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Article

Food habits of Yellow Perch, Smallmouth Bass, and Northern Pikeminnow in Lake Cascade, Idaho

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ABSTRACT

Objective: Yellow Perch *Perca flavescens* was first encountered in Lake Cascade, Idaho, in 1957. Since its introduction, the abundance of Yellow Perch in Lake Cascade has been highly variable. Historically, declines in Yellow Perch abundance were attributed to predation by Northern Pikeminnow *Ptychocheilus oregonensis*. In the 1990s, Smallmouth Bass *Micropterus dolomieu* became established in Lake Cascade. Although Yellow Perch abundance has been high and currently supports a world-class fishery, the Idaho Department of Fish and Game has documented poor Yellow Perch recruitment in recent years, concerning regional managers. An investigation into the food habits of Yellow Perch, Smallmouth Bass, and Northern Pikeminnow was conducted to better understand the importance of juvenile Yellow Perch to predator diets.

Methods: In Lake Cascade, gill nets were deployed monthly from April 2022 to May 2023. Ageing structures and stomach contents were removed from Yellow Perch, Smallmouth Bass, and Northern Pikeminnow. Diet composition was quantified and then summarized by species, cohort, and season. Bioenergetics modeling, coupled with estimates of predator abundance, was used to evaluate overall consumption of Yellow Perch.

Results: In total, stomach contents were extracted from 1,099 Yellow Perch, 440 Smallmouth Bass, and 980 Northern Pikeminnow. Food habits varied by season and predator length, but Yellow Perch was a primary prey item of all study species. The energetic contribution of Yellow Perch to Yellow Perch varied from 10% to 80% across seasons. Smallmouth Bass consumed fewer Yellow Perch than either Yellow Perch or Northern Pikeminnow. The highest average per capita consumption of Yellow Perch (i.e., across seasons) was observed for 500–600-mm Northern Pikeminnow (five Yellow Perch/Northern Pikeminnow). Energetic contribution of Yellow Perch to Northern Pikeminnow diets was highest in spring 2023, yet Northern Pikeminnow consumed the highest average number of Yellow Perch in July. Bioenergetics modeling estimated that per-capita annual consumption of Yellow Perch was 6.0 kg for Yellow Perch, 3.4 kg for Smallmouth Bass, and 9.9 kg for Northern Pikeminnow. In total, estimated consumption of all study species was as high as 37% of the estimated total number age-0 Yellow Perch produced.

Conclusions: Yellow Perch was an important prey item for all three species, particularly Yellow Perch and Northern Pikeminnow. Results from this study provide important information on the predation of Yellow Perch in Lake Cascade. Further, this work will bolster a growing body of research on the food habits of and interactions between native and nonnative predators in western reservoir systems.

KEYWORDS: bioenergetics model, nonnative species, predation, recruitment, trophic ecology

LAY SUMMARY

A diet analysis was conducted to estimate the consumption of Yellow Perch by three predator species in Lake Cascade, Idaho. The results indicated that Yellow Perch and Northern Pikeminnow consumed the greatest quantity of Yellow Perch and may contribute to variable Yellow Perch recruitment.

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INTRODUCTION

Yellow Perch *Perca flavescens* is a widely distributed percid in North America. Its native distribution extends from Nova Scotia, Canada, to South Carolina, United States, on the east coast, and its western distribution arcs southeast from Great Slave Lake, Canada, to eastern Kansas, United States. Its native distribution also includes most of the Great Lakes and upper Midwest regions of the United States and the Canadian Provinces of Alberta, Saskatchewan, Manitoba, Ontario, and Quebec (Lee et al., 1980). Yellow Perch typically occupies coolwater lakes and streams with vegetated, littoral habitats (Krieger et al., 1983). Yellow Perch has plastic food habits; it usually experiences an ontogenetic diet shift such that juvenile fish consume small planktivorous items and large Yellow Perch eat macroinvertebrates or small-bodied fishes (Brown et al., 2009). Government agencies and private individuals began stocking Yellow Perch outside its native distribution around the turn of the 20th century (Heidinger & Kayes, 1993). Leach (1928) reported that 15 states stocked 208 million juvenile Yellow Perch in 1925. Given the generalist food and habitat requirements of Yellow Perch, introductions were often successful in establishing novel populations across North America. Currently, Yellow Perch has been introduced in 35 states across the United States, where populations support important recreational fisheries. Throughout its distribution, Yellow Perch provides both cultural (Kraft, 1982) and economic value (Stepien et al., 2015). Economically, Yellow Perch is important for both recreational (Diana et al., 1987; Sohngen et al., 2015) and commercial (Lauer et al., 2008) fisheries.

A system of particular importance where Yellow Perch was successfully introduced is Lake Cascade, a large reservoir in central Idaho. Yellow Perch was first reported by anglers in Lake Cascade in 1957 (Welsh, 1975). Yellow Perch is thought to have entered Lake Cascade via entrainment from Payette Lake, an upstream water body on the North Fork Payette River (Casey, 1962). Since its introduction in Lake Cascade, Yellow Perch abundance has been highly variable, resulting in periods of high angler catch rates and periods of near extirpation (Bennett, 2004). In the 1950s and 1960s, Lake Cascade was primarily a put-and-grow salmonid fishery, with high catch rates of Rainbow Trout *Oncorhynchus mykiss*, Coho Salmon *O. kisutch*, and kokanee *O. nerka* (lacustrine Sockeye Salmon) (Casey, 1962; Lindland, 1971). However, anglers were dissatisfied with high catches of Northern Pikeminnow *Ptychocheilus oregonensis*, a native species that thrives in reservoirs but is generally not desirable for sportfishing (Keating, 1961). In 1958, the Idaho Department of Fish and Game (IDFG) began treating two of the four major tributaries with Squoxin, a piscicide specific to Northern Pikeminnow (MacPhee & Ruelle, 1969; Welsh, 1975). Nearly one million Northern Pikeminnow were removed during the operation. The IDFG completed several additional piscicide treatments between 1968 and 1974, which removed approximately 450,000 Northern Pikeminnow (Welsh, 1975). Yellow Perch abundance increased following the Northern Pikeminnow removal efforts. The 1970s and 1980s marked years of world-class Yellow Perch angling (Bennett, 2004). The first Smallmouth Bass *Micropterus dolomieu* was sampled in 1991, and the species was well established by 1994 (Grunder & Anderson, 1991; Janssen et al., 2006). In the same time frame, the Yellow Perch population was in decline (Janssen et al., 2006). Angler effort dropped from 383,242 h in 1992 to just 74,000 h by 2001, and most anglers switched from targeting Yellow Perch to Rainbow Trout (Janssen et al., 1996, 2006). The rapid decline in Yellow Perch abundance prompted several investigations by IDFG. First, long-term limnological data were used to examine major changes that might have affected Yellow Perch abundance. The Idaho Department of Environmental Quality detected high concentrations of phosphorus and subsequently listed Lake Cascade as "water quality limited," though phosphorus was not deemed to be a major factor influencing Yellow Perch survival. Next, Janssen et al. (1996) conducted several small studies on Lake Cascade, including evaluations of parasites and diseases, Yellow Perch spawning habitat and timing, age-0 Yellow Perch body condition, zooplankton quality, and benthic macroinvertebrate abundance. However, none of the studies identified why the Yellow Perch population had abruptly declined. Finally, Bennett (2004) completed an assessment of Northern Pikeminnow population dynamics and food habits in Lake Cascade. Although the study was limited in scope (i.e., sample size, temporal scale), the findings enabled IDFG to establish prescriptions for Northern Pikeminnow removals based on length structure and relative abundance. The prescription stated that Northern Pikeminnow numbers should be "aggressively reduced" if relative abundance is greater than 15 fish/net-night (gill nets) and 75% of the population is greater than 350 mm (IDFG 2006). Thus, IDFG removed another 30,000 Northern Pikeminnow using chemical and physical removal methods (i.e., weirs on spawning tributaries) during 2004–2006. The IDFG also transplanted about 865,000 mature Yellow Perch from nearby systems into Lake Cascade. By 2009, Yellow Perch abundance was increasing, and by 2014, Lake Cascade was once again a premier Yellow Perch fishery (Janssen et al., 2011, 2016).

Following multiple years of excellent Yellow Perch angling, IDFG noticed declines in the abundance of juvenile (age-0 and age-1) Yellow Perch in 2018 (Janssen et al., 2020). Yellow Perch appeared to successfully spawn, but relatively few juvenile fish were sampled during the fall trawling evaluations. Population trends detected in 2018 were similar to those documented prior to the population "collapse" in the 1990s. Although juvenile Yellow Perch abundance in recent years has seemingly returned to that observed in the mid-2010s, the concern of another population decline encouraged IDFG biologists to speculate about mechanisms leading to variable Yellow Perch recruitment. A leading question is the role of predation on juvenile Yellow Perch. The only recent study that provides any insight on predation of juvenile Yellow Perch in Lake Cascade is Bennett (2004). However, Bennett (2004) has several shortcomings. Notably, the study was completed when Lake Cascade had a different fish assemblage; Yellow Perch were virtually absent in the system and Smallmouth Bass was not fully established (Janssen et al., 2020). The scope of the study was also relatively limited, with only 506 Northern Pikeminnow sampled over 4 months (July–October 2002). Of the fish sampled, the author found that Northern Pikeminnow diets were dominated by invertebrates (i.e., 99% by number, 88% by weight). Yellow Perch made up less than 1% by number and 2% by weight of

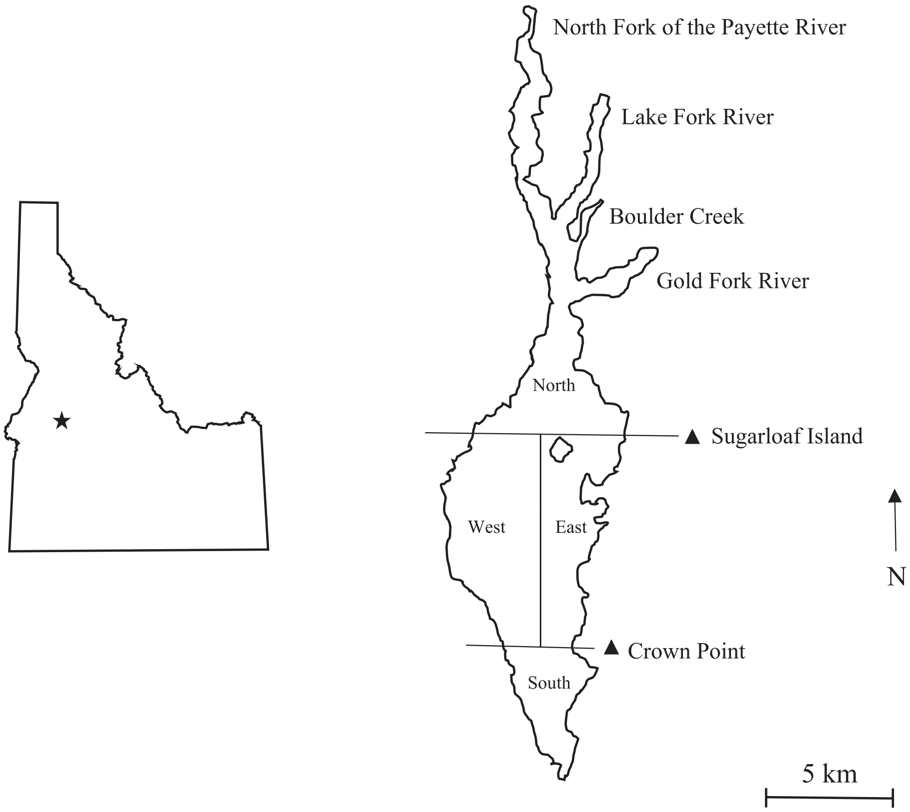

Figure 1. The Lake Cascade system located in central Idaho. This system included Lake Cascade, the North Fork Payette River, Lake Fork River, Boulder Creek, and Gold Fork River. The system was divided into four regions: the area north of Sugarloaf Island, including the four major tributaries (north); the area south of Sugarloaf Island west of the historical North Fork Payette River floodplain north of Crown Point (west); the area south of Sugarloaf Island east of the historical North Fork Payette River floodplain north of Crown Point (east); and the area south of Crown Point (south). Triangles represent landmarks where regional boundaries were drawn.

Northern Pikeminnow diets. Smallmouth Bass and Yellow Perch diets have never been evaluated in Lake Cascade. Yellow Perch recruitment in Lake Cascade has been particularly variable since 2018, so a contemporary evaluation of predator food habits should provide insight on the importance of Yellow Perch in predator diets.

Predation is an important mechanism that can alter sport fish populations. Yellow Perch may consume enough juvenile Yellow Perch to limit recruitment. Tarby (1974) found that Yellow Perch was highly cannibalistic when age-0 Yellow Perch were abundant in Oneida Lake, New York. In addition to changes in Yellow Perch and Northern Pikeminnow populations in Lake Cascade, Smallmouth Bass has recently established and little is currently known about its food habits in the system. Smallmouth Bass reduced the abundance of Yellow Perch in an Ontario lake by 75% in 2 years (Luek et al., 2010). Similarly, Wolf et al. (2022) found that Yellow Perch occurred in over 50% of Smallmouth Bass diets in a small, western reservoir in Utah. Tabor et al. (1993) conducted a diet analysis of Smallmouth Bass and Northern Pikeminnow in the Columbia River, Washington–Oregon, and found that both Smallmouth Bass and Northern Pikeminnow appeared to ingest the same prey items at similar rates. Northern Pikeminnow food habits have been extensively studied within its native distribution, where it often suppresses sport fish populations. For instance, Zimmerman and Ward (1999) found that up to 78% of juvenile salmonid mortality in the Columbia River was attributed to Northern Pikeminnow predation. Thus, to gain an understanding of the importance of Yellow Perch to predator diets, an investigation was initiated on the diets of Yellow Perch, Smallmouth Bass, and Northern Pikeminnow in Lake Cascade. This study aimed to (1) describe the seasonal food habits of Yellow Perch, Smallmouth Bass, and Northern Pikeminnow and (2) estimate the consumption of juvenile Yellow Perch by Yellow Perch, Smallmouth Bass, and Northern Pikeminnow using bioenergetics models.

METHODS

Study area

Lake Cascade began filling in 1948 after the U.S. Bureau of Reclamation constructed an earthen dam on the North Fork Payette River (Janssen et al., 2020). Though it is the fourth largest body of water in Idaho by surface area (122 km^2), the average depth of Lake Cascade is relatively shallow (7.6 m; Griswold & Bjornn, 1989). The reservoir has four major inlets: North Fork Payette River, Lake Fork River, Boulder Creek, and Gold Fork River (Figure 1). Four large embayments are formed where each of the rivers flows into the reservoir. Each of the bays are relatively shallow (~5 m), have steep banks, and are filled with debris (i.e., stumps, aquatic vegetation). All four rivers converge just north of Sugarloaf Island to form the historical

North Fork Payette River floodplain. The historical floodplain divides the reservoir longitudinally and is consistently deeper than the surrounding water. The western portion of Lake Cascade has silt substrate, gradually sloping bathymetry, and abundant macrophytes. The shoreline east of the floodplain is steep, deep (15 m), and rocky. Most of the area south of Crown Point is similar to the western side of the reservoir, with gradual slopes and abundant macrophytes. Conversely, the southern area also has a relatively small area of deep water (~20 m) due to its proximity to Cascade Dam. For this study, the reservoir was divided into four regions to ensure equal sampling effort across habitat types (Figure 1). The regions were defined as (1) the inundated area of all four tributaries and the area extending to the northernmost point of Sugarloaf Island (north); (2) the middle of the historical North Fork Payette River floodplain to the western shore, south of Sugarloaf Island and north of Crown Point (west); (3) the middle of the historical North Fork Payette River floodplain to the eastern shore, south of Sugarloaf Island and north of Crown Point (east); and (4) the remaining area south of Crown Point (south).

Native species in Lake Cascade include Bridgelip Sucker *Pantosteus columbianus*, Largescale Sucker *Catostomus macrocheilus*, Northern Pikeminnow, Mountain Whitefish *Prosopium williamsoni*, Rainbow Trout, kokanee, and Westslope Cutthroat Trout *Oncorhynchus lewisi*. The sport fish assemblage in Lake Cascade is dominated by nonnative species. Popular nonnative sport fish include Coho Salmon, Largemouth Bass *Micropterus nigricans*, Pumpkinseed *Lepomis gibbosus*, Smallmouth Bass, White Crappie *Pomoxis annularis*, and Yellow Perch.

Field sampling

Fish were collected using IDFG's standard gill nets. Nets were 45 m long and 2 m tall and had 7.5-m-long panels of increasing mesh size (1.9-, 2.5-, 3.2-, 3.8-, 5.1-, and 6.4-cm bar-measure mesh; Lamansky & Meyer, 2012). Monthly netting commenced in April 2022 and concluded in May 2023. Each monthly sampling event occurred for 1–2 weeks. Two pairs of nets were deployed in two locations per day (i.e., four total nets per day). In each location, one sinking net and one floating net were deployed in parallel ~100 m apart. Sampling locations were chosen to maximize catch of target species (i.e., Yellow Perch, Smallmouth Bass, Northern Pikeminnow). Gill nets were set perpendicular to shore in littoral habitats. Nets were set in a random manner such that the small or large mesh was not consistently set towards shore. Nets were fished overnight for ~12 h to maximize catch, reduce interactions with the public, and minimize digestion of stomach contents in captured fish (Garvey & Chipps, 2012). Under-ice gill-net surveys were also conducted in January and February 2023. A prairie ice jigger was used to pull a rope under the ice (Hayden et al., 2012). Only sinking nets were set during the winter months to avoid possible complications with ice formation. A temperature logger (ONSET, Bourne, Massachusetts) was attached to each net to provide hourly ambient water temperatures. Although electrofishing is a better technique for sampling Smallmouth Bass (Miranda et al., 2024), boat electrofishing was not conducted due to very low water conductivity (i.e., <20 μS/cm).

Total length (nearest millimeter) and wet weight (nearest 0.1 g) were measured for all captured fish. For each of the target species, five individuals per centimeter length-group were sacrificed per month for ageing structure and stomach extraction. Sagittal otoliths were collected from Yellow Perch and Smallmouth Bass, and the leading pectoral fin ray was taken from Northern Pikeminnow (Wilson et al., 2025). Extracted otoliths were wiped clean and stored in centrifuge tubes for later processing. Fin rays were stored in coin envelopes and allowed to air dry before processing (Quist et al., 2012). Stomach contents were collected from all sacrificed fish captured in sampling events from May 2022 through May 2023. Stomachs (i.e., esophagus to large intestine) were removed and placed in Whirl-Pak bags (Uline, Pleasant Prairie, Wisconsin) with a 10% solution of buffered formalin (Garvey & Chipps, 2012).

Laboratory processing

Ageing structure preparation followed techniques provided in Quist et al. (2012), Wegleitner and Isermann (2017), and Wilson et al. (2025). Ageing structures were sectioned along the transverse plane using an IsoMet Low-Speed Saw (Buehler, Lake Bluff, Illinois; Quist et al., 2012). Otoliths and fin rays were sectioned to approximately 0.8 mm thick. Otolith sections included the nucleus. Fin ray sections were taken near the articulating process to ensure accurate age estimates (Watkins et al., 2015; Wegleitner & Isermann, 2017). Stomach contents were identified to the lowest taxonomic group (e.g., species for fish, order for invertebrates; Chipps & Garvey, 2006). Diagnostic bones were used to identify fish that were partially digested or otherwise unidentifiable (Frost, 2000; Jeter et al., 2019; Scott & Crossman, 1973; Stroud & Scholz, 2014; Traynor et al., 2010; Wallace & Zaroban, 2013; Wydoski & Whitney, 2003). Stomach contents were blotted dry and weighed to the nearest 0.1 g. Total length (nearest mm) was recorded for intact fish and macroinvertebrate specimens, and standard length (nearest mm) was recorded for partially digested individuals (Garvey & Chipps, 2012). When macroinvertebrates were too numerous to count and measure, the first 100 whole individuals that were recovered were measured and weighed. The estimated abundance of taxa remaining in an individual's stomach was calculated by multiplying the weight of the remaining taxa by the quotient of the number measured (i.e., 100) and their weight.

Catch per unit effort, body condition, growth, and age structure

Data were summarized by season and species. Months were grouped into seasons: spring 2022 (April–May 2022), summer (June–August 2022), fall (October–November 2022), winter (January–February 2023), and spring 2023 (May 2023). Catch per unit effort (CPUE) was calculated as the number of fish per net-night. A net-night was defined as one net fished for ~12 h (Pine et al., 2012). Body condition of Yellow Perch and Smallmouth Bass was assessed using relative weight (W_r):

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

where W is the weight of the individual and W_s is the length-specific standard weight predicted by a weight–length regression specific to Yellow Perch (Willis et al., 1991) or Smallmouth Bass (Kolander et al., 1993). Body condition of Northern Pikeminnow was assessed using relative condition factor (K_n ; Neuman et al., 2012):

$$K_n = \left(\frac{W}{W'}\right) \times 100,$$

where W is the weight of the individual and W' is the length-specific standard weight predicted by a weight–length regression fit to data from Northern Pikeminnow sampled across Idaho. Values over 100 indicate above-average body condition for W_r and K_n. Fish were arranged into 100-mm length-groups for summarization of body condition.

Age structure of target species was described as the proportion of sampled individuals assigned to each cohort. Seasonal growth of target species was measured as the change in the average weight by species, cohort, and season. Summarizations were limited for some species and cohort combinations due to low sample size.

Food habits

Data were summarized by season, species, cohort, and length; differences among sampling location were not obvious. Length summarizations were used as an analog for age summarizations in some instances due to wide variations in the distribution of ages. A number of stomach samples from each species had to be discarded due to issues with preservation (i.e., poor-quality formalin). Specifically, Yellow Perch ($n=2$) and Smallmouth Bass ($n=7$) samples from October, November, and May 2023 were discarded. Northern Pikeminnow ($n=161$) samples were discarded from sampling events in May 2022 ($n=4$), June ($n=1$), July ($n=2$), October ($n=51$), November ($n=65$), and May 2023 ($n=38$).

Stomach contents were analyzed by frequency of occurrence (O_i), proportion by weight (PW_i), and proportional energy contribution (PE_i). Frequency of occurrence of each prey item in the sample was calculated as follows:

$$O_i = \frac{J_i}{P},$$

where J_i is the number of fish with prey item i and P is the total number of nonempty stomachs (Amundsen et al., 1996; Garvey & Chipps, 2012; Pope et al., 2001). The percent composition by weight was calculated using the following:

$$PW_i = \frac{W_i}{\sum_{i=1}^{Q} W_i},$$

where W_i is the weight of prey type i and Q is the number of prey types. Percent energy contribution was calculated by multiplying the weight of a prey type by its energy density and dividing by the total energy contributed by all prey types (Probst et al., 1984). Energy densities from the literature were used to estimate energetic contributions (Table S1 [see online Supplementary Material]). Some diet items were grouped into categories for diet analysis due to their relative rarity. Orthoptera, Anisoptera, Baetidae, Buprestidae, Curculionidae, Diplopoda, Ephemeroptera, Formicidae, Coleoptera, Tricoptera, and unknown invertebrates were grouped into the category "other macroinvertebrates." Black Bullhead *Ameiurus melas*, Northern Pikeminnow, Pumpkinseed, Rainbow Trout, Smallmouth Bass, and White Crappie were grouped into the category "other fish." Cladocera, Copepoda, and Leptodora were grouped into the category "zooplankton." Mean energy densities of all fish and macroinvertebrate species were used to estimate the energy density of unidentifiable fish and macroinvertebrates (Courtney et al., 2018).

Diet overlap between all three target species was summarized using Pianka's (1973) index of niche overlap. Pianka's index (G_{ij}) is calculated as follows:

$$G_{ij} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij^2} \sum_i^n p_{ik^2}}},$$

where p_{ij} is the proportion of diet item i in the total resources used by species j, p_{ik} is the proportion of diet item i in the total resources used by species k, and n is the total number of diet items. Pianka's index provides values between 0 (no diet overlap) and 1.0 (complete diet overlap); a value of 0.75 generally indicates high overlap and 0.40 indicates low overlap (Koenig, 2020; Pianka, 1973; Wuellner et al., 2010). Due to sample size limitations, diet compositions of all the individuals of a species captured in a season were grouped to compare overlap between species.

The average length and weight of Yellow Perch in stomachs were summarized for each species and across months. The average number of Yellow Perch identified in predator stomachs by length and month was calculated by dividing the number of Yellow Perch in the stomachs of a given predator in a month or length group by the total number of predator stomachs analyzed in that month or length-group. Month was used instead of season to describe recruitment of age-0 Yellow Perch to the diet of predators.

Bioenergetics

Consumption of juvenile Yellow Perch in Lake Cascade was modeled using Fish Bioenergetics 4.0v1.1.6 (Deslauriers et al., 2017). We used parameter estimates from Kitchell et al. (1977) for Yellow Perch, Whitledge et al. (2003) for Smallmouth Bass, and Petersen and Ward (1999) for Northern Pikeminnow. Bioenergetics models partition food consumed into various biological processes. The general form of the bioenergetics model is as follows:

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

where C is consumption, R is respiration, S is the specific dynamic action, F is fecal egestion, U is nitrogenous excretion, and ΔB is the change in growth (weight) of the individual (Deslauriers et al., 2017; Hanson et al., 1997; Ney, 1993). Models were run for a year beginning on May 15, 2022, and ending on May 15, 2023. The year was divided into four seasons, and separate seasonal models with a daily time step were run to capture seasonal diet trends for each species and groups of cohorts. The spring model ran from day 1 to day 34, the summer model ran from day 35 to day 136, the fall model ran from day 137 to day 244, and the winter model ran from day 245 to day 365. All four seasonal models were run for Yellow Perch. Three seasonal models were run for Smallmouth Bass and Northern Pikeminnow. Spring and summer models were run as described above. Fall and winter models were combined due to low winter catch rates and sample losses in fall and spring 2023. The combined fall–winter model ran from day 137 to day 365. Due to small sample size, many groups of cohorts had to be combined. Yellow Perch cohorts 2002 to 2008 and 2010 to 2014 were combined into two groups. Smallmouth Bass cohorts 2004 to 2014 and Northern Pikeminnow cohorts 1997 to 2013 were combined. Water temperature, predator and prey energy densities, change in predator weight, and predator diet proportions were the required model inputs (Deslauriers et al., 2017; Hanson et al., 1997; Kitchell et al., 1977). Ambient water temperature (°C) was obtained from temperature loggers. Specifically, the average water temperature (across nets) during each sampling event was calculated. Daily water temperatures between sampling events were estimated by calculating a daily increase or decrease in temperature (i.e., quotient of the difference in temperature and number of days between sampling events). Water temperatures varied among seasons: spring 2022 (minimum–maximum; 11.4–15.5°C), summer (14.9–20.6°C), fall (8.9–14.6°C), winter (3.2–9.1°C), and spring 2023 (8.3–9.2°C). As previously described, prey energy densities were obtained from the literature. Seasonal growth was estimated by calculating the difference between the average weights of a given cohort between seasons (Table S2). If the average weight of individuals in a cohort decreased between seasons, no growth was assumed to occur during that time period (e.g., Koenig, 2020; Walrath 2013). Spawning was taken into account for each species. In the model, Yellow Perch from all cohorts older than 2019 lost 12% of their weight on day 2 (Blazer et al., 2013; Henderson et al., 1999). On day 35, Smallmouth Bass from all cohorts older than 2018 lost 7% of their weight (Mackereth et al., 1999; Ridgway et al., 1991) and Northern Pikeminnow from all cohorts 2018 and older lost 4.1% of their body weight (Petersen & Ward, 1999). Spawning expenditures for all three species were average values for male and female individuals (Deslauriers et al., 2017; Hanson et al., 1997). Lastly, several swim speeds are available for Northern Pikeminnow model parameterization (Petersen & Ward, 1999). We ran the Northern Pikeminnow models using the 1.3 cm/s swim speed parameterization to best represent reservoir conditions.

Estimates of per capita total consumption of Yellow Perch (kg) were derived by summing the model outputs for all seasons of a given cohort for each predator. We also calculated population-scale consumption of Yellow Perch (kg) by estimating population abundance for all three species. The IDFG uses a Lincoln estimator (Ulaski et al., 2023) to estimate the population size of Yellow Perch greater than 250 mm using estimates of exploitation to estimate harvest. The most recent estimate was completed in 2022. We supplemented IDFG's estimate by estimating the number of Yellow Perch between 150 and 250 mm. The number of Yellow Perch greater than 150 mm was calculated as the quotient of the IDFG population estimate and the proportion of Yellow Perch greater than 250 mm in our sample, which was summed with the IDFG population estimate. The abundance of Smallmouth Bass has never been estimated in Lake Cascade. Therefore, three scenarios for Smallmouth Bass abundance were evaluated. In scenario 1 (equal Smallmouth Bass catchability), we assumed equal catchability between Smallmouth Bass and Yellow Perch. We found the quotient of Smallmouth Bass CPUE and Yellow Perch CPUE and multiplied that by the Yellow Perch population estimate described above. Smallmouth Bass recruit poorly to gill nets, so the estimate is likely biased low (Beamesderfer & Rieman, 1988; Miranda et al., 2024). Thus, we provided two additional scenarios. In scenario 2 (50% increase) the population estimate from scenario 1 was increased by 50%, and in scenario 3 (100% increase), the population estimate from scenario 1 was increased 100%. Similarly, a current population estimate for Northern Pikeminnow is absent in Lake Cascade, so we considered three scenarios for Northern Pikeminnow. During their yearly index netting, IDFG reports similar CPUE for Yellow Perch and Northern Pikeminnow (A. J. Dangora, IDFG, personal communication). In scenario 1 (equal Northern Pikeminnow catchability), population abundance was estimated by assuming equal catchability between Yellow Perch and Northern Pikeminnow. In scenario 2 (hydroacoustic), data were extrapolated from Janssen et al. (2006), who used a hydroacoustic survey to estimate the abundance of pelagic species in Lake Cascade in 2002. Janssen et al. (2006) paired the hydroacoustic surveys with gill-net catch data to proportionally assign species-level abundance to hydroacoustic estimates. The current population of Northern Pikeminnow in Lake Cascade was estimated by finding the product of the modern Northern Pikeminnow gill-net CPUE and the historical Northern Pikeminnow population estimate from 2002 and dividing that by the historical, 2002 Northern Pikeminnow gill-net CPUE. Because the estimate from the equal catchability is likely biased high and the estimate from the hydroacoustic scenario is likely biased low, the estimated abundance in the third scenario (mean abundance) was found by taking the mean of estimates from scenario 1 (equal Northern Pikeminnow catchability) and scenario 2 (hydroacoustic). We fully recognize that the population estimates are coarse, but they provide a framework to compare the consumption of juvenile Yellow Perch by Yellow Perch, Smallmouth Bass, and Northern Pikeminnow in Lake Cascade.

The total consumption (estimated by bioenergetics modeling) was applied to the population of each predator using the proportional cohort distribution described above to extrapolate to a population-scale consumption of Yellow Perch by each cohort of each species. We then multiplied the weight of Yellow Perch consumed by an individual in a cohort in a year (estimated from the bioenergetics model) by the estimated number of individuals in that cohort in the population to get

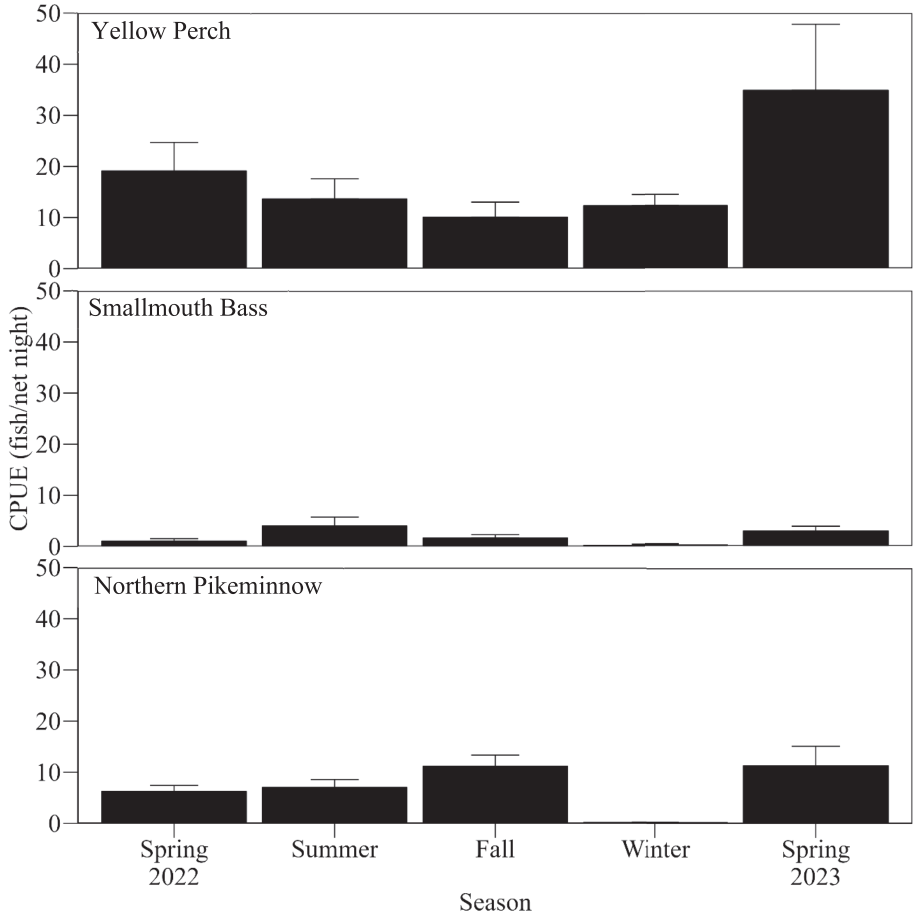

Figure 2. Mean catch per unit effort (CPUE = number of fish [Yellow Perch, Smallmouth Bass, Northern Pikeminnow] per net-night) in Lake Cascade, Idaho, by season and species from April 2022 to May 2023. Bars represent one standard error. Months were grouped into seasons: spring 2022 (April–May 2022), summer (June–August 2022), fall (October–November 2022), winter (January–February 2023), and spring 2023 (May 2023).

a total weight (kg) of Yellow Perch consumed annually by that cohort. We also estimated the number of juvenile Yellow Perch consumed by each cohort. Most Yellow Perch recovered from stomach contents were age 0. We divided the total weight of Yellow Perch (kg) consumed by a cohort in a season by the average weight of intact Yellow Perch observed in predator stomachs from that season to account for seasonal fluctuations in age-0 Yellow Perch weight. We then summed consumption across seasons and cohorts to estimate the total number of Yellow Perch consumed by a predator.

We estimated the total fecundity of Yellow Perch to provide insight on how patterns of predation relate to potential Yellow Perch recruitment. Total fecundity was estimated using a regression equation developed for Yellow Perch in Lake Cascade (Dangora, unpublished data):

$$y = 961.59x - 206{,}303,$$

where y is the predicted fecundity of a Yellow Perch and x is the total length (mm) of that Yellow Perch. We proportionally distributed fish to the Yellow Perch population estimate described above using the length-frequency distribution of Yellow Perch captured in our study. Half of the fish were assumed to be female. The total number of eggs produced was estimated by summing the number of eggs produced by females at each length. Comparisons between patterns of consumption in each predator-specific scenario were made by calculating the percent of age-0 Yellow Perch consumed as the quotient of the number of Yellow Perch consumed and the total number of eggs produced by females. Clady (1976) estimated that in Oneida Lake, New York, up to 18.4% of Yellow Perch eggs failed to reach larval stage. Thus, we made the same calculation described above assuming that 18.4% of Yellow Perch eggs failed to hatch. Nobel (1968) reported a daily mortality rate of 0.056% for larval Yellow Perch 8–20 mm in Oneida Lake, New York. We applied the same daily mortality rate to the estimated number of surviving larvae for 30 d. We then made the same calculation as described above to estimate the percent of remaining larvae after 30 d.

RESULTS

In total, we sampled 3,579 Yellow Perch, 518 Smallmouth Bass, and 1,825 Northern Pikeminnow. We extracted stomachs and ageing structures from 1,099 Yellow Perch, 440 Smallmouth Bass, and 980 Northern Pikeminnow during nine sampling

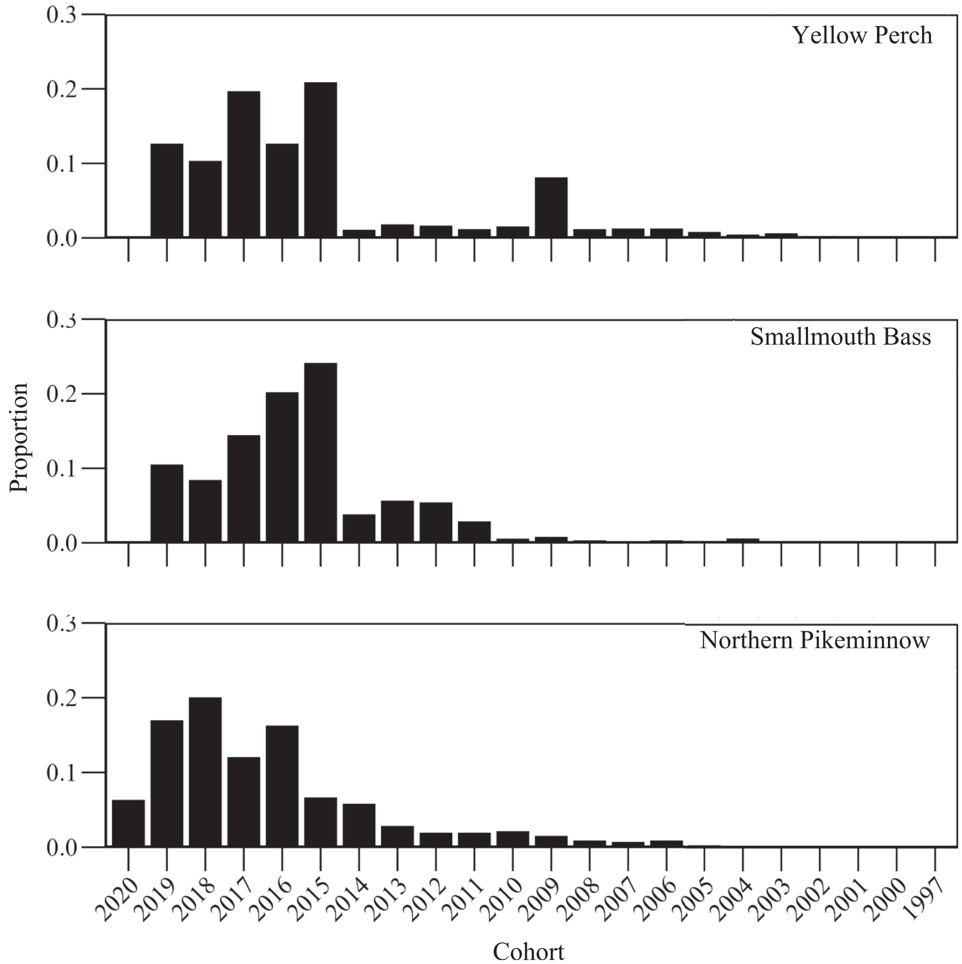

Figure 3. Proportion of Yellow Perch ($n = 1,080$), Smallmouth Bass ($n = 433$), and Northern Pikeminnow ($n = 976$) cohorts sampled in Lake Cascade, Idaho, from April 2022 to May 2023.

Table 1. Overall contribution of prey items to Yellow Perch, Smallmouth Bass, and Northern Pikeminnow diets from Lake Cascade from May 2022 to May 2023. Diet summarizations were frequency of occurance (O_i), proportion by weight (PW_i), and proportion of energy (calories) contributed (PE_i). Taxa were denoted as chironomids (CHR), Yellow Perch (YEP), zooplankton (ZOO), unknown fish (UKF), gastropods (GAS), other macroinvertebrates (MAC), molluscs (MOL), crayfish (CRY), other fish (OTF), and fish eggs (EGG). The symbol "*a*" indicates the proportional contribution was <0.01.

	Yellow Perch			Smallmouth Bass			Northern Pikeminnow		
Taxa	O_i	PW_i	PE_i	O_i	PW_i	PE_i	O_i	PW_i	PE_i
CHR	0.48	0.31	0.28	0.36	0.03	0.02	0.53	0.38	0.17
YEP	0.28	0.46	0.50	0.42	0.59	0.49	0.43	0.52	0.72
ZOO	0.18	0.03	0.03	0.04	*a*	*a*	0.06	*a*	*a*
UKF	0.17	0.05	0.03	0.32	0.06	0.04	0.06	*a*	*a*
GAS	0.17	0.10	0.08	0.01	*a*	*a*	*a*	*a*	*a*
MAC	0.12	0.02	0.02	0.22	0.02	0.03	0.24	0.03	0.04
MOL	0.10	0.01	*a*	*a*	*a*	*a*	*a*	*a*	*a*
CRY	0.02	0.02	0.04	0.17	0.20	0.26	0.02	0.03	0.03
OTF	0.01	*a*	0.01	0.04	0.01	0.16	*a*	0.02	0.02
EGG	*a*	*a*	*a*	–	–	–	–	–	–

events. Catch per unit effort of Yellow Perch was highest in spring and decreased through summer, fall, and winter (Figure 2). Catch rates of Smallmouth Bass and Northern Pikeminnow were highest in spring 2023 and lowest in winter. Yellow Perch varied in length from 85 to 396 mm (mean length ± SD = 270 ± 67 mm). Smallmouth Bass and Northern Pikeminnow had similar length distributions; Smallmouth Bass varied from 125 to 517 mm (317 ± 84 mm) and Northern Pikeminnow varied from 132 to 587 mm (323 ± 81 mm). Relative weight of Yellow Perch varied from 63 to 140 (94.0 ± 11.2) and from 65 to 157 (963.9 ± 12.9) for Smallmouth Bass. Relative condition varied from 55 to 156 for Northern Pikeminnow and averaged 106.2 (SD = 12.7).

Yellow Perch varied in age from 1 to 21 years, Smallmouth Bass varied from 2 to 17 years, and Northern Pikeminnow varied from 1 to 24 years (Figure 3; Table S3). For all three species, approximately 80% of the fish were age 6 or younger. Yellow Perch cohorts from 2019 to 2015 exhibited the greatest change in average weight between summer and fall (~30%); cohorts from 2014 to 2005 had minimal changes in weight over the sampling period (Table S2). The greatest change in average weight for Smallmouth Bass was observed between summer and fall. The oldest cohorts of Smallmouth Bass increased their average

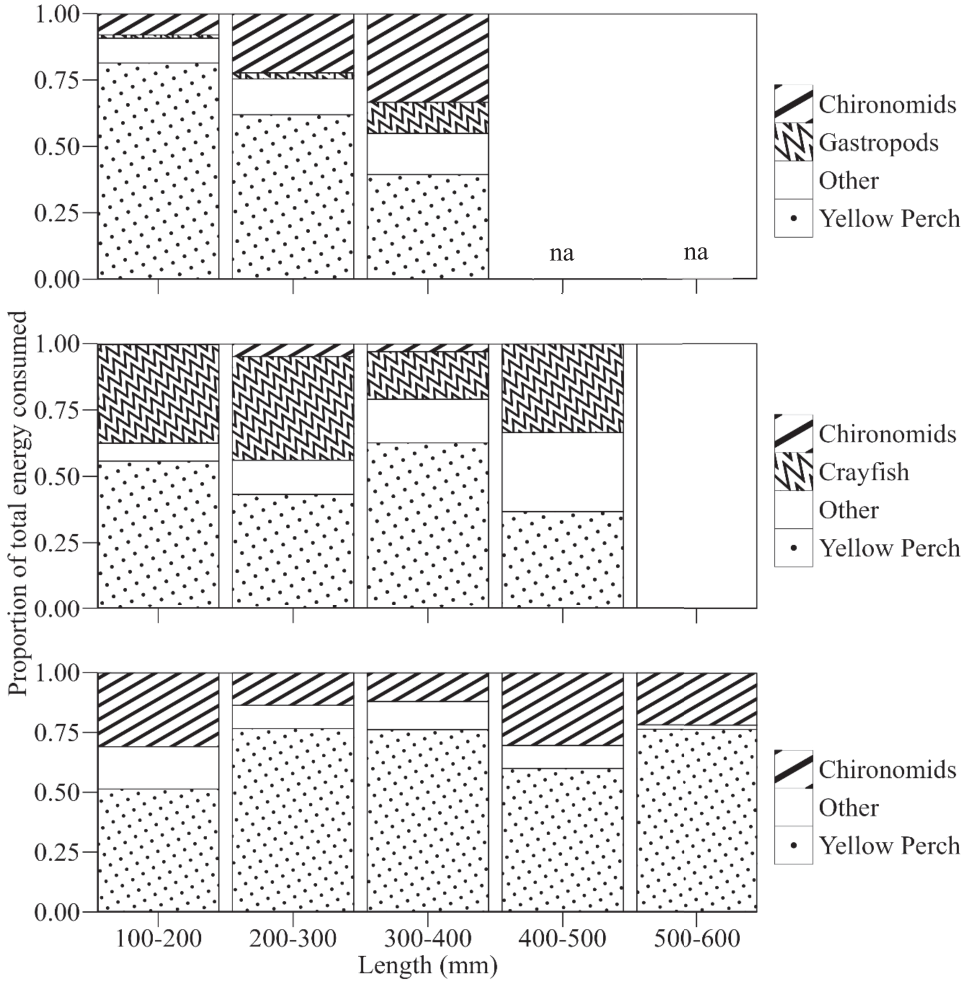

Figure 4. Proportion of energy contributed to the diets of Yellow Perch ($n = 666$; top panel), Smallmouth Bass ($n = 277$; middle panel), and Northern Pikeminnow ($n = 514$; bottom panel) by 100-mm length-group sampled in Lake Cascade, Idaho, from May 2022 to May 2023. Prey items were limited to the three most important taxa for Yellow Perch and Smallmouth Bass and the two most important taxa for Northern Pikeminnow. For all three species, all taxa not listed in the figure legend were grouped into the "other" category.

weight by about 10%, and the youngest cohorts increased their average weights by as much as 60%. Between spring and summer and between summer and fall, Northern Pikeminnow cohorts from 2019 to 2013 had similar increases in average weight (~25%). A clear trend was not observed in average weights of Northern Pikeminnow cohorts from 2012 to 2007.

Stomach contents varied by species (Table 1; Tables S4–S7). Yellow Perch had the lowest proportion of empty stomachs (27%), followed by Northern Pikeminnow (29%) and Smallmouth Bass (34%). Chironomids and Yellow Perch were the most common items in Yellow Perch and Northern Pikeminnow diets. Chironomids occurred more frequently than crayfishes (order Decopoda) in Smallmouth Bass diets but did not contribute meaningfully to the total energy consumed by Smallmouth Bass. Other prey types such as unknown fish, gastropods, and other macroinvertebrates were frequently observed in all three predator stomachs, but none contributed more than 8% to the total energy ingested by each species. Across all three target species, Yellow Perch contributed the greatest proportion of energy to predator diets (Table 1). In Yellow Perch and Northern Pikeminnow diets, chironomids contributed the second highest proportion of energy even though they occurred more frequently than Yellow Perch. Crayfish contributed the second highest proportion of energy to Smallmouth Bass diets.

The proportion of energy contributed by different prey items varied by the length of Yellow Perch (Figure 4). Interestingly, the proportion of energy contributed by Yellow Perch to Yellow Perch decreased from approximately 80% in fish that were 100–200 mm to approximately 40% in fish that were 300–400 mm. Energy from chironomids made up the difference. Similar patterns in length were not observed for Smallmouth Bass and Northern Pikeminnow. Yellow Perch made up 45% of the energy contribution to 100–500-mm Smallmouth Bass diet, whereas crayfish made up 40%. Approximately 70% of the energy in Northern Pikeminnow diets was from Yellow Perch. Chironomids made up approximately 25% of the remaining energy in all length-groups. Cohort-level trends were harmonious with length summarizations (Tables S4–S6).

Predator diets also varied seasonally (Figure 5). In spring 2022 and summer, over 50% of the energy consumed by Yellow Perch was from chironomids. Yellow Perch made up about 25%

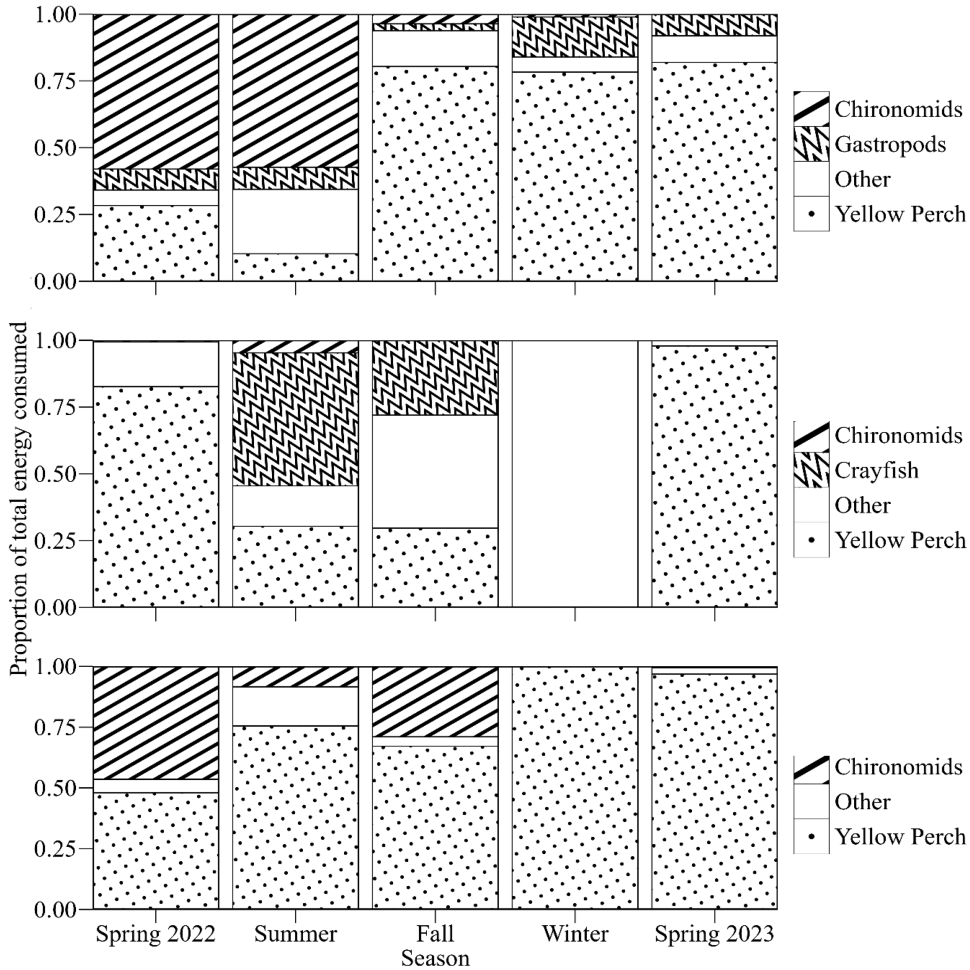

Figure 5. Proportion of energy contributed to the diets of Yellow Perch ($n = 666$; top panel), Smallmouth Bass ($n = 277$; middle panel), and Northern Pikeminnow ($n = 514$; bottom panel) in each season sampled in Lake Cascade, Idaho, from May 2022 to May 2023. Months were grouped into seasons: spring 2022 (May 2022), summer (June–August 2022), fall (October–November 2022), winter (January–February 2023), and spring 2023 (May 2023). Prey items were limited to the three most important taxa for Yellow Perch and Smallmouth Bass and the two most important taxa for Northern Pikeminnow. For all three species, all taxa not listed in the figure legend were grouped into the "other" category.

of the energy consumed by Yellow Perch in spring 2022 but below 10% in the summer. The remaining energy came from other species. Yellow Perch made up approximately 75% of the energy ingested by Yellow Perch during the fall, winter, and spring 2023. Smallmouth Bass diets were relatively consistent during the summer and fall, consisting of Yellow Perch, crayfish, and small amounts of other prey. However, Yellow Perch made up approximately 85% of the energy consumed by Smallmouth Bass during spring of 2022 and 2023. Yellow Perch contributed at least 50% of the total energy to Northern Pikeminnow diets across seasons. Chironomids made up a minority of the total energy contributed in spring 2022, summer, and fall but were scarce in the winter and spring 2023. Seasonal trends in percent weight contribution mirrored trends in energy contribution (Table S7).

Diet overlap was high ($G > 0.75$) among species and seasons (Table 2). The only exception was between Yellow Perch and Smallmouth Bass in the fall, which had moderate overlap ($G = 0.65$). Overall, the season with the highest average diet overlap was the spring 2023 ($G = 0.92$). The species interaction with the highest average overlap was between Yellow Perch and Northern Pikeminnow ($G = 0.89$).

The number of Yellow Perch in stomachs varied by predator length and month (Figure 6). Yellow Perch consumption by Yellow Perch was consistently 0.3 Yellow Perch/Yellow Perch across all length-groups. Smallmouth Bass consumption was about 0.4 Yellow Perch/Smallmouth Bass for fish that were 100–300 mm but doubled to approximately 1.0 Yellow Perch/Smallmouth Bass for Smallmouth Bass that were 300–500 mm. Northern Pikeminnow in the 500–600-mm length-group consumed the highest number of Yellow Perch (5.0 Yellow Perch/Northern Pikeminnow), followed by 300–500-mm fish (1.6 Yellow Perch/Northern Pikeminnow), 200–300-mm fish (0.5 Yellow Perch/Northern Pikeminnow), and 100–200-mm fish (0.2 Yellow Perch/Northern Pikeminnow). For all three species, Yellow Perch were nearly absent from the diets in June but increased in July. Yellow Perch consumed 0.3 Yellow Perch/Yellow Perch from May 2022 through February 2023. In May 2023, consumption tripled to approximately 1.0 Yellow Perch/Yellow Perch. Smallmouth Bass consumption of Yellow Perch

Table 2. Pianka's index of niche overlap depicting the strength of diet overlap between Yellow Perch, Smallmouth Bass, and Northern Pikeminnow during each season in Lake Cascade from May 2022 to May 2023. Months were grouped into seasons: spring 2022 (May 2022), summer (June–August 2022), fall (October–November 2022), winter (January–February 2023), and spring 2023 (May 2023).

Season	Yellow Perch × Smallmouth Bass	Yellow Perch × Northern Pikeminnow	Northern Pikeminnow × Smallmouth Bass
Spring 2022	0.88	0.89	0.77
Summer	0.86	0.93	0.82
Fall	0.65	0.85	0.88
Winter	–	0.85	–
Spring 2023	0.84	0.95	0.98
All	0.79	0.92	0.76

was highest in May 2022 (1.8 Yellow Perch/Smallmouth Bass) and May 2023 (2.0 Yellow Perch/Smallmouth Bass) but averaged about 0.3 Yellow Perch/Smallmouth Bass for the remainder of the year. Northern Pikeminnow consumption of Yellow Perch averaged 0.5 Yellow Perch/Northern Pikeminnow during all months except July (3.3 Yellow Perch/Northern Pikeminnow) and August (1.5 Yellow Perch/Northern Pikeminnow).

The total estimated annual consumption of Yellow Perch by all cohorts was 6.0 kg by Yellow Perch, 3.4 kg by Smallmouth Bass, and 9.9 kg by Northern Pikeminnow. Consumption (by weight) of Yellow Perch by Smallmouth Bass in all three abundance scenarios was lower than Yellow Perch or Northern Pikeminnow consumption of Yellow Perch (Table 3). In the highest consumption scenario for Smallmouth Bass (100% increase), Smallmouth Bass consumed one-fifth as much Yellow Perch as Yellow Perch. Consumption of Yellow Perch by Yellow Perch was most similar to Northern Pikeminnow consumption in Northern Pikeminnow abundance scenario 3 (mean abundance). The difference in consumption between Yellow Perch and Northern Pikeminnow scenario 3 was only 1,000 kg of Yellow Perch. By number of Yellow Perch consumed, the difference was approximately 147,320,000 individuals. When catchability was assumed equal between Yellow Perch and Northern Pikeminnow, Northern Pikeminnow consumed about 350,000 kg more Yellow Perch than Yellow Perch.

The estimated number of eggs produced by Yellow Perch in Lake Cascade was 27,434,053,956. When consumption in the highest abundance scenarios was summed across species, predators consumed approximately 5.5% of the larval Yellow Perch produced (Table 2). Assuming an 18.4% egg mortality, the estimated number of larvae produced was 22,386,188,028. Predators in Lake Cascade would consume about 6.6% of the larval Yellow Perch produced under the highest consumption scenarios. Assuming a daily mortality rate of 0.056% over 30 d, 3,973,195,877 larvae would reach 20 mm. Under maximum consumption conditions, approximately 37% of the larvae that reached 20 mm would be consumed in the first year by all three predators.

DISCUSSION

Since the introduction of Yellow Perch to Lake Cascade, its abundance has been highly variable. Two historical studies have documented Northern Pikeminnow food habits in Lake Cascade, but neither identified fish as an important prey resource (Bennett, 2004; Casey, 1962). Recent declines in Yellow Perch recruitment sparked a novel investigation into Yellow Perch, Smallmouth Bass, and Northern Pikeminnow food habits in Lake Cascade. Our study found that Yellow Perch was an important prey resource for the study species, particularly Yellow Perch and Northern Pikeminnow. Chironomids were the second most common prey item in Yellow Perch and Northern Pikeminnow diets and contributed substantially to the total energy consumed. Crayfish was the second most common diet item in Smallmouth Bass diets. Other prey taxa (i.e., unknown fish, gastropods, other macroinvertebrates) occurred frequently in the diets of all three study species but did not contribute meaningfully to total energy consumption.

Although Yellow Perch often experience notable ontogenetic diet shifts (Brown et al., 2009), major shifts in diet were not observed for Yellow Perch in Lake Cascade. The diet of Yellow Perch of all lengths was dominated by chironomids and Yellow Perch. Interestingly, the energetic contribution of chironomids to Yellow Perch diets increased with length. Similar trends are not well documented in the literature, considering that Yellow Perch usually become increasingly piscivorous with length. For instance, Hilling et al. (2018) found that the diets of age-0 and age-1 Yellow Perch contained no fish, whereas 40% of the diet was comprised of fish for age-2 and older Yellow Perch in a West Virginia reservoir. Similarly, Clady (1974) noted that the diet of Yellow Perch shorter than 150 mm was composed of 55% chironomids by weight. The diet of fish larger than 150 mm was composed of 55% fish by weight. Several mechanisms may be facilitating the pattern of high chironomid consumption with length in Lake Cascade. One explanation is that age-0 fish are not available as a prey item because they do not overlap with adult Yellow Perch. Feucht et al. (2023) found that age-0 Yellow Perch in Crystal Lake, Wisconsin, occupied vegetated, littoral habitat and adult Yellow Perch used pelagic habitats. In Lake Cascade, Yellow Perch were found in the stomachs of Yellow Perch captured in variable habitats. Another possible mechanism may be gape limitation of large (>300 mm) Yellow Perch (Hoyle & Keast, 1987). Gape limitation seems unlikely, as Paszkowski and Tonn (1994) noted that in laboratory conditions, Yellow Perch as small as 190 mm consumed equal amounts of small (43–55 mm) and large (71–80 mm) fish prey. Alternatively, the increase in chironomid consumption may be due to the relative ease of capturing chironomids (Lammens & Hoogenboezem, 1991) and/or the relative abundance of

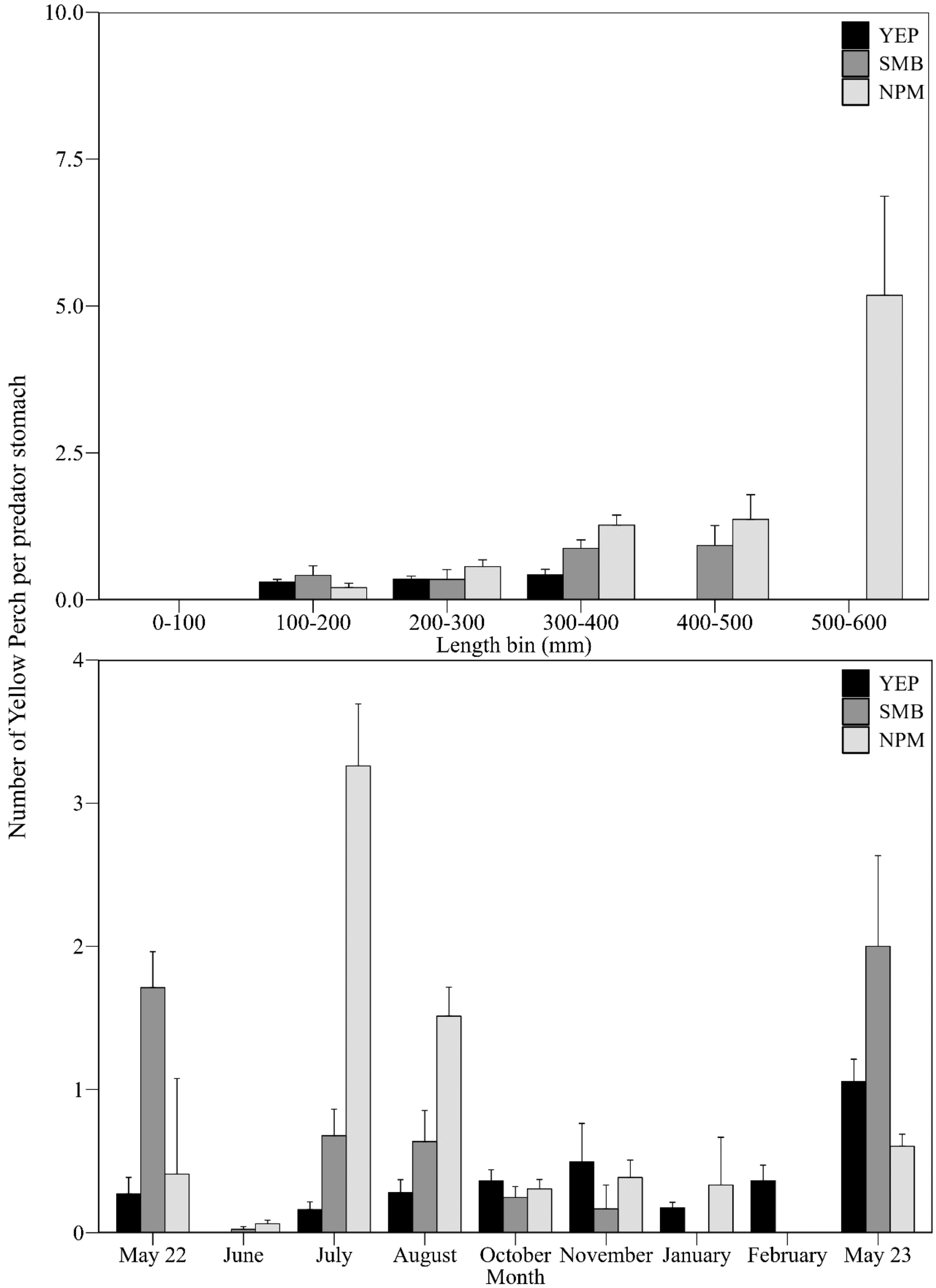

Figure 6. Average number of Yellow Perch consumed by Yellow Perch (YEP), Smallmouth Bass (SMB), and Northern Pikeminnow (NPM) by length (mm; top panel) and month (bottom panel) in Lake Cascade, Idaho, from May 2022 to May 2023. Bars represent one standard error.

chironomids (McCord & Kuhl, 2013). Hayes et al. (1992) found that after the removal of White Suckers *Catostomus commersonii* from a Michigan lake, chironomid abundance increased 13- to 18-fold and growth of Yellow Perch increased. In Lake Cascade, the largest Yellow Perch consumed fewer Yellow Perch than expected. Rather, the majority of energy contributed to large Yellow Perch diets was from chironomids, suggesting that chironomids are abundant and easy to capture for large Yellow Perch.

Cannibalism by Yellow Perch varied seasonally. In Lake Cascade, age-0 Yellow Perch (i.e., 30 mm long) first appeared in Yellow Perch diets in July. The time that age-0 Yellow Perch appeared in Yellow Perch diets coincides with the length and approximate time that age-0 Yellow Perch begin using littoral habitats (Paradis et al., 2014; Power & Van Den Heuvel, 1999). In other systems, age-0 Yellow Perch are often not an important diet item until fall (Fullhart et al., 2002; Knight et al., 1984; Langford & Martin, 1941; Tarby, 1974; White & Facey, 2009). In those systems, juvenile fish from other taxonomic groups (i.e., Clupeidae, Cyprinidae, Percidae, Gasterosteidae, Centrarchidae) are important prey items for Yellow Perch in the spring and early summer. The diversity of fishes in western

Table 3. Estimated abundance of predators, estimated weight (kg) of Yellow Perch consumed, and estimated number of Yellow Perch consumed by Yellow Perch, Smallmouth Bass, and Northern Pikeminnow in scenarios 1, 2, and 3 from May 2022 to May 2023 in Lake Cascade. The percent of the total estimated number of Yellow Perch consumed by each species in each scenario is shown, assuming no egg mortality, high egg mortality (18.4%), and high daily larval mortality (0.056%). Abbreviation: IDFG = Idaho Department of Fish and Game.

Scenario	Abundance estimate	Weight	Number age-0 Yellow Perch	No egg mortality	High egg mortality	High daily larval mortality
Yellow Perch						
Scenario 1—IDFG estimate Smallmouth Bass	890,000	663,514.8	451,518,441	1.6	2.0	11.4
Scenario 1—equal Smallmouth Bass catchability	82,500	59,739.52	48,562,135	0.2	0.2	1.2
Scenario 2—50% increase	124,000	89,790.3	72,990,361	0.3	0.3	1.8
Scenario 3—100% increase	165,000	119,479.0	97,124,270	0.4	0.4	2.4
Northern Pikeminnow						
Scenario 1—equal Northern Pikeminnow catchability	890,000	1,049,493.0	949,183,046	3.5	4.2	23.9
Scenario 2—hydroacoustic	233,000	274,754.2	248,493,424	0.9	1.1	6.3
Scenario 3—mean abundance	561,500	662,123.7	598,838,517	2.2	2.7	15.1

reservoir systems is much lower than water bodies in most other regions of the United States (Miranda & Bettoli, 2010; Rahel, 2000). Consequently, the dearth of "traditional" Yellow Perch prey species in Lake Cascade may increase the importance of age-0 Yellow Perch as a prey resource. Another notable observation was that consumption of Yellow Perch in Lake Cascade was much higher in May 2023 than May 2022. The difference may reflect annual variability in chironomid abundance (McCord & Kuhl, 2013), variable juvenile Yellow Perch abundance (Forsythe et al., 2012; Hanchin et al., 2011; Honsey et al., 2016), and/or differences in growth of age-0 Yellow Perch (Kaemingk et al., 2014; Power & Van Den Heuvel, 1999).

Smallmouth Bass diets varied by length and season but were always dominated by Yellow Perch and crayfish. Our findings are consistent with other studies on the diet of Smallmouth Bass (Buynak et al., 1982; Liao et al., 2004; Margetts & Heise, 2024). Once Smallmouth Bass reach ~100 mm, their diet typically shifts from an insect-dominated diet to one dominated by fish and crayfish (Dauwalter & Fisher, 2008; Weidel et al., 2011). Despite similar energy contributions from Yellow Perch and crayfish, the numeric consumption of Yellow Perch in Smallmouth Bass stomachs in our study doubled after Smallmouth Bass reached 300 mm. Seasonally, Smallmouth Bass was a generalist in Lake Cascade and, similar to other studies, appeared to be opportunistic (Dembkowski et al., 2015; Frey et al., 2003; Pflug & Pauley, 1984; Wolf et al., 2022; Zimmerman, 1999). Crayfish were important in the diet of Smallmouth Bass during summer and fall, which likely reflects the availability of crayfish. Most crayfishes hibernate during cold periods and may be unavailable to Smallmouth Bass in the winter and spring (Bubb et al., 2004). In spring, most of the energy consumed by Smallmouth Bass was provided by Yellow Perch. Fayram and Sibley (2000) reported that juvenile Sockeye Salmon made up 30–40% of Smallmouth Bass diets during the spring in Lake Washington, Washington. The authors attributed Smallmouth Bass consumption of Sockeye Salmon to habitat overlap in the spring rather than preference for fish. In Lake Cascade, Smallmouth Bass likely consumed the most readily available prey in each season.

Yellow Perch made up at least 50% of the energy contributed to Northern Pikeminnow diets in Lake Cascade. Hansen et al. (2022) used stable isotopes to describe the diet of several predator species in Kachess Lake, Washington. The authors reported that Northern Pikeminnow smaller than 200 mm were most similar to Largescale Suckers, whereas Northern Pikeminnow larger than 400 mm occupied the same isotopic space as 300–400-mm, piscivorous Burbot *Lota lota*. Similarly, Clarke et al. (2005) found that Northern Pikeminnow less than 150 mm in Lake Pend Oreille, Idaho, primarily consumed benthic invertebrates. Northern Pikeminnow longer than 300 mm consumed 25% more fish and 38% more kokanee compared to smaller Northern Pikeminnow. Two historical diet studies have been conducted on Northern Pikeminnow in Lake Cascade, and only Casey (1962) summarized Northern Pikeminnow diets by length. He found that fish were only consumed by Northern Pikeminnow that were 305–406 mm (fork length). Smaller Northern Pikeminnow primarily consumed chironomids. Despite the relatively similar energetic contributions of Yellow Perch to Northern Pikeminnow of all lengths in our study, the number of Yellow Perch consumed increased with predator length. Northern Pikeminnow that were 500–600 mm long consumed approximately five times more Yellow Perch than those that were 400–500 mm.

The proportion of energy contributed to Northern Pikeminnow diets by Yellow Perch increased over the duration of the study. In spring 2022, about 50% of the energy consumed by Northern Pikeminnow was from Yellow Perch and 50% was from chironomids. By spring 2023, nearly 100% of the energy contributed to Northern Pikeminnow diets was from Yellow Perch. Seasonal diet composition of Northern Pikeminnow in other systems is inconsistent. Several studies have shown that Northern Pikeminnow consumption of macroinvertebrates decreases from spring to fall and consumption of fish increases (Hansen et al., 2022; Sorel et al., 2016). Other studies have reported that the highest consumption of fish is in the spring, with a subsequent decline during the remainder of the year (Collis et al., 1995; Zimmerman, 1999). In the Columbia River, Northern Pikeminnow consumed high numbers of juvenile salmonids during spring out-migration (Isaak & Bjornn, 1996; Zimmerman, 1999). Studies that reported increased fish consumption in the fall have been in reservoir systems that lack anadromous fishes. Although some fish were consumed by large Northern Pikeminnow, Casey (1962) reported that fish were not a dominant prey item in Lake Cascade. Bennett (2004) found that the number of Yellow Perch consumed by Northern Pikeminnow increased from July to October, but Yellow Perch were never a major component (by weight) in Northern Pikeminnow diets. In the current study, the number of Yellow Perch consumed by Northern Pikeminnow was highest in July–August and low in other months. Juvenile Yellow Perch typically transition from pelagic habitat to littoral areas in July and August, where they are likely particularly vulnerable to predation by Northern Pikeminnow (Paradis et al., 2014; Power & Van Den Heuvel, 1999).

In Lake Cascade, diet overlap was high among all three study species. Despite the findings of our research, diet overlap between Yellow Perch, Smallmouth Bass, and Northern Pikeminnow varies based on the habitat in which the interaction occurs. For example, Clady (1974) showed relatively little diet overlap between Yellow Perch and Smallmouth Bass in two Michigan lakes. Specifically, the author noted that Yellow Perch consumed juvenile Yellow Perch and macroinvertebrates, whereas Smallmouth Bass had a more diverse diet primarily composed of crayfish and other fishes. Similarly, Liao et al. (2002) observed that Yellow Perch and Smallmouth Bass both had diverse diets in Spirit Lake, Iowa. The staple food items for Yellow Perch were amphipods and crayfish, and Yellow Perch was the dominant prey in Smallmouth Bass diets. Conversely, Vigg et al. (1991) and Zimmerman (1999) found that in Columbia River impoundments, Washington–Oregon, Smallmouth Bass and Northern Pikeminnow consumed similar quantities of fish (e.g., Cottidae, Salmonidae) across systems and seasons. Prey biodiversity in a system is an important determinant of the degree of diet overlap between predators (Feiner et al., 2019; Winters & Budy, 2015). Based on our analysis, prey diversity in Lake Cascade was relatively low. Yellow Perch, chironomids, and crayfish were the dominant diet items for all study species. Thus, the high diet overlap observed in Lake Cascade likely reflects the relatively low diversity of prey resources.

Although our estimates of abundance are admittedly coarse, Yellow Perch, Smallmouth Bass, and Northern Pikeminnow in Lake Cascade may consume up to 37% of the Yellow Perch reaching 20 mm. Hartman and Margraf (1992) found similar consumption levels in Lake Erie, Ohio, where Walleye *Sander vitreus* consumed 28–90% of the Yellow Perch produced. Further, the authors concluded that predation could play a major role in structuring year-class strength of Yellow Perch in the system. Likewise, Brandt et al. (1987) identified predation by Alewife *Alosa pseudoharengus* as a potential factor limiting Yellow Perch recruitment in Lake Ontario, New York. In Lake Cascade, Northern Pikeminnow may influence Yellow Perch year-class variability more than Yellow Perch, although both likely play a much larger role than Smallmouth Bass. Similar to our study, Dembkowski et al. (2015) concluded that Smallmouth Bass predation did not independently limit age-0 Yellow Perch recruitment in two South Dakota lakes. Likewise, Fetzer et al. (2015) showed that Smallmouth Bass, Largemouth Bass, and Walleye only suppressed Yellow Perch populations when all three species were present. Unlike Smallmouth Bass, studies have demonstrated that Yellow Perch and Northern Pikeminnow predation can influence sport fish recruitment. For example, Sanderson et al. (1999) found that adult Yellow Perch in an oligotrophic, Wisconsin lake suppressed age-0 Yellow Perch, creating a population that cycled every 5 years. Likewise, Clark (2017) found that Northern Pikeminnow consumed up to 37% of the juvenile Sockeye Salmon produced in Lake Washington and potentially limited recruitment. Although the estimated consumption of Yellow Perch in Lake Cascade is compelling, several assumptions were made during the calculation of the Smallmouth Bass and Northern Pikeminnow abundance estimates. Nevertheless, the estimates provide a framework to compare the consumption of Yellow Perch, Smallmouth Bass, and Northern Pikeminnow. Future efforts focused on accurately estimating the abundance of Smallmouth Bass and Northern Pikeminnow in Lake Cascade would be useful. Further, an investigation into the effects of altering Northern Pikeminnow removal prescriptions would provide insight into the effectiveness of potential Northern Pikeminnow removal projects on Lake Cascade.

Our study adds to the growing body of literature documenting the food habits of native and nonnative fishes in western reservoirs. Similar to systems within the native distribution of Yellow Perch (e.g., Dauwalter & Fisher, 2008; Weidel et al., 2011; White & Facey, 2009), juvenile Yellow Perch were an important prey resource to predators in Lake Cascade. Northern Pikeminnow appeared to consume more Yellow Perch by weight than either Yellow Perch or Smallmouth Bass in the highest Northern Pikeminnow abundance scenario (equal Northern Pikeminnow catchability). In Northern Pikeminnow scenario 3 (mean abundance), consumption of Yellow Perch by weight was equal between Yellow Perch and Northern Pikeminnow. Though the native distributions of Northern Pikeminnow and Yellow Perch do not overlap, predation by both Yellow Perch and Northern Pikeminnow may be related to recruitment variability of Yellow Perch in Lake Cascade. Further, the influence of predation on Yellow Perch is likely exacerbated by the apparently low prey biodiversity in Lake Cascade. Thus, predation on juvenile Yellow Perch in Lake Cascade may play a larger role in recruitment variation than in systems within the native distribution of Yellow Perch.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *North American Journal of Fisheries Management* online.

DATA AVAILABILITY

Data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The study was conducted in accordance with the guidelines for experimental procedures in animal research from the University of Idaho Animal Care and Use Committee (Protocol 2021-82).

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CONFLICTS OF INTEREST

The authors declare that there is no conflict of interest in connection with this article.

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