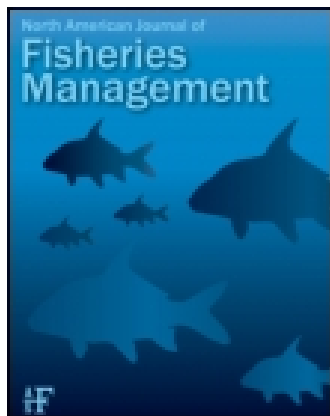


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ARTICLE

Trophic Ecology of Nonnative Northern Pike and their Effect on Conservation of Native Westslope Cutthroat Trout

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Abstract

Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* in Coeur d'Alene Lake, Idaho, have declined in recent years; predation by Northern Pike *Esox lucius*, a nonnative sport fish, is thought to be a causative mechanism. The goal of this study was to describe the seasonal food habits of Northern Pike and determine their influence on Westslope Cutthroat Trout in Coeur d'Alene Lake by using a bioenergetics modeling approach. Fish were sampled monthly from March 2012 to May 2013 using pulsed-DC electrofishing and experimental gillnetting in four bays. Northern Pike catch rates from electrofishing were generally low but increased slightly each season and were highest in the southern portion of the lake; catch rates from gillnetting were approximately 50% higher during the two spring sampling periods compared with the summer and fall. Seasonal growth and food habits of 695 Northern Pike (TL = 16.2–108.0 cm; weight = 24–9,628 g) were analyzed. Diets primarily consisted of kokanee *O. nerka*, Westslope Cutthroat Trout, and Yellow Perch *Perca flavescens*. Results of a bioenergetics model estimated that Westslope Cutthroat Trout represented approximately 2–30% of the biomass consumed by age-1–4 Northern Pike. Total Westslope Cutthroat Trout biomass consumed by Northern Pike (2008–2011 year-classes) across all seasons sampled was estimated to be 1,231 kg (95% CI = 723–2,396 kg), and the total number consumed was 5,641 (95% CI = 3,311–10,979). The highest occurrence of Westslope Cutthroat Trout in Northern Pike diets was observed during spring. Thus, reducing Northern Pike predation on Westslope Cutthroat Trout would be one tool worth considering for conserving Westslope Cutthroat Trout populations in Coeur d'Alene Lake.

The Cutthroat Trout *Oncorhynchus clarkii* historically had one of the most widespread distributions of any North American salmonid; however, Cutthroat Trout populations have been declining since the 19th century and are now a major focus of management and conservation (Gresswell 1988; Dunham 2002). A primary factor contributing to the decline of Cutthroat Trout is a reduction in habitat quality and quantity (Liknes and Graham 1988; Marnell 1988; Shepard et al. 2005;

Gresswell 2011). The construction of dams has created movement barriers that interfere with spawning and other important life history events (Liknes and Graham 1988). Many populations also exist in watersheds with extensive agriculture, where channel dewatering and sedimentation are common (Moeller 1981; Liknes and Graham 1988). Changes in water quality and damage to riparian habitat from livestock grazing have been shown to exert negative effects on Cutthroat Trout populations

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(Peterson et al. 2010). In addition, the Cutthroat Trout was among the most common fish species encountered by European settlers in the 19th century and as a result was important for subsistence and commerce (Behnke 1988). The high catchability of Cutthroat Trout and a lack of harvest regulations for this species caused many populations to be overexploited in less than 100 years (Behnke 1988).

Nonnative fishes have been shown to negatively affect Cutthroat Trout populations through competition, predation, and hybridization (Rich 1992; Shepard et al. 2005; Tabor et al. 2007; Muhlfeld et al. 2008). As populations of Cutthroat Trout have become less abundant, water bodies have often been stocked with nonnative species to create or supplement fisheries. One of the greatest factors contributing to the decline of Cutthroat Trout is their interaction with nonnative Rainbow Trout *O. mykiss*, which compete and hybridize with Cutthroat Trout (Marnell 1988; Allendorf et al. 2004; Shepard et al. 2005; Muhlfeld et al. 2009). Many remaining genetically pure populations of Westslope Cutthroat Trout *O. clarkii lewisi* exist only in headwater streams where movement barriers protect them from nonnative species (Rasmussen et al. 2010). In fact, Westslope Cutthroat Trout populations known to be genetically pure currently inhabit less than 10% of this subspecies' historic distribution in the United States and less than 20% of its historic distribution in Canada (Shepard et al. 2005). Other species, such as Brown Trout *Salmo trutta* in large streams, Brook Trout *Salvelinus fontinalis* in small streams, and Lake Trout *Salvelinus namaycush* in lake systems, have also replaced Cutthroat Trout across the species' distribution (Behnke 2002; Quist and Hubert 2004). In addition to salmonids, various warmwater and coolwater species have been introduced into systems containing Cutthroat Trout, primarily to diversify recreational angling opportunities. Some of these species include Smallmouth Bass *Micropterus dolomieu*, Largemouth Bass *M. salmoides*, Northern Pike *Esox lucius*, Walleye *Sander vitreus*, and Sauger *Sander canadensis*. Nonnative top-level predators not only have an influence on native fishes but also can greatly alter prey population structure and dynamics (Tabor et al. 2007; Muhlfeld et al. 2008).

Introductions of nonnative species have contributed to declines in Cutthroat Trout populations, particularly Westslope Cutthroat Trout, across much of the Pacific Northwest (Rich 1992; Naughton et al. 2004; Tabor et al. 2007; Muhlfeld et al. 2008). In Idaho, Westslope Cutthroat Trout are native to the Kootenai, Pend Oreille, Spokane, Clearwater, and Salmon River systems in the northern part of the state. Historically, Westslope Cutthroat Trout were abundant in Idaho and as a result were important for subsistence and commerce (Wallace and Zaroban 2013). In addition, Westslope Cutthroat Trout have cultural significance to Native Americans. In the past, the Coeur d'Alene Tribe in northern Idaho relied on Westslope Cutthroat Trout for subsistence, harvesting roughly 42,000 fish per year from Coeur d'Alene Lake and the St. Joe River

(Firehammer et al. 2012). However, Westslope Cutthroat Trout in Coeur d'Alene Lake have declined drastically, and conservation efforts have been initiated.

Over the last 10–15 years, the Coeur d'Alene Tribe has implemented restoration practices in Lake and Benewah creeks (i.e., two tributaries to Coeur d'Alene Lake) to recover populations of adfluvial Westslope Cutthroat Trout. The Coeur d'Alene Tribe is focused on restoring stream spawning and rearing habitat by increasing sinuosity, creating deep pools, enhancing large woody debris, and reconnecting streams to their floodplains (Firehammer et al. 2012). Stream renovations were initiated to increase instream survival, but there is a critical knowledge gap associated with the survival of adfluvial Westslope Cutthroat Trout once they out-migrate to Coeur d'Alene Lake as juveniles and return to spawn as adults. Recently, the Coeur d'Alene Tribe embarked on an intensive PIT-tagging study to better understand juvenile survival and adult return rates. Of the 5,300 out-migrating juveniles that were tagged during 2005–2010, only 1.7% returned as adults to Lake Creek and 2.3% returned to Benewah Creek (Firehammer et al. 2012). These juvenile-to-adult return rates are 8–12 times lower than estimates obtained using similar techniques in comparable systems (Huston et al. 1984; Stapp and Hayward 2002; Muhlfeld et al. 2009). The mechanism responsible for the poor survival of adfluvial Westslope Cutthroat Trout is unknown, but it is hypothesized to be the result of predation by nonnative species, particularly Northern Pike, in Coeur d'Alene Lake (Rich 1992; Naughton et al. 2004; Tabor et al. 2007; Muhlfeld et al. 2008).

Northern Pike are top-level predators with a circumpolar distribution. Due to their popularity in recreational fisheries, Northern Pike have been introduced into systems across North America (Crossman 1978). In addition to being stocked for sport fishery enhancement, Northern Pike have also been introduced to reduce densities of "nuisance" species, such as the Common Carp *Cyprinus carpio* and Gizzard Shad *Dorosoma cepedianum* (Pflieger 1997). Northern Pike are ambush predators that require littoral habitat with abundant vegetation for successful spawning (Crossman 1978; Casselman and Lewis 1996). They are also opportunistic predators that prefer soft-rayed fishes (Eklöv and Harrin 1989).

In the Coeur d'Alene River basin of northern Idaho, shallow, vegetated habitat and sloughs are common where tributaries enter Coeur d'Alene Lake. Juvenile adfluvial Westslope Cutthroat Trout out-migrate to Coeur d'Alene Lake during spring and must pass through habitat that is highly suitable for Northern Pike. Thus, there is the potential for spatial and temporal overlap between Westslope Cutthroat Trout and Northern Pike in areas where tributaries enter the lake. Given the need to better understand factors influencing Westslope Cutthroat Trout in Coeur d'Alene Lake, our objectives were to describe the seasonal food habits of Northern Pike in the lake and to estimate their consumption of Westslope Cutthroat Trout and other prey taxa.

METHODS

Coeur d'Alene Lake is the second-largest natural lake in Idaho, with a surface area of 12,700 ha (Figure 1). The lake has a mean depth of approximately 24 m and a maximum depth of 61 m (Rich 1992; Vitale et al. 2004). Primary tributaries to Coeur d'Alene Lake are the Coeur d'Alene and St. Joe rivers; many small streams also contribute to the system. Post Falls Dam was constructed on the outlet of Coeur d'Alene Lake in 1906 and raised the water level of the lake by 2.5 m, creating an abundance of shallow, vegetated habitats (Rich 1992). The lake has been classified as mesotrophic based on nutrient concentrations; however, heavy metals from 100 years of mining and ore processing in the watershed limit biological production (National Research Council 2005). Fisheries in Coeur d'Alene Lake are co-managed by the Coeur d'Alene Tribe and the Idaho Department of Fish and Game.

Native sport fish species in Coeur d'Alene Lake include Westslope Cutthroat Trout, Bull Trout *Salvelinus confluentus*, and Mountain Whitefish *Prosopium williamsoni*. Currently, sport fishes are primarily nonnative species, such as kokanee

O. nerka, Chinook Salmon *O. tshawytscha*, Rainbow Trout, Brook Trout, Largemouth Bass, Smallmouth Bass, Black Crappie *Pomoxis nigromaculatus*, Pumpkinseed *Lepomis gibbosus*, Yellow Perch, Brown Bullhead *Ameiurus nebulosus*, Black Bullhead *Ameiurus melas*, and Northern Pike. Other notable native species in the basin include Northern Pike-minnow *Ptychocheilus oregonensis* and Longnose Sucker *Catostomus catostomus*. Tench *Tinca tinca*, a nonnative species in North America, is also common in Coeur d'Alene Lake.

Four major bays (i.e., Wolf Lodge Bay, Cougar Bay, Windy Bay, and Benewah Lake) in Coeur d'Alene Lake were selected for this study because they are the primary areas where Northern Pike are common or because they represent important areas for sport fish management (Figure 1; Rich 1992; 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. A sampling event consisted of sampling 18 nonoverlapping sections composed of 12 gillnetting sites and 6 electrofishing sites. Sampling occurred once per month in Cougar and Wolf Lodge bays from March 2012 to May 2013. Windy Bay and Benewah Lake were sampled once per month during June–November 2012 and twice per month from March to May in both 2012 and 2013. Spring biweekly sampling was performed to increase the resolution in Windy Bay and Benewah Lake, where the Coeur d'Alene Tribe is intensely monitoring Westslope Cutthroat Trout in tributaries (i.e., Lake and Benewah creeks). Hazardous lake conditions prevented us from sampling during winter (December 2012–February 2013).

Northern Pike were sampled using pulsed-DC electrofishing and experimental gill nets. Electrofishing was conducted using a 5,000-W generator mounted in an aluminum boat with Smith-Root equipment (Smith-Root, Inc., Vancouver, Washington). Power output was standardized to 2,750–3,250 W based on ambient water conductivity ($\mu\text{S}/\text{cm}$; Miranda and Boxrucker 2009). In an effort to minimize mortality and prey digestion, gill nets (46 × 1.8 m, with panels of 2.5-, 3.2-, 3.8-, 4.4-, and 5.0-cm bar-measure mesh) were fished for 1.5–2.0 h. Kobler et al. (2008) found that Northern Pike movement was more homogeneous during winter months than in other months, with slightly higher movement occurring during the day. Those authors also reported that Northern Pike were most active at dawn and dusk during the summer. Therefore, we conducted sampling at dusk in May–September and during the day in October–April. Additionally, operation of a boat at night with low water levels and ice became hazardous during fall and winter.

All Northern Pike were measured for TL to the nearest millimeter and were weighed to the nearest gram. Each Northern Pike was marked by completely removing the left pelvic fin (Nielson 1992; Guy et al. 1997). Age structures (i.e., left pelvic fin ray) were collected from 10 fish per centimeter



FIGURE 1. Coeur d'Alene Lake, located in northern Idaho. The Idaho Department of Fish and Game manages the lake north of the Coeur d'Alene River mouth; the Coeur d'Alene Tribe manages the lake south of the river mouth as well as the Lake Creek watershed. Sampling sites were located in Cougar Bay, Wolf Lodge Bay, Windy Bay, and Benewah Lake.

length-group (Laine et al. 1991; Quist et al. 2012). Fin rays were placed into coin envelopes and were allowed to air dry before processing (Koch and Quist 2007). Cleithra from Northern Pike were collected to corroborate ages from pelvic fin rays. Agreement between cleithrum ages and pelvic fin ray ages was 100%.

Half of the captured Northern Pike were tagged by using an individually numbered, nonreward FD-94 T-bar anchor tag (7.6 cm; Floy Tag, Inc., Seattle) inserted near the posterior end of the dorsal fin. All other Northern Pike were tagged with an individually numbered, nonreward Carlin dangler tag (0.6 × 1.6 cm; Floy Tag; Quist et al. 2010) in the caudal peduncle. Individually numbered tags were used to obtain individual recapture histories, which were used to estimate Northern Pike population abundance in Program MARK (Cooch and White 2010).

Stomach contents were obtained via gastric lavage from 5 fish per centimeter length-group during each sampling event in each bay. A 12-V, 14.4-L/min pump (Fimco, North Sioux City, South Dakota) equipped with a pressure gauge, changeable hose fittings, and a pressure-release valve was used to flush stomachs (Light et al. 1983; Bowen 1996; Venturelli and Tonn 2006). Large prey items that were not flushed from the stomach were removed using forceps. Filtered water held in an on-board container was used for the lavage process to ensure that samples were not contaminated with organisms from the lake. Before a fish was released, a gastroscope was inserted through the esophagus and into the stomach to ensure the removal of all prey items, water, and air. If prey items were observed, the lavage process was repeated until the stomach was empty. Stomach contents were fixed with 10% buffered formalin (Garvey and Chipps 2012). The efficiency of removing all prey items from stomachs with the pulsed gastric lavage technique was evaluated by dissecting mortalities and examining their stomachs for any remaining content; efficiency was 98%. Stomach contents were also scanned for PIT tags by using an Allflex ISO compact reader (Allflex, San Antonio, Texas), as adfluvial Westslope Cutthroat Trout in Lake and Benewah creeks are PIT-tagged.

In the laboratory, vertebrate diet items were counted and identified to species, and invertebrate diet items were counted and identified to order. Lengths of prey items were measured to the nearest 0.002 cm by using a caliper (Mitutoyo, Aurora, Illinois). Wet and dry weights were measured to the nearest milligram. For partially digested items, total lengths and weights were estimated from hard structures (e.g., vertebrae and head capsules) by using published length–weight equations (Duke and Crossley 1975; Dumont et al. 1975; Smock 1980; Evenson and Kruse 1982; Rust 1991; Garvey and Stein 1993; Ganihar 1997; Altindag et al. 1998; Behnke et al. 1999; Sabo et al. 2002; Anders et al. 2003; Baumgartner and Rothhaupt 2003; Wigley et al. 2003).

Relative weight (W_r) was used to evaluate body condition of Northern Pike:

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

where W is the weight of an individual and W_s is the standard weight from a species-specific length–weight regression (Neumann et al. 2012). A W_r value greater than 100 indicates above-average body condition.

Food habits data were pooled by season based on water temperature: spring (March–May), summer (June–August), and fall (September–November). All data were summarized by Northern Pike year-class for those year-classes that were represented by at least five individuals in each season (i.e., the 2008–2011 year-classes). Frequency of occurrence, percent by number, percent energy contribution, and prey-specific energy contribution were used to summarize the 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 energy of that taxon by the total energy of all prey items. Prey-specific energy contribution was the percentage of energy contributed by a prey taxon to total energy (all taxa) for only those stomachs in which the prey taxon occurred (Amundsen et al. 1996). Only Northern Pike with identifiable prey items in their stomachs were used in the food habits analysis. Unidentifiable prey items were rare (<1%) and therefore removed from further analysis.

To gain insight on prey importance, feeding strategy, and components of diet niche width for Northern Pike in Coeur d'Alene Lake, we used a modification of the Costello method, which plots the prey-specific energy contribution of a prey taxon against its frequency of occurrence (Amundsen et al. 1996). Feeding strategies can be defined as follows: (1) rare taxa occur at low frequencies, contribute little energy, and are typical of a generalist diet; (2) prey taxa that occur at high frequencies and that contribute substantial amounts of energy indicate specialization at the population level; and (3) prey taxa with low frequencies of occurrence and high prey-specific energy contributions indicate specialization by individuals (Amundsen et al. 1996).

Bioenergetics modeling conducted with Fish Bioenergetics 3.0 (Hanson et al. 1997) was used to estimate the weights of various taxa consumed by Northern Pike. Bioenergetics models are popular for understanding the growth and trophic ecology of fishes and are based on the generalized equation

$$C = (R + A + S) + (F + U) + (\Delta B + G),$$

where C = consumption, R = respiration, A = active metabolism, S = specific dynamic action, F = egestion, U = excretion, ΔB = somatic growth, and G = gonad production (Hanson et al. 1997). The simulation covered 440 d (from March 15, 2012, to May 31, 2013) with a daily time step and

TABLE 1. Biomass (g) of individual prey types consumed by Northern Pike in Coeur d'Alene Lake, Idaho, as estimated with bioenergetics models. Estimates are provided for each Northern Pike year-class (2008–2011) and each season. Months were grouped together based on water temperature: spring (March–May), summer (June–August), and fall (September–November).

Taxon	2011 year-class				2010 year-class			
	Spring 2012	Summer 2012	Fall 2012	Spring 2013	Spring 2012	Summer 2012	Fall 2012	Spring 2013
Invertebrates								
Annelida	28.88	0.00	0.00	0.05	0.00	0.00	0.00	0.01
Coleoptera	0.00	0.00	0.00	0.00	0.07	0.90	0.00	0.00
Decapoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
Fish								
Catostomidae								
Largescale Sucker	7.04	0.00	0.00	0.00	30.31	1.47	58.50	0.00
Centrarchidae								
Black Crappie	30.20	0.00	0.00	1.18	0.00	0.00	8.67	29.42
Bluegill	0.00	0.00	549.67	4.82	0.00	0.00	18.02	0.00
Largemouth Bass	0.00	87.63	0.00	0.00	0.00	0.08	7.66	0.00
Unknown species	0.00	0.00	0.00	0.00	0.00	0.00	12.38	0.00
White Crappie <i>Pomoxis annularis</i>	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.00
Clupeidae								
Pacific Herring <i>Clupea pallasii</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.81
Cottidae								
Sculpin	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cyprinidae								
Northern Pikeminnow	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tench	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Esocidae								
Northern Pike	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
Ictaluridae								
Brown Bullhead	0.00	17.82	0.00	0.00	17.77	0.00	17.27	0.74
Percidae								
Yellow Perch < 15.0 cm	24.50	134.96	264.77	32.25	46.59	19.33	97.55	196.65
Yellow Perch ≥ 15.0 cm	0.00	0.00	0.00	155.60	106.07	92.76	174.83	77.91
Salmonidae								
Kokanee	0.00	0.00	0.00	94.53	238.26	55.03	108.86	98.50
Unknown species	0.00	0.00	0.00	0.68	0.00	0.00	0.00	3.88
Westslope Cutthroat Trout	0.00	0.00	0.00	26.80	216.79	345.48	0.00	96.55
Other								
Idaho giant salamander <i>Dicamptodon aterrimus</i>	0.00	0.00	0.00	0.00	0.00	0.00	1.99	0.00
Detritus	32.99	46.24	0.00	0.00	0.00	12.23	0.01	0.00

was divided into four periods (i.e., spring, summer, and fall 2012; and spring 2013) to better represent seasonal trends in consumption and growth for each Northern Pike year-class. Bioenergetics models were not developed for winter (i.e., December 1, 2012–March 14, 2013) because no sampling occurred during that period.

The two most common uses of bioenergetics models are for estimating how environmental conditions affect growth and

estimating the weight of prey consumption by predators (Hartman and Kitchell 2008). The models require water temperature data, prey energy densities, predator energy densities, and cohort-specific information on diet proportions, initial weights, final weights, and physiological parameters for the focal species (e.g., Hanson et al. 1997; Muhlfeld et al. 2008). Water temperature was recorded by three Onset temperature loggers (Model H08-001-02; Onset, Cape Cod, Massachusetts)

TABLE 1. Extended.

Taxon	2009 year-class				2008 year-class			
	Spring 2012	Summer 2012	Fall 2012	Spring 2013	Spring 2012	Summer 2012	Fall 2012	Spring 2013
Invertebrates								
Annelida	0.24	0.00	0.00	64.88	0.21	0.00	0.00	0.00
Coleoptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Decapoda	0.00	196.72	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Odonata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fish								
Catostomidae								
Largescale Sucker	0.00	0.00	35.57	19.95	0.00	0.00	0.00	0.00
Centrarchidae								
Black Crappie	0.00	0.00	53.73	0.00	0.21	0.00	0.00	22.87
Bluegill	0.00	0.00	53.05	0.00	0.00	0.00	0.00	0.00
Largemouth Bass	18.63	0.00	230.66	0.00	0.00	0.00	0.00	0.00
Unknown species	0.00	0.00	0.00	0.00	0.00	0.00	9.76	64.19
White Crappie <i>Pomoxis annularis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Clupeidae								
Pacific Herring <i>Clupea pallasii</i>	0.00	0.00	0.00	113.99	0.00	0.00	0.00	0.00
Cottidae								
Sculpin	0.00	0.00	0.00	0.00	0.52	0.00	0.00	0.00
Cyprinidae								
Northern Pikeminnow	0.00	0.00	44.36	12.82	0.00	0.00	0.00	0.00
Tench	0.00	0.00	0.00	125.10	36.29	0.00	0.00	0.00
Esocidae								
Northern Pike	0.00	0.00	0.00	0.00	13.16	0.00	0.00	0.00
Ictaluridae								
Brown Bullhead	18.05	217.82	38.88	0.00	0.05	0.00	0.00	16.56
Percidae								
Yellow Perch < 15.0 cm	76.59	3.68	210.26	95.65	41.55	0.00	0.22	0.00
Yellow Perch ≥ 15.0 cm	50.40	118.98	29.73	87.16	16.76	73.15	160.93	129.20
Salmonidae								
Kokanee	233.62	186.63	339.03	181.87	80.85	786.76	296.44	178.93
Unknown species	13.44	0.00	0.00	0.00	37.31	0.00	56.42	0.00
Westslope Cutthroat Trout	142.29	4.80	128.28	52.04	74.39	18.66	287.11	160.69
Other								
Idaho giant salamander <i>Dicamptodon aterrimus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Detritus	0.00	0.00	0.02	0.00	0.00	36.72	0.00	0.00

in each of the four bays. Temperature loggers were placed at depths varying from 0.9 to 10.7 m across bays and recorded the temperatures that were likely to be experienced by Northern Pike. The loggers recorded a water temperature (°C) every 6 h to generate a mean daily temperature. Caloric densities for prey items and predators were obtained from the published literature (Cummins and Wuycheck 1971; Yule and Luecke 1993; Bryan et al. 1996; Hanson et al. 1997; Liao et al. 2004; Antolos et al. 2005; Muhlfeld et al. 2008). Dietary

information for each sampling day was aggregated across all individual Northern Pike by year-class and was input into the model as the proportion by weight of prey taxa consumed. Initial and final weights of Northern Pike for each period and year-class were estimated using the median weights of individuals from each year-class. If an initial or final weight was less than the previous value, the weight was assumed to be the same as that recorded for the previous period. Physiological parameters from Bevelhimer et al. (1985) were developed for

TABLE 2. Total biomass (g) of individual prey types consumed by Northern Pike in Coeur d'Alene Lake, as estimated with bioenergetics models. Estimates are presented for each Northern Pike year-class (2008–2011) as well as summed across year-classes.

Taxon	Year-class				Total
	2011	2010	2009	2008	
Invertebrates					
Annelida	28.93	0.01	65.12	0.21	94.27
Coleoptera	0.00	0.97	0.00	0.00	0.97
Decapoda	0.00	0.00	196.72	0.00	196.72
Hymenoptera	0.00	0.00	0.00	0.04	0.04
Odonata	0.00	0.04	0.00	0.00	0.04
Fish					
Catostomidae					
Largescale Sucker	7.04	90.27	55.52	0.00	152.83
Centrarchidae					
Black Crappie	31.39	38.09	53.73	23.08	146.29
Bluegill	554.49	18.02	53.05	0.00	625.57
Largemouth Bass	87.63	7.74	249.29	0.00	344.66
Unknown species	0.00	12.38	0.00	73.95	86.33
White Crappie	0.41	0.00	0.00	0.00	0.41
Clupeidae					
Pacific Herring	0.00	3.81	113.99	0.00	117.80
Cottidae					
Sculpin	0.00	0.00	0.00	0.52	0.52
Cyprinidae					
Northern Pikeminnow	0.00	0.00	57.18	0.00	57.18
Tench	0.00	0.00	125.10	36.29	161.39
Esocidae					
Northern Pike	0.00	0.02	0.00	13.16	13.17
Ictaluridae					
Brown Bullhead	17.82	35.78	274.75	16.61	344.96
Percidae					
Yellow Perch < 15.0 cm	486.48	360.13	386.19	41.77	1,274.56
Yellow Perch ≥ 15.0 cm	155.60	451.57	286.28	380.04	1,273.48
Salmonidae					
Kokanee	94.53	500.65	941.14	1,342.98	2,879.31
Unknown species	0.68	3.88	13.44	93.73	111.73
Westslope Cutthroat Trout	26.80	658.82	327.40	540.85	1,553.86
Other					
Idaho giant salamander	0.00	0.35	0.00	0.00	0.35
Detritus	79.23	12.24	0.02	36.72	128.22
All prey	1,571.02	2,196.74	3,198.94	2,599.93	

Northern Pike varying from 12.8 to 22.7 cm TL and from 9.5 to 53.2 g. Bean (2010) demonstrated that there is a risk of overestimating consumption when the parameters developed by Bevelhimer et al. (1985) are applied to larger individuals (i.e., >22.7 cm). Therefore, to correct inaccuracies for larger individuals, Bean (2010) developed parameters for Northern Pike varying from 25.0 to 71.8 cm TL and from 86 to 2,146 g. Thus, physiological parameters from Fish Bioenergetics 3.0 (i.e., Bevelhimer et al. 1985) were used for the 2011 year-class, whereas parameters from Bean (2010) were used for the

2008–2010 year-classes. Bioenergetics models were not developed for the 2005–2007 year-classes, as fewer than five individuals were captured during each season.

After all species- and site-specific data were entered, the proportion of maximum consumption (P_c) was calculated as

$$P_c = \frac{C}{(C_{max} \times r_c)},$$

where C is the estimated consumption, C_{max} is the maximum consumption of a specific ration at a given temperature, and r_c

TABLE 3. Estimates of total Westslope Cutthroat Trout (WCT) biomass consumed by Northern Pike (2008–2011 year-classes) in Coeur d'Alene Lake from March 15, 2012, to May 31, 2013 (excluding December 1, 2012–March 15, 2013). Northern Pike age composition percentages were derived from an age–length key. The 95% CIs are shown in parentheses for Northern Pike abundance (N) and total WCT biomass.

Year-class	Age composition (%)	Northern Pike N	Total WCT biomass (kg)
2011	19.5	637 (358–1,240)	17.1 (9.6–33.2)
2010	31.4	1,026 (576–1,997)	676.1 (379.8–1,315.8)
2009	30.8	1,007 (565–1,959)	329.6 (185.1–641.4)
2008	11.8	386 (217–751)	208.6 (117.2–405.9)
Total	93.5	3,056 (1,717–5,947)	1,231.3 (691.7–2,396.4)

is a temperature-dependent proportional adjustment of the consumption rate (Hanson et al. 1997). In the present model, P_c was estimated by solving the equation with observed growth and temperature data.

Program MARK (Cooch and White 2010) was used to estimate the population abundance of Northern Pike in each of the study bays in Coeur d'Alene Lake by using closed-population capture–recapture models. Closed capture models include a single mixture, so only two parameters are used: the capture probability (p_i) and the recapture probability (c_i). We used this method to estimate population abundance with four models: M_0 , M_b , M_r , and M_{tb} . Model M_0 was the null model, with constant detection probabilities. Model M_b assumed that p_i was equal to c_i . Model M_r also assumed that c_i and p_i were equal, but the values were allowed to vary through time. In model M_{tb} , p_i and c_i were modeled as constant offsets of one another. The four candidate models were compared in an information theoretic framework by using Akaike's information criterion corrected for small sample size (Burnham and Anderson 2002). The abundance of Northern Pike in each bay was aggregated to estimate the total population abundance. Total abundance of Northern Pike in each year-class was calculated by multiplying the estimated total population abundance by the percent age composition derived from an age–length key.

The total weight of Westslope Cutthroat Trout consumed seasonally by Northern Pike was estimated as follows: (population abundance of Northern Pike [2008–2011 year-classes]) \times (the corresponding estimate of Westslope Cutthroat Trout biomass consumed by an individual Northern Pike). The estimated total number of Westslope Cutthroat Trout consumed by Northern Pike was derived from the Westslope Cutthroat Trout's (1) estimated total consumed biomass, (2) length–weight relationship, and (3) frequency of consumption.

RESULTS

Sampling was performed on 138 d, and 15,645 individual fish representing 24 species were captured. Electrofishing effort totaled 62.4 h, and 638 gill nets were fished for 1,166.0 h. In total, 58 Northern Pike were sampled with electrofishing and 678 were sampled with gillnetting. Although

electrofishing catch rates varied greatly among season and among bays, Northern Pike catch rates were consistently higher in Benewah Lake than in the other bays (Figure 2). Northern Pike catch rates from gillnetting during the two spring sampling periods were twice as high as the catch rates observed during summer and fall. The data suggest that body condition (W_r) of Northern Pike decreased between summer and fall and increased the following spring (Figure 3). Additionally, Northern Pike in Windy Bay tended to be in better condition than those in the other bays across all seasons. Among the 736 Northern Pike captured, 573 were marked, 98 were recaptured, and 73 were mortalities. The recapture rate of Northern Pike was highest (38%) in Windy Bay, whereas the recapture rate in the other bays was roughly 9%.

Seasonal growth and food habits were analyzed from 695 Northern Pike (including recaptures) varying from 16.2 to 108.0 cm TL and from 24 to 9,628 g. Age of Northern Pike varied from 1 to 7 years; approximately 95% of individuals were ages 1–4. In general, the majority of growth occurred between fall and spring for most of the Northern Pike year-classes (Figure 4).

The proportion of empty stomachs varied among year-classes and seasons but was highest for most year-classes during spring 2012 (Figure 5; Appendix Table A.1). For Northern Pike belonging to the 2011 year-class, the diet was dominated by warmwater species (i.e., Yellow Perch, Bluegills *Lepomis macrochirus*, and Brown Bullheads). Salmonids became an important prey taxon for the 2011 year-class during the spring of 2013 and accounted for approximately 40% of the total energy consumed by that year-class. For older Northern Pike (2008–2010 year-classes), the diets were dominated by salmonids (i.e., kokanee and Westslope Cutthroat Trout). Throughout the year, kokanee represented the highest frequency of occurrence, percent by number, and energy contribution to the diet. Kokanee were consumed at the highest rate during summer, accounting for 87% of the total energy consumed. Northern Pike consumption of Westslope Cutthroat Trout was highly variable among seasons. During spring 2012, Westslope Cutthroat Trout occurred in approximately 25% of Northern Pike stomachs but contributed roughly 75% of the total energy consumed (Figure 5). During summer and fall,

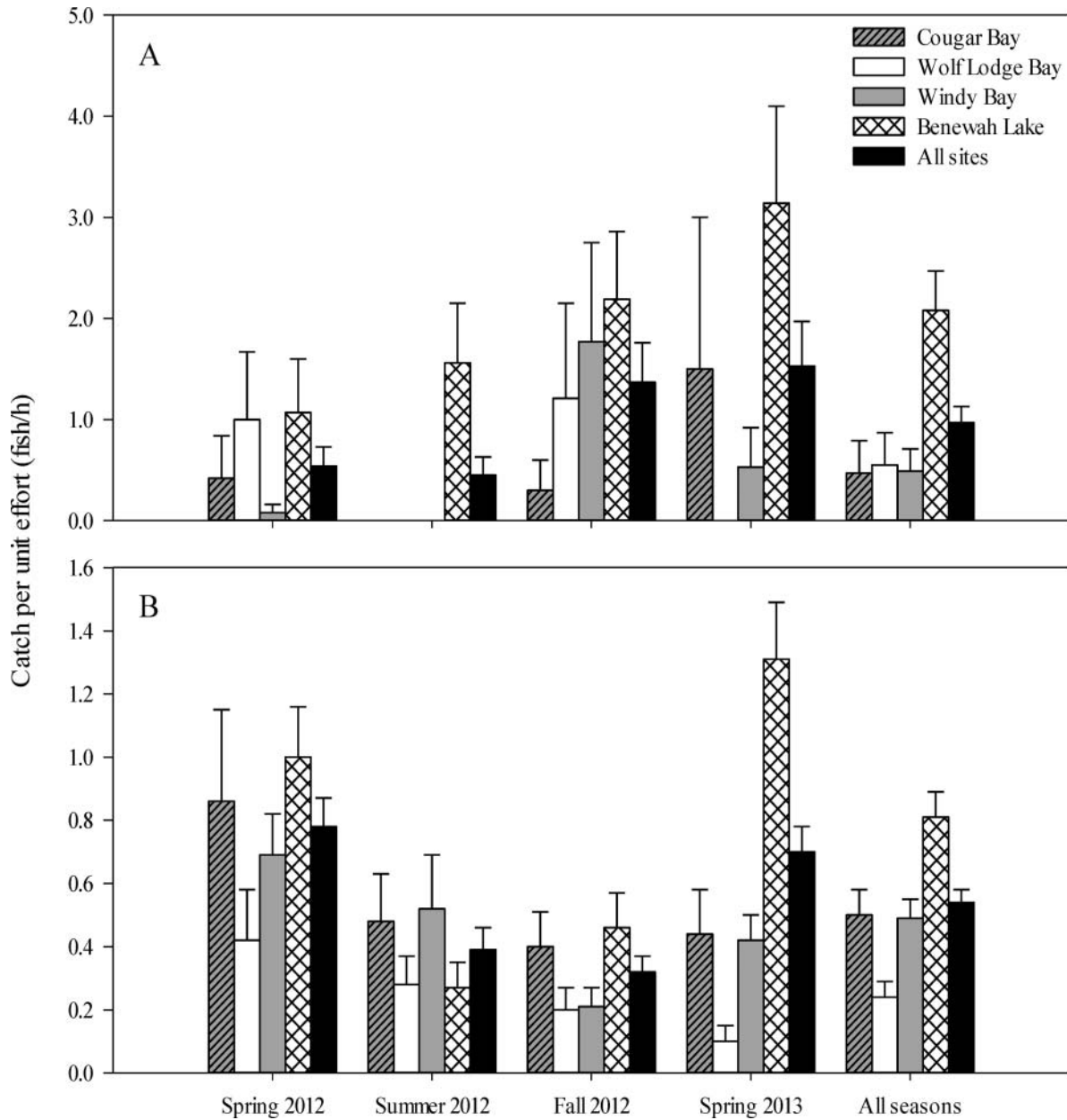


FIGURE 2. Mean (+SE) Northern Pike catch per unit effort (fish/h) with (A) electrofishing and (B) gillnetting by season in Coeur d'Alene Lake from March 2012 to May 2013. Months were grouped together based on water temperature: spring (March–May), summer (June–August), and fall (September–November).

percent occurrence and energy contribution of Westslope Cutthroat Trout in the diet decreased by about 50%. In spring 2013, the occurrence of Westslope Cutthroat Trout in Northern Pike diets increased again relative to summer and fall (Figure 5). The bioenergetics models estimated that Westslope Cutthroat Trout contributed approximately 2–30% of the biomass consumed by age-1–4 Northern Pike (Tables 1, 2). Seasonal P_c values for Northern Pike in Coeur d'Alene Lake were generally highest during spring and lowest during summer (Figure 6).

The estimate of Northern Pike abundance generated by the best candidate model was 3,268 fish (95% CI = 2,000–6,361) across the four study bays. For the Northern Pike year-classes used in the bioenergetics model (i.e., the 2008–2011 year-classes), abundance was estimated at 3,056 fish (95% CI = 1,793–5,947; Table 3). The TL of Westslope Cutthroat Trout consumed by Northern Pike varied from 8.7 to 43.7 cm and averaged 25.0 cm (Figure 7). The TLs of Westslope Cutthroat Trout consumed by Northern Pike were highly variable across seasons and generally increased with Northern Pike TL

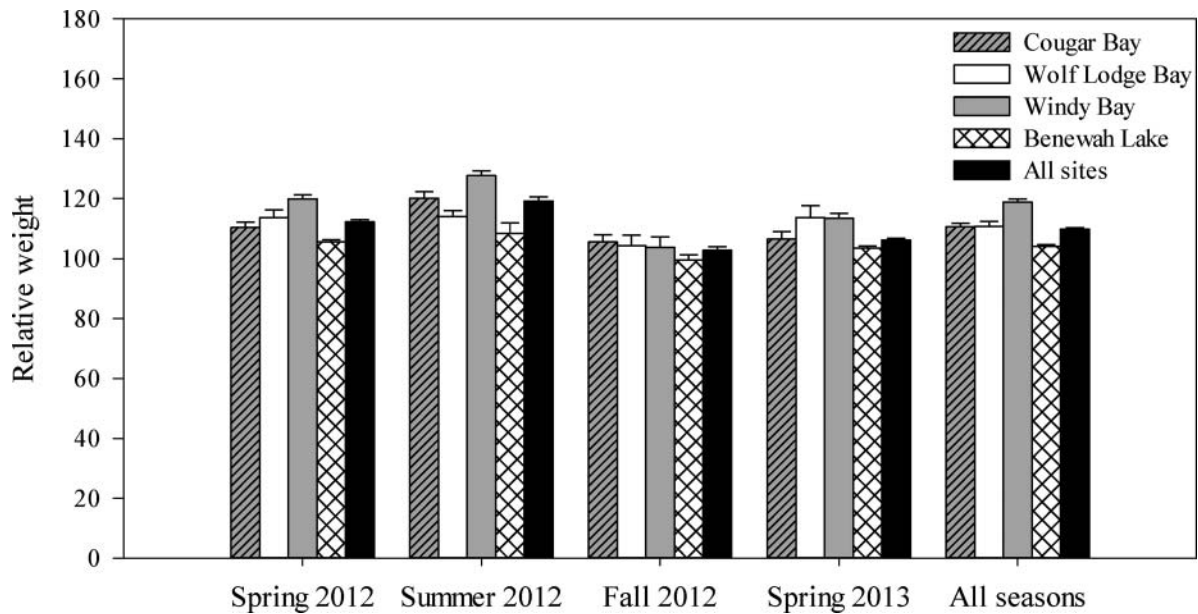


FIGURE 3. Mean (+SE) relative weights of Northern Pike captured in four bays of Coeur d'Alene Lake from March 2012 to May 2013. Means were calculated for each season as well as for each site across all seasons. Months were grouped together based on water temperature: spring (March–May), summer (June–August), and fall (September–November).

(Figure 8). The total Westslope Cutthroat Trout biomass consumed seasonally by Northern Pike (2008–2011 year-classes) in the four bays was estimated to be 1,231 kg (95% CI = 723–2,396 kg), and the total number of Westslope Cutthroat Trout consumed was estimated at approximately 5,641 fish (95% CI = 3,311–10,979).

DISCUSSION

Northern Pike have been introduced into many watersheds to create recreational fishing opportunities throughout North America, including Coeur d'Alene Lake. Unfortunately, many studies have found that Northern Pike can have detrimental effects on native fishes (Muhlfeld et al. 2008; Sepulveda et al. 2013). Therefore, an understanding of the effects of Northern Pike on native fishes is critical for developing management strategies to balance recreational sport fisheries with efforts to conserve native fishes, particularly species like the Westslope Cutthroat Trout.

The food habits of Northern Pike have been extensively studied throughout the species' distribution; although Northern Pike are generally piscivorous, they are highly opportunistic (Frost 1954; Soupier et al. 2000; Venturelli and Tonn 2006). For example, Soupier et al. (2000) reported that invertebrates were common in Northern Pike diets when the availability and abundance of fish were low in six lakes within Voyageurs National Park, Minnesota. Similarly, in three eutrophic lakes in northeast Alberta that lacked prey fishes, introduced Northern Pike consumed leeches and other invertebrates (Venturelli and Tonn 2006). Northern Pike in the current study consumed

a diversity of food items, including invertebrates, fish, and salamanders. Invertebrates were consumed sporadically throughout the year but contributed little to the overall amount of energy consumed by Northern Pike in Coeur d'Alene Lake. Rather, kokanee had the greatest energy contribution to the diets in each season. Westslope Cutthroat Trout were consumed at the highest frequency during spring. Northern Pike also preyed on spiny-rayed fishes (e.g., Yellow Perch and Black Crappies) throughout the year, with the highest occurrence in fall 2012 and spring 2013, likely a result of prey availability. Eklöv and Harrin (1989) reported that Northern Pike preferred soft-rayed fishes and that Northern Pike switched to spiny-rayed fishes or cannibalism when preferred prey types were unavailable.

Ontogenetic changes in the diet are common for Northern Pike (Frost 1954; Miller and Kramer 1971). The only exception appears to be in systems with simple fish assemblages (Soupier et al. 2000). In Coeur d'Alene Lake, ontogenetic shifts in the food habits of Northern Pike were apparent, particularly between ages 1 and 2. For the 2011 year-class, diets primarily consisted of Yellow Perch less than 15.0 cm, Brown Bullheads, and centrarchids during fall 2012. In spring 2013, the diets of the 2011 year-class shifted toward large Yellow Perch (i.e., ≥ 15.0 cm) and salmonids. Although the data suggest that Northern Pike undergo an ontogenetic shift in feeding habits toward salmonids at a young age, factors such as prey availability, habitat, and gape size also likely play a role in the shift (Nilsson and Bronmark 2000).

Growth of Northern Pike in Coeur d'Alene Lake varied among year-classes and among seasons. Most year-classes

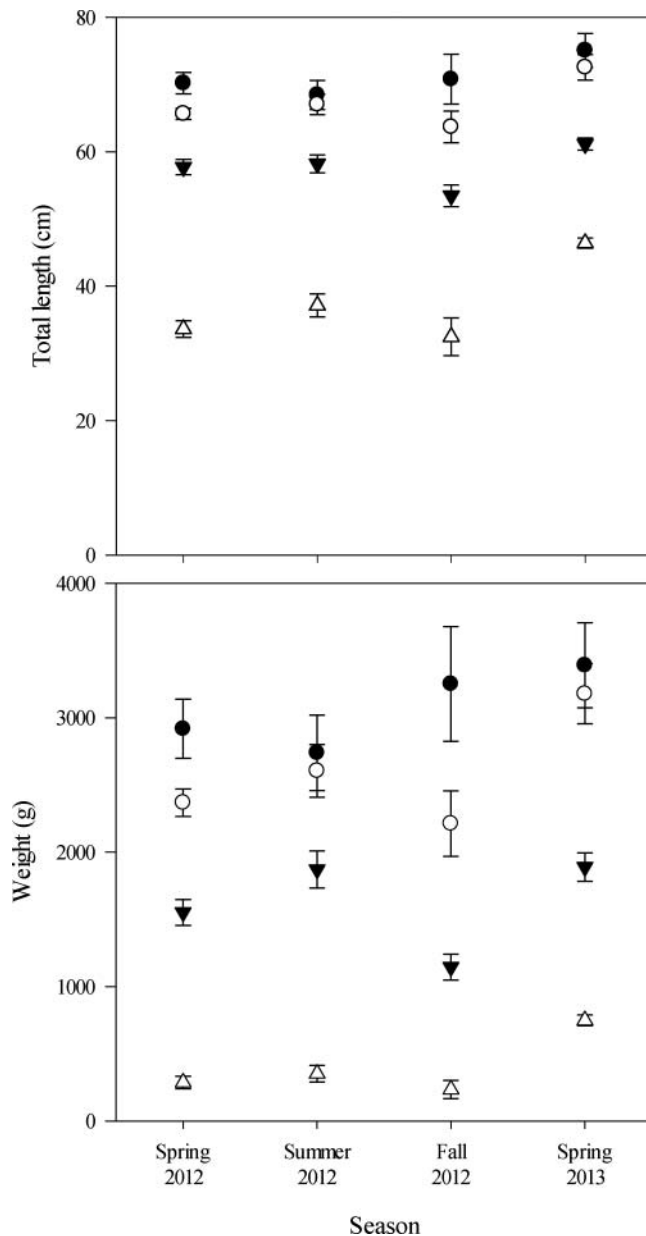


FIGURE 4. Mean (\pm SE) TLs and weights of Northern Pike from four year-classes (black shaded circles = 2008; open circles = 2009; black shaded triangles = 2010; open triangles = 2011) sampled in Coeur d'Alene Lake from March 2012 to May 2013. Months were grouped together based on water temperature: spring (March–May), summer (June–August), and fall (September–November).

increased in weight from spring to summer, but weight then decreased in the fall. Interestingly, about 50% of the annual growth in weight was achieved between fall and the beginning of the next spring. Headrick and Carline (1993) reported similar results, with Northern Pike losing weight from May to October and then gaining weight from October to March. Other coolwater species have also been observed to exhibit the majority of their growth in the fall. For example, Quist et al.

(2002) reported that for Walleyes in Glen Elder Reservoir, Kansas, approximately 80% of length and weight was achieved between August and October.

Percentage of C_{max} reflects the intensity of predation and prey availability (Rice et al. 1983). Seasonal P_c values were consistently highest for the 2011 year-class of Northern Pike in Coeur d'Alene Lake, likely due to the increased metabolic demand in juveniles (Bean 2010). We also observed a seasonal pattern in which estimates of P_c were generally highest during spring for all cohorts. The high estimates of P_c for spring likely reflect the availability of salmonids as prey and the post-spawn feeding intensity of Northern Pike. Low P_c values for Northern Pike in the summer and fall are probably attributable to a decrease in prey availability and the lower metabolic rates achieved by Northern Pike as they move to cooler water during those seasons (Bevelhimer et al. 1985).

As concerns over nonnative species increase, many such species have been the focus of removal or suppression efforts (Mueller 2005; Spens and Ball 2008; Kolar et al. 2010). However, a high density of other nonnative species may actually assist in the recovery of native fish populations. When a predator's preferred prey is depleted, predators often switch to another prey type, thereby allowing the preferred prey type to recover (Sinclair et al. 2006). The current study suggests that some nonnative species may act as a predation buffer for Westslope Cutthroat Trout throughout much of the year. Specifically, kokanee and Yellow Perch (nonnative species) each accounted for 30% of the total annual biomass consumed by Northern Pike. The occurrence of a predation buffer has also been reported for other aquatic systems. Stapanian and Madenjian (2007) determined that when Sea Lampreys *Petromyzon marinus* began preying on Lake Trout in Lake Erie, Burbot *Lota lota* increased in abundance.

Nonnative prey species may create a predation buffer for Westslope Cutthroat Trout, but numerous studies in the Pacific Northwest have shown that Northern Pike consume large quantities of Westslope Cutthroat Trout when present. For example, Muhlfeld et al. (2008) estimated that Northern Pike in the upper Flathead River system, Montana, consumed approximately 13,000 Westslope Cutthroat Trout annually. Similarly, Rich (1992) reported that Westslope Cutthroat Trout contributed about 45% of the prey weight consumed by Northern Pike in Killarney Lake, Idaho. More importantly, the ability of Northern Pike to consume large quantities of Westslope Cutthroat Trout suggests that high densities of Westslope Cutthroat Trout may not be feasible in a system that contains Northern Pike. An exception was provided by Sepulveda et al. (2013), who reported that salmonid escapement objectives were met in Wood River Lake, Alaska, despite a high level of predation by Northern Pike. Sepulveda et al. (2013) hypothesized that salmonid and Northern Pike habitats were spatially segregated.

Northern Pike predation on Westslope Cutthroat Trout in Coeur d'Alene Lake decreased in the summer and fall,

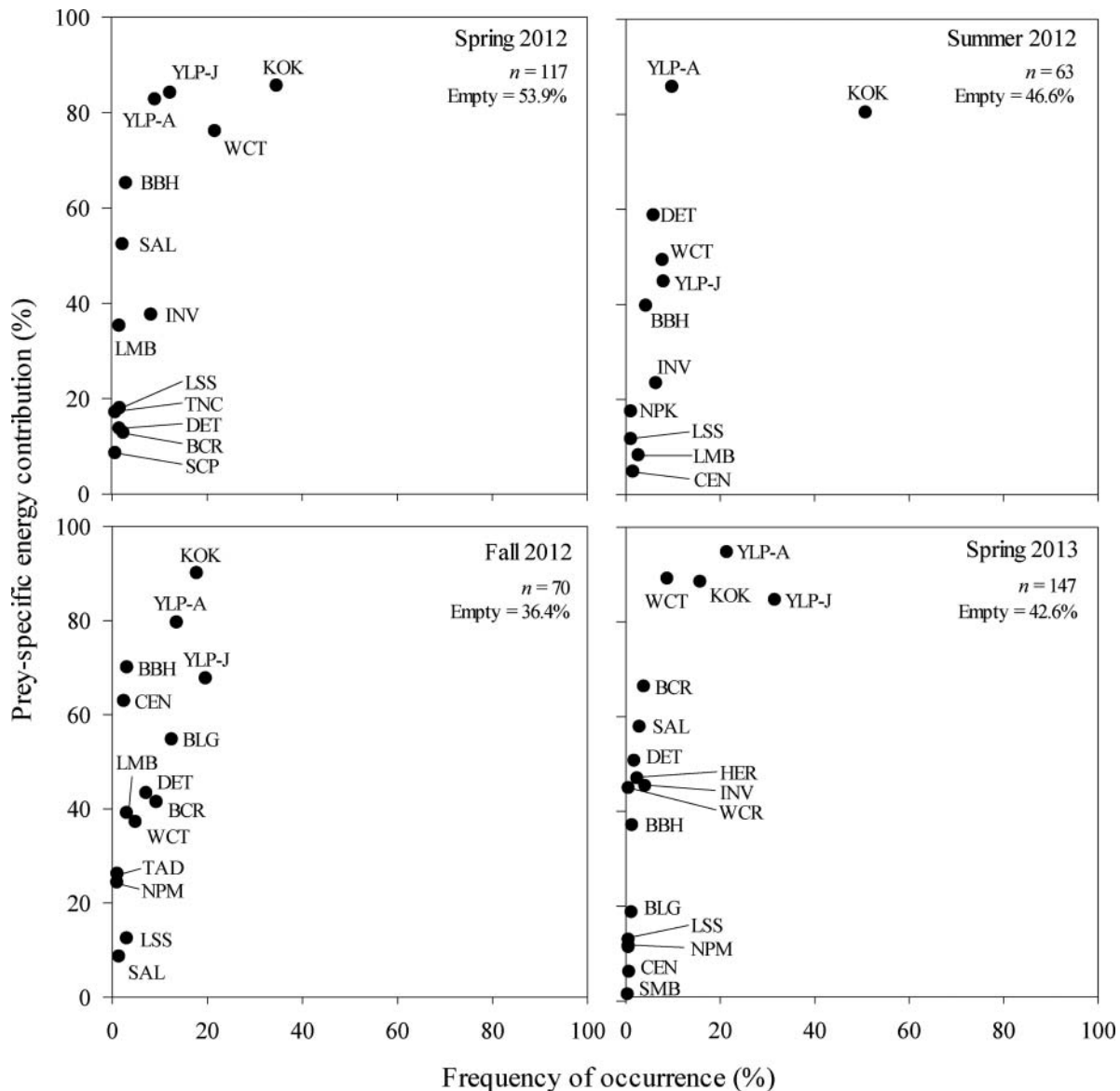


FIGURE 5. Frequency of occurrence and prey-specific energy contribution of prey types in the diets of Northern Pike sampled from Coeur d'Alene Lake during spring, summer, and fall 2012 and spring 2013. The seasonal frequency of empty stomachs and the sample size (n ; the number of Northern Pike stomachs with diet contents) are also provided (INV = invertebrates; LSS = Largemouth Sucker; BCR = Black Crappie; BLG = Bluegill; LMB = Largemouth Bass; WCR = White Crappie; CEN = Centrarchidae; HER = Pacific Herring; SCP = sculpin; NPM = Northern Pikeminnow; TNC = Tench; NPK = Northern Pike; BBH = Brown Bullhead; YLP-A = Yellow Perch ≥ 15.0 cm; YLP-J = Yellow Perch < 15.0 cm; KOK = kokanee; WCT = Westslope Cutthroat Trout; SAL = Salmonidae; DET = detritus; TAD = tadpole; SMB = Smallmouth Bass).

suggesting habitat segregation during those periods. Habitat segregation between salmonids and Northern Pike is possible because salmonids typically spend minimal time in the shallow, vegetated areas commonly occupied by Northern Pike (D'Angelo and Muhlfeld 2013). Unfortunately, the increased occurrence of Westslope Cutthroat Trout in Northern Pike diets during spring may negate any benefits obtained from habitat segregation during other time periods. Although the period of spatial overlap appears to be relatively short (i.e., April and May) based on Northern Pike diets, previous

research has shown that Northern Pike can consume large quantities of prey over a short time period. In a study of the Danish River, Denmark, Jepsen et al. (1998) found that Northern Pike predation over a 3-week period was responsible for 56% of Atlantic Salmon *Salmo salar* smolt mortalities. In Coeur d'Alene Lake, approximately 80% of the predation on Westslope Cutthroat Trout in 2012 occurred during spring. However, the potential effects of Northern Pike predation on Westslope Cutthroat Trout varied depending on the study location. Although only 29% of the Northern Pike were captured in

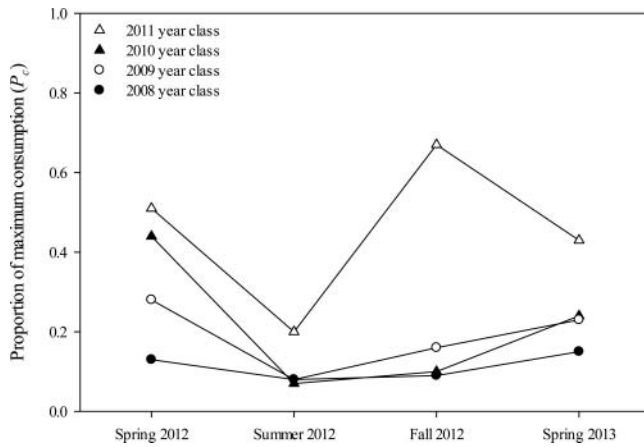


FIGURE 6. Proportion of maximum consumption (P_c) from the bioenergetics model used to estimate consumption and growth of four year-classes of Northern Pike in Coeur d'Alene Lake from March 2012 to May 2013. Months were grouped together based on water temperature: spring (March–May), summer (June–August), and fall (September–November).

Windy Bay, those fish accounted for 75% of the Westslope Cutthroat Trout that were consumed. Based on our estimates of abundance and consumption, Northern Pike consumed approximately 335 adult Westslope Cutthroat Trout (≥ 30.0 cm) in Windy Bay during spring 2012. In Lake Creek, the tributary that enters Windy Bay, the estimated abundance of spawning adult Westslope Cutthroat Trout was 410 fish (SE = 85; Firehammer et al. 2012). Similar estimates are not available for 2013 or for tributaries of the other bays. Estimates of Westslope Cutthroat Trout consumption by Northern Pike are also conservative since no sampling occurred during winter. Nevertheless, the observed predation by Northern Pike is of concern and may explain the low juvenile-to-adult return rates

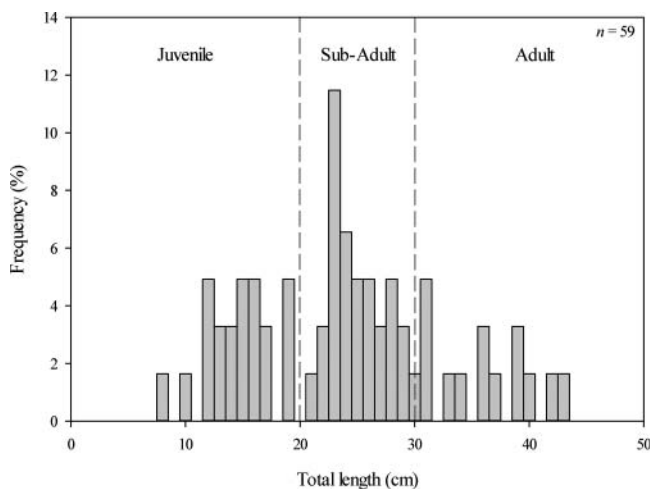


FIGURE 7. Length frequency histogram of adfluvial Westslope Cutthroat Trout consumed by Northern Pike in Coeur d'Alene Lake from March 2012 to May 2013. Dashed lines delineate the TL (cm) classes corresponding to juvenile, subadult, and adult Westslope Cutthroat Trout.

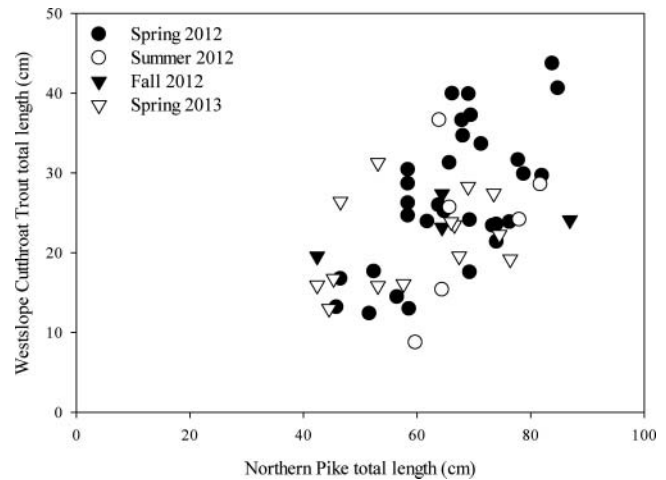


FIGURE 8. Relationship between Northern Pike TL (cm) and the TLs of Westslope Cutthroat Trout consumed seasonally in Coeur d'Alene Lake from March 15, 2012, to May 31, 2013.

of Westslope Cutthroat Trout (Firehammer et al. 2012). Fortunately, intense seasonal predation on Westslope Cutthroat Trout might be alleviated by reducing Northern Pike densities near the tributaries used by spawning Westslope Cutthroat Trout.

Various mechanical removal methods have been used or recommended to reduce densities of nonnative predators (Broughton and Fisher 1981; Mann 1985; Kulp and Moore 2000; Mueller 2005). Suppressing a nonnative predator such as Northern Pike may be important for conserving salmonids and other native fish species. However, desired effects from suppression efforts are usually diminished because the remaining individuals of the target species typically display compensatory increases in recruitment, survival, and growth (Kolar et al. 2010). Additionally, the amount of resources needed to reduce piscivore biomass in larger systems is generally prohibitive (Goeman et al. 1993). In some systems, complete eradication of nonnative piscivores is required for achieving viability of salmonid populations (Spens and Ball 2008); however, eradication of Northern Pike from large systems has been unsuccessful (Aguilar et al. 2005). Additionally, the Northern Pike is an important sport fish in Coeur d'Alene Lake, and anglers are likely to show substantial opposition to a removal plan. Future research should focus on management strategies (i.e., harvest regulations) that might be used in Coeur d'Alene Lake to reduce Northern Pike densities at small spatial and/or temporal scales.

Results of the present study have important implications for the management of Northern Pike and the conservation of Westslope Cutthroat Trout. The primary limitation of our study was the inability to estimate the lakewide abundance of Westslope Cutthroat Trout. Unfortunately, given the size of the lake and its major tributaries, attempts to estimate absolute abundance of Westslope Cutthroat Trout are unlikely.

Nevertheless, we determined that Northern Pike consumption of Westslope Cutthroat Trout varies across seasons and that Westslope Cutthroat Trout could account for up to 30% of the total biomass consumed by Northern Pike. High spatial and temporal overlap between these two species during spring resulted in relatively large quantities of Westslope Cutthroat Trout being consumed in some areas. Thus, the Coeur d'Alene Tribe's management objective—to restore Westslope Cutthroat Trout to a level that allows for subsistence harvest, maintains genetic diversity, and increases the probability of persistence despite anthropogenic influences—might be achieved if predation by Northern Pike near tributaries used by adfluvial Westslope Cutthroat Trout can be reduced during the spring.

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Appendix: Taxonomic Composition and Energy Contribution of Prey Consumed by Northern Pike in Coeur d'Alene Lake

TABLE A.1. Frequency of occurrence (%O), percent by number (%N), and percent energy contribution (%EC) of prey types consumed by Northern Pike from four year-classes (YC) in Coeur d'Alene Lake, Idaho, March 2012–May 2013. Sample size (*n*) and the percentage of empty stomachs are presented for each YC and season.

Variable or taxon	2011 YC			2010 YC			2009 YC			2008 YC		
	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Spring 2012												
Sample size	17			54			129			36		
Empty	64			44			57			44		
Invertebrates												
Annelida	17	29	^a	0	0	0	6	3	^a	8	5	^a
Coleoptera	0	0	0	6	10	^a	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0
Odonata	0	0	0	3	4	^a	2	1	^a	0	0	0
Fish												
Catostomidae												
Largescale Sucker	17	14	76	3	1	^a	0	0	0	0	0	0
Centrarchidae												
Black Crappie	17	14	3	0	0	0	0	0	0	4	3	^a
Bluegill	0	0	0	0	0	0	0	0	0	0	0	0
Largemouth Bass	0	0	0	0	0	0	3	2	1	0	0	0
Unknown species	0	0	0	0	0	0	0	0	0	0	0	0
White Crappie	0	0	0	0	0	0	0	0	0	0	0	0
Clupeidae												
Pacific Herring	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae												
Sculpin	0	0	0	0	0	0	0	0	0	4	3	^a
Cyprinidae												
Northern Pikeminnow	0	0	0	0	0	0	0	0	0	0	0	0
Tench	0	0	0	0	0	0	0	0	0	4	3	20
Esocidae												
Northern Pike	0	0	0	0	0	0	0	0	0	4	3	2
Ictaluridae												
Brown Bullhead	0	0	0	3	1	^a	3	2	1	4	3	^a
Percidae												
Yellow Perch < 150 mm	33	29	21	6	2	^a	15	12	1	8	5	0
Yellow Perch ≥ 150 mm	0	0	0	11	3	5	6	4	2	8	13	3
Salmonidae												
Kokanee	0	0	0	51	71	68	35	61	54	28	45	36
Unknown species	0	0	0	0	0	0	3	2	9	4	3	3
Westslope Cutthroat Trout	0	0	0	17	7	26	26	14	31	20	13	36
Other												
Idaho giant salamander	0	0	0	0	0	0	0	0	0	0	0	0
Detritus	17	14	^a	0	0	0	0	0	0	4	3	^a
Summer 2012												
Sample size	9			47			37			15		
Empty	44			53			46			33		

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TABLE A.1. Continued.

Variable or taxon	2011 YC			2010 YC			2009 YC			2008 YC		
	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Invertebrates												
Annelida	0	0	0	3	1	^a	0	0	0	0	0	0
Coleoptera	0	0	0	3	72	^a	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	4	3	^a	0	0	0
Hymenoptera	0	0	0	0	0	0	0	0	0	10	27	^a
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0
Odonata	0	0	0	3	2	0	0	0	0	0	0	0
Fish												
Catostomidae												
Largescale Sucker	0	0	0	3	1	3	0	0	0	0	0	0
Centrarchidae												
Black Crappie	0	0	0	0	0	0	0	0	0	0	0	0
Bluegill	0	0	0	0	0	0	0	0	0	0	0	0
Largemouth Bass	20	20	11	3	1	^a	0	0	0	0	0	0
Unknown species	0	0	0	0	0	0	0	0	0	0	0	0
White Crappie	0	0	0	0	0	0	0	0	0	0	0	0
Clupeidae												
Pacific Herring	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae												
Sculpin	0	0	0	0	0	0	0	0	0	0	0	0
Cyprinidae												
Northern Pikeminnow	0	0	0	0	0	0	0	0	0	0	0	0
Tench	0	0	0	0	0	0	0	0	0	0	0	0
Esocidae												
Northern Pike	0	0	0	3	1	^a	0	0	0	0	0	0
Ictaluridae												
Brown Bullhead	20	20	57	0	0	0	9	7	1	0	0	0
Percidae												
Yellow Perch < 150 mm	20	20	31	10	2	^a	4	3	^a	0	0	0
Yellow Perch ≥ 150 mm	0	0	0	7	1	2	9	7	2	20	13	4
Salmonidae												
Kokanee	0	0	0	50	17	80	65	72	93	50	47	90
Unknown species	0	0	0	0	0	0	0	0	0	0	0	0
Westslope Cutthroat Trout	0	0	0	10	2	14	9	7	3	10	7	6
Other												
Idaho giant salamander	0	0	0	0	0	0	0	0	0	0	0	0
Detritus	40	40	^a	3	1	^a	0	0	0	10	7	^a
Fall 2012												
Sample size	8			41			34			19		
Empty	50			22			50			37		
Invertebrates												
Annelida	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0
Odonata	0	0	0	0	0	0	0	0	0	0	0	0

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TABLE A.1. Continued.

Variable or taxon	2011 YC			2010 YC			2009 YC			2008 YC		
	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Fish												
Catostomidae												
Largescale Sucker	0	0	0	2	1	2	8	7	7	0	0	0
Centrarchidae												
Black Crappie	0	0	0	16	19	2	8	7	^a	0	0	0
Bluegill	60	67	63	9	28	1	13	25	0	0	0	0
Largemouth Bass	0	0	0	2	1	1	8	7	^a	0	0	0
Unknown species	0	0	0	2	1	^a	0	0	0	8	8	1
White Crappie	0	0	0	0	0	0	0	0	0	0	0	0
Clupeidae												
Pacific Herring	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae												
Sculpin	0	0	0	0	0	0	0	0	0	0	0	0
Cyprinidae												
Northern Pikeminnow	0	0	0	0	0	0	4	4	8	0	0	0
Tench	0	0	0	0	0	0	0	0	0	0	0	0
Esocidae												
Northern Pike	0	0	0	0	0	0	0	0	0	0	0	0
Ictaluridae												
Brown Bullhead	0	0	0	5	3	3	4	4	1	0	0	0
Percidae												
Yellow Perch < 150 mm	40	33	37	28	25	10	8	7	1	8	8	^a
Yellow Perch ≥ 150 mm	0	0	0	14	8	33	13	11	10	25	23	7
Salmonidae												
Kokanee	0	0	0	9	6	48	21	18	63	33	38	82
Unknown species	0	0	0	0	0	0	0	0	0	8	8	5
Westslope Cutthroat Trout	0	0	0	0	0	0	8	7	10	17	15	5
Other												
Idaho giant salamander	0	0	0	0	0	0	0	0	0	0	0	0
Detritus	0	0	0	12	7	^a	4	4	^a	0	0	0
Spring 2013												
Sample size	112			93			28			16		
Empty	41			46			32			44		
Invertebrates												
Annelida	3	2	^a	2	1	^a	5	8	^a	0	0	0
Coleoptera	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	3	5	^a	0	0	0	0	0	0	0	0	0
Odonata	0	0	0	0	0	0	0	0	0	0	0	0
Fish												
Catostomidae												
Largescale Sucker	0	0	0	0	0	0	5	2	15	0	0	0
Centrarchidae												
Black Crappie	4	3	^a	4	4	1	0	0	0	13	8	14
Bluegill	3	4	^a	0	0	0	0	0	0	0	0	0
Largemouth Bass	0	0	0	0	0	0	0	0	0	0	0	0
Unknown species	0	0	0	0	0	0	0	0	0	13	8	^a
White Crappie	1	3	^a	0	0	0	0	0	0	0	0	0

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TABLE A.1. Continued.

Variable or taxon	2011 YC			2010 YC			2009 YC			2008 YC		
	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC	%O	%N	%EC
Clupeidae												
Pacific Herring	0	0	0	2	4	1	14	27	3	0	0	0
Cottidae												
Sculpin	0	0	0	0	0	0	0	0	0	0	0	0
Cyprinidae												
Northern Pikeminnow	0	0	0	0	0	0	5	19	1	0	0	0
Tench	0	0	0	0	0	0	5	2	3	0	0	0
Esocidae												
Northern Pike	0	0	0	0	0	0	0	0	0	0	0	0
Ictaluridae												
Brown Bullhead	0	0	0	2	1	^a	0	0	0	13	8	5
Percidae												
Yellow Perch < 150 mm	41	42	8	31	30	2	19	8	1	0	0	0
Yellow Perch ≥ 150 mm	23	16	51	20	19	13	14	10	6	25	15	10
Salmonidae												
Kokanee	12	19	24	19	23	73	19	17	68	25	46	65
Unknown species	1	1	1	6	4	3	0	0	0	0	0	0
Westslope Cutthroat Trout	5	5	15	11	9	6	14	6	4	13	15	6
Other												
Idaho giant salamander	0	0	0	2	2	^a	0	0	0	0	0	0
Detritus	3	2	^a	2	2	^a	0	0	0	0	0	0

^aFrequency < 1%.