

Articles

Population Characteristics and the Potential Suppression of Common Carp in Lake Spokane, Washington

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Abstract

Common Carp *Cyprinus carpio* is a nonnative species that often has deleterious effects on aquatic systems. As such, there is interest in suppressing nonnative Common Carp populations in areas where humans have introduced them. The objectives of this study were to 1) provide insight on efficient techniques for capturing Common Carp, 2) describe their population demographics and dynamics, 3) evaluate whether temperature and water elevation were related to growth and recruitment, and 4) develop an age-structured population model for evaluating different management scenarios of Common Carp removal in Lake Spokane, Washington. Catch rates of Common Carp varied among sampling gears with slightly higher catch rates in monofilament (mean \pm SD; 15.5 ± 9.8 fish/net night) vs. multifilament (12.7 ± 7.3 fish/net night) gill nets. Catch rates of Common Carp with nighttime electrofishing (0.3 ± 0.4 fish/min) were higher than daytime electrofishing (0.1 ± 0.2 fish/min). Common Carp in Lake Spokane exhibited variable recruitment, rapid growth, large-length structure, high longevity (i.e., age 18 y), and low total annual mortality (17.0%). Air temperature was positively associated with annual growth increments ($R^2 \leq 0.25$). Neither air temperature nor water elevation was highly correlated ($R^2 \leq 0.20$) to recruitment of Common Carp. A Beverton–Holt yield-per-recruit model suggested that yield declined with increasing exploitation. Recruitment overfishing would occur at exploitation rates of 20–40% for all targeted minimum length categories (i.e., 150, 300, 450 mm) except 600 mm. Results from this study provide important information on the ecology of Common Carp that can be used to guide management efforts (e.g., suppression) in western systems.

Keywords: Common Carp; *Cyprinus carpio*; nonnative; suppression

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Introduction

Fisheries managers throughout most of the United States recognize Common Carp *Cyprinus carpio* as a nuisance species that humans have introduced through legal and illegal stocking (Rahel 2004). For example, the U.S. Fish Commission was established in 1871 with a mission to increase fishery resources in the United States through species propagation and stocking (Nielsen 1999). One of the primary fish species introduced to lentic and lotic systems was Common Carp. However, fisheries managers quickly curtailed new introductions of Common Carp due to the many deleterious effects they had on aquatic systems.

Common Carp are highly adaptable to new environments and can alter the abiotic and biotic integrity of aquatic ecosystems (Bajer et al. 2012). Common Carp are benthic feeders that consume macrophytes and invertebrates (King and Hunt 1967; Crivelli 1981; Scheffer et al. 1993; Parkos et al. 2003; Miller and Crowl 2006). During feeding, Common Carp destabilize substrate, and resuspend sediments and nutrients into the water column, which increases turbidity (Loughheed et al. 1998; Zambrano and Hinojosa 1999; Zambrano et al. 2001; Fischer et al. 2013). Previous research on Cootes Paradise Marsh in Lake Ontario, Canada, estimated that turbidity increased proportionally with total Common Carp biomass (Loughheed et al. 1998). Increased water turbidity ultimately limits the amount of light penetrating the water and thus reduces the growth of various macrophytes (Hootsmans et al. 1996). Common Carp can also negatively influence fish assemblage structure (Jackson et al. 2010; Wahl et al. 2011). For instance, a study conducted in Danish lakes suggested that sight-feeding fishes were less abundant in turbid waters that contained benthivorous fishes (e.g., Common Carp) than those without benthivores (Jeppesen et al. 2000). Moreover, Common Carp are highly fecund and long lived, making them a dominant species in both lentic and lotic environments (Cahn 1929; Panek 1987).

Due to their negative effects, Common Carp are often the focus of removal efforts. Bajer et al. (2011) demonstrated how researchers could use radiotelemetry to locate large aggregations of radio-tagged Common Carp, which fisheries personnel could then exploit. Similarly, Penne and Pierce (2008) conducted a radiotelemetry study in Clear Lake, Iowa, and reported that Common Carp exhibited repeatable patterns in their seasonal distribution and habitat selection that would allow for a variety of removal techniques. Other studies have demonstrated the use of commercial harvest as a management tool for Common Carp (Weber et al. 2011; Colvin et al. 2012). Although suppression of Common Carp is a major focus of many studies, effectively suppressing Common Carp populations is difficult due to their rapid growth, high recruitment, and low natural mortality (Brown and Walker 2004; Weber et al. 2011). An understanding of Common Carp population dynamics is necessary for managers to predict how populations will react to management actions, including suppression.

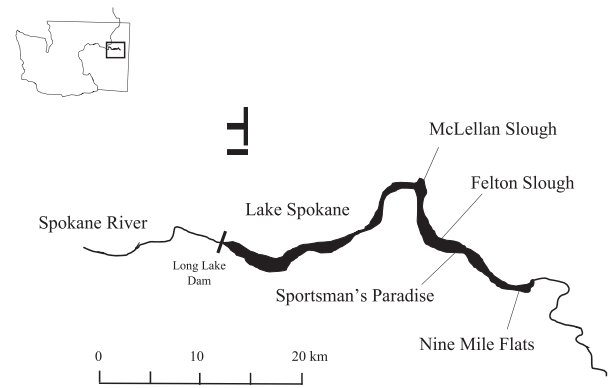


Figure 1. Lake Spokane, Washington, and the four sampling locations (McLellan Slough, Felton Slough, Sportsman's Paradise, and Nine Mile Flats) used to sample Common Carp *Cyprinus carpio* during May 2017.

Information on population demographics (e.g., age structure) and dynamics (e.g., growth, mortality, and recruitment) is critical for assessing fish management strategies (Ricker 1975; Allen and Hightower 2010). Specifically, insight on the age, growth, and recruitment of Common Carp is valuable for evaluating environmental factors that may hinder growth and recruitment. These data also provide information for population models that managers can use to examine different suppression scenarios. The objectives of this study were 1) to provide insight on efficient techniques for capturing Common Carp, 2) describe the population demographics and dynamics of Common Carp, 3) evaluate whether temperature and water elevation were related to the growth and recruitment of Common Carp, and 4) develop an age-structured population model to evaluate different removal scenarios for Common Carp in Lake Spokane.

Methods

Study area

Lake Spokane is located 15 km northwest of Spokane, Washington, and was formed in 1915 when the Spokane River was impounded by Long Lake Dam (Figure 1). At full pool, the reservoir has a surface area of 20.8 km², is approximately 34.5 km in length, and has a maximum depth of 54.9 m (Thomas and Soltero 1977). Water elevation is typically 468 m and fluctuates by an average of 4 m and temperature varies from -4.4 to 26°C (Avista 2015). The lake is known for having shallow littoral habitats with nearly a dozen species of aquatic plants, including a variety of native (e.g., tape grass *Vallisneria spiralis*) and nonnative plants (e.g., Eurasian watermilfoil *Myriophyllum spicatum*; Avista 2011). The lake includes both nongame (e.g., Northern Pikeminnow *Ptychocheilus oregonensis*, Largescale Sucker *Catostomus macrochilus*, and Chiselmouth Chub *Acrocheilus alutaceus*) and sport fish species (e.g., Yellow Perch *Perca flavescens*, Smallmouth Bass *Micropterus dolomieu*). Other common fishes

in the system include Northern Pike *Esox lucius* and Common Carp.

In the past, fisheries personnel have focused little attention on Common Carp in Lake Spokane. In recent years, fishery managers have declared a need to remove Common Carp from Lake Spokane due to the many deleterious effects Common Carp have on the ecosystem, such as destabilization of substrate and decreased water quality. Additionally, Common Carp influence phosphorus loading during feeding, excretion, and die offs. In Lake Spokane, phosphorus loading has led to algae blooms and poor water quality. As such, managers have proposed Common Carp suppression as a strategy to reduce phosphorus levels in Lake Spokane. In 2014, a telemetry study of Common Carp in Lake Spokane identified areas of high Common Carp density in the winter and spring (Avista 2015). During the spawning season (June–July), Common Carp were found actively spawning in the littoral zone (≤ 2 m) of six vegetated flats: Nine Mile Flats (river kilometer [rkm] 87.5–89.0, measuring from the mouth of the Spokane River), Sportsman's Paradise (rkm 79.0–82.0 southern bank), Felton Slough (rkm 77.5–79.0 northern bank), McLellan Slough (rkm 71.0–73.0), extended vegetated flats on the north bank (rkm 62.8–64.4), and Woody Slough (rkm 57.0–59.0; Figure 1). During other seasons, Common Carp were widely dispersed around the lake.

Field sampling

We sampled Common Carp in May 2017 at four previously identified spawning locations in Lake Spokane (i.e., Nine Mile Flats, Sportsman's Paradise, Felton Slough, and McLellan Slough; Figure 1). Each of the four sampling locations was roughly 400 m long and was divided into multiple sampling reaches along the shoreline (i.e., Nine Mile Flats = 5, Sportsman's Paradise = 12, Felton Slough = 6, and McLellan Slough = 6). Sampling occurred over an 8-d period. We sampled all reaches using gill nets, daytime electrofishing, and nighttime electrofishing.

Gill nets were 60 m long and 3 m tall. Each gill net was constructed of four 15-m-long panels (127, 152, 177, 203 mm stretch-measure mesh). A monofilament and multifilament gill net were tied together to form a “gang.” Gangs were constructed to evaluate the influence of mesh type on catch per unit effort ($\text{CPUE}_{\text{GN}} = \text{fish per net}$). We placed one or two gangs randomly at each of the four locations. We set gangs perpendicular to shore and systematically randomized the mesh type closest to the shore. We set gangs at sunset and pulled them early the next morning (~12-h set). We set four to eight gangs every night over six nights.

We conducted daytime and nighttime electrofishing using a 5-m-long boat equipped with a 5,000 W generator and Smith-Root VVP-15B electrofisher (Smith-Root, Incorporated, Vancouver, WA). Electrofishing power output was standardized (Miranda 2009). We sampled each reach in its entirety or until “electrified” time

reached 10 min. Sampling commenced at the downstream-most point of each reach and continued upstream in a zig-zag pattern. We estimated electrofishing catch rates (CPUE_{EF}) as the number of fish per minute of pedal-down time.

We measured total length (nearest mm) and weight (nearest g) from all Common Carp. We also recorded net type (i.e., monofilament or multifilament) for Common Carp captured in gill nets. We recorded sex and maturity status (immature or mature) for all individuals. We removed the dorsal spine from 10 Common Carp per centimeter-length group (Quist et al. 2012; Yates et al. 2016; Miranda and Colvin 2017). We cut dorsal spines at the junction with the body wall (Watkins et al. 2015), placed them into individually marked envelopes, and returned them to the University of Idaho for processing. We mounted spines in epoxy and transversely sectioned them following Koch and Quist (2007).

Data summarization and analysis

We tested differences in CPUE_{GN} between monofilament and multifilament gill nets using a paired *t*-test, whereas we used a Student *t*-test to test for differences in CPUE_{EF} between day and nighttime electrofishing (Ott and Longnecker 2008). We summarized length structure of Common Carp using proportional size distribution (Neumann et al. 2012). We estimated proportional size distribution values as the number of fish in a specified length category divided by the number of fish greater than or equal to stock length (≥ 280 mm), multiplied by 100 (Neumann et al. 2012). Length categories for Common Carp included quality (410 mm), preferred (530 mm), memorable (660 mm), and trophy (840 mm).

Length structure of Common Carp was similar between gill netting and electrofishing samples, and gill netting provided a much larger sample of Common Carp than electrofishing. Therefore, we used only data collected from gill netting in further analyses. We evaluated body condition of Common Carp captured in gill nets using relative weight. We estimated relative weight as 100 times the weight of a fish divided by the length-specific standard weight of an individual (Neumann et al. 2012). We estimated standard weight for Common Carp in the following way:

$$\log_{10}(W_s) = -4.639 + 2.920 \times \log_{10}(L),$$

where W_s is the standard weight of fish of total length L (Neumann et al. 2012). We summarized relative weight by length category to provide insight on length-related patterns in body condition.

We examined cross-sections (0.875 mm) of mounted dorsal spines using a dissecting microscope with transmitted light and an image analysis system (Image-Pro Plus; Media Cybernetics, Silver Spring, MD). Yates et al. (2006) noted that Common Carp dorsal spines are easily interpreted and between-reader agreement was high. In the current study, annuli were enumerated by one reader and a subsample ($n = \sim 75$ fish) was

corroborated by a second experienced reader; agreement in ages between readers was 100%. We used an age-length key to estimate age structure of Common Carp (Quist et al. 2012; Paukert and Spurgeon 2017). We estimated total annual mortality of Common Carp using a weighted catch curve (Chapman and Robson 1960; Smith et al. 2012). Age-4 and older fish were considered fully recruited to the sampling gear.

We estimated back-calculated length at age of Common Carp using the Dahl-Lea method (Quist et al. 2012; Shoup and Michaletz 2017):

$$L_i = \frac{S_i}{S_c} \times L_c,$$

where L_i is the back-calculated length of the fish when the i th increment was formed, L_c is the length of the fish at capture, S_i is the radius of the spine at the i th increment, and S_c is the radius of the spine at capture (Francis 1990; Shoup and Michaletz 2017). We also estimated the relative growth index to provide insight on how growth of Common Carp in Lake Spokane compared to other populations across their distribution. We estimated the relative growth index as 100 times the observed back-calculated length at age divided by the age-specific standard length (Jackson et al. 2008). We estimated the standard length for Common Carp using the following equations (Jackson et al. 2008):

$$L_s = 632.4 \left[1 - e^{-0.283(\text{age} + 0.053)} \right]$$

where L_s is the age-specific standard length in millimeters. We further summarized the growth of Common Carp using a von Bertalanffy growth model (von Bertalanffy 1938; Haddon 2001; Ogle et al. 2017):

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)} \right]$$

where L_t is length at time t , L_∞ is the theoretical mean maximum length of the fish in the population, k is the growth coefficient, t is age, and t_0 is the theoretical age when length equals 0 mm (Quist et al. 2012; Ogle et al. 2017). We fit models using the fisheries stock assessment package (FSA, Ogle 2017) in R statistical software (R Development Core Team 2017).

We used a repeated-measures mixed-effect model to evaluate the effects of temperature and water level on growth of Common Carp in Lake Spokane (Weisberg et al. 2010). Year was the random effect, age was a fixed effect, and we took repeated measures from individual fish. We used the estimated growth coefficients as dependent variables in a linear regression model. We used linear regression to estimate how three candidate models (temperature, water elevation, and temperature + water elevation) explained growth of Common Carp. Unfortunately, water temperature data were unavailable. Therefore, we gathered air temperature data (°C) from a National Oceanic and Atmospheric Administration weather station located approximately 20 km southeast of Lake Spokane. We estimated mean air temperature for

each year from 1999 to 2017 and used that as an independent variable in regression models. We obtained the mean annual water surface elevation (m) from years 1999 to 2017 from a U.S. Geological Survey gaging station at Lake Spokane (USGS 12422500) and used that as an independent variable in regression models. We truncated growth increments at age 7 since even modest imprecision in annulus measurements resulted in considerable error in the evaluation of incremental growth (see Watkins et al. 2015). In addition to evaluating growth of Common Carp, we also evaluated year-class strength. We used residuals from the catch curve as an index of recruitment to estimate how environmental factors were relative to year-class strength (Maceina 1997; Quist and Spiegel 2012; Watkins et al. 2015). We used Akaike's information criterion corrected for small sample size (AIC_c) to rank candidate models (Burnham and Anderson 2002). Top models had an AIC_c value that was within 2.0 of the best model (i.e., ΔAIC_c). We evaluated top models using the Akaike weight (w_i) and further evaluated models using the coefficient of determination (R^2).

We used Beverton-Holt yield-per-recruit models to evaluate fluctuations in potential yield and spawning potential ratio (SPR) under different removal strategies. We constructed models using the Fishery Analysis and Modeling Simulator v. 1.64 (FAMS; Slipke and Maceina 2014). Yield-per-recruit models used a variety of input parameters. Input parameters included growth, which we calculated from the von Bertalanffy growth model, as well as total annual mortality. Input parameters also included longevity and the length-weight relationship (i.e., $\log_{10}[\text{weight}] = -4.589 + 2.916 \times \log_{10}[\text{length}]$). The SPR is used to estimate the influence of exploitation on the productivity of a population and is calculated as the ratio of fished to unfished mature eggs that are produced in an average recruit's lifetime (Goodyear 1993). We considered populations to be experiencing recruitment overfishing when SPR was below 0.20 (i.e., 80% reduction in lifetime egg production; Goodyear 1993). Spawning potential ratio calculations required additional parameters including fecundity-length relationship estimates and age at maturation. Since a fecundity-length relationship was not available for Common Carp in Lake Spokane, we used the equation from Sivakumaran et al. (2003): $\text{fecundity} = -1.269 + 0.00359 \times \text{length}$. Based on our data, approximately 80% of females were mature at age 2 and 100% were mature by age 3.

Due to the lack of fishing mortality in Lake Spokane, we assumed conditional natural mortality to be equal to A . Therefore, conditional natural mortality was set at 0.10 and 0.20 to encompass the estimated total annual mortality rate of 0.17. We allowed conditional fishing mortality (cf) to vary from 0.00 to 0.95 in increments of 0.05. We input an arbitrary initial population of 1,000 individuals as the number of recruits. We used models to examine four different management scenarios. Specifi-

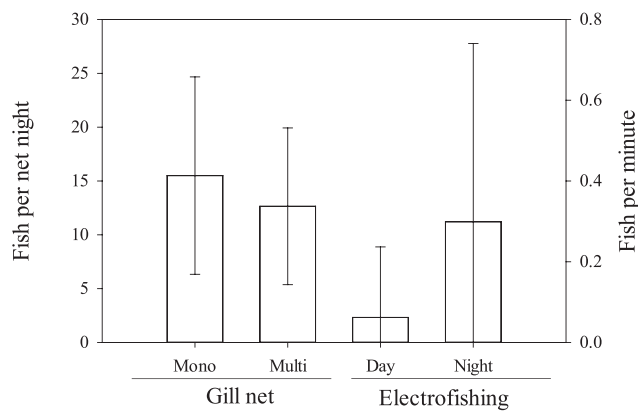


Figure 2. Catch per unit effort of Common Carp *Cyprinus carpio* sampled using monofilament and multifilament gill nets (fish/net night) and daytime and nighttime electrofishing (fish/min) during May 2017, in Lake Spokane, Washington. Error bars represent one standard deviation.

cally, we evaluated yield and SPR with the assumption that the minimum lengths that fish were available for harvest were 150, 300, 450, or 600 mm. Minimum lengths roughly corresponded to harvest of age-1 and older (150 mm), age-2 and older (300 mm), and age-3 and older (450 mm) Common Carp. The 600-mm minimum length represents the approximate modal length from our sampling efforts.

Results

In total, we collected 1,072 Common Carp during sampling, with 968 captured in gill nets and 105 sampled using electrofishing (Table S1, *Supplemental Material*). Catch per unit effort in gill nets was slightly higher in monofilament nets (mean \pm SD; 15.5 ± 9.8 fish/net night) than in multifilament nets (12.7 ± 7.3 fish/net night), but differences were not significant ($P = 0.08$;

Figure 2; Table S2, *Supplemental Material*). Catch rates of Common Carp with daytime electrofishing were significantly ($P < 0.0001$) lower (0.1 ± 0.2 fish/min) than with nighttime electrofishing (0.3 ± 0.4 fish/min). Length structure was similar between sampling methods (Figure 3; Table S3, *Supplemental Material*). Common Carp captured in gill nets were between 325 mm and 872 mm; whereas fish captured by electrofishing varied in length from 390 mm to 808 mm. Regardless of capture method, length structure was skewed toward long individuals. Common Carp were in good body condition with mean relative weight values greater than 100 for all length categories (Figure 4).

Common Carp age estimates varied from 2 to 18 y and the majority of fish (82%) were age 4 or older (Table 1; Table S4, *Supplemental Material*). Recruitment was highly variable among years (Figure 5). Year classes produced in 2003–2009 were relatively strong (positive residuals), whereas those in 2011 and 2012 were comparatively weak (negative residuals; Figure 5). We estimated total annual mortality as 17%.

Common Carp grew quickly and obtained an average length of 612.4 mm by age 6 (Figure 6; Table 1). We estimated the theoretical maximum length of a Common Carp in Lake Spokane as 793.3 mm using the von Bertalanffy growth model. Mean relative growth index values of all ages of Common Carp were above 100 with the exception of age-1 fish indicating relatively fast growth (Table 1).

Mixed-effect models provided insight on the growth of Common Carp. Growth increments were highly variable among years for Common Carp in Lake Spokane. Temperature best explained variability in growth (Table 2). However, temperature only explained 25% of the variation in growth of Common Carp. Similarly, the top model predicting recruitment contained temperature, but temperature explained little variation in year-class strength of Common Carp ($R^2 = 0.15$).

Yield of Common Carp generally declined as rates of exploitation increased (Figure 7). When conditional

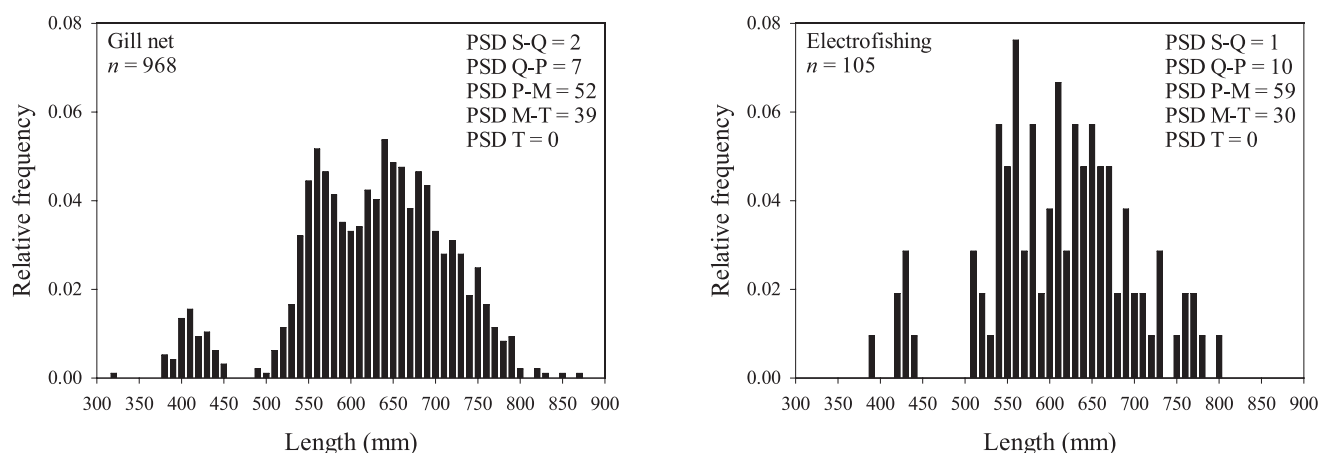


Figure 3. Length-frequency distribution of Common Carp *Cyprinus carpio* sampled using gill nets and electrofishing during May 2017, from Lake Spokane, Washington. Proportional size distribution (PSD) values were estimated using incremental length groups (S–Q, Q–P, P–M, M–T, T). S = stock (≥ 280 mm); Q = quality (410 mm); P = preferred (530 mm); M = memorable (660 mm); T = trophy (840 mm).

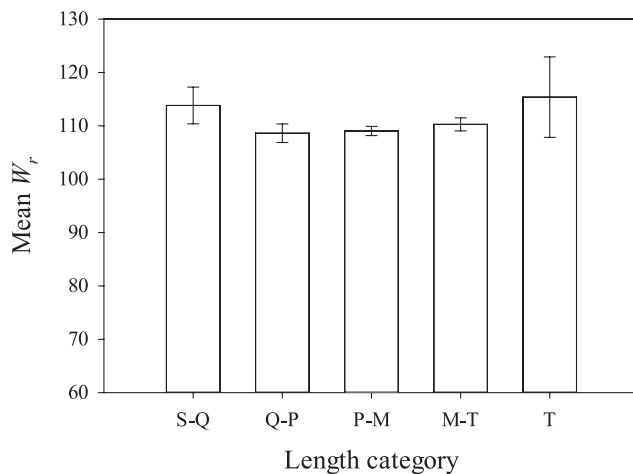


Figure 4. Mean relative weight (W_r) of Common Carp *Cyprinus carpio* sampled using gill nets during May 2017, from Lake Spokane, Washington. Relative weight was summarized by length category (S–Q, Q–P, P–M, M–T, T). Error bars represent one standard deviation. S = stock (≥ 280 mm); Q = quality (410 mm); P = preferred (530 mm); M = memorable (660 mm); T = trophy (840 mm).

mortality was set at 0.10 and 0.20, yield decreased with increased exploitation for all targeted length categories except 600 mm. When conditional mortality was 0.10, exploitation had to be ~ 0.20 –0.30 to cause recruitment overfishing ($SPR \leq 0.2$) for targeted lengths of 150, 300, and 450 mm fish (Figure 8). Exploitation would need to be roughly 0.90 to cause recruitment overfishing when targeting 600-mm Common Carp. When conditional mortality was 0.20, exploitation would need to be 0.20–

0.40 to cause recruitment overfishing for targeted lengths of 150-, 300-, and 450-mm fish. Recruitment overfishing would not occur if managers targeted only 600-mm and longer Common Carp for removal.

Discussion

Common Carp sampled by gill nets and electrofishing in Lake Spokane resulted in similar length-frequency distributions with a preponderance of large individuals. Large Common Carp were likely more susceptible to capture than smaller fish due to the selectivity of the large mesh size of gill nets (Pope et al. 2010) and electrofishing (Dolan and Miranda 2003). Other studies have also reported difficulties in sampling small Common Carp, which has led to length-frequency distributions skewed toward large individuals. Bajer et al. (2011) sampled Common Carp with seines and caught only a few fish less than 440 mm. Colvin et al. (2012) reported that the mean length of Common Carp sampled with trawls was 603 mm. Pinto et al. (2005) primarily captured large Common Carp (> 400 mm) via gill netting in the Botany Wetlands, Australia. Bajer and Sorensen (2012) sampled Common Carp by electrofishing in small Midwestern lakes and only caught fish that were 400 to 700 mm in length. In addition to gear selectivity, we sampled Common Carp in areas where Common Carp are thought to spawn, as supported by the high percentage of sexually mature fish (96%). However, Common Carp grow relatively fast in the system and mature early (ages 2–3) suggesting that the sample probably adequately described the length structure of Common Carp in the system.

Table 1. Mean back-calculated length at age by year class for Common Carp *Cyprinus carpio* sampled using gill nets during May 2017, from Lake Spokane, Washington. Numbers in parentheses represent one standard deviation for all values except for the overall mean where the value represents one standard error. Relative Growth Index (RGI) values are also provided.

Year class	Age	n	Mean back-calculated length at age (mm)								
			1	2	3	4	5	6	7	8	9
2015	2	54	225.5 (6.0)	417.9 (2.6)	—	—	—	—	—	—	—
2014	3	8	171.4 (19.4)	380.8 (27.7)	475.0 (26.4)	—	—	—	—	—	—
2013	4	87	152.2 (6.3)	402.8 (3.8)	519.5 (3.0)	563.2 (3.4)	—	—	—	—	—
2012	5	5	119.5 (19.3)	284.1 (43.9)	430.7 (10.0)	512.3 (12.9)	555.0 (14.6)	—	—	—	—
2011	6	7	152.7 (19.8)	414.0 (9.5)	505.0 (6.4)	550.9 (10.9)	590.7 (11.1)	615.1 (11.6)	—	—	—
2010	7	19	166.8 (11.8)	403.4 (6.9)	495.8 (6.2)	553.0 (6.4)	587.5 (7.7)	613.3 (8.7)	641.7 (10.3)	—	—
2009	8	16	151.2 (9.6)	397.3 (7.5)	488.7 (7.1)	545.6 (8.1)	580.4 (9.3)	604.0 (10.2)	630.1 (10.5)	650.8 (10.0)	—
2008	9	19	135.4 (13.3)	379.1 (12.3)	484.7 (9.8)	537.3 (8.7)	567.9 (8.5)	594.0 (8.4)	617.5 (8.5)	641.3 (8.6)	664.8 (8.7)
2007	10	24	176.2 (13.1)	374.9 (9.1)	474.4 (6.2)	522.3 (5.5)	551.9 (6.0)	584.5 (5.8)	609.6 (6.4)	630.2 (6.8)	652.7 (7.3)
2006	11	28	163.0 (13.4)	372.1 (9.7)	476.5 (8.8)	530.2 (8.8)	563.5 (9.2)	596.3 (7.9)	621.5 (7.7)	646.7 (7.2)	669.5 (7.4)
2005	12	22	138.9 (10.8)	347.4 (12.5)	458.8 (11.5)	521.6 (11.0)	558.8 (10.2)	593.5 (9.9)	621.2 (9.7)	642.9 (9.1)	667.5 (8.0)
2004	13	21	156.2 (16.2)	361.5 (12.2)	475.8 (8.7)	531.3 (7.4)	565.5 (7.9)	601.0 (7.1)	630.9 (7.6)	651.85 (7.3)	674.4 (7.1)
2003	14	16	142.3 (16.1)	360.6 (14.8)	477.5 (10.2)	539.8 (10.1)	580.4 (9.5)	613.9 (9.1)	637.4 (8.8)	659.2 (8.2)	678.6 (8.0)
2002	15	5	137.9 (26.9)	322.7 (23.7)	454.1 (15.7)	515.3 (12.0)	546.4 (11.5)	585.6 (11.2)	614.7 (12.3)	640.0 (12.2)	666.7 (14.1)
2001	16	8	128.8 (17.6)	341.8 (18.7)	476.0 (13.7)	541.7 (13.9)	580.1 (13.2)	616.9 (13.2)	651.1 (13.3)	674.6 (13.5)	698.3 (14.8)
2000	17	1	108.6 (a)	384.6 (a)	521.9 (a)	574.2 (a)	614.8 (a)	643.6 (a)	686.7 (a)	695.9 (a)	711.6 (a)
1999	18	3	105.9 (25.2)	312.9 (33.1)	445.9 (33.8)	509.8 (30.8)	557.0 (33.6)	587.0 (33.6)	608.9 (34.1)	629.1 (29.7)	651.9 (31.9)
Mean			149.0 (6.9)	368.2 (9.0)	478.8 (6.2)	536.6 (4.9)	571.4 (5.0)	603.8 (4.6)	630.9 (6.3)	651.1 (5.9)	673.6 (5.9)
RGI			91	132	131	124	119	116	115	115	115

^a Not estimable.

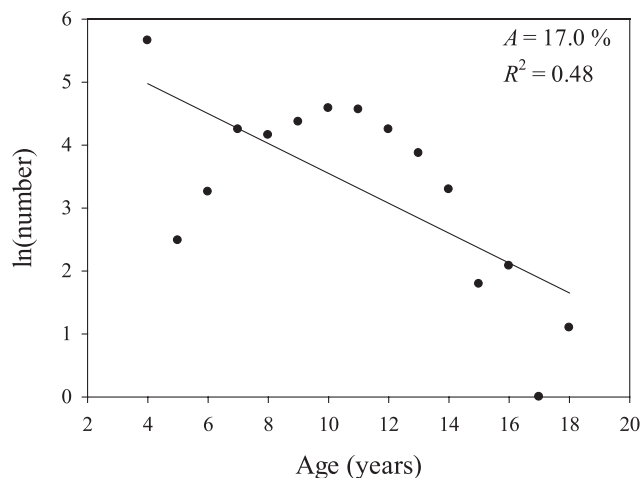


Figure 5. Catch curve of Common Carp *Cyprinus carpio* sampled using gill nets during May 2017, from Lake Spokane, Washington. Points above the regression line suggest high recruitment of Common Carp. Total annual mortality (A) is also provided.

Although gill nets and electrofishing captured Common Carp in Lake Spokane that were similar in length, catch rates of Common Carp varied among gear types. Catch rates were greater with monofilament than multifilament gill nets but differences were not significant. Previous researchers have evaluated catch rates between different filament types for other species and have drawn similar results. Collins (1979) deployed monofilament and multifilament gill nets in the North Channel of Lake Huron and estimated greater catch rates of Lake Whitefish *Coregonus clupeaformis* in monofila-

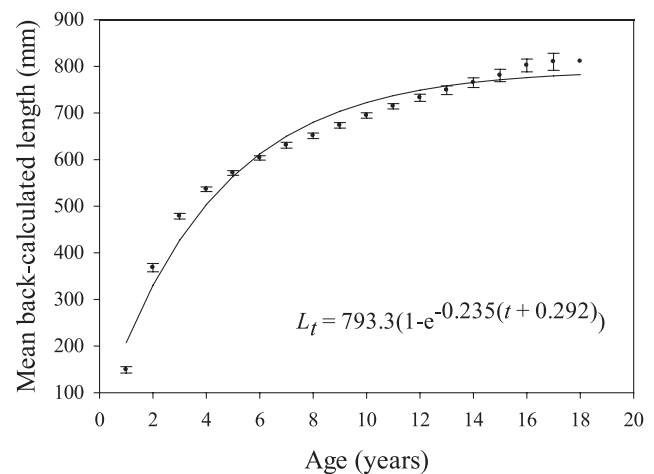


Figure 6. Mean back-calculated length at age and von Bertalanffy growth model of Common Carp *Cyprinus carpio* sampled using gill nets during May 2017, from Lake Spokane, Washington. Error bars represent one standard deviation.

ment gill nets, but results were not statistically significant. Ayaz et al. (2006) suggested that catch rates of several marine fishes were greater in monofilament than multifilament gill nets. Regardless of whether researchers use monofilament or multifilament gill nets, they should not use these filament types interchangeably when monitoring Common Carp populations. Rather, one filament type should be selected (based on cost and durability) and used for research and monitoring (Bonar et al. 2009). In addition to gill nets, electrofishing catch rates of Common Carp in Lake Spokane were higher during the night than the day. Other studies have

Table 1. Extended.

Mean back-calculated length at age (mm)								
10	11	12	13	14	15	16	17	18
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
676.8 (8.0)	—	—	—	—	—	—	—	—
688.3 (7.4)	706.9 (7.9)	—	—	—	—	—	—	—
687.5 (7.7)	709.5 (7.4)	727.8 (6.9)	—	—	—	—	—	—
692.3 (6.9)	708.0 (6.8)	726.8 (6.9)	744.0 (7.3)	—	—	—	—	—
696.6 (7.9)	714.7 (8.1)	730.8 (7.8)	746.0 (7.5)	762.6 (7.2)	—	—	—	—
684.8 (14.8)	702.0 (15.1)	715.2 (15.1)	728.9 (13.9)	740.9 (13.9)	755.2 (12.2)	—	—	—
719.5 (14.8)	735.5 (15.4)	748.2 (14.5)	760.6 (13.7)	775.3 (11.9)	790.0 (11.3)	807.1 (11.6)	—	—
727.3 (a)	743.0 (a)	769.1 (a)	787.5 (a)	799.2 (a)	813.6 (a)	822.8 (a)	828.0 (a)	—
678.8 (35.3)	697.1 (36.5)	711.0 (37.3)	726.6 (36.9)	747.7 (36.9)	763.3 (32.5)	776.3 (32.1)	791.5 (32.1)	810.7 (27.0)
694.7 (5.8)	714.6 (5.7)	732.7 (7.6)	748.9 (9.2)	765.1 (10.4)	780.5 (13.3)	802.1 (13.7)	809.7 (18.3)	810.7 (a)
117	118	120	121	123	125	128	129	129

Table 2. Multiple-regression models predicting growth and recruitment of Common Carp *Cyprinus carpio* sampled from Lake Spokane, Washington, 2017. Independent variables include the mean annual water elevation and mean air temperature during the growing season (i.e., 1 April to 30 September). Akaike's information criterion corrected for small sample size (AIC_c) and Akaike's weight (w_i) were used to evaluate candidate models. The AIC_c values were calculated from the number of model parameters and sample size. The coefficient of determination (R^2) is provided to describe model fit.

Independent variable	Variable(s)	k	AIC_c	ΔAIC_c	w_i	R^2
Growth	Temp	3	152.07	0.00	0.67	0.25
	Temp + water elevation	4	153.89	1.83	0.27	0.32
	Water elevation	3	156.85	4.79	0.06	0.00
Recruitment	Temp	3	52.22	0.00	0.65	0.15
	Water elevation	3	54.60	2.38	0.20	0.00
	Temp + water elevation	4	55.10	2.88	0.15	0.20

k = number of model parameters; AIC_c = Akaike's information criterion corrected for small sample size; w_i = Akaike's weight; R^2 = coefficient of determination.

documented differences in day and night electrofishing catch rates across a variety of species. Paragamian (1989) reported that catch rates of Smallmouth Bass were significantly higher during nighttime than daytime electrofishing in Maquoketa River, Iowa. Similarly, Dumont and Dennis (1997) reported that catch rates of Largemouth Bass *Micropterus salmoides*, Bluegill *Lepomis macrochirus*, and Gizzard Shad *Dorosoma cepedianum* in Texas reservoirs were generally higher with nighttime electrofishing compared to electrofishing during the daytime. Differences in daytime and nighttime catch rates of fishes, such as Common Carp, may be partially associated with water transparency (Reynolds 1983; Dumont and Dennis 1997). Similar to gill nets, sampling during a specific time of day will ensure sampling efforts are standardized (Bonar et al. 2009).

Growth of Common Carp is highly variable throughout their distribution. In Lake Spokane, growth was relatively fast compared to other systems with fish reaching lengths of 600 mm by age 6. Karatas et al. (2007) estimated that Common Carp in Almus Dam Lake, Tokat-Turkey, reached lengths of 356 mm by age 7. Likewise, Crivelli (1981) estimated Common Carp in Etang du Vaccares, Camargue, France, to be roughly 578 mm in length by age 13. Results from our study also suggested that growth after age 1 was approximately 15–30% faster than other Common Carp populations, such as fish in the Murray-Darling basin, Australia (Brown and Walker 2004) and Common Carp in Iowa lakes (Jackson et al. 2010). Differences in growth among populations are likely related to factors associated with density dependence and environmental conditions (e.g., temperature; Weber and Brown 2013).

Recruitment was highly variable in Lake Spokane. Researchers have reported similar results for Common Carp across their distribution (Phelps et al. 2008). For example, Weber and Brown (2013) conducted a study of 13 lakes in eastern South Dakota and reported that recruitment of Common Carp was highly variable. Bajer and Sorenson (2010) suggested that recruitment of Common Carp varied among interconnected lakes in Minnesota. Similarly, Coulter et al. (2008) suggested that recruitment of Common Carp in Pelican Lake, Nebraska, was highly variable. In Lake Spokane, data suggested that year classes produced in 2003–2009 were strong and those in 2011 and 2012 were comparatively weak.

Although the mechanisms responsible for fast growth and recruitment of Common Carp in Lake Spokane are unknown, we hypothesized temperature and water level as important predictors of growth and recruitment. Growth is often related to temperature, whereby reduced temperatures result in lower growth rates (Fine et al. 1996; Oyugi et al. 2012). For example, Kilambi and Robison (1979) reported that Grass Carp *Ctenopharyngodon idella* had slower growth rates in low water temperatures compared to high temperatures. Similarly,

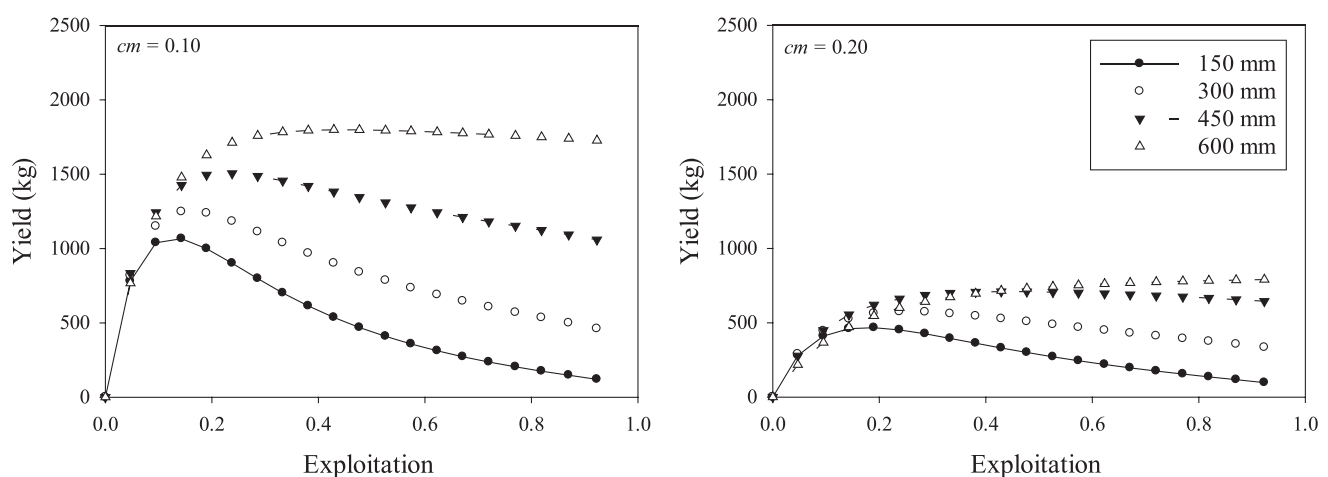


Figure 7. Yield per recruit of Common Carp *Cyprinus carpio* in Lake Spokane at two levels of conditional natural mortality (cm). Lines represent potential minimum lengths targeted for removal. Parameter estimates were obtained from Common Carp sampled during May 2017.

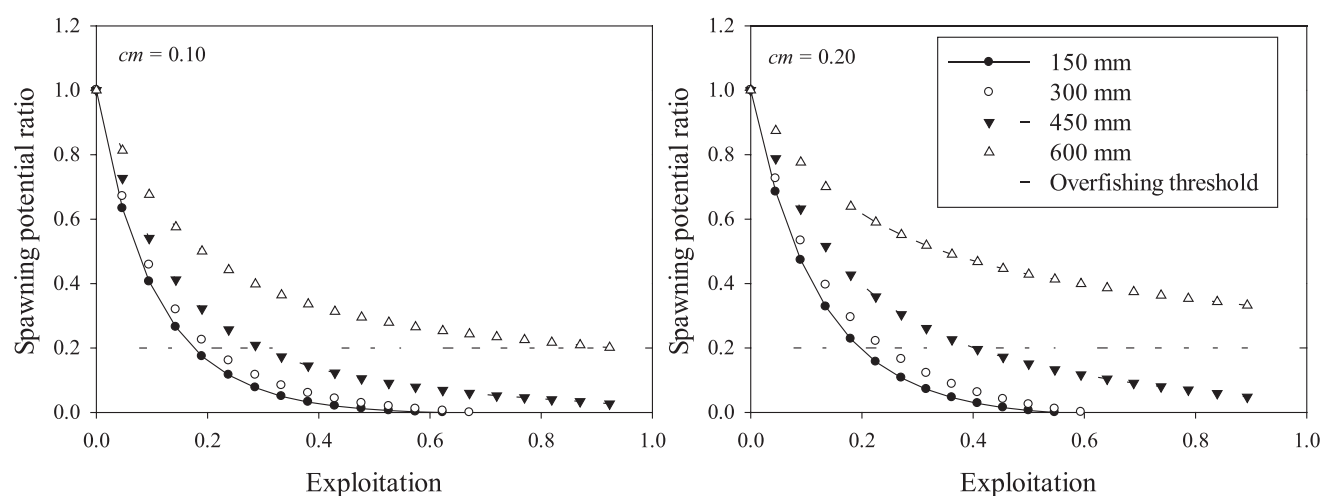


Figure 8. Spawning potential ratio of Common Carp *Cyprinus carpio* in Lake Spokane at two levels of conditional natural mortality (cm). Lines represent potential minimum lengths targeted for removal. The horizontal dashed line represents the theoretical point where a population starts to experience recruitment overfishing. Parameter estimates were obtained from Common Carp sampled during May 2017.

Goolish and Adelman (1984) suggested that Common Carp growth rates decreased with decreasing water temperatures. Moreover, water temperature commonly influences growth, whereas water level frequently influences recruitment. Previous research has suggested that successful recruitment of fishes is correlated with high-water years, which provide more spawning sites and habitat for larval fishes (Bennett 1954). Hudon et al. (2010) suggested that in the St. Lawrence River, Quebec, Canada, a rapid drop in water levels resulted in high Common Carp mortality, thus influencing recruitment. Other studies have also suggested that low water levels would limit Common Carp reproduction and influence year-class strength (Shields 1958). In Lake Spokane, temperature and water level explained little variability in growth and year-class strength of Common Carp. Unfortunately, long-term water temperature data were not available for Lake Spokane so we used air temperature as a surrogate. The imperfect relationship between air and water temperatures hindered our ability to effectively evaluate the influence of water temperature on growth. Additionally, water levels were not useful in explaining recruitment variability of Common Carp, likely because water levels fluctuate little in the system due to dam operations. Furthermore, it is likely that additional abiotic and biotic factors (e.g., water discharge or prey availability) influence growth and recruitment (Nunn et al. 2003).

Overfishing can suppress Common Carp (Weber et al. 2011). Growth overfishing occurs when yield decreases with increasing levels of exploitation, since fisheries personnel and anglers harvest fish before reaching their maximum growth potential (Goodyear 1993). Mirza et al. (2012) reported that expected yield of Common Carp steadily increased with exploitation until exploitation rates were greater than 0.63. Garvey et al. (2006) suggested that relatively high (≥ 0.5) exploitation rates of Silver Carp *Hypophthalmichthys molitrix* (≤ 300 mm in length) would reduce expected yield. In our study,

growth overfishing occurred when exploitation rates were 0.15 for the majority of minimum-length scenarios. More important than growth overfishing is recruitment overfishing, which occurs when fisheries personnel harvest fish from a population at a rate where fish can no longer replace themselves (Goodyear 1993). Weber et al. (2011) estimated that exploitation rates of Common Carp (≥ 575 mm in length) would need to be between 0.20–0.40 in Lake Herman, South Dakota, to cause recruitment overfishing. Additionally, the authors suggested that successful suppression efforts of Common Carp would require the removal of smaller fish (≤ 575 mm). Seibert et al. (2015) reported that recruitment overfishing of nonnative Silver Carp (≥ 300 and ≥ 400 mm in length) in several midwestern U.S. rivers would occur at exploitation rates of 0.27–0.33 and 0.22–0.44. In our study, recruitment overfishing of Common Carp would be achievable for all minimum-length scenarios (with the exception of 600-mm fish) if exploitation rates were approximately 0.20–0.40. As such, moderate levels of exploitation of relatively small Common Carp will be beneficial in reducing the number of Common Carp in Lake Spokane.

Our results indicate that variable recruitment, rapid growth, high longevity, and low annual mortality best describe Common Carp in Lake Spokane. Like other systems where humans have introduced them, Common Carp will likely persist in Lake Spokane without focused removal efforts. Results from the Beverton–Holt yield-per-recruit model suggest that recruitment overfishing would be plausible at moderate to high levels of exploitation. In an effort to maximize removal rates, suppression efforts may focus on removing smaller individuals (≤ 300 mm in length). However, sampling relatively small Common Carp is difficult, which may require further research into other removal strategies (e.g., embryo electroshocking; Simpson et al. 2018). Continual efforts of sampling Common Carp on their spawning grounds using nighttime electrofishing and monofilament gill nets would likely be beneficial.

Future research may consider evaluating additional factors (e.g., water discharge, prey availability) to better describe variations in growth and recruitment. Furthermore, information on Common Carp population characteristics will be useful when predicting how a population will respond to management strategies such as suppression efforts.

Supplemental Material

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Table S1. Data Common Carp *Cyprinus carpio* collected from Lake Spokane, Washington, during May 2017. The individual fish (fish #), length, weight, sex, location of sampling (Sportsmans, McLellan, Nine Miles, and Felton), and survey (gill net [GN] and electrofishing [EF]) are included.

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S1> (106 KB XLSX).

Table S2. The catch per unit effort (CPUE) of Common Carp *Cyprinus carpio* in monofilament and multifilament gill nets from Lake Spokane, Washington, during May 2017. The table includes the individual net, sampling time (h), total number of fish caught, and CPUE in net night (12-h set).

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S1> (106 KB XLSX).

Table S3. The catch per unit effort (CPUE) of Common Carp *Cyprinus carpio* in day and night electrofishing from Lake Spokane, Washington, during May 2017. The table includes the individual electrofishing (E-fish) sample, sampling time (min), total number of fish caught, and CPUE in minutes.

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S1> (106 KB XLSX).

Table S4. Data Common Carp *Cyprinus carpio* collected from gill nets in Lake Spokane, Washington, during May 2017. The individual fish (fish #), length (mm), weight (kg), age at capture in years are included. Additionally, the growth increments (pixels) estimated from the dorsal spine are included for each annulus (e.g., Anu1).

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S1> (106 KB XLSX).

Reference S1. Avista. 2011. Lake Spokane and Nine Mile Reservoir aquatic weed management program. Spokane, Washington: Spokane River Hydroelectric Project. FERC Project 2545-091.

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S2> (11.41 MB PDF).

Reference S2. Avista. 2015. Lake Spokane dissolved oxygen water quality attainment plan 2014 annual

summary report. Spokane, Washington: Spokane River Hydroelectric Project. FERC Project 2545.

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S3> (2.39 MB PDF).

Reference S3. Garvey JE, DeGrandchamp KL, Williams CJ. 2006. Life history attributes of Asian Carps in the upper Mississippi River system. Vicksburg, Mississippi: U.S. Army Corps of Engineer Research and Development Center. ANSRP Technical Notes Collection ERDC/EL ANSRP-06.

Found at DOI: <https://doi.org/10.3996/122018-JFWM-114.S4> (513 KB PDF).

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