Habitat

SMB CPUE by habitat was highest for rocky substrate, submerged logs and bare substrate within the Vancouver Island study lakes, which is consistent with studies of SMB in other regions (Edwards et al. 1983, Pflug and Pauley 1984, Armour 1993, Etnier and Starnes 1993, Downen 1999). Within the individual study lakes SMB CPUE was negatively correlated with sampling depth (m) and is consistent with SMB primarily residing in the warmer littoral zone (<6m depth) of lakes during the summer months (Scott and Crossman 1973). Many lakes supporting SMB populations in both the Cariboo region (e.g. Beaver and Opheim Lakes) and on Vancouver Island (e.g. Spider Lake) have large percent littoral zones (>50%; FISS 2013). The results from this research demonstrate that lakes with large percent littoral zones likely provide increased suitable habitat for supporting non-native SMB populations in British Columbia.

SMB growth

Temperature data revealed a shortened SMB growing season (degree days >10°C) of 62 fewer days for SMB at their northern limit in the Cariboo region relative to the southern Vancouver Island study lakes. SMB length at age was significantly different between the northern Cariboo (length/age=130.8±3.0, n=57) and southern Vancouver Island study lakes (length/age=56.6±1.26, n=302) therefore we can reject the null hypothesis. However, contrary to what we might expect SMB length at age was significantly larger for SMB from the Cariboo region compared to SMB from Vancouver Island, despite the shortened growing season. These results are however consistent with a common adaptation for SMB populations at the northern limit of their range to reach larger sizes at age (Ultsch 1989, Shuter and Post 1990, Dunlop and Shuter 2006).

Increased size at age provides juvenile SMB going into their first winter with greater energy reserves in order to improve their chance of surviving a longer starvation period (Ultsch 1989, Shuter and Post 1990, Dunlop and Shuter 2006). The observed growth curves from the Cariboo region illustrates the importance of sufficient juvenile growth in the successful establishment of SMB populations at the northern limit of their range (Shuter et al. 1980, Shuter et al. 1983, Jackson and Mandrak 2002, Dunlop and Shuter 2006).

The increased size at age for SMB at their northern limit could be linked with higher primary productivity levels (chlorophyll a) in Beaver Lake relative to the Vancouver Island lakes based on data from 2010 and 2011 (FISS 2013). Studies have reported that increased food availability for SMB populations at the northern limit of their range may outweigh the benefits from warmer waters experienced in southern latitudes (Keating 1970, Shuter and Post 1990). Introduced SMB populations in Nova Scotia display slower growth rates and mature later and at larger sizes (McNeil 1995) relative to the average North American introduced SMB populations assessed by Beamsderfer and North (1996). The slower growth rates for SMB populations in Nova Scotia are associated with the combination of a shorter growing season and unproductive lakes (Alexander et al. 1986, McNeil 1995) further emphasizing the importance of high productivity in lakes at the northern limit of SMB.

Observed differences in SMB size at age between the Vancouver Island study lakes and Beaver Lake in the Cariboo could also be linked with differences in the date of SMB first establishment in the lakes. It is possible that the more recently introduced SMB populations in the Cariboo may not have adapted to increases or decreases in prey availability and/or competition with other fish species in the newer environment (Dunlop and Shuter 2006). In more recently established non-native SMB populations the native predator fish species community may not recognize SMB nests and fry as a prey; leading to increased survival of juvenile SMB (Dunlop and Shuter 2006).

It is important to take into consideration that the SMB growth curves are from 2012 while productivity data is from 2010 and 2011. Unfortunately, prey abundance and lake productivity levels were not measured at the time of SMB sampling in 2012, therefore productivity levels cannot be directly compared to the growth curves for 2012. Productivity levels were, however, consistently higher in the Cariboo study lake compared to Vancouver Island study lakes across both 2010 and 2011 suggesting a similar trend occurred in 2012.

Trophic Profile

Within the Vancouver Island study lakes the prey species composition of the SMB diet did not differ significantly between months or years, therefore we could not reject the null hypothesis. It is important to take into consideration that sample size was very small for the early summer months (May and June) and sampling only took place across a two-year period. This data provides a snapshot of the diet of SMB across a temporal gradient, however a larger data set spanning several years would be required for a more thorough assessment of temporal changes in the SMB diet. In addition, stable isotope analysis could be used in the future to assess long-term trends in the trophic profile of the SMB diet (Vander Zanden et al. 1999b).

The prey species composition of the SMB diet did not have a biologically meaningful difference between individual lakes or regions and we could not reject the null hypothesis. The greater within-region similarity than between-regions similarity in the SMB diet is likely due to localized similarities in the prey species community composition. The SMB diet did show significantly higher overall prey species diversity in the Cariboo region relative to the Vancouver Island and Okanagan regions. The higher prey diversity in the SMB diet for Beaver Lake in the Cariboo was likely driven by the juvenile SMB primarily feeding on smaller prey items such as mayflies, plankton and other aquatic insects such as beetle larvae. The results from Beaver Lake are consistent with SMB undergoing an ontogenetic shift from juveniles feeding on smaller prey (e.g. plankton) to adults feeding on larger prey (e.g. fish; Lachner 1950, Keating 1970, Livingstone and Rabeni 1989).

The prey species abundance was not measured in the study lakes and the regional similarities cannot be directly linked to the prey species community composition and abundance. Future research that could really build on this project's data would be to quantify both the SMB diet and prey species abundance levels to assess if percent contributions of prey in the SMB diet reflects prey abundance and availability.

Trophic Overlap

Comparisons between the trophic profiles of SMB and other fish species in the Vancouver Island study lakes revealed no biologically meaningful trophic overlap *(*$\alpha \leq 0.6$) and we could not reject the null hypothesis. The diet of CCT in Cusheon Lake showed very little trophic overlap with the diet of SMB and was dominated by cladocera *(Daphnia spp.)* for both juveniles and adult CCT, despite CCT being a known piscivorous species (Hazzard and Madsen 1933, Nielsen and Lentsch 1988, Reimchen

1990). Weston Lake (SMB free) provides a snapshot of a much more energetically rich diet for CCT that includes threespine stickleback when SMB are not present.

In Cusheon Lake SMB predation on threespine stickleback may have reduced their abundance to levels that precludes CCT from feeding on them. In several lakes on Vancouver Island supporting non-native SMB populations there have been reported declines in threespine stickleback abundance with SMB predation assumed to be the primary cause (McPhail 2007a). In lakes throughout North America SMB have been found to heavily predate on small-bodied fish and drastically reduce their abundance (Robinson and Tonn 1989, Findlay et al. 2000, Weidel et al. 2000, MacRae and Jackson 2001, Jackson and Mandrak 2002). Prey abundance estimates were not measured in Weston and Cusheon Lakes therefore threespine stickleback abundance levels could not be compared between the two lakes.

While not significant, the diets of SMB and RB from Spider Lake showed the greatest degree of trophic overlap across all the interspecific trophic profile comparisons. Correspondingly, gillnet catch data from Spider Lake showed the greatest degree of spatial overlap between SMB and trout (RB or CT) relative to Shawnigan and Cusheon Lakes. RB are a cold-water species and in the Vancouver Island systems trout spend most of the warmer summer months in the deeper and colder depths and then rise to the cooler surface waters during the winter (Scott and Crossman 1973). The observed spatial and trophic overlap between SMB and RB is likely attributed to the large percent littoral zone of Spider Lake (68%; FISS 2013).

In Spider Lake, the greatest trophic overlap occurred between smaller sized SMB and RB feeding on odonates and dipterans, but was not biologically significant ($\alpha \leq 0.6$).

Both RB and juvenile SMB are known to typically feed on smaller prey such as odonates and dipterans (Scott and Crossman 1973), conversely adult SMB typically switch to primarily feeding on larger prey such as prey fish and crayfish when they are available (Lachner 1950, Keating 1970, Livingstone and Rabeni 1989). When larger and more energetically valuable prey such as crayfish are available for adult SMB to feed on this likely contributes to the decrease in the degree of trophic overlap between larger sized SMB and RB.

Interspecific trophic profile comparisons between SMB and YP from Shawnigan Lake revealed no significant trophic overlap between SMB and YP. The degree of trophic overlap did not differ between small versus large sized SMB and YP; which contradicts previous studies that have reported the greatest dietary overlap occurs between juvenile SMB and YP (Johnson 1983). The lack of significant trophic overlap between juvenile SMB and YP could be linked with prey species availability in Shawnigan Lake. Across all the three Vancouver Island study lakes crayfish levels in the SMB diet were highest in Shawnigan Lake and made up 33.5% of the juvenile SMB diet. The availability of crayfish for SMB to predate on in Shawnigan Lake may have reduced the degree of trophic overlap between juvenile SMB and YP. In order to further assess trophic overlap between SMB and YP, prey species abundance estimates are required to establish if levels in the diet reflects prey abundance in Shawnigan Lake.

Signal Crayfish

When crayfish are available in Vancouver Island lakes they serve as an important prey resource for SMB. Conversely when crayfish relative abundance levels were very low (e.g. Cusheon Lake) odonate larvae serve as important prey for SMB. Crayfish percent contribution in the SMB diet was positively correlated with crayfish relative abundance estimates but was not statistically significant and we could not reject the null hypothesis. The sample size for crayfish relative abundance estimates was very small with only three study lakes therefore future research looking across a larger sample size is necessary. The very low relative abundance of signal crayfish in Cusheon Lake could be linked with habitat availability. Signal crayfish are primarily associated with rocky, bare or woody debris habitats and less associated vegetated habitat; which is dominant in Cusheon Lake (Downen 1999, Bondar et al. 2005). None of the three Vancouver Island study lakes contain additional predator fish species (native or introduced) that are known to feed on signal crayfish (FISS 2013), therefore reduced crayfish abundance due to predation by other fish species is not likely in Cusheon Lake.

Interestingly, crayfish were absent from the diet of SMB in the Okanagan lakes, despite having confirmed signal crayfish populations in the study lakes (Bondar et al. 2005). The lack of crayfish in the SMB diet for the Okanagan study lakes could be a result of prolonged SMB predation on crayfish causing a decrease in the crayfish abundance levels over time, which is consistent with many other studies that have linked the introduction of SMB with reductions in crayfish populations (Stein and Magnuson 1976, Mather and Stein 1993, Somers and Green 1993).

In addition, the Okanagan study lakes have much higher fish species diversity relative to the Vancouver Island study lakes (FISS 2013) and SMB may have targeted fish because they were more abundant. The optimal foraging theory states that prey density is closely linked with determining the predator's prey choice in order to maximize both feeding efficiency and energy gain (Sih and Christensen 2001, Mittelback

2012). Without taking into account the energetic costs of time spent foraging and prey handling time, crayfish provided higher energetic value per gram consumed than prey fish in the SMB diet. The lack of crayfish in SMB diet in the Okanagan study lakes could be linked with SMB maximizing feeding efficiency. SMB may have consumed more of the lower-value prey fish due to a combination of (1) low abundance levels of the higher value crayfish and (2) high abundance of prey fish in the Okanagan study lakes. These are only hypothesis and cannot be confirmed with the data collected from this project as fish and crayfish abundance estimates were not measured for the Okanagan study lakes at the time of sampling.

Quantitative diet analysis of SMB populations throughout BC revealed that when available crayfish serve as an important resource. However in the Cariboo region where crayfish are not available SMB have adapted to feeding on other smaller prey resources. The shift in the SMB diet to smaller prey could potentially lead to increased trophic overlap between SMB and other predator fish species in the Cariboo region. Other fish species present in Beaver Lake, that are known to feed on smaller prey items (i.e. dipterans, mayflies and plankton) includes; lake whitefish (*Coregonus clupeaformis*), longnose and largescale suckers (*Catostomus spp*.), northern pikeminnow (*Ptychocheilus oregonensis*), redside shiner (*Richardsonius balteatus*) and rainbow trout (*Oncorhynchus mykiss*) (Johannes and Larkin 1961, Scott and Crossman 1973, Dauble 1986, FISS 2013). On going monitoring of SMB in Beaver Lake will be important in order assess the degree of trophic overlap between SMB and the other fish species, and how this may impact the surrounding freshwater community.

SMB salmon predation

Spring samplings in the Okanagan study lakes (Skaha and Osoyoos Lakes) revealed that SMB did not spatially or temporally overlap with kokanee or sockeye fry in the Okanagan study lakes (SMB CPUE=0). At the time of sampling surface water temperatures were around 9-10°C (Environment Canada 2013) and well below the minimum temperature threshold of 15°C when SMB typically become active in spring following the winter starvation period (Shuter et al. 1980). YP; a piscivorous non-native species introduced into 59 lakes in BC (Runicman and Leaf 2009) were captured during gillnet sampling in Osoyoos Lake and were predating on kokanee fry. The minimum temperature threshold for spawning and growth in YP is 8°C, which is 7°C lower than the minimum temperature threshold of SMB (Shuter and Post 1990). Additional research is needed in order to further assess the degree of spatial and temporal overlap between YP and salmonids during the spring runs in the Okanagan Lakes.

SMB and BC stocking program

The results from the field stocking experiment highlights the ability for SMB to significantly increase the amount (J/g) of prey they are consuming immediately following (twelve to twenty four hours) a pulse of forage (stocking event). The total energetic value of prey consumed by SMB was significantly higher at the 12hr. interval relative to the pre-stocking sampling; therefore, the null hypothesis was rejected. The observed peak in trout consumed per SMB at the 24hr. sampling interval is likely a reflection of SMB reaching their maximum satiation and consumption rates. The rapid decrease in trout fry consumption by SMB at the 36hr. sampling interval is likely associated with decreases in trout fry abundance. A decrease in trout fry abundance could be linked with; (1) SMB predation levels on trout fry and (2) dispersal of trout fry into the deeper and colder waters (Lee et al. 2006). The total energetic value of all prey in the average SMB stomach was significantly lower for the post-stocking sampling compared to the pre-stocking sampling, suggesting that the SMB diet had returned to the pre-stocking baseline levels.

Despite the large pulse of available trout fry following the stocking event, SMB were still feeding on signal crayfish across the entire duration of the field stocking experiment. This could be associated with crayfish providing higher energetic value in the SMB diet compared to prey fish, however time spend foraging and prey handling time was not taken into account when looking at the energetic value of crayfish and fish. The results from the field stocking experiment show preliminary data of how a pulse of forage following a stocking event may influence a predator's (i.e. SMB) prey choice in order to maximize feeding efficiency (i.e. optimal diet; Schoener 1971, Emlen 1973, Maynard Smith 1974, Pulliman 1974, Werner and Hall 1974). A more thorough assessment of the optimal foraging diet of SMB would include looking at both prey abundance levels and handling times of the prey species in the SMB diet.

It is important to take into consideration that the field stocking experiment took place in mid-September when maximum surface water temperatures peaked around 20°C. When hatchery trout fry are released into the warmer surface waters during a summer stocking event they will rapidly disperse into deeper and colder depths (Lee et al. 2006) which reduces the window of time when SMB and trout fry overlap spatially in the littoral zone (Lee et al. 2006). The results from this experiment highlights the importance of the timing and location of stocking events in order to mitigate predation on trout fry when they are stocked into BC lakes containing SMB.

The results from this field stocking experiment supports current hypotheses that reduced survival of hatchery trout fry in SMB lakes on Vancouver Island is due to predation by SMB. The reduced survival of trout fry has forced stocking programs to switch to stocking lakes containing SMB with larger catchable sized trout, which comes at an increased cost (FFSBC 2013). In 2012, approximately 146,100 catchable sized rainbow trout were stocked into 17 lakes with confirmed introduced SMB populations on Vancouver Island (FFSBC 2013). Based on very preliminary data provided by FFSBC (Melinda Barnes and Ginny Acheson 2013) the approximate cost from production to release of hatchery rainbow trout is $1.00 per trout fry and $5.00 per catchable sized trout. This amounts to an increased cost of $4 per trout to stock catchable size trout. The estimated cost associated with hatchery programs switching to stocking SMB lakes on Vancouver Island with larger catchable sized trout was around $584,480 for 2012 (Melinda Barnes and Ginny Acheson 2013). These projected values illustrate the increased costs associated with stocking larger versus smaller hatchery rainbow trout and should be taken into consideration for provincial policy planning and management of SMB within BC.

The results from this research suggest that larger lakes with increased primary productivity and high percent littoral zone are important characteristics of lakes at the northern limit of SMB within British Columbia. Lakes with preferred SMB habitats such as; submerged logs, rocky substrate and covered areas are more likely to support SMB at their northern limit. Additional research is necessary in order to determine the critical threshold for productivity levels and lake size below which SMB will no longer survive in northern parts of British Columbia. However, large/deep lakes with a small percent littoral zone and low primary productivity are less likely to support SMB at the northern limit of their range.

Conclusion

The results from interspecific trophic profile comparisons emphasize the role of lake morphology in determining the degree of spatial and trophic overlap between SMB and other fish species. Coupling prey abundance estimates and diet analysis in future research will be important for assessing if non-native SMB populations may be triggering shifts in the diets of other fish species (RB, CCT and YP).

As displayed in the field stocking experiment the opportunistic and plastic nature of the SMB diet allows them adapt and maximize their consumption during pulses of prey. This research provides the first quantitative data to support current hypotheses that SMB are predating on hatchery trout fry following a stocking event. In addition the field stocking experiment highlights the increased costs associated with stocking lakes with larger catchable sized trout due to SMB predation on hatchery trout fry and should be taken into consideration for provincial policy and planning.

Temperature levels in the Cariboo region do not appear to be limiting SMB growth despite being at the species global northern most limit. The results from this research show the critical importance of sufficient lake productivity in order for the successful establishment of SMB in more northern parts of BC. Important future research will be to couple the fine scale quantitative data from this research with larger scale provincial data in order to predict lakes at greatest risk of SMB establishment in northern parts of BC. This research provides the first quantitative data on the trophic profile and habitat characteristics of SMB in lakes throughout BC. These results serve as critical data to be taken into consideration for management of non-native SMB in lakes throughout BC, in particular at the northern limit of their distribution.

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Appendix

Sample site characteristics

Table 1A. Lake characteristics of SMB study lakes sampled in 2011 and 2012, data was obtained from the Ministry of Environment online database (FISS 2012).

Lake Name	Region	Surface Area (Ha)	Max Depth (m)	Number of Fish Species*	Fish Species Present
Osoyoos Lake	Okanagan	2299	63	14	Rainbow trout, Steelhead, Sockeye, Kokanee, Largemouth bass, Yellow perch, Black catfish, Pumpkinseed, Carp, Mountain whitefish, Northern pikeminnow, Lake Whitefish, Goldfish, Black crappie
Skaha Lake	Okanagan	2010	57	12	Rainbow trout, Chiselmounth, Sockeye, Kokanee, Burbot, Peamouth chub, Carp, Mountain whitefish, Northern pikeminnow, Lake Whitefish, Sculpin, Largescale sucker
Vaseux Lake	Okanagan	275	27	11	Rainbow trout, Sockeye, Kokanee, Largemouth bass, Largescale sucker, Northern pikeminnow, Peamouth chub, Yellow perch, Pumpkinseed, Mountain Whitefish, Carp
Beaver Lake	Cariboo	185	35	7	Rainbow trout, Bridgelip sucker, Mountain Whitefish, Redside shiner, Kokanee, Peamouth chub, Northern pikeminnow
Chambers Lake	Cariboo	111	29.6	7	Longnose Sucker, Northern Pikeminnow, Peamouth Chub, Redside Shiner, Whitefish (General), Kokanee, Rainbow trout,
Cusheon Lake	Vancouver Island	27	9	2	Cutthroat, Threespine stickleback
Shawnigan Lake	Vancouver Island	537	50	8	Rainbow trout, Brown catfish, Pumpkinseed, Cutthroat trout, Kokanee, Yellow perch, Dolly varden, Prickly sculpin
Spider Lake	Vancouver Island	58	13	3	Rainbow trout, Steelhead, Prickly sculpin

**Number of fish species does not include smallmouth bass.*

Table 2A. Lake characteristics of the three trout reference lakes (SMB free) on Vancouver Island that were sampled during the 2012 field season (FISS 2012).

Reference Lake	Smallmouth bass Lake	Surface Area (Ha)	Maximum Depth (m)	Number of Fish Species	Fish Species Present
Weston Lake	Cusheon Lake	18.5	12.2	3	Rainbow trout, Cutthroat trout, Threespine stickleback
Reginald	Spider Lake	32.3	27.9	1	Rainbow trout
Maple lake	Shawnigan Lake	28	12.8	1	Rainbow trout

Bathymetric maps

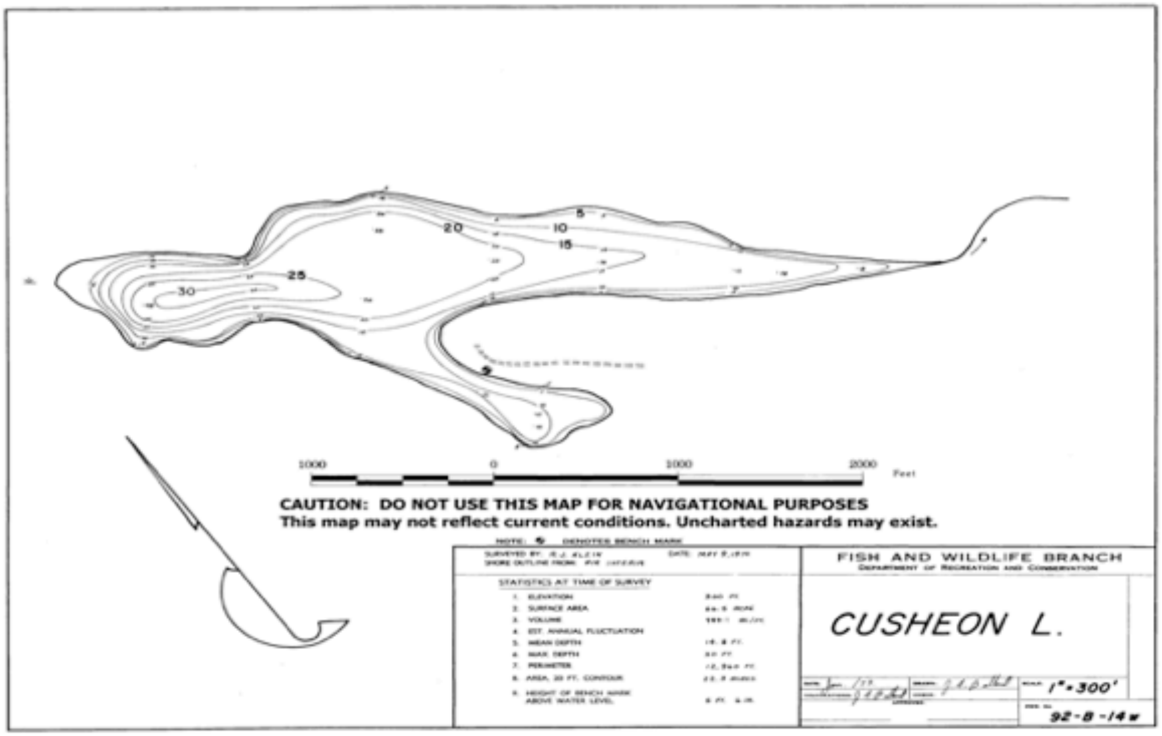

Figure 1A. Bathymetric map of Cusheon Lake (FISS 2012) located on Salt Spring Island in the southern Gulf Islands (48°48'57.57"N, 123°28'12.85"W).

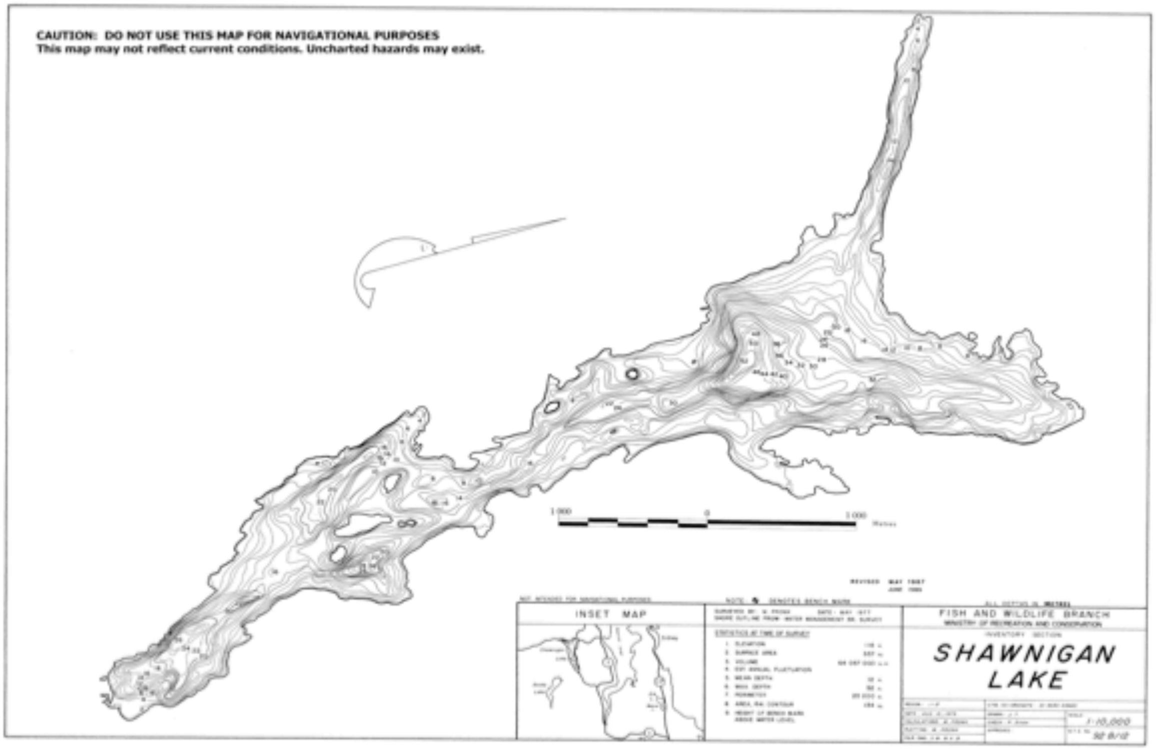

Figure 2A. Bathymetric map of Shawnigan Lake (FISS 2012) located on Southern Vancouver Island (48°38'8.67"N, 123°38'29.04"W).

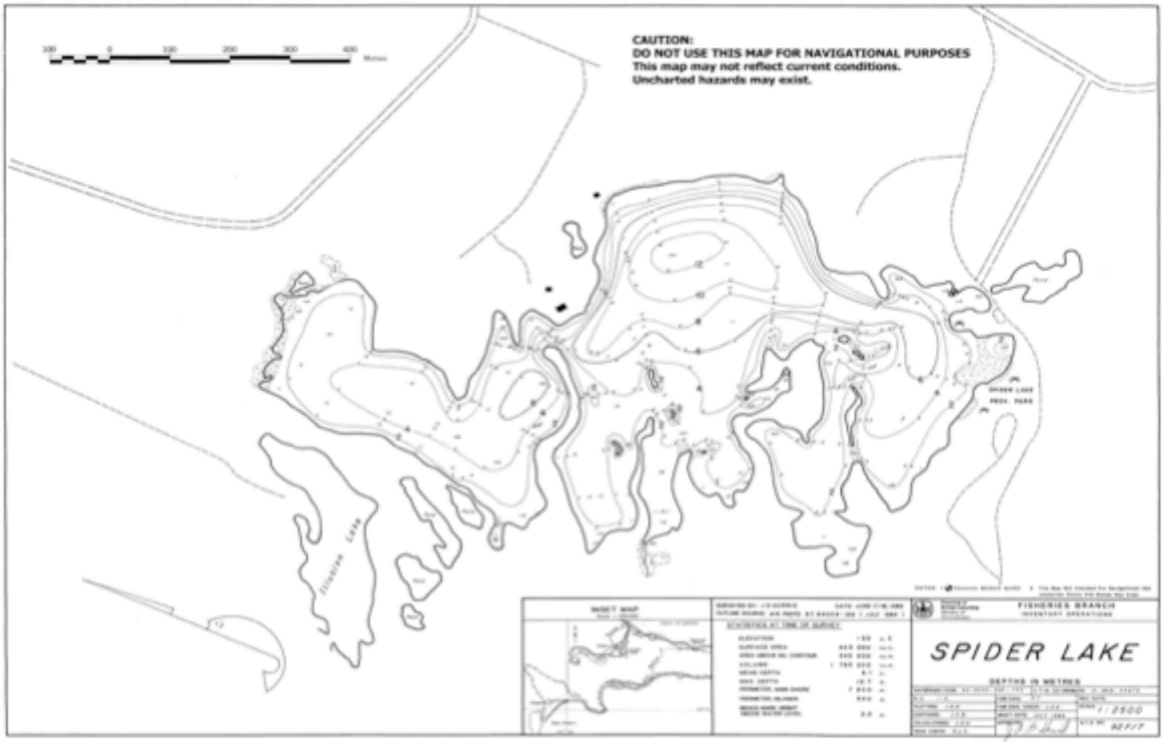

Figure 3A. Bathymetric map of Spider Lake (FISS 2012) located just north of Nanaimo on Vancouver Island (49°20'49.54"N, 124°37'25.18"W).

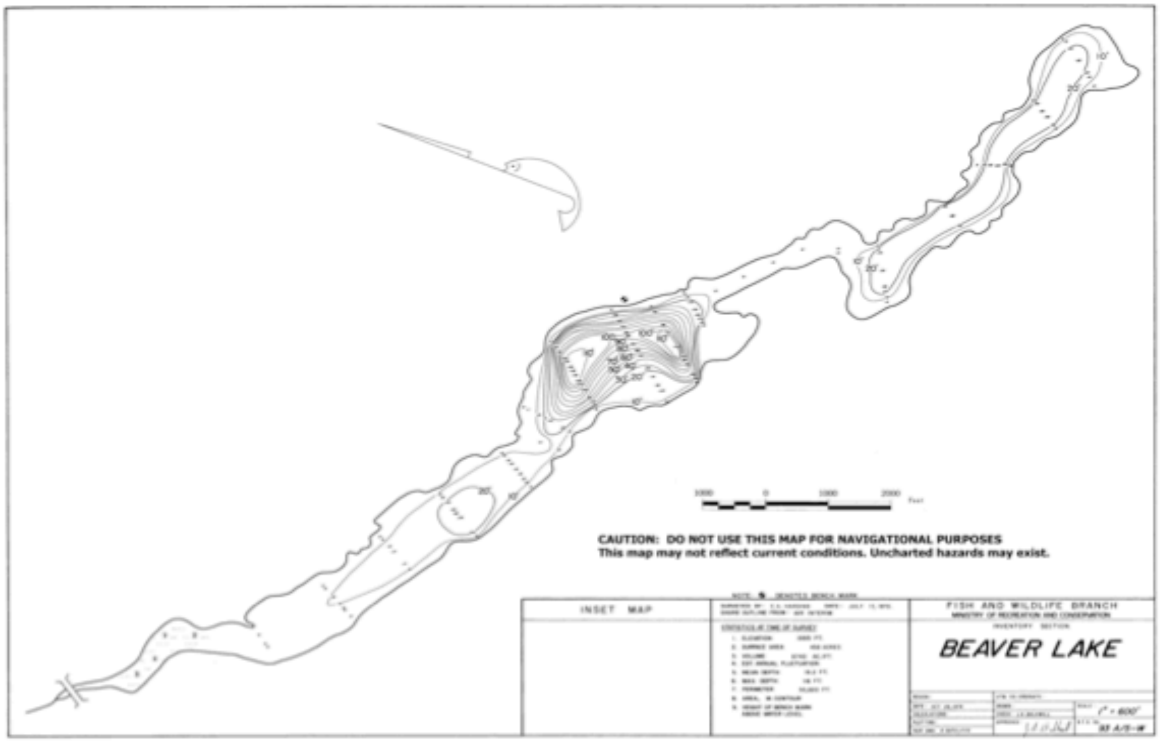

Figure 4A. Bathymetric map of Beaver Lake (FISS 2012) located in the Cariboo Region (52°27'28.12"N, 121°49'38.27"W).

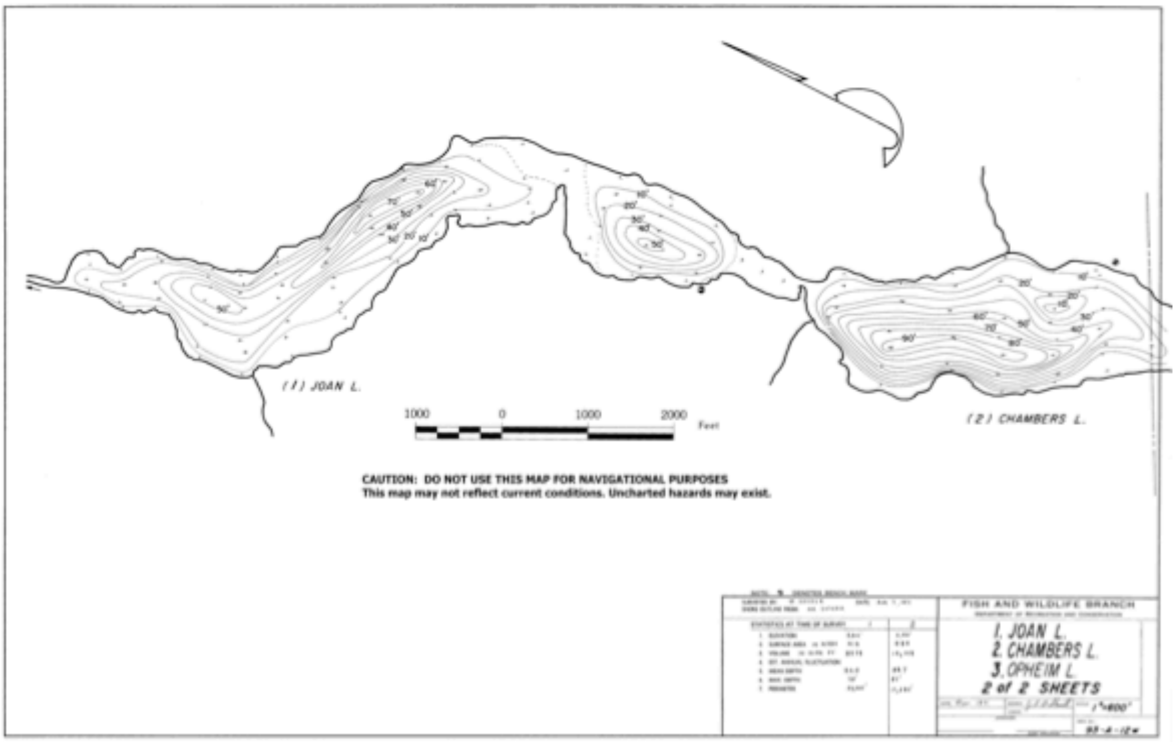

Figure 5A. Bathymetric map of Chambers Lake (FISS 2012) located in the Cariboo Region (52°32'48.11"N, 121°56'11.00"W).

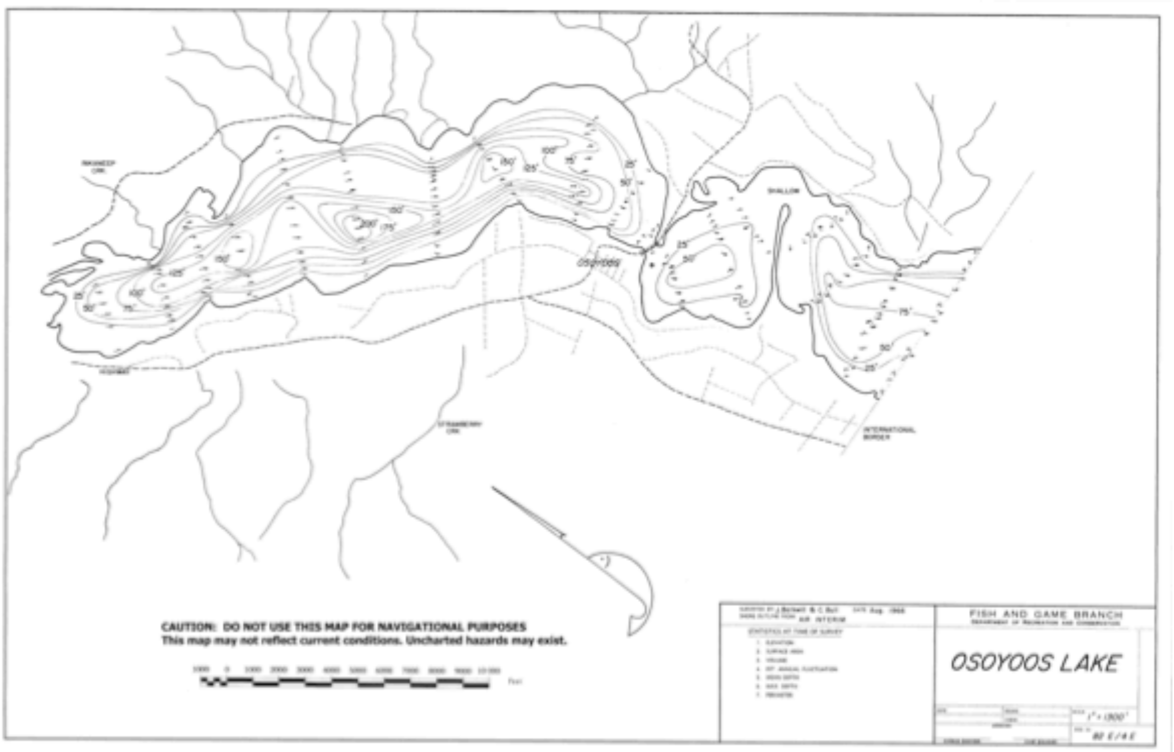

Figure 6A. Bathymetric map of Osoyoos Lake (FISS 2012) located in the Okanagan Region (49° 2'20.72"N, 119°27'30.81"W).

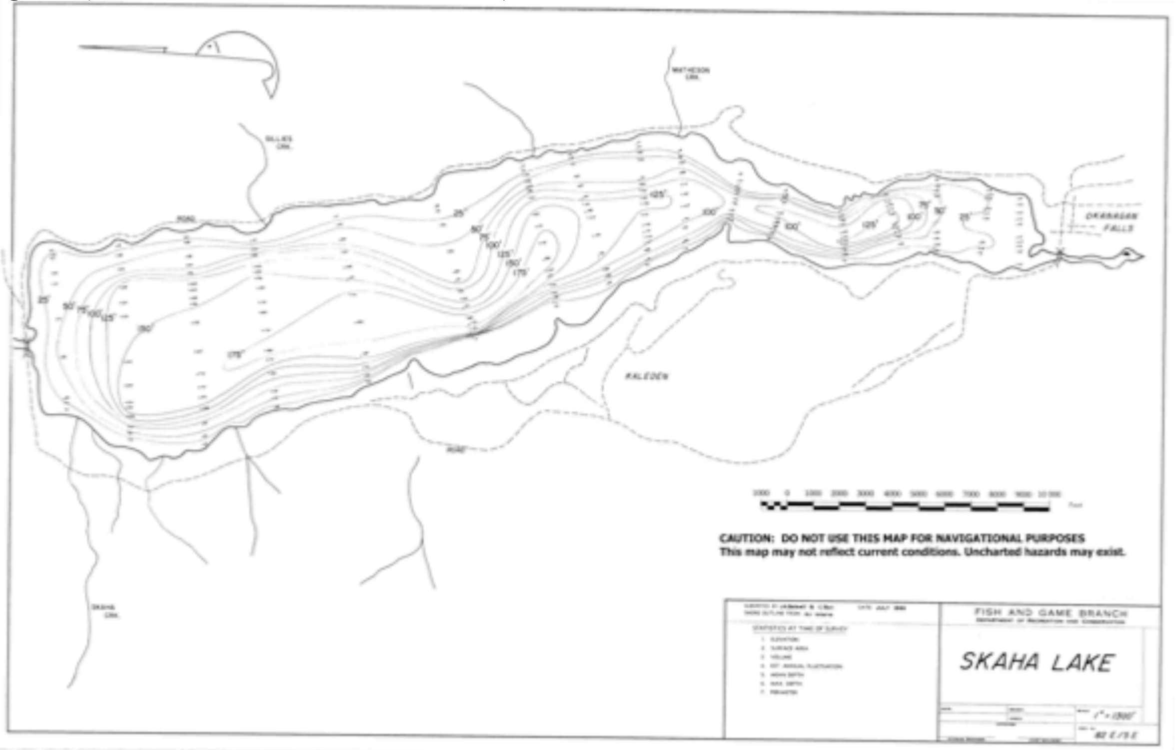

Figure 7A. Bathymetric map of Skaha Lake (FISS 2012) located in the Okanagan Region (49°25'17.44"N, 119°35'33.57"W).

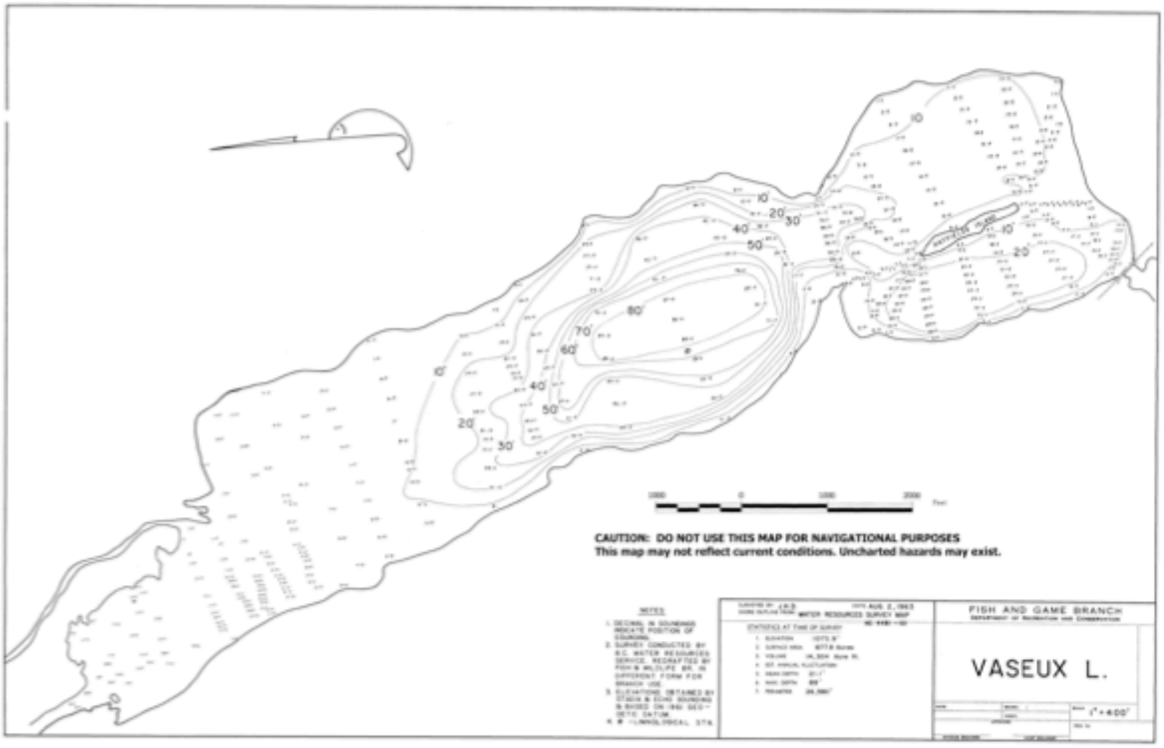

Figure 8A. Bathymetric map of Vaseux Lake (FISS 2012) the smallmouth bass sample site located in the Southern Okanagan Region (49°17'33.02"N, 119°31'52.71"W).

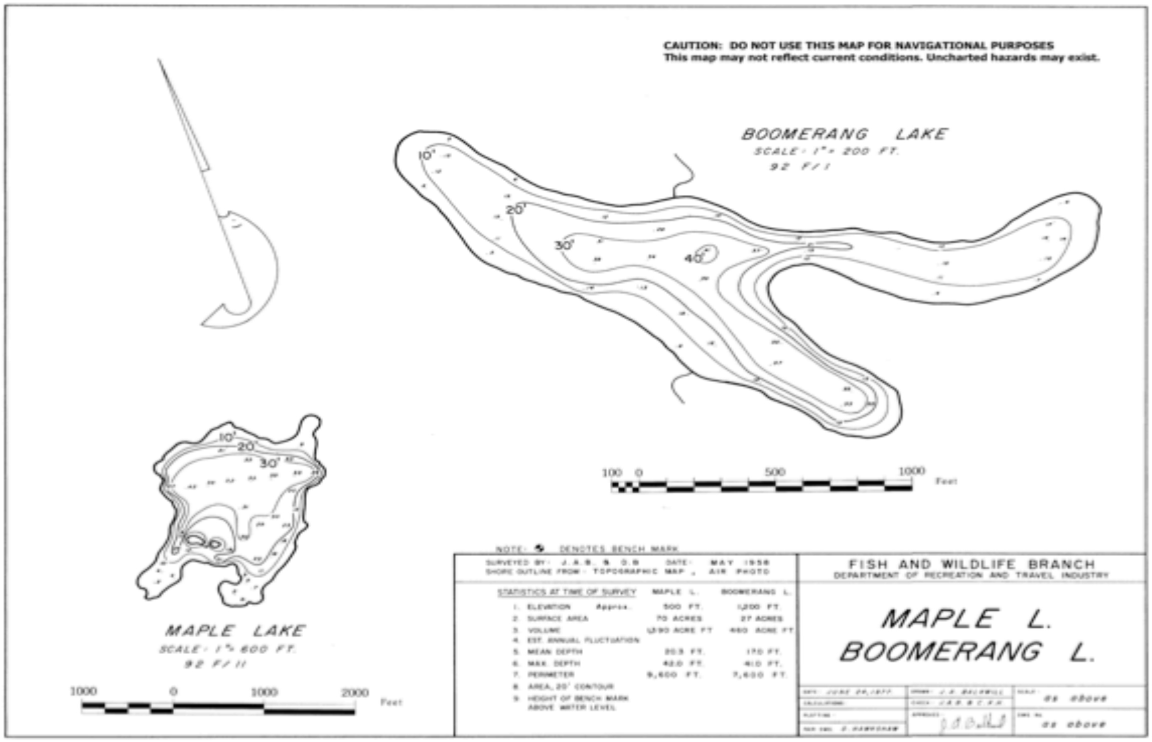

Figure 9A. Bathymetric map of Maple Lake (FISS 2012) the rainbow trout reference lake located in Central Vancouver Island (49°38'18.79"N, 125° 0'56.20"W).

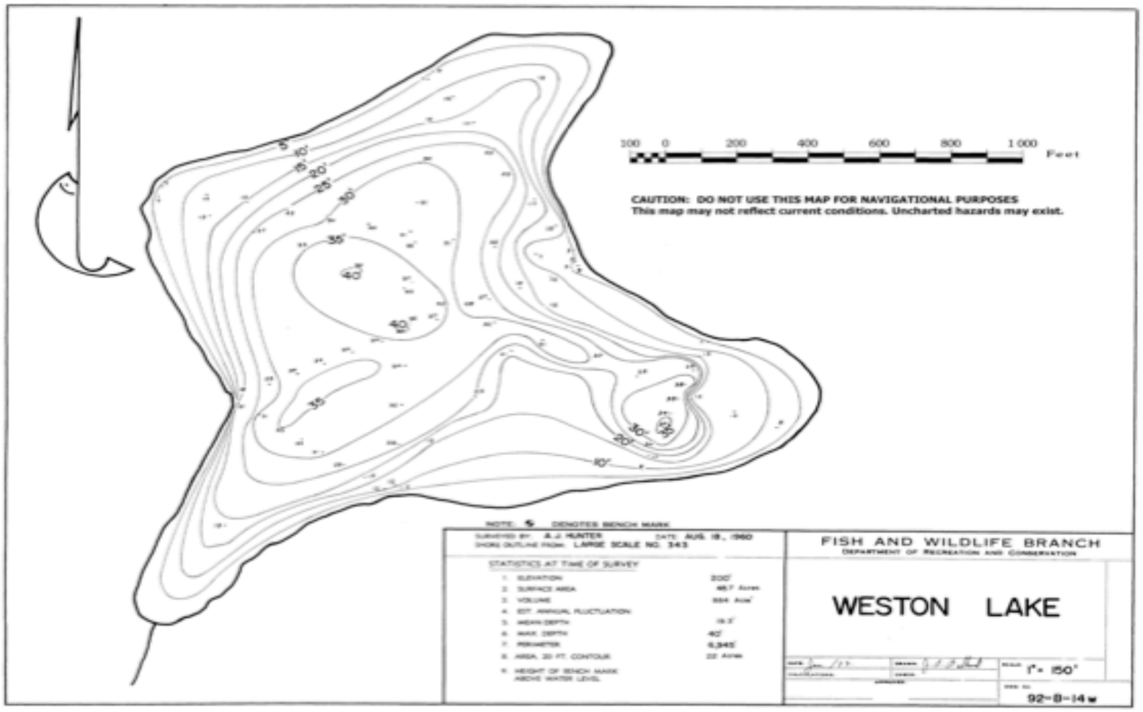

Figure 10A. Bathymetric map of Weston Lake (FISS 2012) the cutthroat trout reference lake (SMB free) located on Salt Spring Island (48°47'2.41"N, 123°25'28.78"W).

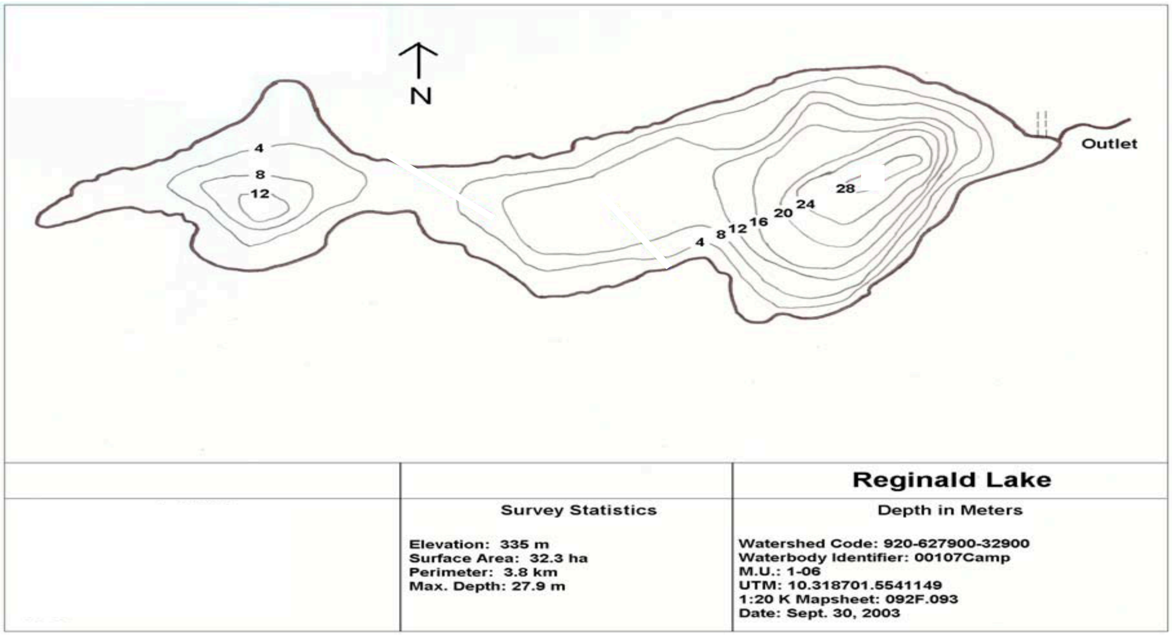

Figure 11A. Bathymetric map of Reginald Lake (FISS 2012) the rainbow trout reference lake (SMB free) located on Central Vancouver Island (49°59'38.54"N, 125°32'23.12"W).

Field stocking experiment study sites

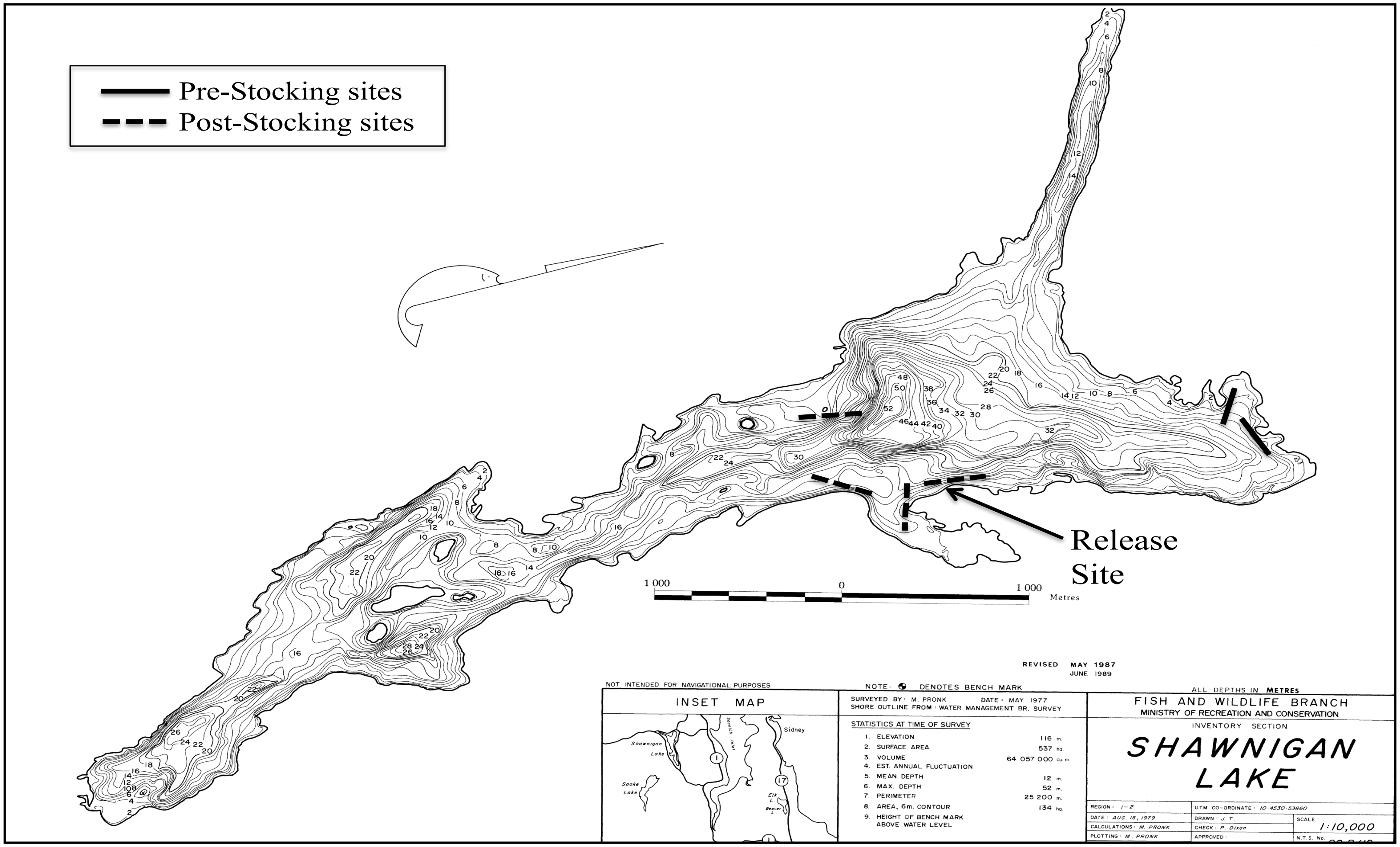

Figure 12A. Bathymetric map (FISS 2012) of Shawnigan Lake with the location of the release site, pre-stocking (solid lines), and post-stocking sample sites (dashed lines).

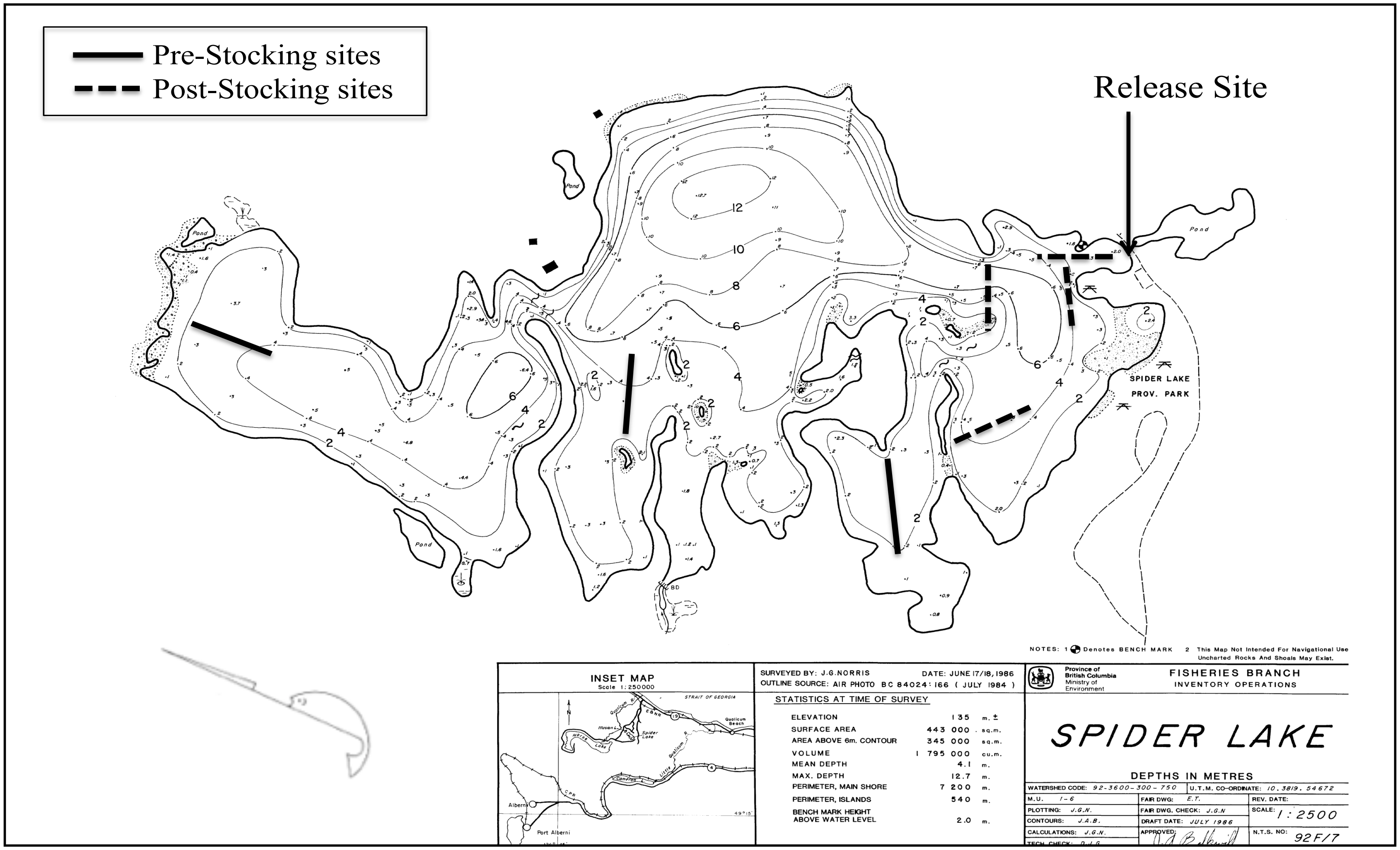

Figure 13A. Bathymetric map (FISS 2012) of Spider Lake with the location of the release site, pre-stocking (solid lines), and post-stocking sample sites (dashed lines).

Snorkel transect sites

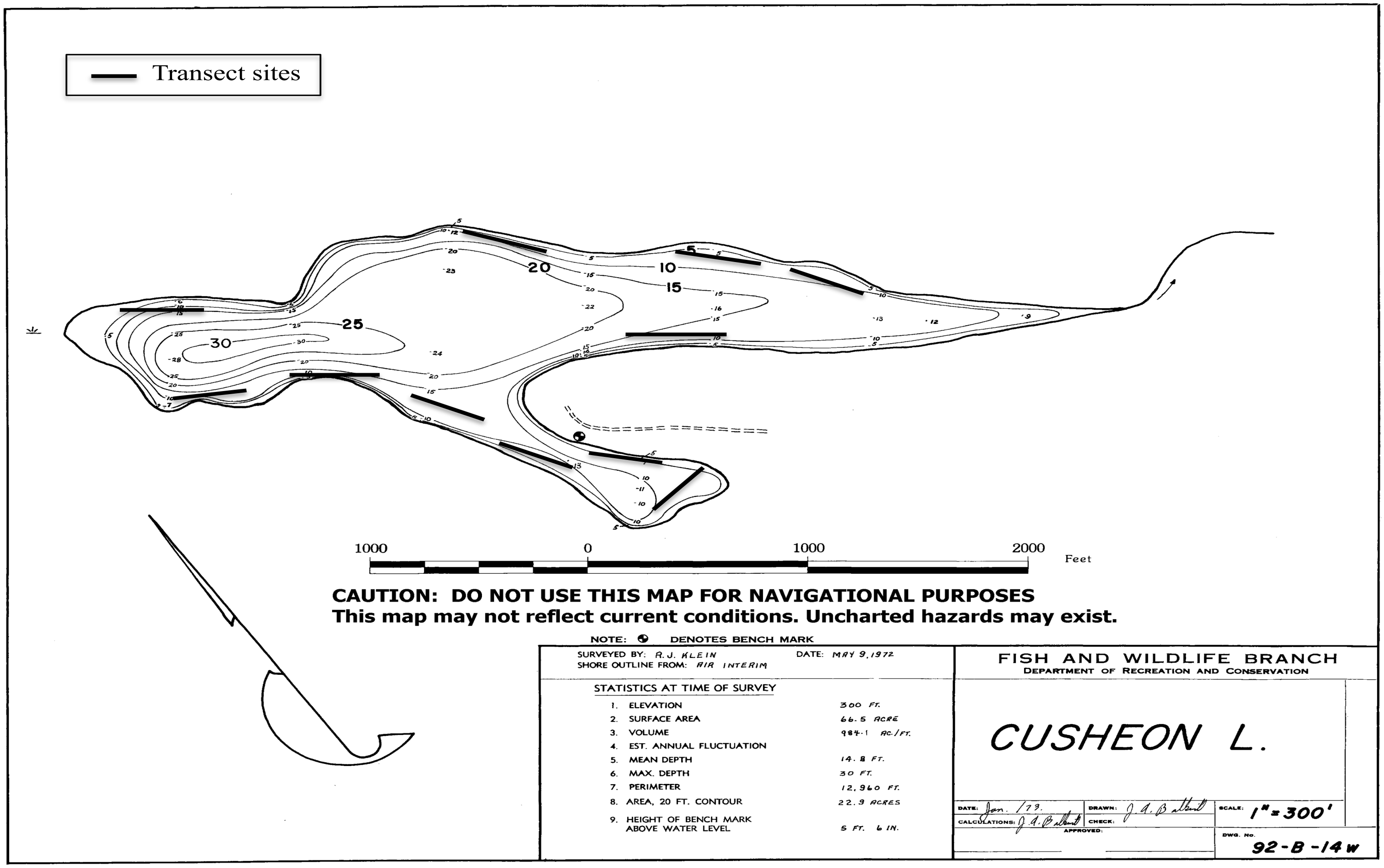

Figure 14A. Bathymetric map (FISS 2012) of Cusheon Lake, with the locations of the crayfish snorkel transects completed from July to September 2012.

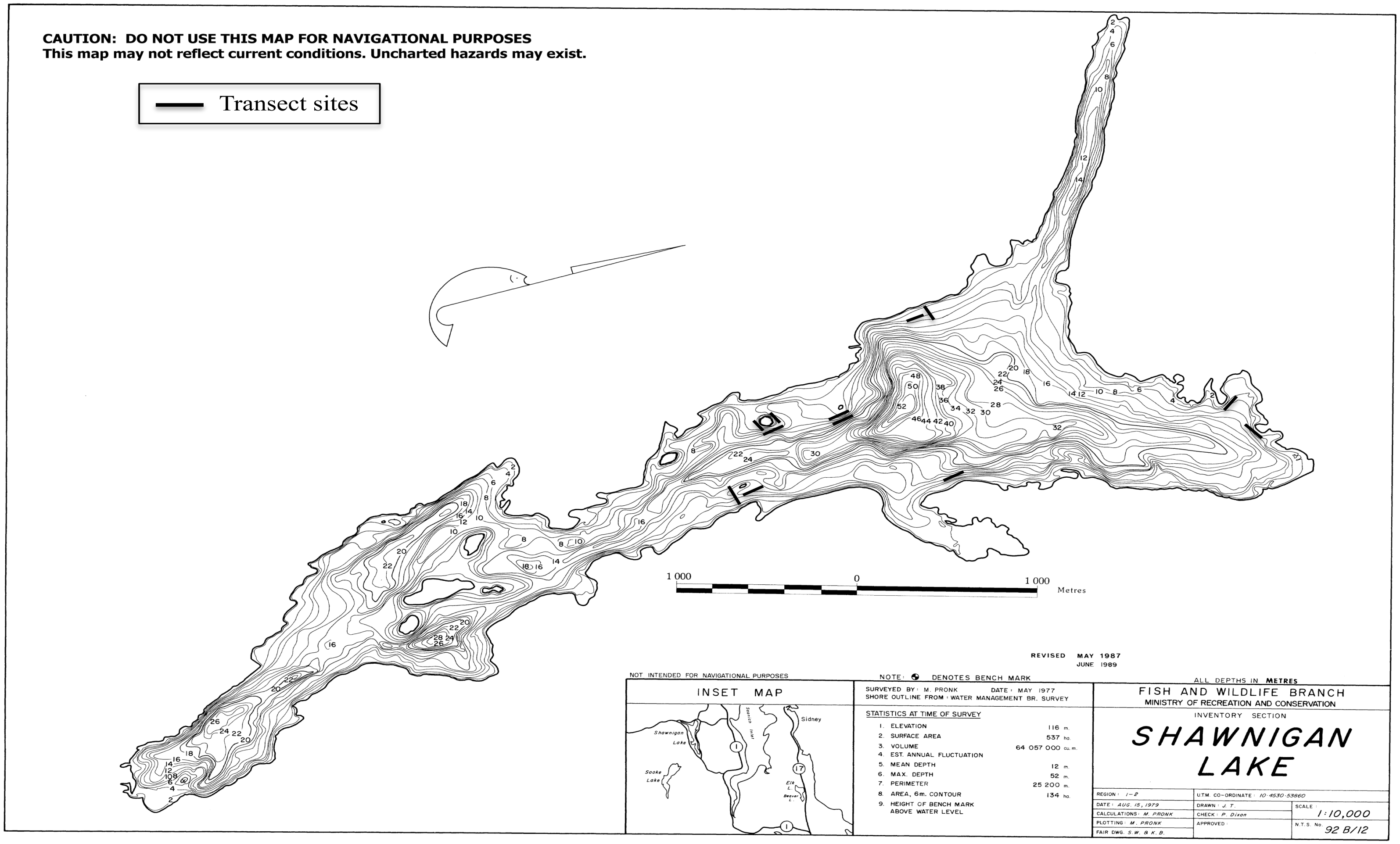

Figure 15A. Bathymetric map (FISS 2012) of Shawnigan Lake, with the locations of the crayfish snorkel transects completed from July to September 2012.

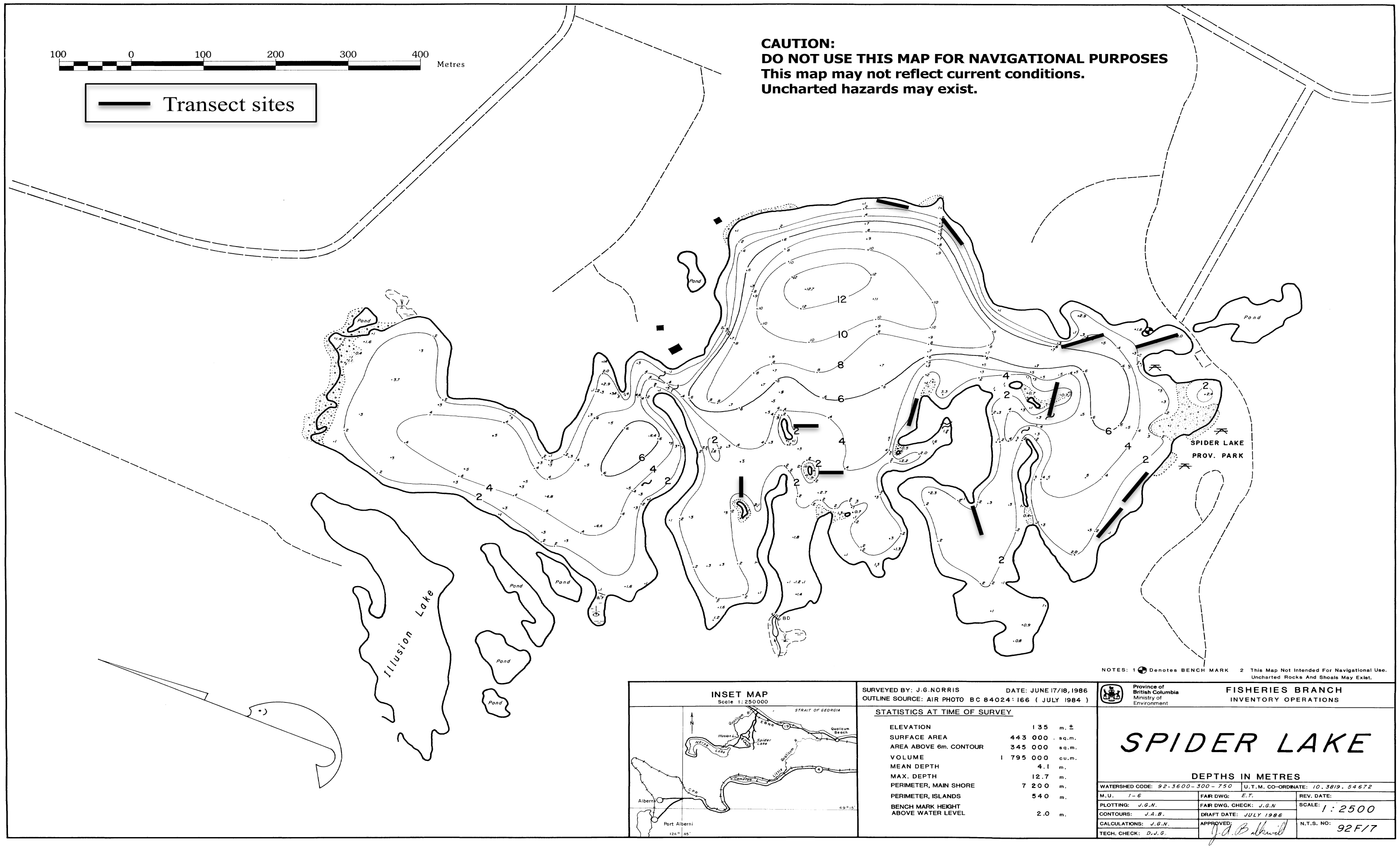

Figure 16A. Bathymetric map (FISS 2012) of Spider Lake, with the locations of the crayfish snorkel transects completed from July to September 2012

Temperature data for Vancouver Island lakes

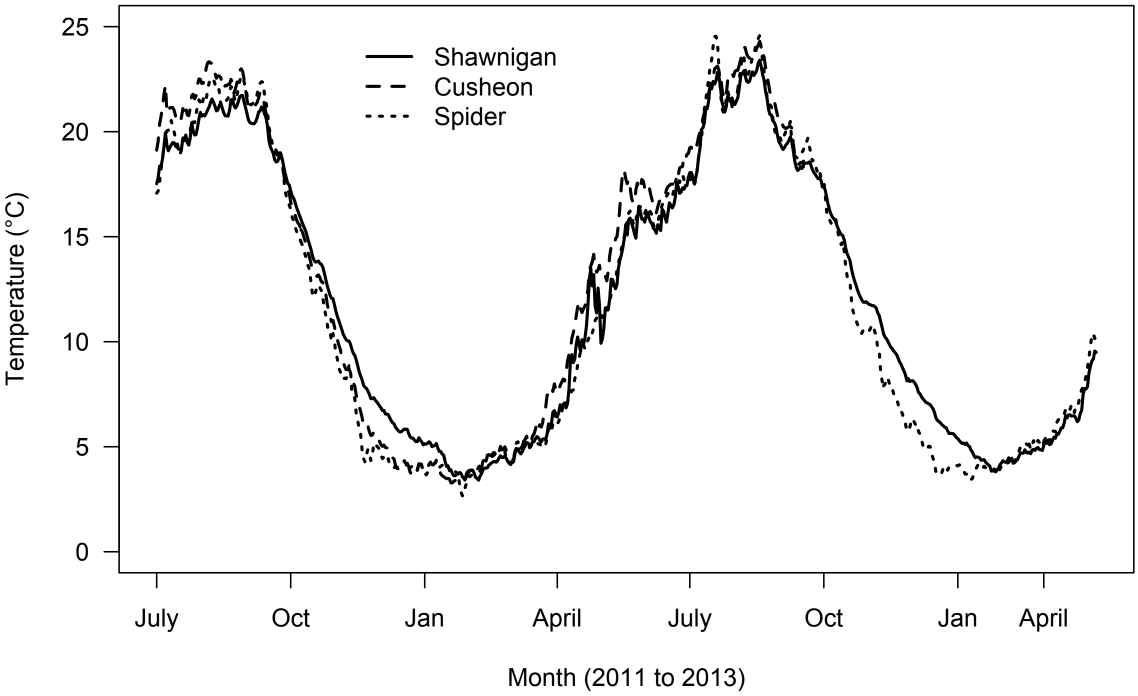

Figure 1A. Mean daily surface (°C) temperature from Tidbit temperature loggers at near shore depths (~1m) for the three Vancouver Island (Cusheon, Spider, Shawnigan) study lakes from July 2011 to April 2013

SMB otolith data and images

Table 1A. Age analysis (years) completed by the Sclerochronology Lab, at the Pacific Biological Station (PBS) for a subsample of SMB otoliths collected from the three Vancouver Island study lakes (Shawnigan, Cusheon and Spider Lakes) and Beaver Lake in the Cariboo region from 2012 catch data (Sclerochronology Lab 2012).

Study Lake	Fork Length (mm)	Weight (g)	Comments	Otolith Age (Years)
Shawnigan	173	80.8	1otolith crystalized, vague 3rd	4(4+) F+/-1
Shawnigan	269	301.9	5th on edge?	4(4+) F+/-1
Shawnigan	281	314.5	1 otolith crystalized, vague 5th	5(5+)F+/-1
Shawnigan	332	484.4	2 otolith crystallized	5(5+)FG
Shawnigan	348	622.2		7(7+)F+/-1
Shawnigan	350	600.2		6(6+)FG

Shawnigan	357	676.1		7(7+)F+/-1
Shawnigan	358	618.9		6(6+)FG
Shawnigan	371	703.4	small 1st	8(8+)F+/-1
Shawnigan	383	799.1	1 otolith crystalized, vague 1st	8(8+)F+/-1
Shawnigan	404	1060.0	photos bass #7 & #8	8(8+)F+/-2
Shawnigan	408	928.6	1 otolith crystalized, edge?	9(9+)F+/-1
Shawnigan	410	992.8	2 otolith crystallized	8(8+)F+/-1
Shawnigan	422	1192.4	1 otolith crystalized, photo bass #9	9(9+) FG
Shawnigan	454	1277.7	1 otolith crystalized	12(12+) FG
Beaver	247	243.2	photo bass 10	3(3+)FG
Beaver	250	299.4		3(3+)F+/-1
Beaver	250	277.5		3(3+)FG
Beaver	257	238.8		3(3+)FG
Chambers	268	339.2	large 1st?	4(4+)F+/-1
Beaver	269	256		3(3+)FG
Chambers	271	321.5	small vague1st or large 1st?	4(4+)F+/-1
Beaver	278	304.4		3(3+)FG
Beaver	308	425.9		4(4+)FG
Beaver	317	497.2		4(4+)F+/-1
Beaver	319	481		4(4+)FG
Beaver	340	722.3	1otolith crystalized	4(4+)FG
Beaver	345	652.9		4(4+)F+/-1
Beaver	422	1620.4	photo bass #11	8(8+)F+/-1
Beaver	271	308.5	piece missing from otolith	3(3+)FG
Spider	296	464.7		3(3+)FG
Spider	288	401.3		3(3+)F+/-1
Spider	321	552.3	off centered break, small 1st	4(4+)F+/-1
Spider	310	526.7		3(3+)FG
Spider	230	199.2		3(3+)F+/-1
Spider	306	514.6		3(3+)FG
Spider	142	45.1		1(1+)F+/-1
Spider	449	1603.6		14(14+)F+/-1
Spider	240	198.5		2(2+)FG
Spider	147	44		1(1+)FG
Spider	370	875.4	1otolith crystalized	5(5+)F+/-1
Spider	309	484.1	small 5th yr.	3(3+)FG
Spider	310	520.7		4(4+)F+/-1

Spider	352	796.8	1 otolith crystalized	4(4+)FG
Spider	166	80	2 otolith crystallized	2(2+)FG
Cusheon	148	51		1(1+)FG
Cusheon	139	38.9	photo bass #12	1(1+)FG
Cusheon	152	48.0		1(1+)FG
Cusheon	167	72.2	1 otolith crystalized	1(1+)FG
Cusheon	142	45	photo bass #13	1(1+)FG
Cusheon	150	54.9		1(1+)FG
Cusheon	165	59.8	1 otolith missing	1(1+)FG
Cusheon	165	63.9		1(1+)FG
Cusheon	156	68.1		1(1+)FG
Cusheon	290	398.1	vague 1st	3(3+)F+/-1
Cusheon	159	63.6	1 otolith crystalized	1(1+)FG
Cusheon	343	648.9		4(4+)FG
Cusheon	129	32.2		1(1+)FG
Cusheon	279	331.8		3(3+)FG
Cusheon	448	1417.2	photo- bass#14 &15, yellow sticker on vial	19(19+)F+/-1

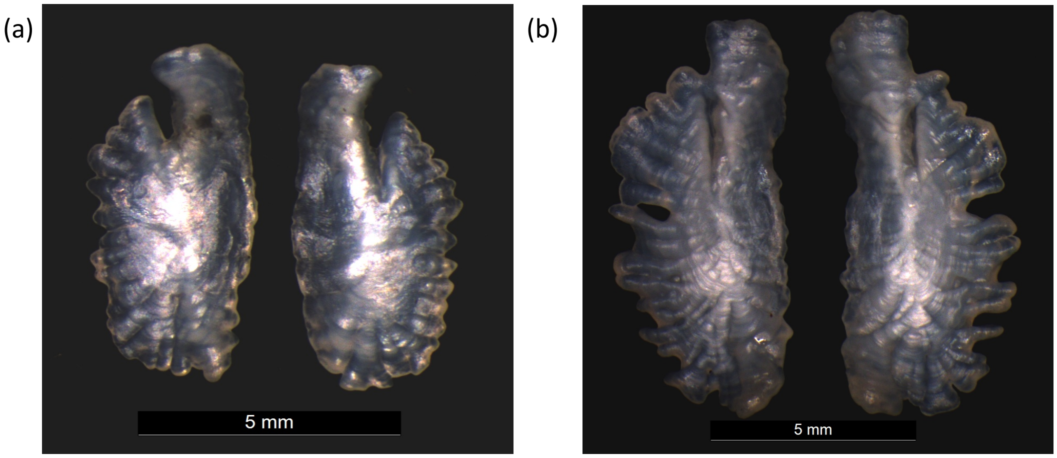

Figure 2A. Distal surface of SMB otolith samples from Beaver Lake in the Cariboo region for (a) three year old SMB (fork length=247mm and weight=243.2g) and (b) eight year old SMB (fork length=422mm and weight=1620.4g) (Sclerochronology Lab 2012).

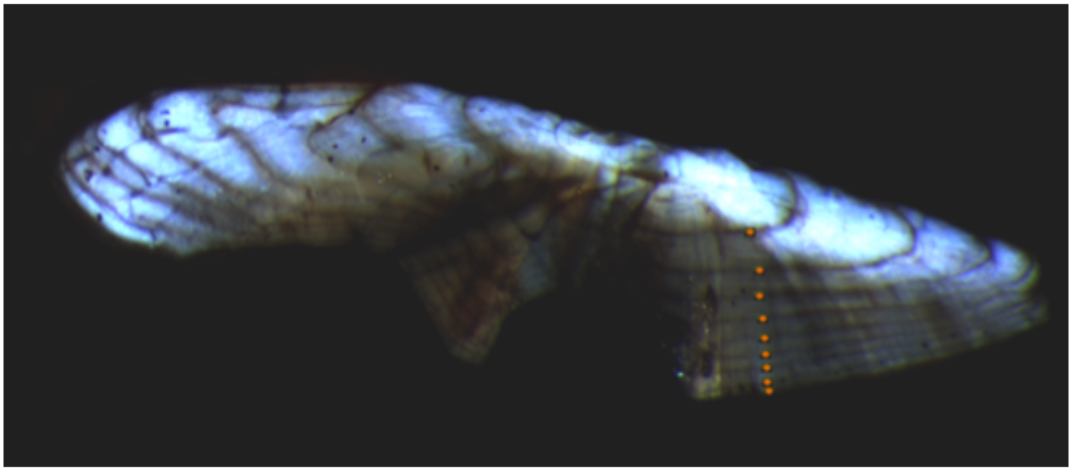

Figure 3A. Lateral view of SMB otolith sample from Shawnigan Lake on Vancouver Island, aged at 9 years old (Fork length=422mm, weight=1192.4g). Annuli are marked with red symbols. Break and burn method was used to expose the annuli from the lateral view (Sclerochronology Lab 2012).

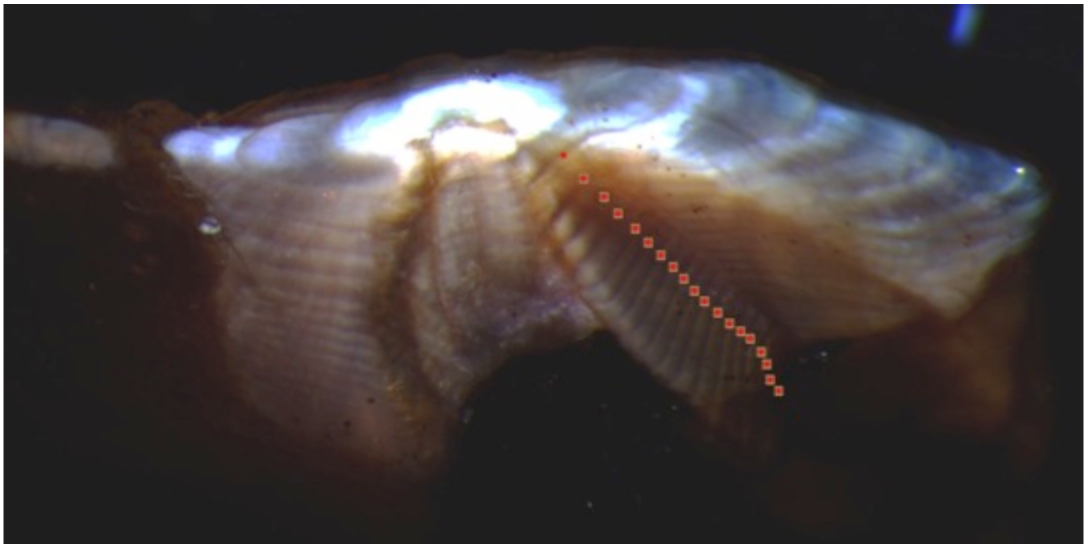

Figure 4A. Lateral view of otolith sample for an SMB from Cusheon Lake on Vancouver Island, aged at 19 years old (Fork length= 448mm, weight=1417.2g). Annuli are marked with red symbols. Break and burn method was used to expose the annuli from the lateral view (Sclerochronology Lab 2012).

Table 1A. Central tendency measures of age Summary of the von Bertalanffy growth equation parameters (k, L∞ and t_0*) and the growth curve slope and intercept values (a and b) for the SMB catch data from Shawnigan, Spider, Cusheon and Beaver Lakes for the 2012 field season.

Variables	Shawnigan	Spider	Cusheon	Beaver
Median age (yrs.)	3.340	3.577	3.277	0.713
Mean age (yrs.)	3.896	4.574	4.140	1.684
Max age (yrs.)	12.844	16.043	19	8
Min age (yrs.)	1.327	2.139	1.980	0.583
SD (yrs.)	2.075	2.799	3.147	1.479
a	-0.350	-0.033	0.317	-1.127
b	0.257	0.339	0.104	0.669
k	0.257	0.339	0.104	0.669
L∞ (cm)	48.3	45.3	50.5	42.7
t_0	0.023	0.023	0.023	0.023

** k = b the slope of the growth curve, L∞ = asymptotic length (length of largest fish captured) and t0 = -a/b the point in time when fish has zero length.*

SMB diet diversity and feeding evenness

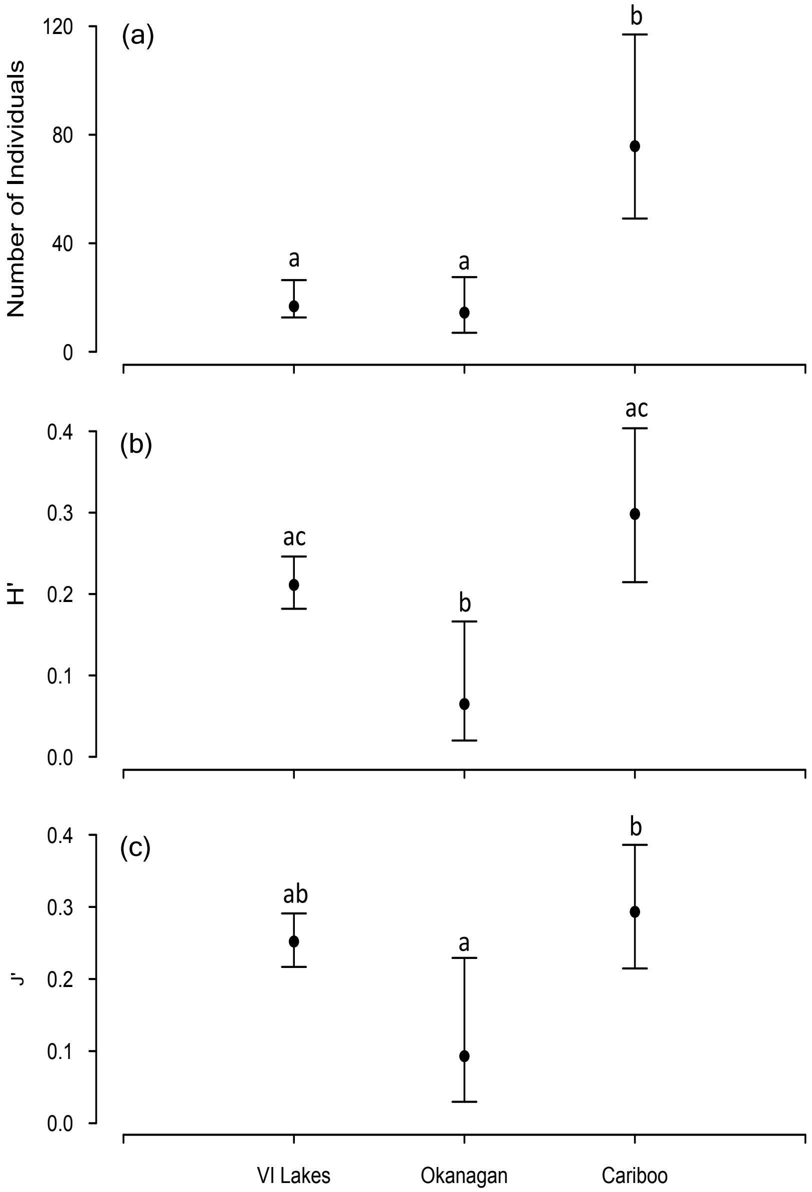

Figure 5A. Mean ± 95%C.I. (a) number of individuals per stomach sample, (b) Shannon's diversity index (H') and (c) Pielou's feeding evenness index (J') for SMB diet across the three geographic sampling regions in BC (Vancouver Island Lakes, Okanagan and Cariboo). The mean values containing the same lower-case letters are not significantly different (P>0.05, according to the Kruskal-Wallis test).

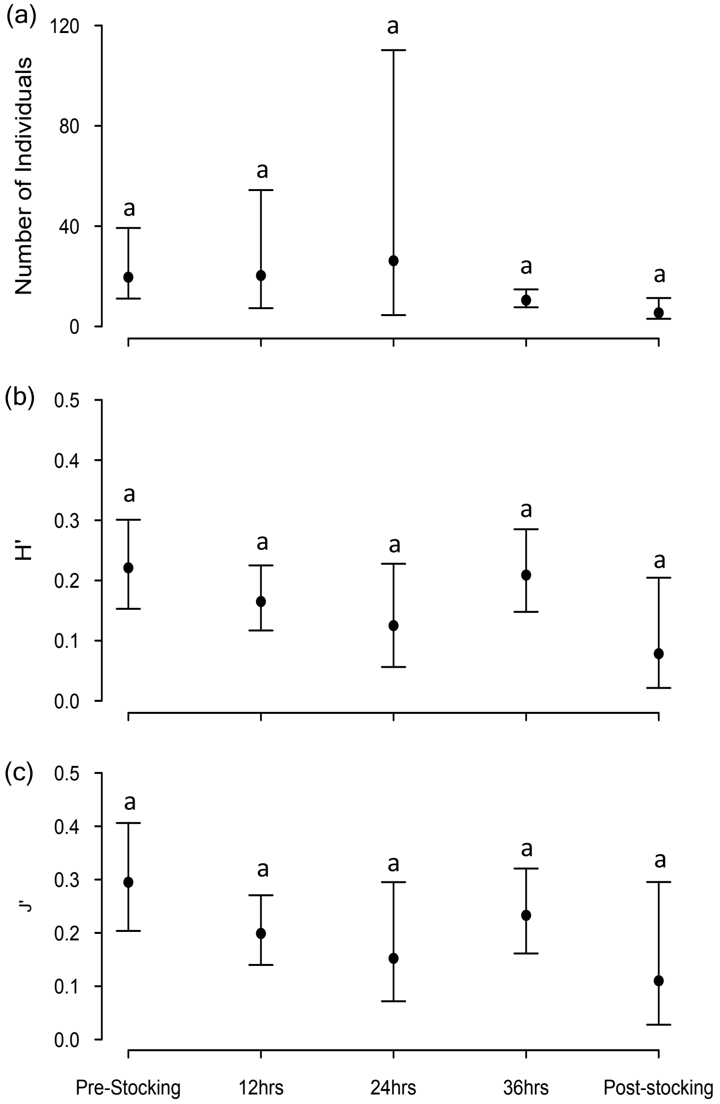

Figure 6A. Mean ± 95%C.I. (a) number of individuals per stomach sample, (b) Shannon's diversity index (H') and (c) Pielou's feeding evenness index (J') across the stocking sampling time intervals. The mean values containing the same lower-case letters are not significantly different (P>0.05, according to the Kruskal-Wallis test).