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Food Habits of Nonnative Smallmouth Bass in Coeur d'Alene Lake, Idaho

Abstract

Smallmouth Bass (*Micropterus dolomieu*) has been widely introduced beyond its native distribution where interactions with other organisms are largely unknown. We examined the food habits of Smallmouth Bass in Coeur d'Alene Lake, Idaho. Smallmouth Bass were sampled monthly from March 2012 to May 2013 using short duration (1–2 hr sets) gill netting and electrofishing. In total, food habits were evaluated from 904 Smallmouth Bass varying in total length from 39 to 492 mm using gastric lavage. Diet composition varied by season and age. Smallmouth Bass less than 100 mm had diets dominated by invertebrates, particularly Ephemeroptera, Odonata, and Diptera. Fishes were increasingly important in the diet of Smallmouth Bass longer than 100 mm. Interestingly, crayfish (Decapoda) were virtually absent in Smallmouth Bass stomachs; only eight Smallmouth Bass had crayfish in their diet. Native vertebrates were also rare in Smallmouth Bass diets. Rather, kokanee (*Oncorhynchus nerka*), a nonnative species, was generally the most commonly consumed fish prey item (present in 5–15% of Smallmouth Bass across seasons). Kokanee contributed the highest percentage of total energy (approximately 45% of all energy) of any prey item. Results of this study suggest that native fishes of conservation concern are a minor component of Smallmouth Bass diets and that kokanee is important in meeting the energy demands of nonnative Smallmouth Bass. Further research on the distribution and abundance of crayfish in the system and on the population-level effects of Smallmouth Bass predation on kokanee would be insightful and help guide management actions in Coeur d'Alene Lake and similar systems in western North America.

Keywords: crayfish, diet, introduced species, kokanee

Introduction

Smallmouth Bass (*Micropterus dolomieu*) is a socially and economically important species across its distribution. The native distribution of Smallmouth Bass is the central and eastern United States where it extends from the Great Lakes and St. Lawrence River system through the Mississippi River and its tributaries (Scott and Crossman 1973, Brewer and Orth 2015). Smallmouth Bass has long been among the most popular sport fishes in North America. Consequently, Smallmouth Bass has been introduced to freshwater systems across most of the United States, southern Canada, and in nine other countries (Brewer and Orth 2015). The mechanism of dispersal has included a mixture of intentional and unintentional stockings, as well as volitional movement from established populations (Borden and Krebs 2009, Carey et al. 2011). In the western United States, the first recorded introduction occurred in 1874 in California (Lampman 1946). In Idaho, Munther (1970) reported that Smallmouth Bass was introduced to the Snake River in the late 1800s somewhere along the Idaho–Oregon border, but the specific location is unknown. In 1905, the U.S. Bureau of Fisheries introduced Smallmouth Bass to Muldoon Lake, Idaho, but a population was never established (Simpson and Wallace 1982). In the

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Pacific Northwest around 1925, approximately 400 Smallmouth Bass were stocked into the Willamette River, Oregon, and approximately 5,000 Smallmouth Bass were released into the Yakima River, Washington (Lampman 1946, LaVigne et al. 2008). The first well-documented introduction of Smallmouth Bass was in the Snake River in 1942 by the Idaho Department of Fish and Game (IDFG; Keating 1970). Since that time, Smallmouth Bass populations have increased in the Snake River basin, enhanced by the construction of the Hells Canyon Hydroelectric Projects in the 1950s and 1960s. Legal introductions of Smallmouth Bass in Idaho ceased in the 1980s, but illegal introductions and volitional movements continued to occur. For instance, the Montana Department of Fish, Wildlife, and Parks introduced Smallmouth Bass into Noxon Reservoir on the Clark Fork River in the mid-1980s. Smallmouth Bass moved downstream and are now well established in Lake Pend Oreille and the Pend Oreille River, Idaho, and have moved upstream into the Priest Lake system (Sigler and Zaroban 2018). Smallmouth Bass is now one of the most widespread species in Idaho.

The introduction of Smallmouth Bass to provide recreational opportunity can be considered both a success and a challenge. Although Smallmouth Bass is a popular sportfish outside its native distribution, it has had several deleterious effects on native species. Jackson (2002) summarized the effects of Largemouth Bass (*M. nigricans*) and Smallmouth Bass in north temperate lakes of the United States and Canada. The author reported that the introduction of *Micropterus* spp. often altered aquatic systems through direct reductions in small-bodied fish diversity via predation and cascading effects to plankton and macroinvertebrate communities. Vander Zanden et al. (2009) provided a detailed assessment of the consequences of Smallmouth Bass introductions to Canadian lakes where diversity and density of prey fishes declined following establishment of Smallmouth Bass. Native Lake Trout (*Salvelinus namaycush*) in lakes with nonnative Smallmouth Bass had a plankton-based diet compared to a fish-based diet in uninvaded lake systems.

The negative effects of nonnative Smallmouth Bass are perhaps most evident in the Pacific Northwest where Smallmouth Bass overlap in distribution with Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*). In the Columbia and Snake river systems of Idaho–Washington–Oregon, Smallmouth Bass are common and abundant, given favorable habitat conditions (Naughton et al. 2004, LaVigne et al. 2008). Carey et al. (2011) summarized findings from multiple studies in the Columbia River basin and reported that individual Smallmouth Bass consume up to 3.9 juvenile salmon per day. The effects of Smallmouth Bass on anadromous fishes are expected to increase as Smallmouth Bass populations expand in distribution and abundance. Despite the widespread occurrence of Smallmouth Bass, surprisingly few studies have been conducted on the food habits of nonnative Smallmouth Bass introduced to lentic systems in western North America. As such, the goal of this study was to describe the food habits of Smallmouth Bass in Coeur d'Alene Lake, Idaho. We were particularly interested in the consumption of fishes that have conservation or recreational importance in the system.

Methods

Coeur d'Alene Lake is a large natural lake located in northern Idaho with a surface area of 12,700 ha (Figure 1). Mean depth of the lake is approximately 24 m and maximum depth is 61 m (Rich 1992, Vitale et al. 2004). The Coeur d'Alene and St. Joe rivers are the primary tributaries to Coeur d'Alene Lake, but many smaller streams also contribute to the system. In 1906, Post Falls Dam was constructed on the outlet of Coeur d'Alene Lake, which raised the water level of the lake by 2.5 m (Rich 1992). Historical nutrient concentrations classify the lake as mesotrophic; however, biological production has been limited with the input of heavy metals from over a century of mining in the watershed (National Research Council 2005). Fisheries in Coeur d'Alene Lake are comanaged by the Coeur d'Alene Tribe and IDFG.

Sport fisheries in Coeur d'Alene Lake are primarily focused on nonnative species such as kokanee (*O. nerka*), Chinook Salmon

(*O. tshawytscha*), Rainbow Trout (*O. mykiss*), Largemouth Bass, Black Crappie (*Pomoxis nigromaculatus*), Pumpkinseed (*Lepomis gibbosus*), Yellow Perch (*Perca flavescens*), Brown Bullhead (*Ameiurus nebulosus*), and Northern Pike (*Esox lucius*). The first documented presence of Smallmouth Bass in Coeur d'Alene Lake was in 1990 near the city of Coeur d'Alene, Idaho (Fredericks et al. 2000). The prevailing hypothesis is that Smallmouth Bass was illegally introduced from nearby Hayden Lake where Smallmouth Bass was introduced by IDFG in 1983. Since that time, Smallmouth Bass in Coeur d'Alene Lake has steadily increased in abundance and it now supports a popular sport fishery. Native sport fish species in Coeur d'Alene Lake include Westslope Cutthroat Trout (*O. lewisi*), Bull Trout (*Salvelinus confluentus*), and Mountain Whitefish (*Prosopium williamsoni*). Other notable native species in the basin include Northern Pikeminnow (*Ptychocheilus oregonensis*) and Longnose Sucker (*Catostomus catostomus*). Westslope Cutthroat Trout is a species of particular conservation concern in the system and has been the focus of extensive research by the Coeur d'Alene Tribe (Firehammer et al. 2012, Walrath et al. 2015a). Similarly, Bull Trout is listed as threatened under the Endangered Species Act and has experienced dramatic declines in abundance in the Coeur d'Alene basin (USFWS 2015).

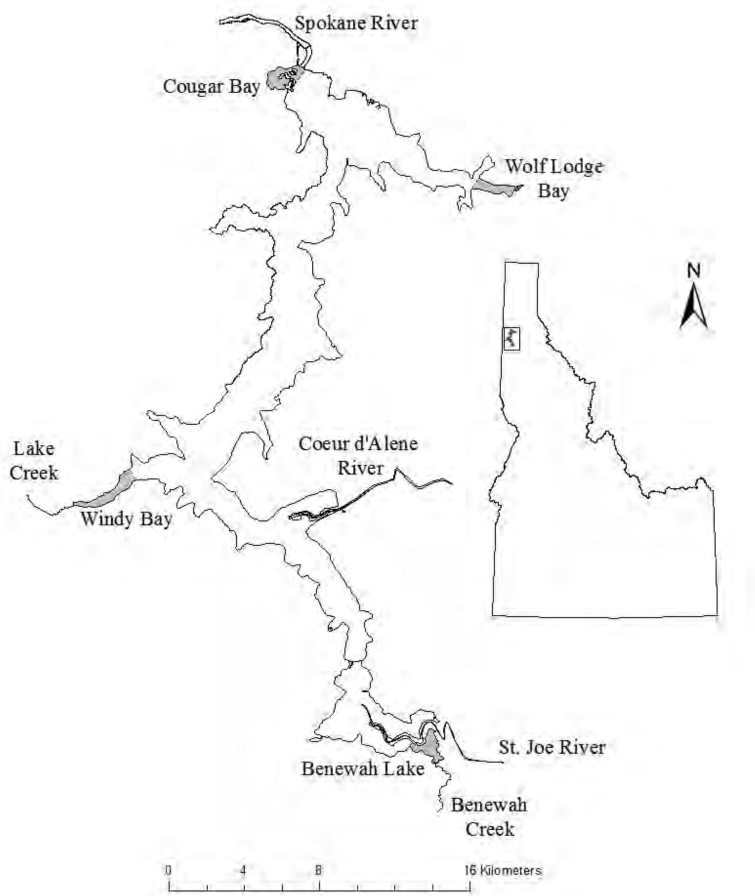

Figure 1. Map of Coeur d'Alene Lake in northern Idaho. Idaho Department of Fish and Game manages the lake north of the mouth of the Coeur d'Alene River. The Coeur d'Alene Tribe manages the lake south of the mouth of the Coeur d'Alene River as well as the Lake Creek watershed. Sampling sites (shaded gray) were located in Cougar, Wolf Lodge, and Windy bays, and Benewah Lake.

Bays were selected as part of our study to evaluate the diet of nonnative piscivores in Coeur d'Alene Lake, particularly with respect to their consumption of native salmonids. Four major bays (i.e., Wolf Lodge, Cougar, and Windy bays, and Benewah Lake) were selected for this study because they provided a diversity of habitats and were representative of important areas for management (Figure 1; Rich 1992, Firehammer et al. 2012, Walrath et al. 2015a). In addition, at least two of the bays (Benewah Lake and Windy Bay) contain tributaries that are used by adfluvial Westslope Cutthroat Trout (Firehammer et al. 2012). Stratified random sampling was used to select sampling sites by dividing the shoreline of each bay into 300-m sections and randomly assigning a gear type to a section. Pulsed-DC electrofishing and experimental gill nets were used to sample Smallmouth Bass. A sampling event consisted of sampling 18 non-overlapping sections composed of six electrofishing and 12 gill netting sites. A sampling event occurred once per month in Cougar and Wolf Lodge bays from March 2012–May 2013. Windy Bay and Benewah Lake were sampled once per month during June–November (2012) and twice per month from March–May (2012 and 2013). Spring bi-weekly sampling was performed to increase the resolution in Windy Bay and Benewah Lake where the Coeur d'Alene Tribe intensely monitors Westslope Cutthroat Trout in tributaries (i.e., Lake and Benewah creeks). Hazardous lake conditions prevented sampling during winter (i.e., December 2012–February 2013).

Electrofishing was conducted using a 5,000 W generator mounted in an aluminum boat with Smith-Root (Smith-Root, Inc., Vancouver, Washington) equipment. Power output was standardized to 2,750–3,250 W based on ambient water conductivity ($\mu S \cdot cm^{-1}$; Miranda 2009). Prey digestion and mortality of Smallmouth Bass were minimized in gill nets (46 m × 1.8 m with panels of 2.5, 3.2, 3.8, 4.4, and 5.0-cm bar-measure mesh) by limiting their soak duration to 1.5–2.0 hours. Sinking gill nets were set perpendicular to shore in littoral habitats. The mesh size closest to shore was randomized to minimize systematic bias in catch.

All sampled Smallmouth Bass were measured to the nearest millimeter (total length). Smallmouth Bass were weighed to the nearest gram with a digital balance (Ohaus FD15H; Ohaus Corporation, Parsippany, New Jersey). Pulsed gastric lavage was used to obtain stomach contents from five fish per centimeter length group. Stomachs were flushed with a 12-volt 14.4 $L \cdot min^{-1}$ pump (Fimco, North Sioux City, South Dakota) equipped with a pressure gauge, changeable hose fittings, and a pressure-release valve (Light et al. 1983, Venturelli and Tonn 2006, Walrath et al. 2015a). Forceps were used to remove large prey items that were not flushed from the stomach. Filtered water, held in an on-board container, was used for the lavage process to ensure samples were not contaminated with organisms from the lake. A gastroscope was inserted through the esophagus and into the stomach to ensure the removal of all prey items, water, and air prior to release. If prey items were observed, the lavage process was repeated until the stomach was empty. Stomach contents were preserved with 10% buffered formalin until they could be further analyzed in the laboratory (Garvey and Chipps 2012). The efficiency of removing all prey items from stomachs using the pulsed gastric lavage technique was evaluated by dissecting mortalities (n = 422 fish; 39–485 mm) and examining their stomach for any remaining content; efficiency was 99% (i.e., based on frequency of occurrence by number). Individual Smallmouth Bass stomach contents were also scanned for passive integrated transponder (PIT) tags (i.e., adfluvial Westslope Cutthroat Trout in Lake and Benewah creeks are PIT tagged) using an Allflex ISO compact reader (Allflex, San Antonio, Texas). No PIT tags were detected in Smallmouth Bass stomachs. Dorsal spines were collected from all Smallmouth Bass that were sampled for stomach contents. In an effort to better describe age structure and growth, we also removed dorsal spines from fish that were not sampled for stomach contents. We sampled at least 10 fish per centimeter length group during each sampling event across bays (Quist et al. 2012, Walrath et al. 2015b). Spines were placed into coin envelopes and allowed to air dry before processing (Koch and Quist 2007). Sagittal otoliths from Smallmouth Bass mortalities were collected to corroborate ages from dorsal spines; agreement was 100% between otoliths and dorsal spines (n = 45).

In the laboratory, dorsal spines were mounted in epoxy and approximately 0.5 mm thick sections were cut using a Buehler low-speed saw (Buehler, Lake Bluff, Illinois; Koch and Quist 2007). Sections of spines were sanded with 400–1,200 grit sandpaper until annuli were clearly visible. Cross sections were viewed with a dissecting microscope using transmitted light and ages were assigned by a single reader. A subsample of sections (n = 80) was read independently by two readers; agreement in age estimates was 100%.

Vertebrate diet items were identified to species and invertebrates to order. Lengths of intact prey items were measured to the nearest 0.02 mm using calipers (Mitutoyo, Aurora, Illinois). Wet and dry weights were measured to the nearest milligram. Total lengths and weights of partially digested taxa were estimated using published length–weight equations using hard structures (e.g., vertebrae, head capsule; Duke and Crossley 1975, Dumont et al. 1975, Smock 1980, Rust 1991, Garvey and Stein 1993, Ganihar 1997, Altindag et al. 1998, Benke et al. 1999, Anders et al. 2003, Baumgartner and Rothhaupt 2003, Wigley et al. 2003).

Body condition of Smallmouth Bass was evaluated using relative weight (W_r):

$$W_r = \left(\frac{W}{W_s}\right) \times 100 \tag{1}$$

where W is the weight of an individual and W_s is the standard weight from a species-specific length–weight regression (Kolander et al. 1993, Neumann et al. 2012). Relative weight was only estimated for fish ≥ 150 mm (Kolander et al. 1993). A W_r value greater than 100 indicates that an individual fish is heavier than an average fish of the same length and a value less than 100 indicates that the fish is lighter than an average fish (Neumann et al. 2012). Values over 85 generally indicate that fish are in good body condition.

Food habits data were summarized by season: spring (March, April, May), summer (June, July, August), and fall (September, October, November). All data were summarized by age for those year classes represented by at least five individuals in each season (i.e., 2005–2012 year classes). Frequency of occurrence, percent by number, and percent energy contribution were used to summarize diet data (Garvey and Chipps 2012). Percent energy contribution was estimated by multiplying the weight of a taxon by its caloric value and then dividing the total taxon energy by the total energy of all prey items. Caloric densities for prey items were obtained from published literature (Cummins and Wuycheck 1971, Bryan et al. 1996, Hanson et al. 1997, Liao et al. 2004, Antolos et al. 2005, Muhlfeld et al. 2008, Yule and Luecke 1993). Only fish with identifiable prey items in their stomach were used in the food habits analysis. Unidentifiable prey items were rare (< 1%) and removed from further analysis.

Results

Electrofishing effort totaled 62.4 hours and 638 gill nets were fished for 1,166.0 hours. Electrofishing sampled 1,316 Smallmouth Bass (39–442 mm) and gill nets sampled 102 Smallmouth Bass (181–492 mm). Electrofishing catch rates for Smallmouth Bass were consistently high in Wolf Lodge Bay and low in Cougar Bay and Benewah Lake across all seasons (Figure 2). Electrofishing catch rates of Smallmouth Bass did not typically show a consistent trend except for in Windy Bay where catch rates increased across seasons. Catch rates of Smallmouth Bass with gill nets were relatively low for all seasons and highest in Wolf Lodge Bay except during spring 2013 (Figure 2). Mean W_r varied from 74.7 to 113.0 and averaged 88.1 (SE = 0.5) across locations and seasons (Figure 3), indicating that Smallmouth Bass were in good body condition.

Food habits data were collected from 904 Smallmouth Bass varying in length from 39 to 492 mm and representing eight year-classes (i.e., 2005–2012; Table 1, Figure 4). The percentage of empty stomachs averaged 19.5% across ages and was highest in fall (34.1%) followed by spring 2012 (26.6%), spring 2013 (13.2%), and summer (10.8%; Table 1). Diet composition varied greatly by age and season (Table 1), but several important patterns were observed. All ages of Smallmouth Bass consumed invertebrates, which were dominated by ephemeropterans, odonates, amphipods, and dipterans (Figure 5). Interestingly, crayfish (Decapoda) were exceptionally rare in Smallmouth Bass stomachs, occurring sporadically in diets during summer and fall (Table 1). Vertebrates were consumed by all but the youngest Smallmouth Bass. Kokanee was the primary fish species consumed, but juvenile Yellow Perch (i.e., < 150 mm), Brown Bullhead, and sculpin (*Cottus* spp.) were also important to some ages. A single Westslope Cutthroat Trout (107 mm total length) was observed in the diet and was consumed by a 281 mm Smallmouth Bass. No Bull Trout were

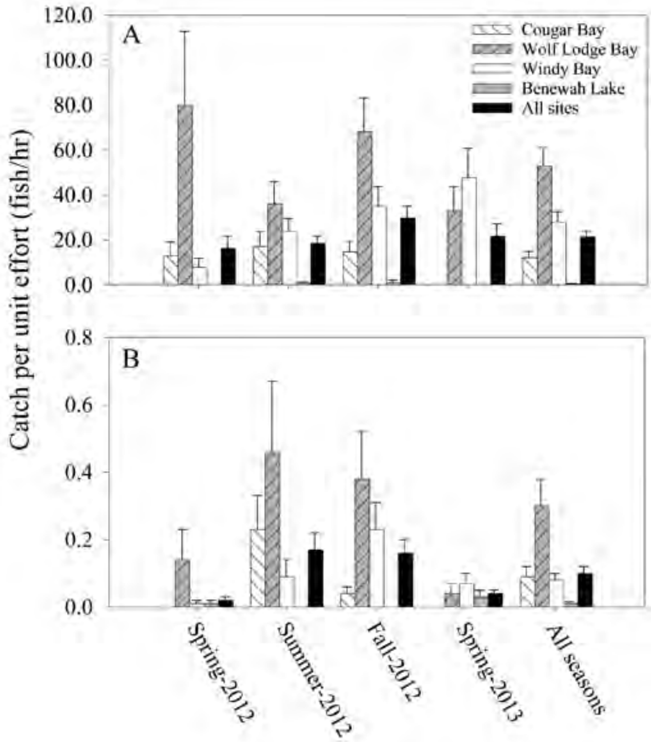

Figure 2. Mean catch per unit effort (fish·hr^{-1}) of Smallmouth Bass sampled using (A) electrofishing and (B) gill nets by season in Coeur d'Alene Lake, Idaho, during 2012 and 2013. Months were pooled by season: spring (March, April, May), summer (June, July, August), and fall (September, October, November). Error bars represent one standard error.

observed in Smallmouth Bass stomachs. For all but age-1 Smallmouth Bass, kokanee was the most important prey item in terms of energy contribution. Even when frequency of occurrence was low, kokanee often made up over 50% of the energy consumed and exceeded 70% for some ages (Figure 5).

Across seasons, ephemeropterans were often the most common prey item in Smallmouth Bass diets (Figure 6). Odonates were common in all seasons except fall. Kokanee was the most common fish in Smallmouth Bass diets in spring and summer 2012, whereas juvenile Yellow Perch was most common in fall. Brown Bullhead was most common in spring 2013. The energy contribution of prey items was dominated by kokanee in all seasons except spring 2013 when Brown Bullhead had the highest energy contribution of all prey items (Figure 6).

Invertebrates, particularly ephemeropterans and odonates, were the most common prey across seasons and year classes but contributed little (< 7%) to the total energy consumed (Figure 7). Although frequency of occurrence was similar among kokanee, juvenile Yellow Perch, and sculpin (approximately 5–6%), kokanee contributed 45.4% of the total energy consumed across seasons and year classes. The next taxa with the highest energy contributions were juvenile Yellow Perch (11.2%) and Brown Bullhead (9.5%).

Discussion

Smallmouth Bass is considered an opportunist carnivore. Larval and juvenile Smallmouth Bass primarily consume zooplankton and small invertebrates (Coble 1975, Dunsmoor et al. 1991, Easton et al. 1996, Margetts and Heise 2024). As the gape of Smallmouth Bass increases, diets are typically dominated by large macroinvertebrates, crayfishes, and fishes (Brewer and Orth 2015). Our results are consistent with previous research in that Smallmouth Bass in Coeur d'Alene Lake had a diverse diet composed of invertebrate and vertebrate prey items. Similarly, the diet of Smallmouth Bass varied by size. The diet of small (< 150 mm) Smallmouth Bass was generally dominated by macroinvertebrates, particularly ephemeropterans and odonates. Weidel et al. (2000) reported similar results for Smallmouth Bass in Little Moose Lake, New York, where ephemeropterans, odonates, and dipterans were the most common and numerous prey items in the diets of Smallmouth Bass less than 150 mm. Olson and Young (2003) described diets of Smallmouth Bass in 16 New York lakes and found that the diet of small Smallmouth Bass (< 125 mm) was dominated by macroinvertebrates (i.e., Ephemeroptera, Odonata). In an Oklahoma stream, Smallmouth Bass less than 125 mm primarily consumed ephemeropterans (Dauwalter and Fisher 2008). Nearly all studies focused on Smallmouth Bass diets have found a similar pattern for small Smallmouth Bass regardless of their status as native or nonnative (e.g., Dunsmoor et al. 1991, Liao et al. 2002, Frey et al. 2003, Schultz et al. 2017). The other constant pattern in Smallmouth Bass diets was a shift to larger prey items as Smallmouth Bass attain large sizes. Although we found evidence of fish in the diet of Smallmouth Bass as small as 66 mm, fish did not appear to be a major component of diets until Smallmouth Bass were 100–150 mm. For Smallmouth Bass greater than 200 mm, fishes were generally the most common and important (i.e., energy consumption) prey item for Smallmouth Bass. Similar results have been reported in other systems. For instance, Liao et al. (2002) found that Walleye (*Sander vitreus*) and Yellow Perch were important in the diet of large Smallmouth Bass in Spirit Lake, Iowa. Scott and Angermeier (1998) reported that fishes (e.g., Logperch [*Percina caprodes*]) were the primary prey of Smallmouth Bass greater than 150 mm in the New River, Virginia.

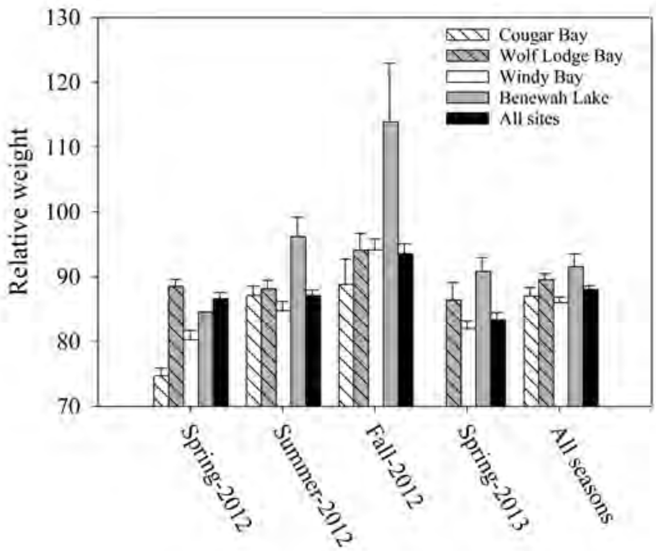

Figure 3. Mean relative weight of Smallmouth Bass by season, captured from each bay in Coeur d'Alene Lake, Idaho, during 2012 and 2013. Means were also calculated for each season and each site across all seasons. Months were pooled by season: spring (March, April, May), summer (June, July, August), and fall (September, October, November). Error bars represent one standard error.

Crayfish often dominate Smallmouth Bass diets. In fact, most studies report that crayfish are the most common and important prey item for large Smallmouth Bass. Weidel et al. (2000) showed that crayfish were in 49% of all Smallmouth Bass diets and in 60% of diets of large (≥ 150 mm) Smallmouth Bass. Olson and Young (2003) reported that crayfish made up over 50% of the biomass consumed by Smallmouth Bass greater than 125 mm and over 75% of the biomass for fish larger than 200 mm in New York lakes. Frey et al. (2003) found that Smallmouth Bass over 130 mm had diets dominated by crayfish (90–93% by weight) in Big Crooked Lake, Wisconsin. Even in western North America, crayfish are a staple of Smallmouth Bass diets. Although fish were the most common prey of Smallmouth Bass in John Day Reservoir, Washington–Oregon, crayfish were present in approximately 35% of Smallmouth Bass stomachs and made up approximately 20% of the biomass consumed (Poe et al. 1991). In Elk Creek, Oregon, crayfish were present in 21% of Smallmouth Bass diets and accounted for 64% of the energy consumed (Schultz et al. 2017). In contrast to virtually all diet studies on Smallmouth Bass, including those in Idaho (e.g., Bennett et al. 1991, Dunsmoor et al. 1991), crayfish were largely absent from the diet of Smallmouth Bass in Coeur d'Alene Lake where only eight Smallmouth Bass varying in length from 90 to 390 mm (only two were < 200 mm) consumed 12 individual crayfish. The reason for this lack of crayfish in Smallmouth Bass diets is unknown. Smallmouth Bass may have simply selected against crayfishes in the system, but this is highly unlikely given the importance of crayfish in almost every study that has evaluated Smallmouth Bass diets.

The status of crayfish is unknown in Coeur d'Alene Lake, but densities may be low given the history of heavy metal contamination in the basin. From the 1800s to the 1980s, the Coeur d'Alene

Table 1. Frequency of occurrence (%O), percent by number (%N), and percent energy contribution (%EC) of prey items consumed by Smallmouth Bass in Coeur d'Alene Lake, Idaho (March 2012 to May 2013). Sample size (n), length (mm; minimum–maximum), and the percentage of empty stomachs are provided for each age and season. The letter 'a' reflects frequency < 1%. Only taxa that were detected in at least one year class are shown.

	Age (year class)																				
	1 (2011)			2 (2010)			3 (2009)			4 (2008)			5 (2007)			6 (2006)			7 (2005)		
Summary of taxa	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Season										Spring 2012											
Sample size	2			27			52			25			19			11			7		
Length	55–72			91–164			101–233			124–328			128–361			143–286			247–418		
Empty	50			30			40			16			16			18			14		
Invertebrates																					
Amphipoda	0	0	0	16	6	a	12	6	a	0	0	0	0	0	0	0	0	0	0	0	0
Annelida	0	0	0	8	2	16	2	a	a	0	0	0	5	2	a	15	4	a	0	0	0
Diptera	0	0	0	0	0	0	10	34	a	4	33	a	0	0	0	0	0	0	13	66	a
Ephemeroptera	100	100	100	40	77	22	41	51	4	42	55	1	24	55	a	23	57	a	13	3	a
Isopoda	0	0	0	8	6	a	5	4	a	4	5	a	0	0	0	0	0	0	0	0	0
Odonata	0	0	0	16	6	19	17	4	a	13	3	a	19	13	a	8	9	a	0	0	0
Plecoptera	0	0	0	4	1	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tricoptera	0	0	0	4	1	a	2	a	a	0	0	0	0	0	0	0	0	0	0	0	0
Fish																					
Centrarchidae																					
Green Sunfish	0	0	0	0	0	0	0	0	0	4	a	1	0	0	0	0	0	0	0	0	0
Smallmouth Bass	0	0	0	4	1	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae																					
Sculpin spp.	0	0	0	0	0	0	5	1	1	13	1	5	10	11	4	8	7	4	13	3	a
Percidae																					
Yellow Perch < 150mm	0	0	0	0	0	0	0	0	0	0	0	0	5	3	7	0	0	0	0	0	0
Yellow Perch ≥ 150mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	3	85
Salmonidae																					
Kokanee	0	0	0	0	0	0	5	1	94	21	3	93	24	12	84	39	22	95	38	23	14
Westslope Cut-throat Trout	0	0	0	0	0	0	0	0	0	0	0	0	5	1	4	0	0	0	0	0	0
Other																					
Detritus	0	0	0	0	0	0	2	a	a	0	0	0	10	2	a	8	2	a	13	3	a

Table 1. (*Cont.*).

	Age (year class)																				
	1 (2011)			2 (2010)			3 (2009)			4 (2008)			5 (2007)			6 (2006)			7 (2005)		
Summary of taxa	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Season	Summer 2012																				
Sample size	38			77			103			58			38			21			11		
Length	64–124			100–206			100–269			116–346			128–355			214–449			262–398		
Empty	11			17			11			16			13			10			9		
Invertebrates																					
Amphipoda	20	7	a	22	10	a	11	8	a	4	4	a	2	a	a	0	0	0	0	0	0
Annelida	2	a	a	3	1	a	5	1	a	7	2	a	2	1	a	3	a	a	8	1	a
Arachnida	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera	10	71	a	5	30	a	0	0	0	1	17	a	0	0	0	0	0	0	0	0	0
Coleoptera	0	0	0	0	0	0	1	14	a	0	0	0	0	0	0	3	1	a	0	0	0
Copepoda	4	15	a	2	35	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda	2	a	a	0	0	0	0	0	0	1	a	a	4	2	a	3	1	a	0	0	0
Diptera	4	1	3	7	1	a	7	14	1	5	14	a	2	1	a	7	39	a	0	0	0
Ephemeroptera	14	1	1	14	5	2	12	4	1	20	20	a	10	26	a	16	11	a	15	63	a
Hemiptera	0	0	0	0	0	0	1	a	a	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	4	a	a	9	3	1	7	8	1	4	1	a	0	0	0	0	0	0	0	0	0
Isopoda	4	1	a	3	2	a	4	22	2	7	6	a	4	1	a	0	0	0	0	0	0
Odonata	20	1	90	9	1	4	17	5	4	16	6	2	12	10	1	10	4	1	8	4	a
Plecoptera	10	1	1	6	2	a	5	4	1	1	1	a	0	0	0	0	0	0	0	0	0
Tricoptera	0	0	0	9	9	2	9	17	1	4	23	a	10	32	a	3	31	a	0	0	0
Fish																					
Centrarchidae																					
Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	2	1	a	0	0	0	0	0	0
Cottidae																					
Sculpin spp.	4	a	4	4	a	20	1	a	a	4	1	4	4	1	a	7	1	10	31	22	16
Ictaluridae																					
Brown Bullhead	0	0	0	2	a	13	2	1	6	1	a	a	6	5	2	13	3	8	8	1	21
Percidae																					
Yellow Perch < 150mm	4	a	4	4	a	20	6	1	22	5	2	7	8	10	6	3	1	a	0	0	0
Yellow Perch ≥ 150mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	43	0	0	0
Salmonidae																					
Kokanee	0	0	0	1	a	50	5	1	59	7	2	85	12	5	90	7	2	37	15	5	63
Other																					
Detritus	0	0	0	1	a	a	5	1	a	12	2	a	22	5	a	23	4	a	15	3	a

Table 1. (*Cont.*).

	Age (year class)																				
	1 (2011)			2 (2010)			3 (2009)			4 (2008)			5 (2007)			6 (2006)			7 (2005)		
Summary of taxa	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Season	Fall 2012																				
Sample size	100			79			27			32			6			10			13		
Length	72–174			90–211			102–242			127–318			148–340			208–387			242–492		
Empty	26			46			48			34			0			30			15		
Invertebrates																					
Amphipoda	10	a	a	4	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Annelida	1	a	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arachnida	1	a	a	2	a	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera	11	10	a	8	42	a	6	43	a	0	0	0	0	0	0	0	0	0	0	0	0
Copepoda	24	61	1	8	36	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda	1	a	a	2	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	18	17	18	2	a	a	6	4	1	4	8	a	0	0	0	0	0	0	0	0	0
Ephemeroptera	4	a	a	18	1	2	19	13	a	16	15	a	0	0	0	0	0	0	0	0	0
Hymenoptera	12	10	13	10	13	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	7	1	1	2	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odonata	5	1	3	6	1	1	13	8	1	12	8	4	0	0	0	0	0	0	8	6	a
Orthoptera	0	0	0	0	0	0	0	0	0	0	0	0	9	5	1	0	0	0	0	0	0
Plecoptera	1	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tricoptera	0	0	0	4	a	1	6	13	a	4	10	a	0	0	0	0	0	0	0	0	0
Fish																					
Centrarchidae																					
Black Crappie	0	0	0	0	0	0	6	2	21	0	0	0	9	14	6	0	0	0	0	0	0
Bluegill	0	0	0	0	0	0	0	0	0	4	3	3	18	24	8	0	0	0	0	0	0
Smallmouth Bass	0	0	0	2	a	5	6	4	5	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae																					
Sculpin spp.	1	a	1	16	1	51	13	4	9	4	3	a	9	5	4	13	9	6	23	19	4
Ictaluridae																					
Brown Bullhead	2	a	15	4	a	20	0	0	0	4	3	2	0	0	0	0	0	0	0	0	0
Percidae																					
Yellow Perch < 150mm	1	a	4	12	a	13	25	9	64	28	38	86	36	43	17	25	64	7	23	31	7
Yellow Perch ≥ 150mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	5	24	0	0	0
Salmonidae																					
Kokanee	1	a	37	0	0	0	0	0	0	8	5	6	9	5	64	25	14	50	23	19	62
Unknown species	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	5	13	15	19	27
Other																					
Detritus	0	0	0	2	a	1	0	0	0	16	10	a	9	5	a	13	5	a	8	6	a

Table 1. (*Cont.*).

	Age (year class)																				
	1 (2011)			2 (2010)			3 (2009)			4 (2008)			5 (2007)			6 (2006)			7 (2005)		
Summary of taxa	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Season	Spring 2013																				
Sample size	75			21			16			16			3			9			8		
Length	39–71			82–173			124–207			134–287			189–345			245–363			250–491		
Empty	48			48			0			19			33			11			13		
Invertebrates																					
Amphipoda	5	4	a	0	0	0	5	14	a	8	8	a	0	0	0	0	0	0	0	0	0
Annelida	0	0	0	8	4	9	10	5	2	8	4	2	0	0	0	6	5	a	8	4	a
Cladocera	10	38	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	20	24	a	8	22	6	10	16	2	0	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	24	10	a	15	9	2	25	35	2	39	60	6	0	0	0	6	10	a	0	0	0
Hymenoptera	0	0	0	0	0	0	0	0	0	7	2	a	0	0	0	0	0	0	8	7	a
Isopoda	17	10	a	23	39	5	10	5	a	8	16	1	0	0	0	0	0	0	0	0	0
Odonata	17	10	a	23	13	17	15	14	5	8	2	a	0	0	0	19	14	1	17	11	a
Plecoptera	5	3	a	0	0	0	5	2	a	0	0	0	0	0	0	0	0	0	0	0	0
Tricoptera	0	0	0	8	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish																					
Centrarchidae																					
Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	7	2
Cottidae																					
Sculpin spp.	0	0	0	8	4	26	0	0	0	0	0	0	0	0	0	7	10	42	8	4	2
Cyprinidae																					
Northern Pike-minnow	0	0	0	8	4	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ictaluridae																					
Brown Bullhead	0	0	0	0	0	0	15	7	89	15	6	90	0	0	0	6	14	11	17	54	11
Percidae																					
Yellow Perch < 150mm	0	0	0	0	0	0	0	0	0	0	0	0	50	50	11	19	19	19	8	4	22
Yellow Perch ≥ 150mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	7	59
Salmonidae																					
Kokanee	0	0	0	0	0	0	0	0	0	0	0	0	50	50	89	13	10	23	0	0	0
Westslope Cut-throat Trout	2	1	99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other																					
Idaho Giant Salamander	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	4	6
Detritus	0	0	0	0	0	0	5	2	a	8	2	1	0	0	0	25	19	3	8	4	a

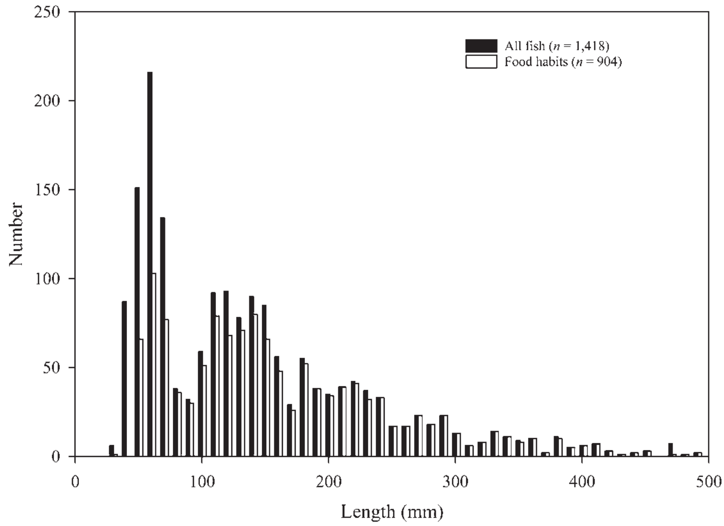

Figure 4. Length–frequency distribution of Smallmouth Bass sampled from Coeur d'Alene Lake, Idaho, during 2012 and 2013. Fish used in the food habits analysis were subsampled from the total (all) fish sampled.

mining district, which includes the Coeur d'Alene River basin, was a global leader in the production of lead, silver, and zinc. Mining, milling, and smelting practices resulted in elevated concentrations of metals that are harmful to plants, humans, and other animals (National Research Council 2005). As might be expected, the effects of heavy metal contamination have been severe with the elimination of all aquatic life in some areas (Farag et al. 1999, Maret and MacCoy 2002). The effects of metals on crayfish in Coeur d'Alene Lake is unknown and could be an important focus of future research. Nevertheless, the lack of crayfish in Smallmouth Bass stomachs is interesting given the inconsistency with other populations across the distribution of Smallmouth Bass.

A primary concern associated with the establishment of Smallmouth Bass in western North America is their potential influence on salmonids. Most of the research on Smallmouth Bass in the western United States has been conducted in systems with anadromous salmonids, particularly in the Columbia River basin. Carey et al. (2011) reported that, across studies in the Columbia River basin, juvenile Pacific salmon were in 0–65% of Smallmouth Bass stomachs and made up 0–89% of the weight consumed by Smallmouth Bass. In some systems, consumption by Smallmouth Bass can represent a substantial component of the run (i.e., outmigration). For instance, Fritts and Pearsons (2004) estimated that 4–35% of the fall Chinook Salmon run (1998–2001) in the Yakima River, Washington, was consumed by Smallmouth Bass. Tiffan et al. (2020) reported that Smallmouth Bass in the Snake River of Idaho–Washington–Oregon upstream of Lower Granite Dam consumed high numbers of juvenile fall Chinook Salmon. Without Smallmouth Bass predation, the authors estimated that adult returns at Lower Granite Dam would be 4–16% higher.

Direct predation on native vertebrates by Smallmouth Bass was uncommon in Coeur d'Alene Lake. In addition to the single Westslope Cutthroat Trout, we observed a single Northern Pikeminnow (34 mm) consumed by a 105 mm Smallmouth Bass, and a 76 mm Idaho Giant Salamander (*Dicamptodon aterrimus*) was found in a 354 mm Smallmouth Bass. Sculpin were the most common native vertebrate taxa in Smallmouth Bass diets. Fifty Smallmouth Bass (86–492 mm) consumed 81 sculpin (20–98 mm). Most of these Smallmouth Bass had a single sculpin in their stomach, but a few fish had ten or more sculpin. Walrath et al. (2015a) found the same native vertebrates in Northern Pike stomachs in Coeur d'Alene Lake, with the addition of Longnose Sucker. In contrast to Smallmouth Bass, Westslope Cutthroat Trout represented 2–30% of the biomass (by year class) consumed by Northern Pike in the system. In nearby Lake Pend Oreille, Idaho, Frawley et al. (2024) found that nonnative Walleye consumed a diversity of native fishes, including sculpin, Longnose Sucker, Northern Pikeminnow, Peamouth (*Mylocheilus caurinus*), and Mountain Whitefish. Although Smallmouth Bass consumed several species of fish in Coeur d'Alene Lake, kokanee was often the most common fish in diets and contributed the most energy to Smallmouth Bass. Kokanee is not native to many lakes in western North America, including Coeur d'Alene Lake, where it supports a highly popular recreational fishery. In addition, kokanee likely serves as an important prey item for large piscivores in Coeur d'Alene Lake, such as Bull Trout (Hansen et al. 2010, McCubbins et al. 2016). The only other diet study focused on piscivores in Coeur d'Alene Lake was conducted on Northern Pike by Walrath et al. (2015a). They found that kokanee was an extremely important component of Northern Pike diets, particularly for age-2 and older fish. More than 50% of the Northern Pike had kokanee in their stomachs and the percentage of energy consumed that was represented by kokanee regularly exceeded 80% depending on the season and year class.

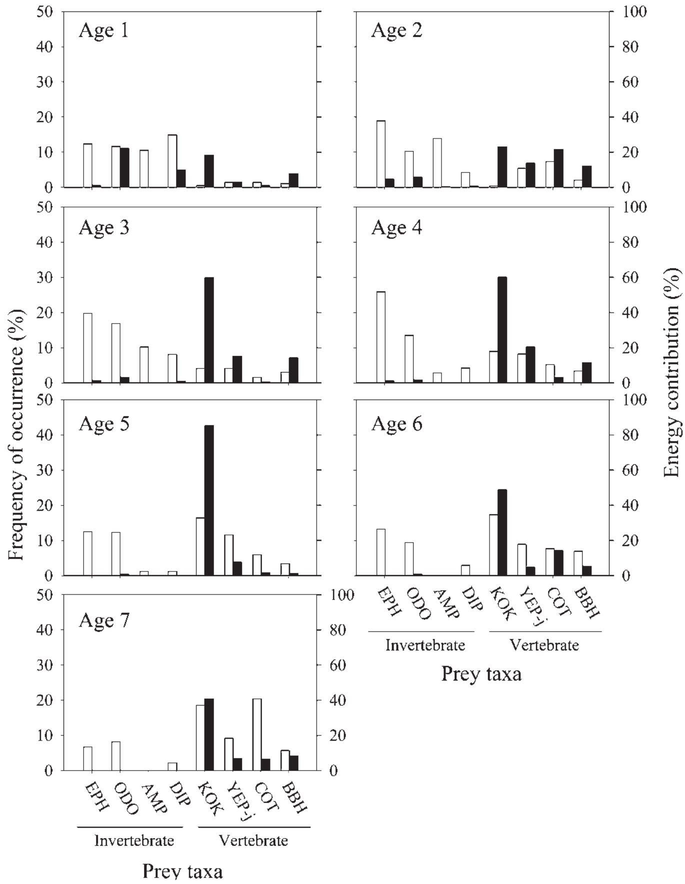

Figure 5. Frequency of occurrence (white bars) and energy contribution (black bars) of prey items in the diets of Smallmouth Bass sampled from Coeur d'Alene Lake, Idaho, during 2012 and 2013. Each panel represents a specific age of Smallmouth Bass. Abbreviations are: EPH (Ephemeroptera), ODO (Odonata), AMP (Amphipoda), DIP (Diptera), KOK (kokanee), YEP-j (Yellow Perch < 15.0 cm), COT (Cottidae), and BBH (Brown Bullhead)

Smallmouth Bass in Coeur d'Alene Lake had diverse diets that generally shifted from invertebrates in young individuals to fishes in large Smallmouth Bass. Native fishes of conservation concern were rare or absent in Smallmouth Bass stomachs. Crayfish were notably rare in Smallmouth Bass diets suggesting that either crayfish densities are low or Smallmouth Bass are avoiding them as prey. A better understanding of the distribution and abundance of crayfish would be insightful. Kokanee was a common and important component of Smallmouth Bass diets. We were unable to evaluate the potential effects of Smallmouth Bass predation on kokanee population dynamics, but such investigations would help inform management actions in Coeur d'Alene Lake and similar systems across western North America. Lastly, although we sampled across two spring seasons and noted variation in relative abundance, body condition, and diet between years, we were unable to fully quantify the role of interannual variation. Future research focused on how the diet of Smallmouth Bass varies through time would provide a more complete understanding of their role in aquatic systems.

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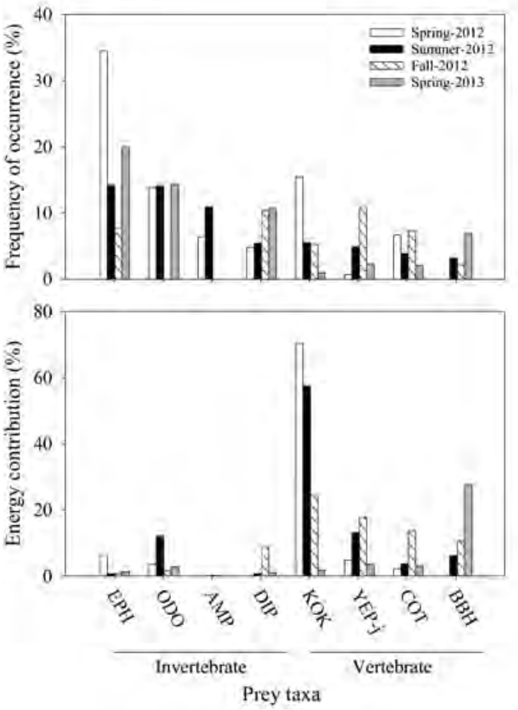

Figure 6. Frequency of occurrence and energy contribution of prey items in the diets of Smallmouth Bass sampled from Coeur d'Alene Lake, Idaho, during 2012 and 2013. Seasons include spring (March, April, May), summer (June, July, August), and fall (September, October, November). Abbreviations are: EPH (Ephemeroptera), ODO (Odonata), AMP (Amphipoda), DIP (Diptera), KOK (kokanee), YEP-j (Yellow Perch < 15.0 cm), COT (Cottidae), and BBH (Brown Bullhead).

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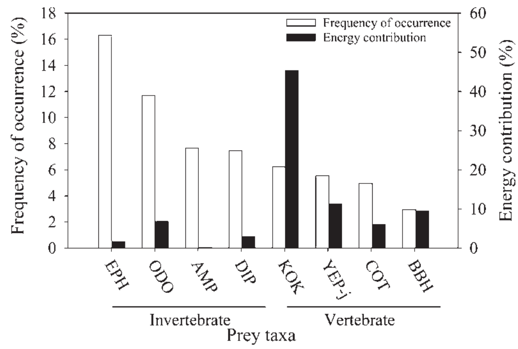

Figure 7. Frequency of occurrence and energy contribution of prey items in the diets of Smallmouth Bass sampled from Coeur d'Alene Lake, Idaho, during 2012 and 2013 (data pooled). Abbreviations are: EPH (Ephemeroptera), ODO (Odonata), AMP (Amphipoda), DIP (Diptera), KOK (kokanee), YEP-j (Yellow Perch < 15.0 cm), COT (Cottidae), and BBH (Brown Bullhead).

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