# WALLEYE AND WHITE BASS RECRUITMENT IN SOUTHWEST NEBRASKA IRRIGATION RESERVOIRS

by

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Walleye *Sander vitreus* and white bass *Morone chrysops* are among the most popular sportfish in the reservoirs of the Great Plains. Despite considerable effort by the Nebraska Game and Parks Commission stocking walleye and managing reservoirs for walleye and white bass, populations of walleye and white bass in southwest Nebraska reservoirs are dynamic, as erratic recruitment has led to "boom and bust" fisheries for these two species. We investigated 1) factors regulating walleye and white bass recruitment during an 18-year period at five reservoirs, and 2) walleye spawning ecology at two reservoirs that differ in their degree of environmental variability. The variables in the candidate model sets for walleye were most-often related to water-level drawdown. The variables in the candidate model sets for white bass were most-often related to adult white bass abundance and condition, and to factors affecting over-winter mortality of juvenile white bass. Despite significant differences in female body and liver masses between reservoirs that differ in environmental variability, we found no difference in reproductive investment measured by egg size and fecundity, which is counterintuitive to life-history theory.

# DEDICATION

I dedicate this work to two Steve Lurtz's who have been so influential in my life.

First and foremost, to GrandPa Lurtz, who showed me the importance of always doing my best, and, whenever I told him about the research I was doing for school, always exclaimed "Wow Jas, that's neat!"

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When God pulls you back, hold tight, aim straight.

"Let us hold tightly without wavering to the hope we
affirm, for God can be trusted to keep his promise."
~ Hebrews 10:23, NLT

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# Chapter 1: INTRODUCTION

## Theoretical framework

Species adapt and evolve in different environments, within varying biotic and abiotic constraints and variables, and therefore exhibit life-history traits that allow them to prosper in those environments. Existing in a variable environment is something with which most organisms must contend. Environmental variability may occur on an hourly or daily temporal scale, or may occur over a much longer period, on the order of seasons, years, or even decades or centuries. Accordingly, seasonal configurations are inherently present in the evolution and ontogeny of many species (Winemiller 1989; Nylin 1992). For organisms living in these variable environments, production of offspring at the proper time is crucial to ensuring the survival of those offspring and the successful passing of genes (Cohen 1966; James and Shine 1985; Seeley and Visscher 1985; Dietz et al. 1994; Komdeur 1996). Thus, one must consider the life history of a species when making inferences about reproductive success.

Recruitment limitations, or “bottlenecks,” are environmental conditions that prohibit or constrain reproductive success, typically exerting influence over larval and juvenile organisms (Werner and Gilliam 1984; Coleman and Fausch 2007). These bottlenecks can be both biotic and abiotic in nature, often relating to the presence and abundance of predators (Köster and Möllmann 2000), availability of prey (Persson and Greenberg 1990), or climatological variables such as temperature and precipitation (Coleman and Fausch 2007). Life-history theory predicts that when an organism inhabits an environment with unfavorable conditions for growth and survival of its offspring, the organism should produce few offspring that are large, as opposed to many offspring that are small (e.g., Johnston and Leggett 2002). Thus, organisms that live in unpredictably variable systems should exhibit different life-history strategies than conspecifics from more predictably variable systems.

## The reservoir environment

The idea of impounding water for human use is not a new one; the earliest known record of humans utilizing reservoirs is in 3000 B.C. near Girnar, India (Rodda and Ubertini 2004). Generally, reservoirs are dynamic systems, often prone to unpredictable and extreme water-level fluctuations (e.g., June 1977). Unfortunately for anglers and fish, management of water levels in reservoirs is typically guided by hydrological and economic factors (e.g., flood control, hydropower generation, and crop irrigation), with little consideration given to fish populations (Sammons et al. 1999; Sammons and Bettoli 2000). This unpredictable variability can cause pronounced changes in availability of spawning and rearing habitat (Beam 1983; Miranda et al. 1984; Ploskey 1986; Willis 1986), turbidity (Martin et al. 1981), and zooplankton abundance (Willis 1986; Naselli-Flores and Barone 1997). Therefore, because of this inherent unpredictability, reservoir fishes often experience large fluctuations in annual survival rates of larvae and juveniles, which leads to large fluctuations in abundance of the adult spawning stock.

## Ecology of fish reproduction

The primary goal of any organism is to perpetuate the species by passing along its individual genetic material to future generations. Fishes typically have discrete spawning seasons that ensure the greatest chance of survival for their young (Wootton 1990). Many fishes take cues from their environment to determine when to spawn (de Vlaming 1972). These cues include water temperature (Graham and Orth 1986; Webb and McLay 1996; Carscadden et al. 1997), lunar or tidal period (Middaugh 1981; Middaugh and Takita 1983), water discharge and velocity (Trépanier et al. 1996), and photoperiod (Duston and Bromage 1986).

Fishes also employ different reproductive strategies to optimize the number of surviving offspring. Fishes are renowned for their fecundity; individuals of most species are capable of producing thousands to millions of eggs every year (Hoar 1969). These eggs are usually either demersal or pelagic (Balon 1975; Wootton 1990), though strategies other than egg laying do exist. Pelagic spawners broadcast semi-buoyant eggs into the water column where they are carried along by currents, whereas demersal spawners scatter eggs near the substrate, sometimes into constructed nests, where they can adhere to vegetation or substrate, or merely settle on the bottom. Demersal spawners also vary in the amount of parental care or guarding they devote to their brood (Smith and Wootton 1995).

Different biotic and abiotic factors may inhibit egg survival of demersal spawners. Cool water temperature increases egg incubation time (Busch et al. 1975), which in turn can expose eggs to a longer period of predation risk (Schaeffer and Margraf 1987;

Steinhart et al. 2004; Steinhart et al. 2005). Wind can cause eggs to become dislodged and stranded (Busch et al. 1975). Suspended fine sediments may diminish the number of eggs laid (Burkhead and Jelks 2001) and impair the hatching of eggs (Auld and Schubel 1978). Deposited fine sediments may smother fish eggs, causing mortality (Lisle 1989; Kock et al. 2006). Low oxygen levels in the water may also impair egg survival (Auer and Auer 1990).

Challenges for fish to recruit are exacerbated by water-level variability (Carline 1986). This is particularly true in irrigation reservoirs, some of which experience unpredictable and often amplified summer draw-downs in response to unpredictable extremes in abiotic conditions (Quist et al. 2003b; Olds et al. 2011). Changing water levels can affect availability of adequate spawning habitat, as well as deposit sediment on eggs or larvae in nests (Miranda et al. 1984; Ploskey 1986; Guy and Willis 1995; Waters and Noble 2004).

### Fish recruitment

From a fishery standpoint, recruitment refers to the supply of fish that becomes available (1) at some particular stage in their life history (often considered to be the age of reproductive viability), or (2) to the commercial or recreational harvest gear used in the fishery (Everhart et al. 1975). Success of recruitment, often considered the relative contribution of annually spawned (or stocked) fish to the population, is generally discussed in terms of year-class strength. Variability in year-class strength is often related to early-life stage survival, typically resulting from interactions of biotic and abiotic factors dealing with size and ontogeny of larval and juvenile fish (Miller et al. 1988; Cushing 1990; Leggett and DeBlois 1994, DeBoer et al. 2013). Year-class strength is also often inherently linked to adult population numbers (Gulland 1982; Sissenwine 1984).

For teleost fishes, natural mortality is often greatest during early-life stages (i.e., larval and juvenile, May 1974; Houde 2002). Understanding factors affecting growth and survival during these stages may be crucial for understanding fish recruitment (Miller et al. 1988; Bremigan and Stein 1994). Successful recruitment is often considered to be a function of successfully navigating a series of sequential events (Neill et al. 1994); a "gauntlet" of sorts. Survival and growth in the larval and juvenile stages are often positively correlated to food availability and avoidance of predation, and negatively correlated to habitat unpredictability, which is itself inherently linked to unpredictability in weather patterns (Houde 1987; Mion et al. 1998; Hoxmeier et al. 2004). Food availability can be related to several factors, including simple prey abundance (Ritchie and Colby 1988; Peterson et al. 2006), overlap with prey availability (the "match/mismatch hypothesis", Cushing 1969; 1975; 1990), conspecific competition (Partridge and DeVries 1999; Knoll 2007), and interspecific competition (Michaletz et al. 1987; Roseman et al. 1996; Garvey and Stein 1998). Predation sources include cannibalistic conspecifics (Chevalier 1973; Fox 1975; Polis 1981; Knoll 2007), as well as interspecific predators (Pope et al. 1996; Quist et al. 2003). Interestingly, one study points to the benefit of a "shading effect" due to higher plankton counts as being an important survival mechanism for larval fish, not only due to increased food availability for larval fish, but also due to reduced predation on larval fish (Fiksen et al. 2002). Habitat unpredictability also affects survival of early-life stages, as changes in factors such as temperature (Rutherford and Houde 1995), turbidity (Chesney 1989), and dissolved oxygen (Breitburg 1994) can have substantial effects on survival of larval and juvenile fish.

In theory, first-year survival, and therefore year-class strength, is inherently less consistent in systems with a high incidence of seasonal and annual unpredictability. Fish in reservoirs are especially vulnerable during early-life stages, often due to unpredictable water fluctuations for which reservoirs are known (June 1977). Irrigation reservoirs in particular, with their history of annual drawdown, can pose a serious challenge to recruitment. Reservoirs often have high ambient levels of turbidity (Bremigan 1997; Gido and Matthews 2000) that can increase even more during periods of high inflow (Mion et al. 1998); these changes can exert direct (mortality) and indirect (stressors) control over larval and juvenile fish. In addition to abiotic challenges, reservoirs can pose other problems for fish during early-life stages. Seasonal changes in reservoir flushing rate can cause changes in zooplankton and phytoplankton abundance; high flushing rate can lead to low zooplankton abundance (*sensu* Watson et al. 1996; Kalff 2003), which could reduce food availability for larval fishes at a critical stage. Although most larval fishes are initially zooplanktivorous (Turner 1984), many species transition to different food sources during growth and development. This size-mediated transition is known as an ontogenetic niche shift, a change in habitat or resource use as an organism increases in size (Werner and Gilliam 1984). Failure to secure enough energy may inhibit fish growth during early-life stages, which may prevent ontogenetic shifts that are necessary for continued growth and survival.

Reservoirs are often stocked with fishes that do not share a common evolutionary history or similar native range. If two species evolved in different regions, one species may be at a disadvantage when the two are introduced into the same system. This lack of co-evolution can pose serious problems in terms of predation and competition, particularly in early-life stages (Galinat et al. 2002; Olson et al. 2007). That is, the biotic influence of one species can constrain recruitment of a second species, even when abiotic conditions are suitable for recruitment of the second (i.e., Biotic-Abiotic-Constraining Hypothesis, Quist et al. 2003).

## Study area

The Republican River is an impounded tributary to the Kansas River; the Republican River basin is contained within three states in the Great Plains region of the USA (Figure 1.1). Bliss and Schainost (1973) identified 37 fish species in the watershed, and 729 km (~40%) of streams were classified as being environmentally degraded, with the primary effects being related to water withdrawal for irrigation. As a result of agricultural over-development (i.e., over-appropriation of groundwater wells for cropland irrigation) in the region, current groundwater and surface water flows are substantially reduced compared to circa-1970 levels throughout the Republican River basin (Szilagyi 1999; 2001). This reduction in flow has been attributed to cropland irrigation, changes in vegetative cover, water conservation practices, and construction of reservoirs and artificial ponds in the basin, all of which increase the amount of water lost to evaporation over the basin (Szilagyi 1999; 2001).

Forty percent of the Republican River basin is in Nebraska (USDA 1978), where the basin drains nearly 25,000 km$^2$ of primarily rangeland and cropland into 1,826 km of streams and rivers (Bliss and Schainost 1973). Catastrophic flooding in 1935 prompted the construction of five large multipurpose reservoirs in the Republican River basin in Nebraska: Enders Reservoir, Harlan County Lake, Medicine Creek Reservoir (Harry D. Strunk Lake), Red Willow Reservoir (Hugh Butler Lake), and Swanson Reservoir. Harlan County and Swanson reservoirs are on the mainstem of the Republican River, whereas Enders, Medicine Creek, and Red Willow reservoirs are on separate tributaries to the Republican River. As a result of the reduction in groundwater and surface water flows, only Medicine Creek Reservoir delivers water for irrigation on an annual basis; the other reservoirs deliver water for irrigation only sporadically when there is sufficient inflow (Table 1.1).

### Enders Reservoir

Enders Reservoir is impounded by Enders Dam, constructed during 1947-1951 on Frenchman Creek, a tributary of the Republican River. Enders Reservoir drains a watershed of 2,841 km$^2$, with an active conservation pool elevation of 948.6 m above sea level. Sportfish present in the reservoir include channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, crappie *Pomoxis* spp., flathead catfish *Pylodictis olivaris*, hybrid striped bass *Morone saxatilis x M. chrysops*, largemouth bass *Micropterus* *salmoides*, northern pike *Esox lucius*, smallmouth bass *M. dolomieu*, walleye *Sander vitreus*, and white bass *Morone chrysops*. Walleye fingerlings and fry were stocked routinely from 1985 to 2011 (Table 1.2), and white bass has never been stocked by the Nebraska Game and Parks Commission (NGPC) in Enders Reservoir.

### Swanson Reservoir

Swanson Reservoir is impounded by Trenton Dam, constructed during 1949-1953 on the mainstem of the Republican River. Swanson Reservoir drains a watershed of 22,326 km$^2$, with an active conservation pool elevation of 838.8 m above sea level. Sportfish present in the reservoir include blue catfish *Ictalurus furcatus*, channel catfish, common carp, crappie, flathead catfish, freshwater drum *Aplodinotus grunniens*, hybrid striped bass, walleye, and white bass. Walleye fingerlings and fry were stocked regularly from 1985 to 2011 (Table 1.2), and white bass has never been stocked by NGPC in Swanson Reservoir.

### Red Willow Reservoir

Red Willow Reservoir (Hugh Butler Lake) is impounded by Red Willow Dam, constructed during 1960-1962 on Red Willow Creek, a tributary of the Republican River. Red Willow Reservoir drains an area of 1,890 km$^2$ (Ferrari 1998), and has an active conservation pool elevation of 801.0 m above sea level. A fissure in the dam at Red Willow Reservoir necessitated an extreme drawdown to ensure the safety of the dam; during November and December 2009, the water level dropped 5.7 meters over a 45-day period. Sportfish present in the reservoir include common carp, channel catfish, crappie, flathead catfish, hybrid striped bass, largemouth bass, northern pike, smallmouth bass, walleye, and white bass. Walleye fingerlings and fry were stocked routinely from 1985 to 2010 (Table 1.2), and white bass has never been stocked by NGPC in Red Willow Reservoir.

### Medicine Creek Reservoir

Medicine Creek Reservoir (Harry D. Strunk Lake) is impounded by Medicine Creek Dam, constructed during 1948-1949 on Medicine Creek, a tributary of the Republican River. Medicine Creek Reservoir drains an area of 2,279 $km^2$, with an active conservation pool elevation of 721.2 m above sea level. Sportfish present in the reservoir include channel catfish, flathead catfish, crappie, walleye, largemouth bass, white bass, hybrid striped bass, and common carp. Walleye fingerlings and fry were stocked routinely from 1985 to 2011 (Table 1.2), and white bass has never been stocked by NGPC in Medicine Creek Reservoir.

### Harlan County Lake

Harlan County Lake is impounded by Harlan County Dam, constructed on the mainstem of the Republican River during 1952. Harlan County Lake drains an area of 18,555 $km^2$, with an active conservation pool elevation of 593.1 m above sea level. Sportfish present in the reservoir include channel catfish, crappie, flathead catfish, hybrid striped bass, northern pike, walleye, and white bass. Walleye fingerlings and fry were stocked routinely from 1985 to 2011 (Table 1.2); Harlan County is the only reservoir of the five in which white bass has been stocked, with 1.5 million fry stocked during May of 1993.

## Study fishes

As we have stated, year-class strength, and thus recruitment, of fishes in unpredictably dynamic systems such as irrigation reservoirs can vary considerably on an inter-annual basis. In southwest Nebraska irrigation reservoirs, year-class strength and recruitment of walleye and white bass are highly variable (DeBoer et al. 2013). Moreover, walleye and white bass are both top-level predators that often flourish in Midwestern reservoirs, have similar life expectancy, and also have similar feeding strategies at multiple life stages. Thus, we chose to study the recruitment dynamics of these two species to make inferences about and gain a broader understanding of recruitment dynamics of fishes in unpredictably dynamic systems.

### Walleye

Walleye is a member of the Percidae family, which includes sauger *Sander canadensis* and yellow perch. Walleye typically inhabits lakes, reservoirs, and large rivers; its native range encompasses much of the eastern half of North America, including Nebraska, where walleye is found in the Republican, Missouri, and Platte River watersheds (Scott 1967; Morris et al. 1972; Scott and Crossman 1973; Williams 1995). As with many species in the USA, its range has been expanded through stocking and transplanting to enhance sportfishing opportunities, particularly in reservoirs (Scott and

Crossman 1973; Colby et al. 1979). In Nebraska, walleye is the preferred species of the majority of anglers (Hurley and Duppong-Hurley 2005).

Male walleye become sexually mature at a smaller size and usually a younger age than do female walleye; most male walleye become sexually mature at age 2 or 3, whereas most female walleye become sexually mature at age 3 or 4 (Carlander 1997). Annual maturation of adult walleye gonads requires water temperatures below 10°C (Colby and Nepszy 1981). If water temperatures are not sufficiently cold enough for a long enough duration, walleye will skip spawning and reabsorb their gametes over the next season. Ova reabsorption interferes with development of the next generation of oocytes, leading to skipping of the next spawning period (Colby et al. 1979). Thus, failure to spawn in one season (due to elevated water temperature during winter) may lead to failure to spawn in the following season, leading to the loss of back-to-back year classes.

Females (and their eggs) are usually the limiting factor in natural reproduction. However, female walleye may be harvested by anglers prior to reaching sexual maturity (Spirk 2012), which may limit natural reproduction. Compared to smaller (i.e., younger) female walleye, larger (i.e., older) female walleye produce more eggs (Johnston et al. 2007) and also larger, higher quality eggs (Johnston 1997; Wiegand et al. 2004) that survive better, and also produce larger fry (Johnston et al. 2007). Thus, it is vital to have an abundance of large female walleye in the population in order to have an increased chance of successful natural reproduction and recruitment (Venturelli et al. 2010). Walleye egg diameter can range from 1.37 to 2.12 mm (Colby et al. 1979), and is negatively affected by poor environmental quality (e.g., low resource abundance, high competition, and high predation; Johnston and Leggett 2002). There is greater egg size variability, both within and among females, when environments are less predictable; thus, females are using variability in egg size to offset the cost of imperfect information when producing smaller eggs (Koops et al. 2003).

Walleye spawn in many different areas, including sandy, gravelly, or rocky wave-washed shallows and shoals in lakes (Scott 1967; Becker 1983), lake tributaries (Pflieger 1997), and riverine upper portions of reservoirs (Quist et al. 2004). Walleye also spawn on the riprap on the face of dams (Grinstead 1971; Morris et al. 1972; Martin et al. 2012), which may not be beneficial to the survival of eggs, and is therefore in conflict with life-history theory. It is possible that dams offer too much depth, pitch, fetch, and cold water to be well-suited for successful natural reproduction, as well as potentially being a long distance from acceptable nursery habitat (*sensu* Jones et al. 2003).

Male walleye typically spawn for longer periods than do female walleye (Ellis and Giles 1965), and arrive at spawning sites up to one month before female walleye (Pflieger 1997). Walleye spawn soon after ice-out, when water temperatures are between 5 and 15°C, with peak spawning between 7 and 12 °C in general (Scott 1967; Pitlo 1989), and between 7 and 10 °C in Nebraska (Morris et al. 1972). Walleye are nocturnal spawners, and eggs and milt are released over substrate in shallow water (Ellis and Giles 1965; Priegel 1970) where the eggs are fertilized and subsequently abandoned; walleye exhibit no parental care (Fahy 1954). Individual females usually spawn in one night (Ellis and Giles 1965).

Walleye eggs are initially adhesive, but will harden after a few hours in the water, and are susceptible to displacement by wind and wave action (Priegel 1970). Constant post-spawn water levels in reservoirs are important for survival of walleye eggs (Groen and Schroeder 1978). In addition, increases in reservoir spring water level are positively correlated with year-class strength of walleye (Cohen and Radomski 1993), and rapidly warming water temperature during incubation leads to better survival of eggs (Colby et al 1979). Hatching can occur as quickly as 7 days, though typically takes longer (12-21 days) depending on water temperature; colder temperatures, like those near dams in reservoirs, can delay hatching (Becker 1983; Pflieger 1997). Delayed hatching subjects eggs to increased risk of predation and sedimentation (Schaeffer and Margraf 1987; Lisle 1989; Steinhart et al. 2004; Kock et al. 2006).

After hatching, larval walleye feed on zooplankton and macroinvertebrates (Hoxmeier et al. 2004), spending much of their time high in the water column (Bulkowski and Meade 1983). Upon attaining 25 mm in total length, juvenile walleye will occupy coves adjacent to the main water body (Grinstead 1971; Becker 1983). Young-of-year walleye compete for resources with young-of-year individuals of other species, including gizzard shad *Dorosoma cepedianum* (Michaletz et al. 1987; Quist et al. 2004), yellow perch, (Michaletz et al. 1987) white bass (Michaletz et al. 1987; Beck et al. 1998), and black crappie (Pope et al. 1996; Galinat et al. 2002). In addition to competitive constraints, young-of-year walleye may also face predation from black crappie (Pope et al. 1996; Galinat et al. 2002), white crappie (Quist et al. 2003), rainbow smelt *Osmerus mordax* (Carpenter et al. 2007) and other piscivorous species.

As a result of reduced inflows, some of these reservoirs do not refill annually, and therefore do not regularly release water for irrigation (Table 1.1). This disparity in refilling and irrigation drawdown leads to seasonal and annual differences in flushing rate within and among reservoirs. Seasonal changes in flushing rate can cause changes in zooplankton and phytoplankton abundance; high flushing rate can lead to low zooplankton abundance (*sensu* Watson et al. 1996; Kalff 2003), which could reduce food availability for larval fish. Likewise, harvest of walleye (Aggus and Bivin 1982), and standing crop, natural reproduction, and spawning success of walleye (Willis and Stephen 1987) were better in reservoirs with low flushing rate (i.e., retention time > 1 year); walleye may not be suitable for stocking into a reservoir with high flushing rate because of a high propensity of being entrained through the dam (Willis and Stephen 1987; Johnson et al. 1988).

### White bass

White bass is a member of the Moronidae family (also known as “temperate basses”), which includes white perch *M. americana*, yellow bass *M. mississippiensis*, and striped bass *M. saxatilis*. Similar to walleye, white bass inhabits lakes, large rivers and streams, and reservoirs (Scott 1967). Unlike walleye, little research has targeted white bass, therefore far less is known about its ecology, especially in reservoirs (Guy et al. 2002). Although its’ native range once included much of the eastern and central USA, including Nebraska, white bass has been introduced in water bodies outside its’ native range for sportfishing (Scott and Crossman 1973). As with walleye, white bass can be found in Nebraska in the Missouri, North Platte, and Republican River watersheds (Morris et al. 1972).

Male white bass become sexually mature at a younger age than do female white bass; most male white bass mature at age 2 or 3, whereas female white bass mature at age 3 or 4 (Carlander 1997). However, female white bass may be harvested by anglers prior to reaching sexually maturity (Spirk 2012), and therefore may limit natural reproduction. Thus, it is important to have an abundance of large female white bass in the population for any chance of successful natural reproduction.

White bass spawn during the spring in tributaries or upper portions of reservoirs when water temperatures are between 12 and 15°C (Webb and Moss 1967; Scott and Crossman 1973; Quist et al. 2002). They spawn in shallow areas with sand, gravel, or cobble for substrate (Scott and Crossman 1973; Willis et al. 2002), with males arriving before females (Pfleiger 1997). Eggs are adhesive, and eggs and milt are broadcast over coarse substrate; like walleye, white bass also exhibits no parental care (Pfleiger 1997). In reservoirs, high spring water levels translate to increased available spawning habitat, which can have a direct benefit on year-class strength (Beck et al. 1997; Pope et al. 1997; DiCenzo and Duval 2002). Alternatively, spring inflow rates that are too high (Quist et al. 2002) or too low (DiCenzo and Duval 2002) can preclude access to ideal spawning habitat. Although white bass eggs are subject to predation and other mortality factors (Steinhart et al. 2004; Kock et al. 2006), they hatch more quickly than do walleye eggs (in as little as 2 days, Scott and Crossman 1973), and thus, are subject to potential threats for a shorter period. *Morone* larvae with longer hatch times are larger, but have, on average, 58% less yolk at hatch (Lochmann et al. 2009).

After hatching, larval white bass will form schools and feed primarily on zooplankton, though they will utilize insects and fish as the summer progresses, including age-0 gizzard shad (Michaletz et al. 1987; Schultz et al. 2002; Willis et al. 2002). Growth of white bass is positively correlated to water temperature and food abundance (Ruelle 1971). Young-of-year white bass compete for resources with young-of-year individuals of other species, including walleye (Michaletz et al. 1987; Beck et al. 1998) and yellow perch (Michaletz et al. 1987). However, in certain systems or years, competition with walleye may be limited, depending on selective feeding traits (Bulkley et al. 1976) or diet divergence (Willis et al. 2002). In addition to competitive constraints, young-of-year white bass likely face predation from similar species as walleye, although specific predators of larval white bass are, as yet, undocumented. White bass populations naturally show high annual variability in year-class strength (Bettoli et al. 1993).

## Need for study

Walleye and white bass are popular sportfish in the reservoirs of the Great Plains states (Stone 1996; Burlingame 1998; Bauer 2002); in a recent angler survey conducted in Nebraska, walleye were the preferred sportfish of the majority of respondents (Hurley and Duppong-Hurley 2005). As such, NGPC dedicates considerable resources for stocking and managing programs for walleye, particularly in these five Southwest reservoirs. However, even though augmented by stocking, walleye year-class strengths in these systems are variable (DeBoer et al. 2013). Likewise, white bass are typically not stocked in these systems, and their year-class strengths are also variable (DeBoer et al. 2013). Irrigation reservoirs are inherently perturbed systems; compounding the difficulty of this assessment, even fish populations in unperturbed systems tend to fluctuate in abundance (Kelso and Bagenal 1977). Hinch et al. (1991) stated a need for more large-scale, multi-lake studies; abiotic variance is problematically reduced with smaller spatial and temporal scales. A multi-reservoir, multi-year study designed to gain a better understanding of walleye and white bass recruitment in these reservoirs will help fishery managers determine proper courses of action, and will provide information on recruitment of fishes in semi-arid regions like the Great Plains.

### Research question 1

What are the biotic and abiotic factors that lead to fluctuations in annual recruitment of walleye in southwest Nebraska irrigation reservoirs?

### Objectives

1. Identify biotic and abiotic factors that influence age-0 walleye abundance in southwest Nebraska irrigation reservoirs.
2. Quantify differences in walleye reproductive condition between two southwest Nebraska irrigation reservoirs.
3. Describe the phenology of walleye spawning at two southwest Nebraska irrigation reservoirs.

### Research question 2

What are the biotic and abiotic factors that lead to fluctuations in annual recruitment of white bass in southwest Nebraska irrigation reservoirs?

### Objectives

4. Identify biotic and abiotic factors that influence age-0 white bass abundance in southwest Nebraska irrigation reservoirs.

### Data collection and use, by chapter

Each of the subsequent chapters is intended to stand alone. Chapter 2 is an analysis of 18 years of NGPC standardized sampling data, with which we model abiotic and biotic factors influencing walleye and white bass recruitment in all five Republican River reservoirs in Nebraska. We used data from NGPC, U.S. Bureau of Reclamation, and the National Oceanic and Atmospheric Administration's National Climatic Data Center (see Table 2.2). Chapter 3 is an analysis of the differences in spawning ecology of female walleye between two reservoirs, Swanson and Medicine Creek, which we perceive have differences in environmental quality. We used adult fish data collected during the spring of 2012 for this chapter. Chapter 4 is a summary of management recommendations and "big picture" contextualization of the preceding chapters.

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Table 1.1. Annual reservoir discharge (millions of $m^3$) during irrigation season (June through September) from 1993 through 2012.

| Year | Enders Reservoir | Swanson Reservoir | Red Willow Reservoir | Medicine Creek Reservoir | Harlan County Lake |
|---|---|---|---|---|---|
| 1993 | 14.4 | 18.9 | 7.8 | 40.4 | 61.0 |
| 1994 | 18.2 | 62.7 | 11.6 | 32.5 | 121.4 |
| 1995 | 19.6 | 70.7 | 13.6 | 41.0 | 207.5 |
| 1996 | 14.7 | 45.9 | 9.3 | 15.2 | 243.6 |
| 1997 | 20.3 | 63.3 | 14.4 | 39.1 | 131.9 |
| 1998 | 19.0 | 59.0 | 13.5 | 36.8 | 124.7 |
| 1999 | 15.2 | 44.1 | 10.7 | 28.2 | 121.2 |
| 2000 | 18.7 | 56.2 | 12.9 | 33.5 | 176.7 |
| 2001 | 11.5 | 25.6 | 16.0 | 31.9 | 106.8 |
| 2002 | 5.7 | 12.6 | 12.3 | 37.0 | 119.8 |
| 2003 | 3.0 | 0.3 | 1.2 | 27.0 | 63.3 |
| 2004 | 0.9 | 0.3 | 1.2 | 29.4 | 0.0 |
| 2005 | 0.9 | 0.3 | 1.2 | 23.7 | 0.0 |
| 2006 | 0.9 | 0.3 | 12.1 | 29.5 | 15.1 |
| 2007 | 2.6 | 0.3 | 1.2 | 47.2 | 26.2 |
| 2008 | 1.5 | 0.3 | 7.0 | 37.6 | 99.9 |
| 2009 | 1.5 | 29.0 | 8.0 | 25.5 | 73.9 |
| 2010 | 1.5 | 24.9 | 8.3 | 25.7 | 123.9 |
| 2011 | 1.5 | 24.6 | 8.9 | 31.5 | 69.6 |
| 2012 | 1.3 | 40.9 | 1.8 | 32.4 | 123.4 |

Table 1.2. Annual stocking data for walleye in the five Nebraska reservoirs of the Republican River. Fish stocked were 2.5-5.0-cm fingerlings, unless otherwise noted.

| Year | Enders Reservoir | Swanson Reservoir | Red Willow Reservoir | Medicine Creek Reservoir | Harlan County Lake |
|---|---|---|---|---|---|
| 1986 | 96240 | 35000 | 169310[C] | 99974[B] | 0 |
| 1987 | 76927 | 153855 | 5733 | 7900 | 270000 |
| 1988 | 7304 | 95000 | 46812[C] | 54180[C] | 0 |
| 1989 | 0 | 72416 | 7539 | 7539 | 0 |
| 1990 | 43648 | 106731 | 57816 | 110783 | 316479 |
| 1991 | 51712 | 150979 | 45420 | 87314 | 5000000[A] |
| 1992 | 47820 | 75000 | 800000[A] | 1400000[A] | 164724 |
| 1993 | 101714 | 284288 | 86948 | 101184 | 374823 |
| 1994 | 125964 | 302850 | 153894 | 188786 | 0 |
| 1995 | 0 | 0 | 81400 | 92015 | 516288 |
| 1996 | 78325 | 256570 | 0 | 0 | 0 |
| 1997 | 0 | 0 | 81400 | 95700 | 616318 |
| 1998 | 89000 | 252504 | 0 | 0 | 0 |
| 1999 | 0 | 0 | 81389 | 92855 | 651300 |
| 2000 | 84000 | 249000 | 0 | 0 | 60000 |
| 2001 | 0 | 0 | 83750 | 92500 | 684950 |
| 2002 | 85400 | 250000 | 0 | 0 | 200000 |
| 2003 | 0 | 0 | 1042000[A] | 93120 | 209221 |
| 2004 | 37600 | 59400 | 1037000[A] | 33125 | 7423000[A] |
| 2005 | 0 | 59400 | 1028000[A] | 0 | 0 |
| 2006 | 909000[A] | 5693125[A] | 2333000[A] | 1457500[A] | 127271 |
| 2007 | 1567800[A] | 2653200[A] | 1192500[A] | 2650000[A] | 11250000[A] |
| 2008 | 1006250[A] | 6031250[A] | 2641100[A] | 1342750[A] | 4168000[A] |
| 2009 | 1762600[A] | 2612425[A] | 1224000[A] | 2723400[A] | 9770200[A] |
| 2010 | 1024020[A] | 6330971[A] | 13923 | 1911500[A] | 15918000[A] |
| 2011 | 1637506[A] | 3477940[A] | 0 | 93556 | 11389430[A] |

[A] Fry

[B] 10.1-12.7-cm fingerlings

[C] 2.5-5.0- and 10.1-12.7-cm fingerlings

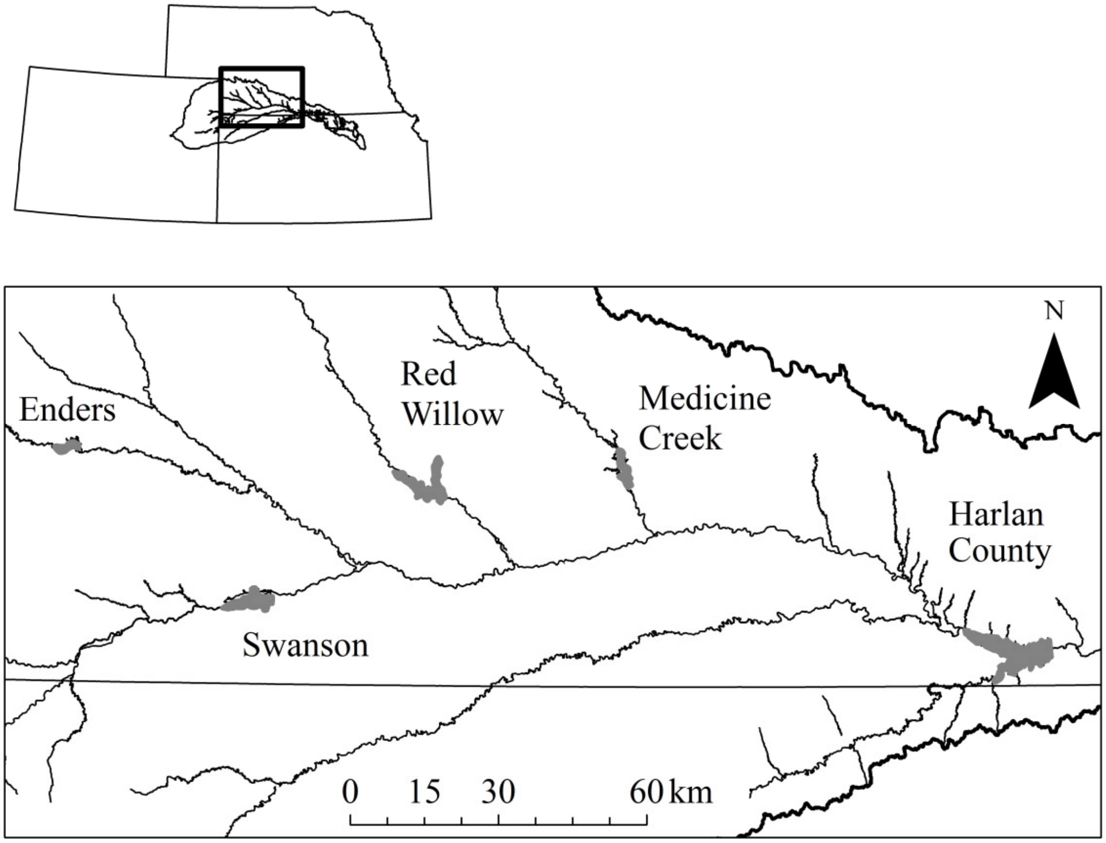

Figure 1.1. Map of the Republican River basin in Colorado, Kansas, and Nebraska, USA, and the five irrigation reservoirs in Nebraska.

# Chapter 2: ENVIRONMENTAL FACTORS REGULATING THE RECRUITMENT OF WALLEYE *SANDER VITREUS* AND WHITE BASS *MORONE CHRYSOPS* IN IRRIGATION RESERVOIRS

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## Abstract

Understanding the environmental factors that regulate fish recruitment is essential for effective management of fisheries. Generally, first-year survival, and therefore recruitment, is inherently less consistent in systems with high intra- and interannual variability. Irrigation reservoirs display sporadic patterns of annual drawdown, which can pose a substantial challenge to recruitment of fishes. We developed species-specific models using an 18-year data set compiled from state and federal agencies to investigate variables that regulate the recruitment of walleye (*Sander vitreus*) and white bass (*Morone chrysops*) in irrigation reservoirs in southwest Nebraska, USA. The candidate model set for walleye included only abiotic variables (water-level elevation, minimum daily air temperature during winter prior to hatching, annual precipitation, spring warming rate and May reservoir discharge), and the candidate model set for white bass included primarily biotic variables (catch per unit effort (CPUE) of black crappie (*Pomoxis nigromaculatus*), CPUE of age-0 walleye, CPUE of bluegill (*Lepomis*

*macrochirus*) and CPUE of age-3 and older white bass), each of which had a greater relative importance than the single abiotic variable (minimum daily air temperature during winter after hatching). Our findings improve the understanding of the recruitment of fishes in irrigation reservoirs and the relative roles of abiotic and biotic factors.

## Introduction

Game management is often predicated on the desire to maintain predictable populations that can sustain consistent harvest over multiple years (Rosenberg et al. 1993; Heino 1998). Unfortunately, in many systems, population variability is the norm rather than the exception (Gaston and McArdle 1994). For example, recruitment – often considered to be the most influential factor governing fish populations (May 1974; Gulland 1982; Donald 1997; Houde 2002) – is inherently less consistent in systems with high intra- and interannual variability. Fish are especially vulnerable during early life stages, particularly in reservoirs where unpredictable water fluctuations are common (June 1977; Beam 1983; Maceina and Stimpert 1998), as habitat constancy is inherently linked to constancy in weather patterns (Houde 1987; Mion et al. 1998; Hoxmeier et al. 2004). Challenges for fish to recruit are exacerbated by water-level variability (Carline 1986), especially in irrigation reservoirs that experience unpredictable and often amplified summer draw-downs in response to sporadic extremes in abiotic conditions (Quist et al. 2003b; Olds et al. 2011).

Abiotic and biotic factors are known to regulate the recruitment of fishes, but specific factors regulating individual species are more difficult to ascertain. Abiotic conditions such as temperature, light, salinity, and oxygen clearly regulate growth rate (Brett 1979) and in some cases survival (Oliver et al. 1979; Post and Evans 1989; Fox and Keast 1991; Johnson and Evans 1991). However, biotic conditions are often equally important although generally more complex. For example, survival and growth generally covary with food availability (Persson and Greenberg 1990; Leggett and DeBlois 1994), which is influenced by prey abundance (Ritchie and Colby 1988; Peterson et al. 2006), temporal and spatial overlap of predator hatching with prey availability (i.e., match/mismatch; Cushing 1990; Chick and VanDenAvyle 1999; Kaemingk et al. 2011), intraspecific competition (Partridge and DeVries 1999; Knoll 2007), and interspecific competition (Michaletz et al. 1987; Roseman et al. 1996; Garvey and Stein 1998; Kaemingk et al. 2012). Similarly, predation also regulates recruitment (Leggett and DeBlois 1994; Köster and Möllmann 2000), and is influenced by cannibalistic conspecifics (Chevalier 1973; Fox 1975; Polis 1981) and interspecific interactions (Pope et al. 1996; Quist et al. 2003b). Ultimately, understanding fish population dynamics, particularly in environments with strong periodic cycles in fish abundance, requires understanding the extent to which biotic and abiotic factors interact to limit fish recruitment.

Walleye *Sander vitreus* and white bass *Morone chrysops* are among the most popular sportfish in the reservoirs of the Great Plains, USA (Stone 1996; Bauer 2002; Hurley and Duppong-Hurley 2005). Despite considerable effort by the Nebraska Game and Parks Commission (NGPC) stocking walleye and managing reservoirs for walleye and white bass, populations of walleye and white bass in southwest Nebraska (USA) reservoirs are dynamic (Huber 2010a-d; Newcomb 2010), as erratic recruitment has led to “boom and bust” fisheries for these two species. Although analyses from regionally similar systems provide some insight (Quist et al. 2002; 2003b), differences exist among systems, and specific reasons for the dynamic nature of these populations are largely unknown. Thus, further knowledge of the factors regulating walleye and white bass recruitment in irrigation reservoirs is required to understand the ecology of these fishes in the semi-arid Great Plains region.

## Methods

### Study area and reservoirs

The Republican River is an impounded tributary to the Kansas River; the Republican River basin is contained within three states (Figure 1.1) in the Great Plains region of the United States of America. Forty percent of the basin is in Nebraska (USDA 1978), where it drains nearly 25,000 km$^2$ of primarily rangeland and cropland into 1,826 km of streams and rivers (Bliss and Schainost 1973). Catastrophic flooding in 1935 prompted the construction of five large multipurpose reservoirs (Table 2.1; Figure 1.1) in the Republican River basin in Nebraska:Enders Reservoir, Harlan County Lake, Medicine Creek Reservoir (Harry D. Strunk Lake), Red Willow Reservoir (Hugh Butler Lake), and Swanson Reservoir. Harlan County and Swanson reservoirs are on the mainstem of the Republican River, whereas Enders, Medicine Creek, and Red Willow reservoirs are on separate tributaries to the Republican River. Species commonly present in these reservoirs include black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, freshwater drum *Aplodinotus grunniens*, flathead catfish *Pylodictis olivaris*, gizzard shad *Dorosoma cepedianum*, hybrid striped bass *M. chrysops* × *M. saxatilis*, largemouth bass *Micropterus salmoides*, northern pike *Esox lucius*, smallmouth bass *Micropterus dolomieu*, walleye, white bass, and white crappie *Pomoxis annularis*. Most of the species present in the reservoirs are indigenous to the drainage; nonindigenous species include black crappie, common carp, hybrid striped bass, largemouth bass, and smallmouth bass (USGS 2009).

As a result of agricultural over-development (i.e., over-appropriation of groundwater wells for cropland irrigation) in the region, flows are substantially reduced compared to circa-1970 levels throughout the Republican River basin (Szilagyi 1999; 2001). This reduction in flow has been attributed to cropland irrigation, changes in vegetative cover, water conservation practices, and construction of reservoirs and artificial ponds in the basin, all of which increase the amount of water lost to evaporation over the basin (Szilagyi 1999; 2001). Thus, only Medicine Creek Reservoir delivers water for irrigation on a regular basis; the other reservoirs deliver water for irrigation only sporadically when there is sufficient inflow.

### Data collection

Data for walleye, white bass, bluegill, black crappie, white crappie, freshwater drum, and gizzard shad were obtained from standardized experimental gillnet surveys conducted by NGPC during autumn 1993-2010. A standard survey consisted of 4-8 gillnets that were set overnight once in each reservoir during autumn of each year. Gillnets were 45.6 m long and 1.8 m deep, with 6 7.6-m panels consisting of 1.9, 2.5, 3.2, 3.8, 5.1, and 7.6 cm bar mesh. We used catch per unit effort (CPUE; number per gillnet night) as an index of abundance. Although trapnets are the standard gear for assessing bluegill and crappie populations, use of the experimental gillnet dataset provided us with both longer-term data and more complete data than use of the trapnet dataset. Ages of captured walleye and white bass were determined by a single reader from NGPC, using scales pressed into acetate slides and a microfiche reader (Smith 1954). Age was not assigned to other fishes. Autumn age-0 fish are often considered an acceptable stage to measure recruitment (Willis 1987); however, here we considered age-1 walleye and age-1 white bass from autumn gillnets to be recruited to the population, as age-1 abundance is a more conservative estimate that considers overwinter mortality (*sensu* Pratt and Fox 2002), among other factors. Furthermore, experimental gillnets do not accurately sample young-of-year walleye or white bass. We obtained hydrological data for reservoirs (e.g., water elevation, irrigation fluctuation, and precipitation; see Table 2.2) for 1993-2009 (1-calendar-year advance of age-1 walleye and age-1 white bass data) from the U.S. Bureau of Reclamation (USBR 2010). We obtained air temperature data (Table 2.2) unique to each reservoir for 1993-2009 (1-calendar-year advance of age-1 walleye and age-1 white bass data) from the National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC 2010).

### Statistical analyses

We used 1-way ANOVA to test for differences in minimum monthly air temperature between the months of April and May during 1994-2009 to verify that minimum air temperature did in fact increase during spring. Likewise, we used 1-way ANOVA to test for differences in extent of range of monthly air temperature (maximum monthly temperature minus minimum monthly temperature during a given year) between the months of April and May during 1993-2009 to verify that temperature fluctuations decreased as spring progressed. We used independent Durbin-Watson tests to test for temporal autocorrelation on residuals in the candidate model sets. We $\log_e$-transformed ($\ln[x + 1]$) CPUE of each species, and transformed independent variables when appropriate. Out of 79 available year-by-reservoir combinations, there were 12 instances of zero catch of age-1 walleye, and 7 instances of zero catch of age-1 white bass (Figure 2.2). All independent variables were assigned a 1-calendar-year advance, so as to model their effect on age-0 walleye and age-0 white bass. From the 51 independent variables (43 for each species, Table 2.2), we developed multiple-linear regression models that best described ln(CPUE) during 1994-2010 for age-1 walleye and age-1 white bass independently (Figure 2.1), using reservoir as a fixed factor. We developed a model set using stepwise multiple linear regression, with variables added based on their adjusted $R^2$. Each model produced by an iteration of the stepwise selection process was included in the model set until a maximum of adjusted $R^2$ for each model set was determined. We then selected a subset of candidate models from among the set of developed models using Akaike's Information Criterion (Akaike 1987) corrected for small sample size ($AIC_c$, Hurvich and Tsai 1989). We excluded models with a $\Delta AIC_c > 2$ from the subset of candidate models (Royall 1997). We assessed relative variable importance (RVI) by summing the $AIC_c$ weights over all models including the explanatory variable. We compared the RVI for all variables included in the candidate model set to evaluate our hypothesis. We conducted statistical analyses using SAS (Version 9.2, SAS Institute

Inc., Cary, NC) and R (Version 2.14.0, The R Foundation for Statistical Computing; Vienna, Austria).

## Results

Durbin-Watson tests for temporal autocorrelation on model residuals were not significant. The minimum temperature in this region during April (-7.5 ± 2.8 °C, mean ± SD) was significantly less (1-way ANOVA, F = 337.3, df = 156, $p < 0.0001$) than during May (0.1 ± 2.4 °C). Furthermore, the mean monthly extent of temperature range during April (37.6 ± 4.4 °C) was significantly greater (1-way ANOVA, F = 28.56, df = 156, $p < 0.0001$) than during May (33.9 ± 4.5 °C).

The candidate model set for walleye (Table 2.3) included two models with a $\Delta AIC_c \leq 2$. There were 5 abiotic and no biotic variables present in the candidate model set; reservoir was also present in the walleye candidate model set. The mean (± SE) adjusted $R^2$ for the walleye candidate model set was 0.67 ± 0.01. Four variables in the candidate model set had an RVI > 0.9; three variables had an RVI > 0.99 (Table 2.4).

The candidate model set for white bass (Table 2.5) included three models with a $\Delta AIC_c \leq 2$. There were 4 biotic variables and 1 abiotic variable present in the candidate model set; reservoir was not present in the white bass candidate model set. The mean adjusted $R^2$ for the white bass candidate model set was 0.33 ± 0.02. Two variables in the candidate model set had an RVI > 0.9 (Table 2.4).

## Discussion

### Walleye recruitment

The most important variable in the candidate model set for walleye was maximum reservoir water level, which was negatively related to year-class strength of walleye. Quist et al. (2003b) also found year-class strength of walleye to be negatively correlated with reservoir elevation, though they were unable to explain the mechanism behind these trends; they hypothesized it may have to do with small (i.e., 1-2 m) increases in reservoir water level during low-water years providing increased spawning habitat or increased production of prey species. In our study reservoirs, high reservoir water levels generally indicated sufficient volume in the reservoir for irrigation discharge. Another variable in the candidate model set was May reservoir discharge, which was also negatively related to year-class strength of walleye. However, annual precipitation was also included in the candidate model set, but it was positively related to year-class strength of walleye. Sufficient volume for irrigation discharge was generally only present in years with abundant annual precipitation, though irrigators need to apply less water in wet years. Thus, discharge was at a lower volume and typically started later in the year, after some of the age-0 walleye had moved away from the dam. Nonetheless, high discharge can entrain age-0 walleye through the dam leading to a direct reduction in the number of potential recruits in the reservoir (Walburg 1971). High discharge levels during May could also lead to low zooplankton abundance (*sensu* Watson et al. 1996; Kalff 2003), which could reduce food availability for larval walleye at a critical stage. Furthermore, previous studies indicate that harvest (Aggus and Bivin 1982), standing crop, natural reproduction, and spawning success of walleye (Willis and Stephen 1987) is greater in reservoirs with low discharge (i.e., retention time > 1 year); as such, larval walleye may not be suitable for stocking into reservoirs with high discharge (Willis and Stephen 1987; Johnson et al. 1988).

The second-most important variable in the candidate model set for walleye was maximum winter temperature (experienced by sexually mature adult walleye prior to spawning), which was negatively related to year-class strength of walleye; recruitment is weak the following year when winter temperatures are warm (Colby and Nepszy 1981). Annual maturation of adult walleye gonads requires water temperatures below 10°C, thus if water temperatures are not sufficiently cold enough for a long enough duration, walleye may skip spawning and resorb their gametes over the next season (Colby and Nepszy 1981). Ova resorption interferes with development of next generation of oocytes, leading to skipping of the next spawning period (Colby et al. 1979). Thus, failure to spawn in one season because of elevated winter water temperature may lead to failure to spawn in the following season, leading to the loss of back-to-back year classes (this was unaccounted for in our models).

The number of spring growing-degree days was positively related to year-class strength of walleye. Warm spring water temperatures may accelerate spawning and shorten egg incubation time (Busch et al. 1975; Colby et al. 1979), and result in greater growth rates for larval walleye (Busch et al. 1975; Colby et al. 1979). These factors allow larval walleye to accelerate their development, switching to piscivory earlier, and therefore increasing their resource intake and ultimately increasing recruitment (*sensu*

Quist 2003a). In previous studies, both spring warming rate (Busch et al. 1975; Madenjian et al. 1996) and mean spring temperature (Quist et al. 2003b) were positively related to recruitment of walleye.

Reservoir, included in the models as a fixed factor, was present in the candidate model set for walleye. Thus, there may be differences among these reservoirs in walleye recruitment. Although age-0 walleye abundance was present in the candidate model set for white bass, age-0 white bass abundance was not present in the candidate model set for walleye. This is most likely because the abiotic factors mentioned above had a greater influence on walleye recruitment. Moreover, we believe the stocking of walleye potentially confounds the relationship between walleye recruitment and abundance of age-3 and older walleye, which is why it was not present in our candidate model set.

Ultimately, these abiotic conditions not only influence walleye, they also influence the entire reservoir community, which in turn affects the walleye population. Thus, it is likely that these abiotic factors act both directly and indirectly on walleye recruitment. If early-season storms or abrupt changes in temperature (an abiotic factor) influence larval walleye production, they likely also influence the production of zooplankton (a biotic factor), in particular the phenology and abundance. Changes in zooplankton composition and abundance could also affect many other age-0 and adult fishes, thus complicating the nature of the relationship between abiotic and biotic factors influencing walleye recruitment.

### White bass recruitment

The most important variable in the candidate model set for white bass was black crappie abundance, which was positively related to year-class strength of white bass. The second-most important variable in the candidate model set for white bass was age-0 walleye abundance, which was also positively related to year-class strength of white bass. Given that larval white bass compete for resources with other age-0 fishes, including walleye (Michaletz et al. 1987; Beck et al. 1998) and black crappie (Pope et al. 1996; Galinat et al. 2002), it is likely that resource conditions (e.g., abundant zooplankton and reservoir inflow) that favor recruitment of one of these species will also benefit the other two. It is also possible that adult crappie and age-0 walleye predation on abundant age-0 gizzard shad (Michaletz 1997; Quist 2003a) reduces competition between age-0 white bass and age-0 gizzard shad for zooplankton (Michaletz et al. 1987). Alternatively, it is possible that large abundances of age-0 walleye may provide a "shading effect" (as alternative prey, *sensu* Forney 1976) for age-0 white bass. White bass, black crappie, and saugeye *Sander vitreus* × *S. canadensis* also respond similarly to reservoir hydrology, producing weak year classes in dry years and strong year classes in wet years (Sammons and Bettoli 2000). As we discussed with walleye, the distinction between abiotic or biotic factors as regulators of recruitment of white bass is complicated.

The third-most important variable in the white bass candidate model set was bluegill abundance, which was negatively related to year-class strength of white bass. Age-0 white bass consume both zooplankton and invertebrates before becoming piscivores (Matthews et al. 1992, Quist et al. 2002). Age-0 bluegill consume primarily zooplankton (Kaemingk et al. 2012) and age-1 and older bluegill consume primarily macroinvertebrates (Olson et al. 2003). This could create scenarios where bluegill and age-0 white bass compete for food resources, which could explain the negative correlation in our model. However, given that year-class strength of white bass was positively correlated to both black crappie abundance and age-0 walleye abundance and negatively correlated to bluegill abundance, further investigation of species-specific interactions in these systems is needed.

Another variable in the white bass candidate model set was abundance of age-3 and older white bass, which was positively related to year-class strength of white bass. Abundance of age-3 and older white bass was used as a surrogate metric for abundance of spawning adults, as no evaluation of the condition of white bass gonads was performed in the field during sampling. The coefficient (≈ 0.3) for this stock-recruit regression (log[WHB]-log[WHB_3_PLUS]) is less than 1; thus, there is likely a density-dependent mechanism that is influencing white bass recruitment. Spawning activity of white bass is positively related to reservoir inflows during spring (Quist et al. 2002), however there was no evidence in these reservoirs of a white bass spawning migration during the spring (Martin et al. 2009) likely because of limited inflows in most of the years studied. Spawning adult abundance is generally considered to be positively related to year-class strength of most fishes (Myers and Barrowman 1996). However, unlike walleye populations, which are regularly augmented by stocking, white bass populations in these systems are self-sustaining, thus leading to the presence of a relationship between white bass recruitment and abundance of age-3 and older white bass.

Minimum winter air temperature (winter after hatching) was the only abiotic variable included in the white bass candidate model set; the relationship was positive, indicating white bass recruitment is positively influenced by milder (i.e., warmer minimum temperatures) winters. Predation and starvation are important overwintering factors for age-0 white perch *Morone americana* (Fitzgerald et al. 2006). In another study, 71% of age-0 white perch died at 2.5° C versus only 11% at 4.0° C, a finding linked to the white perch remaining active but not feeding at 2.5° C, maintaining their basal metabolic rate while reducing their energy intake leading to a net energy deficit (Johnson and Evans 1991). Size-dependent over-winter mortality was also a factor; smaller white perch (Johnson and Evans 1991) and smaller striped bass *Morone saxatilis* (Hurst and Conover 1998; Sutton and Ney 2001) died before larger conspecifics of the same cohort. Other abiotic factors have been related to white bass recruitment, including spring precipitation and air temperature in eastern South Dakota glacial lakes (Pope et al. 1997), spring air temperature in a northwestern South Dakota reservoir (Phelps et al. 2011), and spring inflow in Kansas reservoirs (Quist et al. 2002; Schultz et al. 2002)

### Interspecific differences in spawning period

There is a need to refine existing knowledge about factors that regulate recruitment of fishes, particularly in changing environments (Baccante et al. 2011). Early spawning species are likely more subjected to adverse abiotic conditions because weather in this region is typically more volatile during early spring (i.e., greater likelihood of cold fronts and greater temperature variability during early spring than during late spring;

Coupland 1958). In contrast, late spawning species are likely less subjected to adverse abiotic conditions and likely more subjected to adverse biotic conditions because many species, including numerically dominant common carp and gizzard shad, spawn during this period, and zooplankton abundance declines during this period (Sullivan et al. 2012) and could become limited.

The candidate-model set for walleye (Table 2.3) included only abiotic variables, and the candidate-model set for white bass (Table 2.5) included mostly biotic variables, each of which had a greater relative importance than the single abiotic variable in the candidate-model set. Essentially, we believe earlier-spawning species like walleye spawn during a period typified by predictable biotic conditions and unpredictable abiotic conditions, whereas later-spawning species like white bass spawn during a period typified by unpredictable biotic conditions and predictable abiotic conditions. In most of the reservoirs we studied, walleye was one of the first, if not the first, species to spawn each year; only northern pike spawn earlier among the suite of common species. Thus, in a given year, larval walleye are typically the first to emerge and feed in an environment that is biotically predictable. However, walleye in these systems spawn during a period where early spring storms and cold fronts produce strong winds that can dislodge or damage walleye eggs, increase water turbidity, or present a lingering decrease in air temperature, all of which can negatively affect walleye recruitment. Furthermore, changing temperatures could also lead to reduced hatching success, or alter adult behavior and thus the duration or periodicity of spawning activity.

Alternatively, white bass spawn approximately a month after walleye (Carlander 1997), and the larvae emerge into a dramatically different environment. There are several species that spawn approximately the same time as white bass, including smallmouth bass, black crappie, white crappie, and freshwater drum (Carlander 1977; Bur 1984). Furthermore, common carp and gizzard shad, which also spawn approximately the same time as white bass (Quist et al. 2004), can numerically dominate the age-0 fish community in these systems (Sullivan et al. 2011). Larval white bass must compete for zooplankton with other fishes, in particular hyper-abundant common carp and gizzard shad larvae. Furthermore, zooplankton abundance declines during this period (Sullivan et al. 2011), and could become limited. Therefore, the emergence of these fishes within a short period creates an environment that is biotically unpredictable as compared to when walleye larvae emerged. However, the abiotic environment during this later period is more predictable than when walleye spawn, with milder temperatures and more consistent temperature fluctuations.

We believe that these scenarios offer the most plausible interpretation of the observed patterns. Alternatively, it is possible that adhesive eggs are more vulnerable to abiotic conditions than semi-buoyant eggs, or that demersal spawning activities may be regulated by abiotic factors and pelagic spawning activities may be regulated by biotic factors. However, it is also plausible that abiotic factors regulate recruitment of both walleye and white bass, with white bass recruitment being regulated indirectly by the abundance of other species that are regulated by abiotic conditions. Additional research from other regions and species is needed to provide further evidence and to fully explore inherent complexities.

### Conclusions

Our study provides essential information regarding factors regulating recruitment of walleye and white bass in irrigation-reservoir ecosystems, and indicates that variability in the fish's environment within and among years may be influential in determining the nature of those factors. Our models could be used by biologists and managers to better understand recruitment of walleye and white bass in irrigation reservoirs throughout the southern Great Plains. Understanding the recruitment of fishes is a critical step in improving our knowledge of their ecology, not only in this region, but throughout semi-arid regions of the world.

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Table 2.1. Hydrological characteristics of the Republican River reservoirs in Nebraska, USA. Surface area and maximum depth are based on active conservation pool elevation. Annual fluctuation was the mean ± SE during 1993-2009.

| Reservoir | Surface area (ha) | Maximum depth (m) | Basin (ha) | Annual fluctuation (m) |
|---|---|---|---|---|
| Enders | 485 | 18.3 | 284,100 | 2.6 ± 1.5 |
| Harlan County | 5,362 | 15.2 | 1,855,500 | 2.9 ± 1.8 |
| Medicine Creek | 737 | 13.7 | 227,900 | 4.3 ± 1.8 |
| Red Willow | 659 | 15.8 | 189,000 | 2.3 ± 1.2 |
| Swanson | 2,023 | 14.6 | 2,232,600 | 2.4 ± 1.6 |

Table 2.2. Input variables for models and explanation of variable abbreviations. We obtained hydrological data for reservoirs (e.g., water elevation, irrigation fluctuation, precipitation) for 1993-2009 from the U.S. Bureau of Reclamation. We obtained air temperature data unique to each reservoir for 1993-2009 from the National Oceanic and Atmospheric Administration's National Climatic Data Center. We obtained fish data from standardized gillnet surveys conducted by the Nebraska Game and Parks Commission during autumn 1993-2010. "Annual" refers to January through December, unless otherwise stated. Age groups of fish were pooled, unless otherwise stated.

| Model variable | Explanation |
|---|---|
| PRECIP_MR | March precipitation (cm) |
| PRECIP_AP | April precipitation (cm) |
| PRECIP_MAY | May precipitation (cm) |
| PRECIP_JU | June precipitation (cm) |
| SPR_PRECIP | Spring precipitation[a] (cm) |
| PRECIP_YR | Annual precipitation (cm) |
| Q_AP | April reservoir discharge (millions of $m^3$) |
| Q_MAY | May reservoir discharge (millions of $m^3$) |
| Q_JUNE | June reservoir discharge (millions of $m^3$) |
| SPR_Q | Spring reservoir discharge[a] (millions of $m^3$) |
| Q_YR | Annual reservoir discharge (millions of $m^3$) |
| IN_APRIL | April reservoir inflow ($m^3$) |
| IN_MAY | May reservoir inflow ($m^3$) |
| ACP_APRIL | April reservoir elevation (m, relative to active conservation pool) |
| ACP_MAY | May reservoir elevation (m, relative to active conservation pool) |

Table 2.2. continued.

| Model variable | Explanation |
|---|---|
| ACP_MAX | Maximum reservoir elevation (m, relative to active conservation pool) |
| ACP_MIN | Minimum reservoir elevation (m, relative to active conservation pool) |
| MAY_SEPT | Change in reservoir elevation, May to September (m) |
| MAX_MIN | Change in reservoir elevation, Maximum to Minimum (m) |
| ELV_YR_PRIOR | Annual change in reservoir elevation (April to April) (m) |
| APR_TMIN | Minimum daily air temperature during April (°C) |
| APR_TMEAN | Mean daily air temperature during April (°C) |
| APR_TMAX | Maximum daily air temperature during April (°C) |
| MAY_TMIN | Minimum daily air temperature during May (°C) |
| WIN_TMEAN_ED | Mean daily air temperature during winter prior to hatching[b] (°C) |
| WIN_TMAX_ED | Maximum daily air temperature during winter prior to hatching[b] (°C) |
| WIN_TMIN_OWM | Minimum daily air temperature during winter after hatching[b] (°C) |
| WIN_TMEAN_OWM | Mean daily air temperature during winter after hatching[b] (°C) |
| WIN_TMAX_OWM | Maximum daily air temperature during winter after hatching[b] (°C) |
| APR_GDD | Number of growing-degree days (maximum temperature > 10°C) during April |
| JUN_GDD | Number of growing-degree days (maximum temperature > 10°C) during June |
| SPRING_GDD | Number of growing-degree days (maximum temperature > 10°C) during April-June |
| GSD | Catch per unit effort (CPUE) of gizzard shad (catch per gill net night) |
| BLG | CPUE of bluegill (BLG, catch per gill net night) |
| FWD | CPUE of freshwater drum (FWD, catch per gill net night) |
| BLC | CPUE of black crappie (BLC, catch per gill net night) |
| WHC | CPUE of white crappie (WHC, catch per gill net night) |
| CRP | CPUE of black and white crappie (catch per gill net night) |
| PREDS | CPUE of BLG+FWD+BLC+WHC (catch per gill net night) |
| WAE_3_PLUS | CPUE of walleye ≥ age 3[c] (catch per gill net night) |

Table 2.2. continued.

| Model variable | Explanation |
|---|---|
| WHB_3_PLUS | CPUE of white bass ≥ age 3[c] (catch per gill net night) |
| WAE | CPUE of age-1 walleye[d] (catch per gill net night) |
| WHB | CPUE of age-1 white bass[e] (catch per gill net night) |

[a] Spring includes the months of March, April, and May.

[b] Winter includes the months of December, January, and February.

[c] Fish ≥ age 3 used as a surrogate for spawner abundance; no internal evaluation of fish was performed.

[d] Used as dependent variable for walleye model and independent variable for white bass model.

[e] Used as dependent variable for white bass model and independent variable for walleye model.

Table 2.3. Parameter estimates for variables (Table 2.2) in candidate model sets for recruitment of walleye to age 1. Models with a $\Delta AIC_c > 2$ were excluded from consideration. Data were from the Republican River basin, Nebraska, USA 1993-2009.

| Model | Intercept | ACP_MAX | WIN_TMAX_ED | RES | PRECIP_YR | SPRING_GDD | Q_MAY | Adj. $R^2$ | $\Delta AIC_c$ | $AIC_c$ *w* |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.58 | -0.15 | -0.09 | Enders:0.57<br>Harlan County:0.02<br>Medicine Creek:0.55<br>Red Willow:-0.22<br>Swanson:0.00 | 0.01 | 0.02 | -0.04 | 0.69 | 0 | 0.64 |
| 2 | 0.29 | -0.17 | -0.08 | Enders:0.56<br>Harlan County:-0.05<br>Medicine Creek:0.56<br>Red Willow:-0.20<br>Swanson:0.00 | 0.01 | 0.03 | -[a] | 0.66 | 1.13 | 0.36 |

[a] Variable not included in model.

Table 2.4. Relative variable importance (RVI) for variables (Table 2.2) present in the candidate models sets for recruitment of walleye (Table 2.3) and white bass (Table 2.5) to age 1. Data were from the Republican River basin, Nebraska, USA 1993-2009.

| Variable | RVI |
|---|---|
| **Walleye** | |
| ACP_MAX | 0.999 |
| WIN_TMAX_ED | 0.997 |
| RES | 0.991 |
| PRECIP_YR | 0.939 |
| SPRING_GDD | 0.872 |
| Q_MAY | 0.642 |
| | |
| **White bass** | |
| BLC | 0.950 |
| WAE | 0.948 |
| BLG | 0.824 |
| WHB_3PLUS | 0.731 |
| WIN_TMIN_OWM | 0.604 |

Table 2.5. Parameter estimates for variables (Table 2.2) in candidate model sets for recruitment of white bass to age 1. Models with a $\Delta AIC_c > 2$ were excluded from consideration. Data were from the Republican River basin, Nebraska, USA 1993-2009.

| Model | Intercept | BLC | WAE | BLG | WHB_3PLUS | WIN_TMIN_OWM | Adj. $R^2$ | $\Delta AIC_c$ | $AIC_c$ *w* |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.56 | 0.47 | 0.51 | -0.62 | 0.29 | 0.06 | 0.36 | 0 | 0.51 |
| 2 | 0.35 | 0.47 | 0.44 | -0.63 | 0.28 | -[a] | 0.32 | 1.05 | 0.30 |
| 3 | 1.78 | 0.46 | 0.57 | -0.68 | -[a] | 0.05 | 0.31 | 1.96 | 0.19 |

[a] Variable not included in model

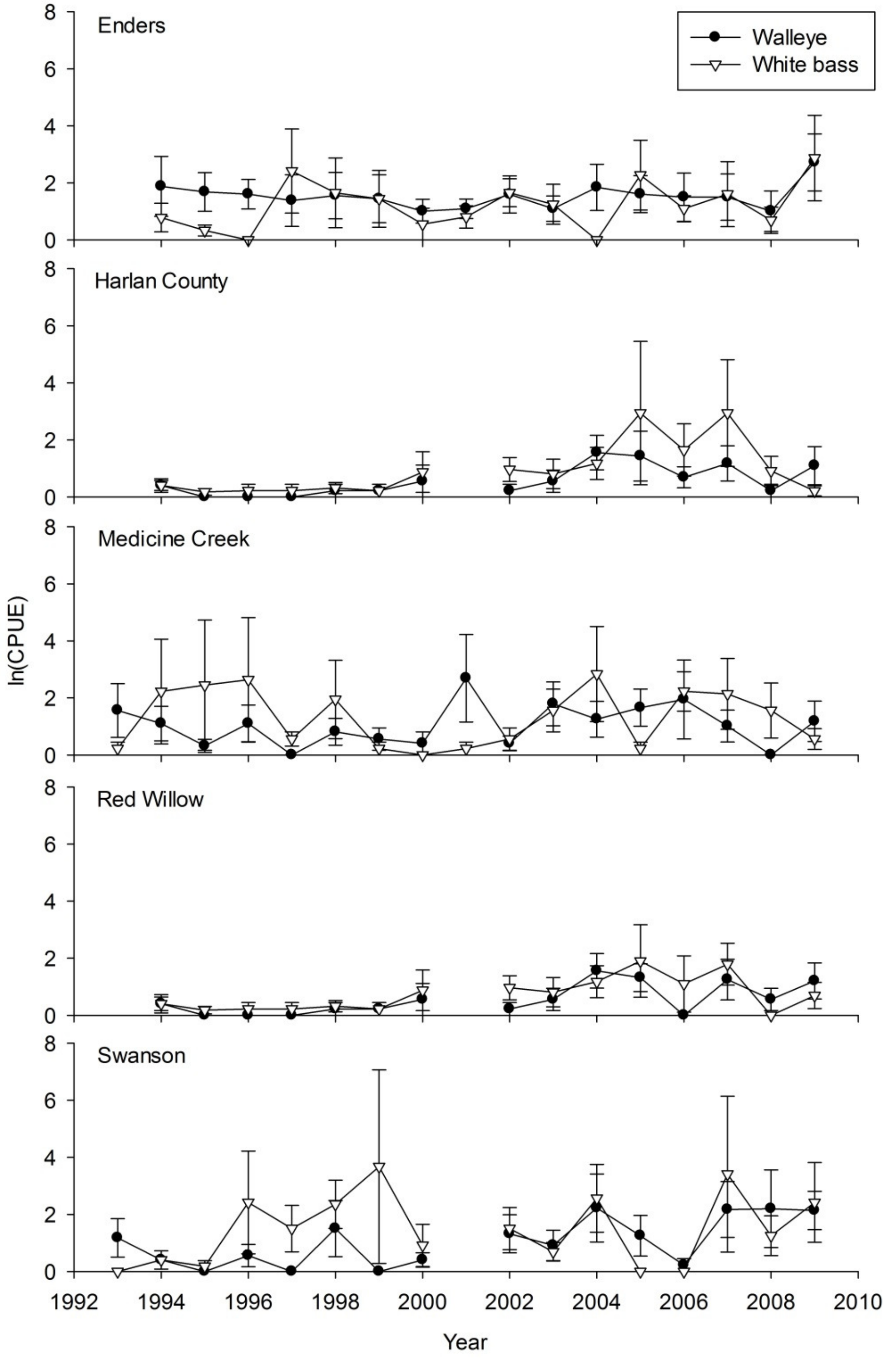

Figure 2.1. Log$_e$-transformed (ln[$x$ + 1]) catch per unit effort (ln(CPUE); number per gillnet night) of age-1 walleye and age-1 white bass during 1994-2010 from the five reservoirs of the Republican River basin in Nebraska, USA.

# Chapter 3: COUNTERINTUITIVE LIFE-HISTORY EXPRESSION IN A HIGHLY VARIABLE ENVIRONMENT

## Abstract

Differing life-history strategies may act as a constraint on reproductive expression that ultimately limits the ability of individual species to respond to changes in the magnitude or frequency of environmental variation, and potentially underlies the variation that is often inherent in phenotypic and evolved responses to anthropogenic change. Alternatively, differential expression of life-history strategies may represent differences in the adaptive capacity to optimize current reproductive value given variation in environmental conditions, if there are environmental cues that predict reproductive potential. We compared several aspects of walleye *Sander vitreus* spawning ecology at two reservoirs that differ in environmental variability (i.e., annual water-level fluctuation) to identify the capacity of phenotypic expression and the corresponding association with age. Despite significant differences in female body and liver masses between reservoirs that differ in environmental variability, we found no difference in reproductive investment measured by egg size and fecundity. Thus, walleye in a highly variable environment appear to exhibit reproductive traits more typical of a short-lived life-history strategy, which may be resultant from the interaction of several factors, including environmental and anthropogenic pressures. This finding emphasizes the need to identify the degree to which life-history expression represents physiological constraints

versus ecological optimization, particularly as anthropogenic change continues to alter environmental conditions.

## Introduction

Life-history theory predicts that environmental variability in resource availability will lead to differential allocation in reproduction (Williams 1966; Trivers 1972; Roff 1992; Stearns 1992); however, relative allocation among species is not equivocal given the same environmental conditions. Along a continuum of slow to fast life-history strategies (e.g., long-lived and low-fecundity versus short-lived and high-fecundity; Stearns 1992), slow-living species are expected to allocate resources to survival and future reproduction, whereas fast-living species are expected to allocate resources to current reproduction (Charlesworth 1980). Differing life-history strategies may thus act as a constraint on reproductive expression that ultimately limits the ability of individual species to respond to changes in the magnitude or frequency of environmental variation, and potentially underlies the variation that is often inherent in phenotypic responses to anthropogenic change (e.g., Kramer 1995; Post and Stenseth 1999; Walther et al. 2002; Schneider et al. 2010). Alternatively, rather than representing a constraint that is optimized among competing physiological functions, differential expression of life-history strategies among species may represent differences in the adaptive capacity to optimize current reproductive value given variation in environmental conditions (i.e., learning; Boag and Grant 1984). Assuming longevity facilitates the matching of phenotypic expression to ecological conditions through learning (*sensu* Buchanan et al. 2013), on the whole, slow-living species exposed to variable environments may express more conservative reproductive strategies that more closely match the benefits of future reproductive investment, whereas fast-living species exposed to variable environments may express more aggressive reproductive strategies that more closely match the benefits of current reproductive investment (Forbes 1991; Bårdsen et al. 2008).

Irrigation reservoirs across the Great Plains are stocked with walleye *Sander vitreus* to provide a recreational fishery for anglers. Walleye evolved in the relatively stable and predictable environs of glacial lakes and rivers (Scott and Crossman 1973; Bailey and Smith 1981), but the abiotic conditions of irrigation reservoirs are highly variable and unpredictable, often based on the nuances of agricultural needs. The 'harsh' environment of irrigation reservoirs leads to significant fluctuation in walleye recruitment, which is closely tied to abiotic conditions, including reservoir water level (DeBoer et al. 2013). Water released from reservoirs for irrigation can carry age-0 walleye and zooplankton through the dam causing a direct reduction in recruits (Walburg 1971) as well as reducing food availability for larval walleye (*sensu* Watson et al. 1996; Kalff 2003), required at this critical life stage. Walleye exhibit reproductive traits of both fast-living and slow-living species: they have small eggs, high fecundity, and provide no parental care, but also delay maturation and spawn once annually. Even using more-complex life-history models (Winemiller and Rose 1992; Winemiller 2005), walleye still exhibit intermediate reproductive traits. It is important to note that life-history continuums are not continuous, but rather have discrete trade-offs that likely lead to among-species zones of concentration in trait expression. Thus, it is very easy to identify the endpoints of the continuum because all of the trade-offs lead to a convergence of life-history expression. More challenging to understand is the manifestation of the 'middle', where trade-offs between life-history traits may lead to differential life-history expression among species, or even among populations, which are experiencing the same ecological conditions. Nonetheless, if there are environmental cues that predict reproductive potential, then we might expect phenotypic adaptation to different abiotic conditions. Furthermore, given the longevity of walleye and the high costs of reproduction, we would predict phenotypic adaptation would increase with age – older walleye should modify their reproductive output more than younger walleye, given the same environmental conditions.

Our goal was to compare aspects of walleye spawning ecology at two reservoirs that differ in environmental variability to identify the capacity of phenotypic adaptation and the corresponding association with age. Specifically, we compared the presence and nature of the relationship between (1) female age and spawning phenology and (2) female condition, size and reproductive investment, in environments that differ in the degree of annual variation in water level. We knew older fish generally spawn first (Miranda and Muncy 1987, and references therein), and that fish are indeterminate growers that exhibit positive allometric relationships between size and condition, and size and gonadal investment. However, gonadal investment in fishes is influenced by environmental factors across populations, as well as by maternal factors within populations (Baltz and Moyle 1982; Johnston and Leggett 2002; Venturelli et al. 2010). Thus, we predicted that (1) older females will spawn before younger females independent of water-level variability, but that females from environments with less annual variation in water level will (2) spawn before females from environments with more-variable water levels independent of female age, (3) be in greater relative condition than females from environments with more-variable water levels, and (4) make a greater relative investment in reproduction than females from environments with more-variable water levels.

## Methods

### Study site and data collection

Nebraska is at the southwestern edge of the walleye's native range (Carlander 1997) and is typified by extreme seasonal variability in temperature and precipitation (Matthews 1988). As a result, reservoirs in the region are subject to a wide range of environmental conditions including extreme changes in water level (June 1977; Willis 1986; Olds et al. 2011), turbidity (Bremigan 1997; Gido and Matthews 2000; Olds et al. 2011), and temperature (Willis 1986; Olds et al. 2011), all of which can be exacerbated by seasonal agricultural irrigation demands. Water temperatures can approach or exceed 30°C during summer, thus walleye in southwest Nebraska likely are at the upper thermal limit at which they can thrive (Colby et al. 1979).

Reservoir water-level data for 2003-2012 were obtained from the U. S. Bureau of Reclamation (USBR 2013) for two reservoirs in the Republican River basin in southwest Nebraska that differed in the relative degree of annual water-level variability over the last 10 years: Swanson Reservoir (mean ± SE annual variation 17% ± 3% of maximum depth) and Medicine Creek Reservoir (annual variation 28% ± 5%). Swanson has a surface area of 1,223 ha, a basin of 2,232,600 ha, and a maximum depth of 9.5 m; Medicine Creek has a surface area of 591 ha, a basin of 227,900 ha, and a maximum depth of 12.5 m. Walleye were collected on alternate nights from March 25 to April 13 of 2012, but because of weather conditions, the actual number of sampling nights at each reservoir differed. Two to three 100-m by 1.8-m monofilament gillnets with 7.6-cm bar mesh were set at approximately sunset in ~2 m of water in close proximity to the dam at each reservoir, the primary spawning site (Martin et al. 2011), and retrieved after approximately a 1-hour deployment. Water temperature was measured at a depth of 1 m at the start of every net deployment. Upon capture, males were released and each female was measured for total length (mm), weighed (g), and had her second dorsal spine removed for aging (DeVries and Frie 1996). Each dorsal spine was later prepared and aged in the laboratory following standard protocol (Logsdon 2007). Individual females usually spawn in one night (Ellis and Giles 1965); therefore, all female walleye captured were assumed to be in breeding condition. All ripe females (i.e., those with distended abdomens that exuded eggs when gentle pressure was applied) were euthanized, and ovaries and the liver were extracted and weighed individually (0.1 g). Walleye exhibit group synchronous ovarian development (Malison and Held 1996), therefore a ~5 mL sample of eggs was collected and weighed (0.1 g) from the posterior third of the right ovary from each euthanized fish to ensure eggs of the same developmental stage were sampled. The egg samples were preserved with 10% buffered formalin phosphate. Egg diameter of the first 25 eggs encountered from each sample was later measured (0.01 mm) in the laboratory using an ocular micrometer on a dissecting microscope; the remaining eggs in each sample were counted.

### Data analyses

Females that had already released their eggs were excluded from analysis (only one such fish was captured). Female age structure was estimated by calculating age-specific daily catch per unit effort (i.e., number of females of each age group captured per hour of netting). To determine if a difference existed between reservoirs, catch per unit effort was modeled as a function of day of year and reservoir. To determine if any relationship existed between age and spawning phenology within a season and between reservoirs, age was modeled as a function of day of year and reservoir. Body condition was compared between reservoirs by modeling body weight as a function of length and reservoir, and by modeling liver weight as a function of somatic weight and reservoir. Reproductive investment was indexed as fecundity, egg size, and gonad weight, all of which were independently modeled as a function of somatic weight and reservoir. Fecundity was estimated by multiplying the number of eggs in each sample by the ratio between total combined ovary weight and egg sample weight. Egg size was indexed as the mean diameter of 25 eggs from each sample. To determine if any relationship existed between water temperature and day of year between reservoirs, mean water temperature (calculated for each sampling date) was modeled as a function of day of year and reservoir. We used SAS (Version 9.2, SAS Institute Inc., Cary, NC) for all analyses, with $\alpha = 0.05$. In all analyses, a significant reservoir term indicated a difference between reservoirs.

**Results**

Reservoirs did not differ in walleye spawning phenology (*F* = 0.96; df = 1, 37; *P* = 0.33) as the majority of walleye were captured during the first four sampling events; nearly half (50% from Swanson, 47% from Medicine Creek) of all fish were captured on a single day at each reservoir (Figure 3.1). We collected 80 female walleye from Swanson and 37 from Medicine Creek: 69 and 29 were unripe, 11 and 7 were ripe, and 0 and 1 were spent, respectively. Female age ranged from 4 to 10 at Swanson and from 5 to 9 at Medicine Creek (Figure 3.1), and there was no difference in mean age between reservoirs (*F* = 0.01; df = 1, 34; *P* = 0.93). Body weight increased with total length at both reservoirs (*F* = 264.7; df = 1, 109; *P* < 0.0001), but females were heavier for a given length at Swanson (*F* = 6.5; df = 1, 109; *P* = 0.01; Figure 3.2).

We obtained ovary and liver weights and egg samples from 11 breeding females at Swanson and 7 at Medicine Creek. Female age ranged from 6 to 10 and mean age did not differ between reservoirs (*F* = 0.43; df = 1, 16; *P* = 0.51). There was no relationship between egg size and somatic weight (i.e., body weight – [liver weight + gonad weight]) (*F* = 0.04; df = 1, 357; *P* = 0.85; Figure 3.3a) or between egg size and reservoir (*F* = 2.14; df = 1, 357; *P* = 0.1; Figure 3.4a); however, liver weight (*F* = 47.7; df = 1, 15; *P* < 0.0001; Figure 3.3b), fecundity (*F* = 7.1; df = 1, 15; *P* = 0.02; Figure 3.3c), and gonad weight (*F* = 10.8; df = 1, 15; *P* = 0.005; Figure 3.4d) increased with somatic weight at both reservoirs. Although females from Swanson had a greater relative liver weight than females from Medicine Creek (*F* = 22.04; df = 1, 15; *P* = 0.0003; Figure 3.3b), there was no difference between reservoirs in fecundity (*F* = 1.53; df = 1, 15; *P* = 0.2; Figure 3.3c) or gonad weight (*F* = 4.04; df = 1, 15; *P* = 0.06; Figure 3.3d). Water temperatures were stable during the sampling season (*F* = 0.06; df = 1, 9; *P* = 0.81), and did not differ between reservoirs (*F* = 0.2; df = 1, 9; *P* = 0.66).

## Discussion

Understanding reproductive effort is a primary focus of life-history studies; life-history theory predicts that large-sized and long-lived organisms should make reproductive decisions that favor survival when faced with energetic constraints (*sensu* Bårdsen et al. 2011). Although reproductive trade-offs are widely documented (Winemiller and Rose 1992; Ricklefs 2000; Shine 2005; Brown and Sibly 2006), there are numerous failures to document the manifestation of trade-offs in life-history expression (Weber and Declerck 1997; Henriksson and Ruohomäki 2000; Milla et al. 2006; Messina et al. 2007). In particular, the interplay between stochastic environmental conditions and life-history expression, including reproductive investment, remains unclear (Messina and Fry 2003; Sgrò and Hoffmann 2004; Bertrand et al. 2006). Life-history theory predicts that slow-living, capital breeders (i.e., those that invest in reproduction via surplus energy, e.g., from visceral fat deposits) such as walleye (Henderson et al. 1996; Moles et al. 2008) in more-variable and lower-quality environments, such as exist at Medicine Creek, would be in relatively poorer condition and thus invest relatively less in reproduction (Roff 1983). Our results supported those predictions; however, despite significant differences in female body mass and liver mass between reservoirs (Figure 3.2, 3.3b) we found no difference in reproductive investment as measured by either egg size or fecundity (Figure 3.3a, c). This evidence is counter to life-history theory and differs from conclusions that reproductive investment by walleye is sensitive to environmental conditions (Johnston and Leggett 2002).

Although there is some evidence to suggest an energetic constraint, at least at the population level, the evidence to suggest adaptive phenotypic matching to environmental conditions is unclear. Life-history theory predicts (Roff 1992; Stearns 1992) and empirical evidence has shown (fish: Hutchings 1991, Johnston and Leggett 2002, Wang et al. 2012; turtles: Rowe 1994; amphipods: Glazier 1999) that when individuals inhabit environments with unfavorable conditions for offspring, selection favors increased investment in fewer progeny. However, we found no difference in egg size or fecundity between reservoirs (Figure 3.3a, c), despite differences in water-level variability and suspected differences in environmental conditions. That we failed to find females adapting egg size to environmental conditions is surprising given previous findings in walleye (Johnston and Leggett 2002) and general indications that fish alter egg size to match environmental conditions (Stearns 1983; Kinnison et al. 1998); however our finding is not without precedence (Morrongiello et al. 2012; Régnier et al. 2013). We also found no difference in egg size among females of different sizes, which is counter to previous studies (Johnston 1997; Wiegand et al. 2004; Venturelli et al. 2010). In general, variation in offspring size within broods can reflect an adaptive strategy for dealing with an unpredictably variable environment (Marshall et al. 2008). Indeed, it is possible that walleye at Medicine Creek cannot produce an egg large enough, within physiological tradeoff bounds, to increase an individual offspring's survival, and are thus not modifying egg size and number relative to females from Swanson.

Even if females from Medicine Creek are not varying offspring size to cope with environmental conditions, successful reproduction still requires timing reproductive events to maximize reproductive potential. Timing breeding to optimize food resources for offspring, for example, is a common reproductive strategy, as the consequences of mismatching are significant (Lack 1950; Cushing 1969, 1975, 1990; Martin 1987; Visser et al. 2006). Differences in food resources between reservoirs would suggest differences in breeding phenology if females are matching ecological conditions. Additionally, we would predict that older walleye would breed earlier to optimize ecological conditions for offspring and allow more recovery time post-breeding (Miranda and Muncy 1987; Schultz 1993; Cargnelli and Neff 2006; Donelson et al. 2008; Sydeman et al. 1991; Clutton-Brock et al. 1987; Sinervo and Doughty 1996). We found no difference in breeding phenology among age groups or reservoirs as the overwhelming majority of females spawned in a 2- or 3-day period, which is also counter to previous studies (Miranda and Muncy 1987, and references therein). That there was little variation in the timing of spawning indicates that there could also be strong selection (e.g., high rates of egg predation; Ims 1990; Eckrich and Owens 1995) favoring breeding synchrony (Estes 1976; Smith 2004). Still, while selection may explain why we failed to see age-differentiated breeding phenology within reservoirs, breeding synchrony between reservoirs is more complex.

Synchrony in walleye breeding phenology between reservoirs suggests a common ecological condition coupled with a common cue that initiates breeding across both reservoirs. Many fish species take cues (e.g., water temperature; Graham and Orth 1986; Webb and McLay 1996; Carscadden et al. 1997) from their environment to determine when to spawn (de Vlaming 1972), so it is reasonable that walleye in both reservoirs are using the same environmental cue, such as moon phase or water temperature, to precisely coordinate spawning activity. It is also possible that walleye do not respond to environmental variability in a linear manner, or that the environmental variability in both reservoirs is above or below some threshold, or that our selected indicator of environmental variability is not related to female walleye egg development.

Female walleye in these systems are likely responding to environmental variability by modifying life-history traits, including age at maturity and whether or not to trade-off between somatic and gonadal investment. However, in addition to coping with abiotic variability, walleye in irrigation reservoirs also experience significant harvest mortality, which is known to have important implications for life-history expression (Ditchkoff et al. 2006; Godfrey and Irwin 2007; Arlinghaus et al. 2009). Even though angling effort for walleye (number of angler-hours per hectare) is nearly twice as high at Medicine Creek, harvest of walleye (number of walleye captured per hectare) is over twice as high at Swanson (C. Chizinski, unpublished data). Thus, walleye at Medicine Creek are not only subject to more extreme abiotic conditions, they are also subject to greater angling pressure, which could have negative synergistic consequences for walleye at Medicine Creek by reducing not only the number of breeding females in the population, but also restricting the number of potential breeding opportunities.

One possibility for our failure to demonstrate a trade-off is that the life-history traits we measured may not inform our understanding of the energetic trade-offs between survival and reproductive investment. Life-history trade-offs are complex and often manifested through indirect pathways. As an example, reduced reproductive investment is not always manifested in reduced fecundity, as there are inherent trade-offs in the size and number of offspring that ultimately shape investment (fish: Hutchings 1991, Johnston and Leggett 2002, Wang et al. 2012; turtles: Rowe 1994; amphipods: Glazier 1999). There are likely many indirect trade-offs that occur in walleye life-history expression, thus we believed it important to study multiple reproductive traits to improve our understanding of these trade-offs. It seems unlikely that females at Medicine Creek are masking alternative trade-offs in life-history expression, as length-corrected mass regularly predicts reproductive investment in other fish species (Carlander 1969; 1977; 1997). Although mass may not always indicate condition (Schulte-Hostede et al. 2005), females from Medicine Creek exhibited many signs of physiological stress, including reduced visceral fat (J. DeBoer, personal observation), which is the primary source of energy for walleye gonadal development (Henderson et al. 1996; Moles et al. 2008).

It is also possible that the production-oriented stocking strategy used to maintain populations of walleye in irrigation reservoirs is constraining local adaptation and variability in life-history expression that might naturally exist. As with many recreational-fishery species, the range of walleye has expanded through stocking and transplanting to enhance opportunities, particularly in reservoirs (Scott and Crossman 1973; Colby et al. 1979). For most fisheries-management agencies, walleye used for propagation are collected during a brief period (i.e., peak spawning activity) and from relatively few water bodies (often a single water body), not only to maximize efficiency of collection, but also to minimize time, effort, and money spent doing so. By limiting the collection window, fisheries managers unintentionally select for walleye that spawn during the same 2- or 3-day period, which is a highly heritable trait (Noordwijk et al 1981; Cooke and Findlay 1982; Gustafsson 1986; Danzmann et al. 1994; Fishback et al. 2000; Leder et al 2006), suggesting the similarity in spawning phenology we observed between reservoirs is possibly the result of artificial selection. This production-oriented stocking strategy could also impose different selection processes for stocked fish that spawn in these reservoirs compared to fish that are naturally produced in these reservoirs. Breeding time is known to be locally adapted for fishes (Otterå et al 2006; Quinn et al. 2000), therefore the continual introduction of individuals from different environments may preclude the ability of walleye in these systems to adapt and effectively modify their breeding time (and other life-history traits) to suit the ecological conditions in a given environment (*sensu* Hansen et al. 2009).

It is also possible that our failure to demonstrate a trade-off is a function of the "artificial" reservoir systems that we sampled in. Given that walleye did not evolve in reservoir ecosystems, it is possible that life-history traits may respond differently in reservoirs as compared to other waters that walleye naturally evolved and reproduce in. Additionally, our sample size of ripe fish was fairly small, which could explain why we did not find differences in egg size or fecundity among reservoirs; increasing the number of fish sampled likely would have provided more information. Also, we only sampled during a single year; additional years of sampling likely would have provided more information by increasing environmental variance.

Although the relative importance of natural reproduction by walleye in these and other irrigation reservoirs is unknown, the patterns we observed are nonetheless interesting. Compared to walleye at Swanson Reservoir, walleye at Medicine Creek Reservoir appear to exhibit reproductive traits more typical of a short-lived life-history strategy, which may be resultant from the interaction of several factors, including environmental and anthropogenic pressures. These factors could affect their population dynamics (Hansen et al. 1998); walleye in Medicine Creek could perceive this harsh environment as a survival constraint, and thus, accordingly modify their somatic and reproductive allocation (McBride et al. 2013). As agricultural needs, and thus demands on irrigation reservoirs, continue to increase, it is imperative to understand the degree to which fish and other organisms can respond to increasingly altered environmental conditions.

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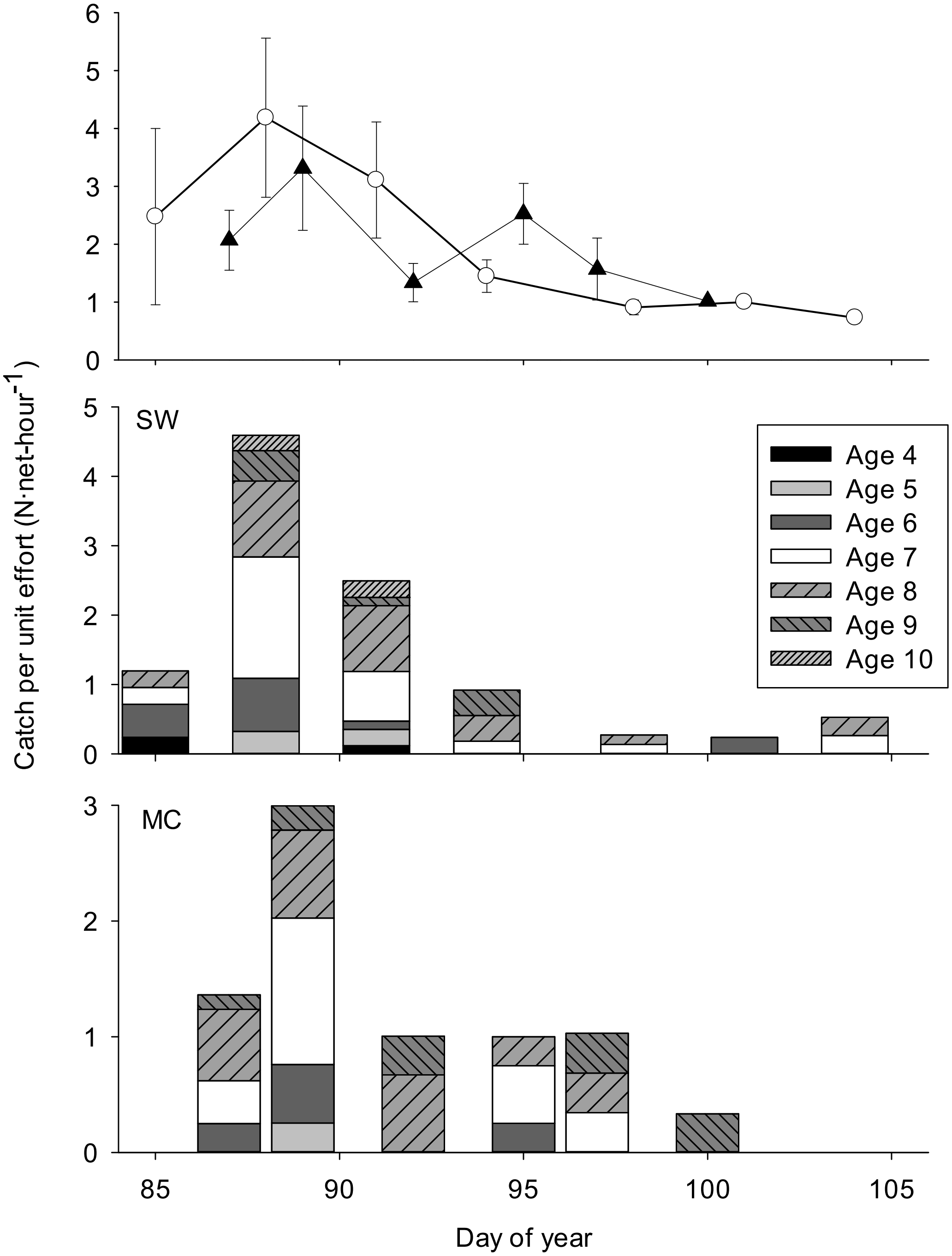

Figure 3.1. Mean ± SE catch per unit effort of female walleye during spring 2012 at Swanson Reservoir (○) and Medicine Creek Reservoir (▲), Nebraska (top panel). Composition of catch per unit effort by age for female walleye collected at Swanson (SW) and Medicine Creek (MC) during spring 2012 (bottom panels). Day 85 was March 25, day 105 was April 14.

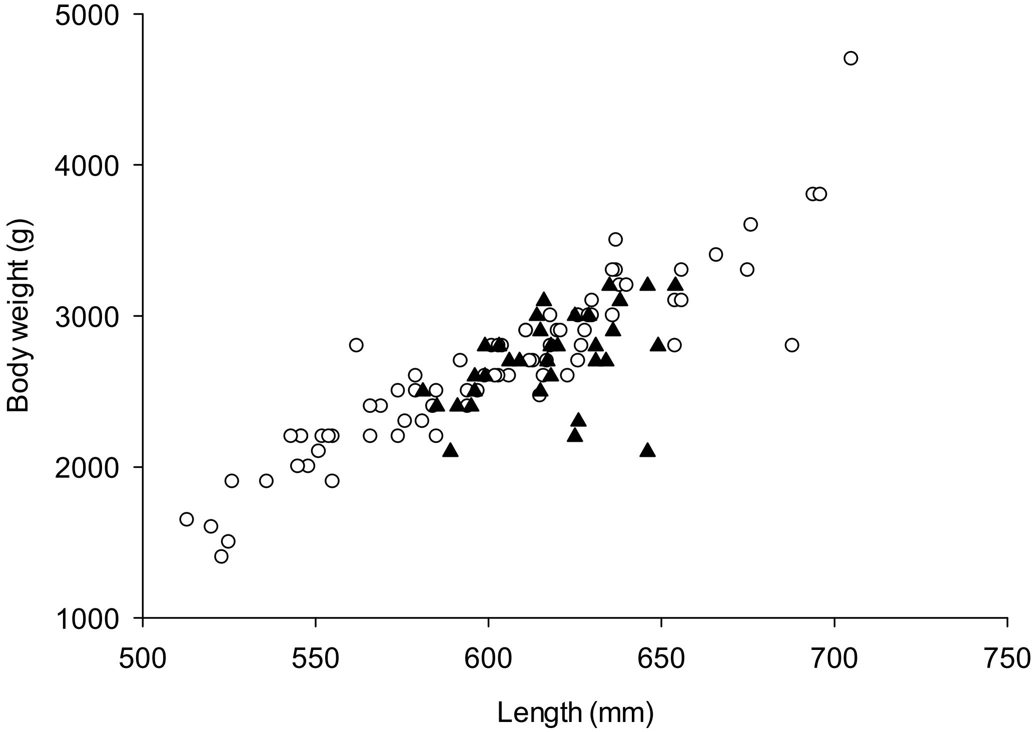

Figure 3.2. Body weight as a function of length for female walleye collected during spring 2012 from Swanson Reservoir (○) and Medicine Creek Reservoir (▲), Nebraska.

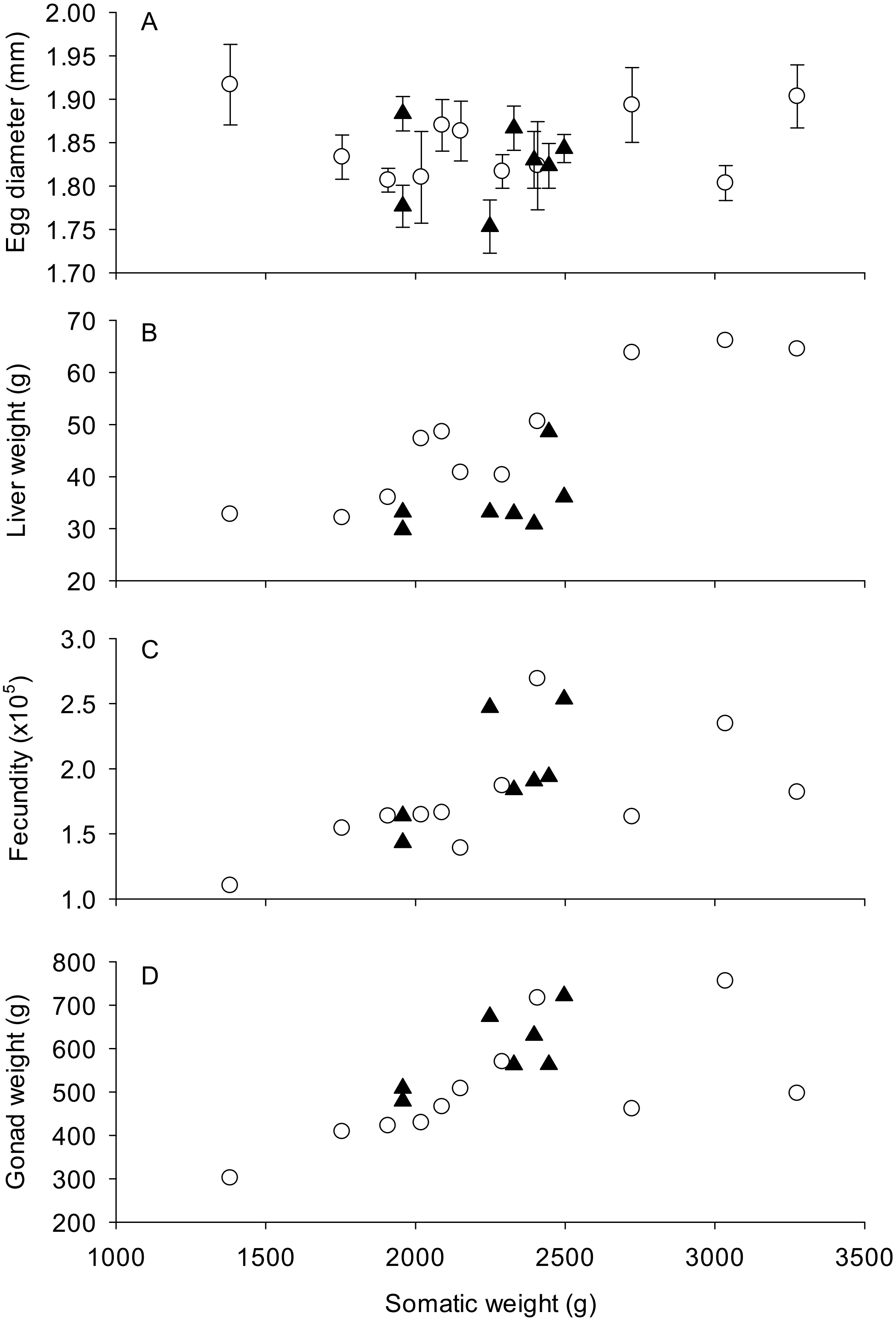

Figure 3.3. Mean ± SE egg diameter (A), liver weight (B), fecundity (C), and gonad weight (D) as a function of somatic weight for female walleye collected during spring 2012 from Swanson Reservoir (○) and Medicine Creek Reservoir (▲), Nebraska.

# Chapter 4: CONCLUSIONS AND RECOMMENDATIONS

Walleye *Sander vitreus* and white bass *Morone chrysops* are among the most popular sportfish in the reservoirs of the Great Plains (Stone 1996; Bauer 2002; Hurley and Duppong-Hurley 2005). Despite considerable effort by the Nebraska Game and Parks Commission (NGPC) stocking walleye and managing reservoirs for walleye and white bass, populations of walleye and white bass in southwest Nebraska reservoirs are dynamic, as erratic recruitment has led to "boom-and-bust" fisheries for these two species. Thus, a better understanding of the factors affecting year-class strength and subsequent recruitment of walleye and white bass in irrigation reservoirs is important for fishery managers.

## General observations

### Long-term modeling

Understanding the environmental factors that regulate fish recruitment is essential for effective management of fisheries. The candidate model set for walleye included only abiotic variables (water-level elevation, minimum daily air temperature during winter prior to hatching, annual precipitation, spring warming rate and May reservoir discharge), and the candidate model set for white bass included primarily biotic variables (catch per unit effort (CPUE) of black crappie *Pomoxis nigromaculatus*, CPUE of age-0 walleye, CPUE of bluegill *Lepomis macrochirus*, CPUE of age-3 and older white bass, and minimum daily air temperature during winter after hatching). Our study provided essential information regarding factors regulating recruitment of walleye and white bass in irrigation-reservoir ecosystems, and indicated that variability in the fish's environment within and among years may be influential in determining the nature of those factors.

Many of the variables in the candidate models sets are difficult to regulate or control (e.g., air temperature and precipitation). Even though reservoir water-level fluctuation may not be directly controllable by NGPC, management can be tailored around it. For example, I believe larval walleye may not be suitable for stocking in irrigation reservoirs that still operate as such (i.e., those with high annual water-level fluctuation like Medicine Creek Reservoir); two of my study reservoirs (i.e., Enders and Swanson reservoirs) do not discharge water regularly (or did not during the study period), and thus may have functioned more like flood-control reservoirs, with abundant littoral macrophytes and more-stable abiotic conditions, which appear to benefit walleye recruitment. I also recommend operating and promoting these five reservoirs as a regional fishery, similar to what is done with the Salt Valley reservoirs around Lincoln, NE. With the regional-fishery concept in mind, I believe it is important to explore the development and promotion of a pelagic piscivore community, featuring striped bass, hybrid striped bass, blue catfish, or some combination thereof, in reservoirs with high annual water-level fluctuation (and thus abundant gizzard shad populations).

### Walleye spawning ecology

I compared several aspects of walleye spawning ecology at two reservoirs that differ in environmental variability (i.e., annual water-level fluctuation) to identify the capacity of phenotypic expression and the corresponding association with age. Despite significant differences in female body and liver masses between reservoirs that differ in environmental variability, I found no difference in reproductive investment measured by egg size and fecundity. Although the relative importance of natural reproduction by walleye in these and other irrigation reservoirs is unknown, the patterns I observed are nonetheless interesting. Walleye at Medicine Creek Reservoir appear to exhibit reproductive characteristics more typical of a short-lived life-history strategy, which may be resultant from the interaction of environmental and anthropogenic pressures. These factors could affect their population dynamics (Hansen et al. 1998); walleye in Medicine Creek Reservoir could perceive this harsh environment as a survival constraint, and thus, accordingly modify their somatic and reproductive allocation (McBride et al. 2013). As agricultural needs, and thus demands on irrigation reservoirs, continue to increase, it is imperative to understand the degree to which fish and other organisms can respond to increasingly altered environmental conditions.

Understanding the contribution of stocked and naturally produced walleye will improve our understanding of walleye recruitment and, thus, management in these reservoirs. First, I believe it is critical for NGPC to determine what proportion of the walleye populations in the state’s major walleye reservoirs (e.g., Sherman, McConaughy, Calamus, Swanson, and Harlan County) are comprised of naturally produced walleye. Although research from Harlan County Lake indicates that naturally produced fish may contribute little to year-class formation in irrigation reservoirs (Uphoff 2012), walleye occasionally produce moderate to strong year classes in years they are not stocked (see

Figure 4.1). Also, the Harlan County Lake study was a single-year effort at a single water body, and there is likely extreme variability in stocking success (and also in natural spawning success) when multiple years and multiple reservoirs are considered. Second, if naturally produced walleye do comprise a substantial proportion of the population in the state's reservoirs, I believe it is important to understand how water-level fluctuation (and consequent water-quality conditions) affects not only adult fish physiology but also fish recruitment in those reservoirs, as my research indicates that water-level fluctuation is an important factor regulating fish recruitment in these reservoirs, and naturally produced fish may be better adapted to the specific ecological conditions in a given system.

## Tangential observations

### Walleye stocking

Despite intensive effort maintaining a stocking program for walleye in these reservoirs, year-class strength of walleye is sporadic. It is possible that the annual stocking of walleye was a confounding factor in my research; walleye were stocked in all years at all reservoirs I studied. I believe it is possible that annual stocking of large numbers of walleye fry may actually be contributing to the erratic recruitment, because of the possibility for density-dependent constraints in years (or reservoirs) when prey availability is limiting. Additionally, there appears to be little consideration regarding the effect of stocking walleye on white bass year-class strength in these reservoirs. I performed a cursory analysis of the efficacy of stocking walleye, and also its effect on white bass recruitment, from 1993-2011 by separately plotting the number of age-1 walleye and white bass captured in fall gillnets the year after stocking, using stocking as 2- and 3-level categorical variables (“yes-no” and “fingerling-fry-no”). Although the data were skewed and there was considerable overlap in the distributions, there was some indication that stocking walleye (rather than not stocking walleye) does result in stronger walleye year classes (Figure 4.1), yet there is clear evidence of recruitment failure in years walleye were stocked. Furthermore, any distinction of a benefit to year-class strength when comparing stocking fingerlings versus stocking fry is even less clear (Figure 4.2). Although there appears to be no difference in white bass year-class strength when I plot stocking as “yes-no” (Figure 4.3), when I plot it as “fingerling-fry-no”, it appears that stocking fingerling walleye may result in weaker white bass year classes (Figure 4.4), perhaps because of competition for food resources, or even predation on age-0 white bass. I believe that a more-detailed statistical analysis of these data needs to be performed to better understand the effects of stocking walleye in these reservoirs, both on walleye and white bass populations.

I believe that stocking walleye the year after a strong year class of walleye is produced may be an ineffective strategy. Given that age-1 walleye still feed primarily on age-0 gizzard shad, a strong year class of age-1 walleye may out-compete the next year class, thus making stocking during the second year less effective, or even ineffective. Incidentally, a strong year class of walleye may be able to support a fishery for multiple years (R. Kill, unpublished data), which would make stocking the year after strong year-class formation unnecessary, both ecologically and financially. I believe it is possible to initially address this question of consecutive strong year classes mathematically, by assessing the incidence of consecutive strong year classes of walleye (and white bass) from data currently available. However, given the difficulty indexing year-class strength of walleye and white bass using age-0 fish (see Chapter 3), I also recommend additional research into developing a reliable method to accurately index year-class strength for walleye and white bass in irrigation reservoirs.

I also believe that stocking walleye fry into reservoirs with increased potential for food competition (e.g., with hyper-abundant gizzard shad (Michaletz et al. 1987; Quist et al. 2004) at Medicine Creek Reservoir) may be an ineffective strategy. However, stocking walleye fingerlings that can feed on hyper-abundant gizzard shad larvae may be a more successful alternative, despite increased hatchery costs. Likewise, stocking walleye fingerlings (rather than fry) might result in greater zooplankton abundance for larval white bass (and other larval fishes), which might improve recruitment of white bass at Medicine Creek. It might also be possible to remove a substantial amount of adult gizzard shad (via piscivorous predator introduction) to reduce predation on zooplankton.

### Potential for egg predation

While sampling for spawning walleye during spring 2012, I observed a prevalent co-occurrence of walleye, river carpsucker *Carpiodes carpio*, and common carp *Cyprinus carpio*. During peak walleye spawning activity, mean daily catch per unit effort (CPUE) of walleye was significantly correlated with combined mean daily CPUE of river carpsucker and common carp ($r = 0.64$, $p = 0.04$; Figure 4.5). I suspect river carpsucker and common carp were preying on walleye eggs, although I did not perform diet analyses of carpsucker or carp. River carpsucker are benthic detritivores with a broad diet, including algae, macroinvertebrates, and zooplankton (Becker 1983; Sublette et al. 1990). In Lake of the Ozarks, river carpsucker are benthic browsers that feed on periphyton associated with submerged rock substrate (Brezner 1958). Although I found no records of river carpsucker feeding on fish eggs, similar species of catostomids are known egg predators (Spiegel et al. 2011). Common carp have a broad diet that includes macroinvertebrates, plant material, and fish (Becker 1983), and are known to prey on fish eggs (Moyle 1976; Taylor et al. 1984; Miller and Beckman 1996; Marsden 1997; García-Berthou 2001). Thus, given that walleye in my study reservoirs are spawning over large rock substrate, and that river carpsucker and common carp appear to be non-selective benthic foragers, I suspect carpsucker and carp were either intentionally or incidentally preying on walleye eggs.

Egg predation is known to negatively affect the recruitment of several species, including lake trout *Salvelinus namaycush* (Fitzsimmons et al. 2002), atlantic salmon *Salmo salar* (Palm et al. 2009), and Baltic cod *Gadus morhua callarias* (Köster and Möllmann 2000). Egg predation is suspected to negatively affect the recruitment of walleye (Schaeffer and Margraf 1987; Roseman et al. 2006), white bass (Schaeffer and Margraf 1987), and sunfishes *Lepomis* spp. (Dorn and Mittelbach 2004). Egg predators can severely decrease the number of potential recruits at an early stage, and thus can negatively and substantially affect fish recruitment. Although research from Harlan County Lake indicates that naturally produced fish may contribute little to year-class formation in irrigation reservoirs (Uphoff 2012), walleye occasionally produce moderate to strong year classes in years they are not stocked (see Figure 4.1). Thus, I believe it is important to evaluate the potential for egg predation if the recruitment of walleye in irrigation reservoirs is to be better understood.

### Standardized sampling recommendations

The following statements were not part of any objective of my study; however, I believe they are important nonetheless. Current NGPC protocols call for an 80% confidence interval on abundance estimates, and also derive fish age estimates using scales. First, an 80% confidence interval generally results in 4-5 gillnet-nights of sampling per reservoir per year for walleye and white bass, which typically produces less than 100 fish (often much less) per sample. I believe this effort and resultant catch are insufficient to accurately quantify abundance and calculate population dynamics for these recreationally important species. Second, I believe scales are an inaccurate and imprecise way to estimate age, particularly for relatively long-lived fishes like walleye and white bass. Dorsal spines are a non-lethally removed structure that are gaining popularity, particularly for aging walleye, although I believe otoliths to be superior to both scales and spines. Otoliths are a validated structure for walleye aging (Erickson 1983; Michaletz 1986), and are also the most time-efficient and precise structure for walleye aging (Isermann et al. 2003). I understand that otoliths are a lethal structure to obtain, but given that many fish are often already dead when gillnets are retrieved, and given the importance of accurately estimating age for making properly informed management decisions, I believe the sacrifice of relatively few fish is inconsequential, particularly when weighed against the cost of inaccurate data from using scales to age fish.

### Detection probability

Accurately determining the abundance and distribution of age-0 sportfish is important for successful fisheries management for various reasons, including characterizing nursery habitats for protection or enhancement, properly identifying reproductive dynamics, and understanding the influences of environmental variables (Brewer and Ellersieck 2011). One of the pervasive shortcomings of fisheries management, particularly in lentic systems, is that we often ignore the effect of detection (or capture) probability on samples used to index relative abundance and on subsequent management recommendations. What little fisheries research has been published on detection probability often focuses on the use of sonar to sample fish (e.g., Mulligan and Kieser 1996; Mulligan 2000), on community-scale metrics such as species richness (Bayley and Peterson 2001; McManamay et al. 2013), or on small lotic systems (Brewer and Ellersieck 2011; Peoples and Frimpong 2011). Nonetheless, comparison of relative abundance of fish throughout space or time is of primary importance in fisheries management. Although relative abundance estimation is dependent on detection probability (MacKenzie and Kendall 2002), most state agencies that index relative abundance of important sportfish as a management technique do not acknowledge detection probability as important. By understanding detection probability, it is possible to estimate true abundance, rather than merely indexing relative abundance (Dauwalter and Fisher 2007).

I believe one of the primary reasons that detection probability is often minimized as a component of lentic fisheries management is that fish are inherently elusive animals to sample, particularly in large, complex water bodies. Compounding that difficulty, detection probability is a function of probability of individual capture, which varies widely with sampling method, fish size, physical habitat, and number of individuals present in a given area (Bayley and Peterson 2001). Particularly for age-0 fish like walleye (Quist et al. 2003; Roseman et al. 2005) and age-0 white bass (Cole and MacMillan 1984; Weaver et al. 1997), which are often patchily distributed, the number of individuals present in a given area can vary dramatically.

I believe it is important to begin addressing this shortcoming as it pertains to both graduate-level research and NGPC sampling in the state of Nebraska. I believe evaluation of multiple sampling-gear types (*sensu* Haynes et al. 2013) would be beneficial, not only for those gears used for sampling small-bodied fishes, such as species of concern and age-0 sportfish, but also for larger-bodied sportfish assessed with routine standardized sampling gears. I believe that a 2- or 4-year graduate research project could address many of these shortcomings by experimentally determining capture efficiency for several species with several gears in multiple water body types, similar to the approaches used by Bayley and Austin (2002), Schoenebeck and Hansen (2005), and Buckmeier and Schlechte (2009). Alternatively, a more-thorough literature search could provide reference values in lieu of actual research; however, given the biases associated with detection probability (Bayley and Peterson 2001), I believe this approach would be inferior.

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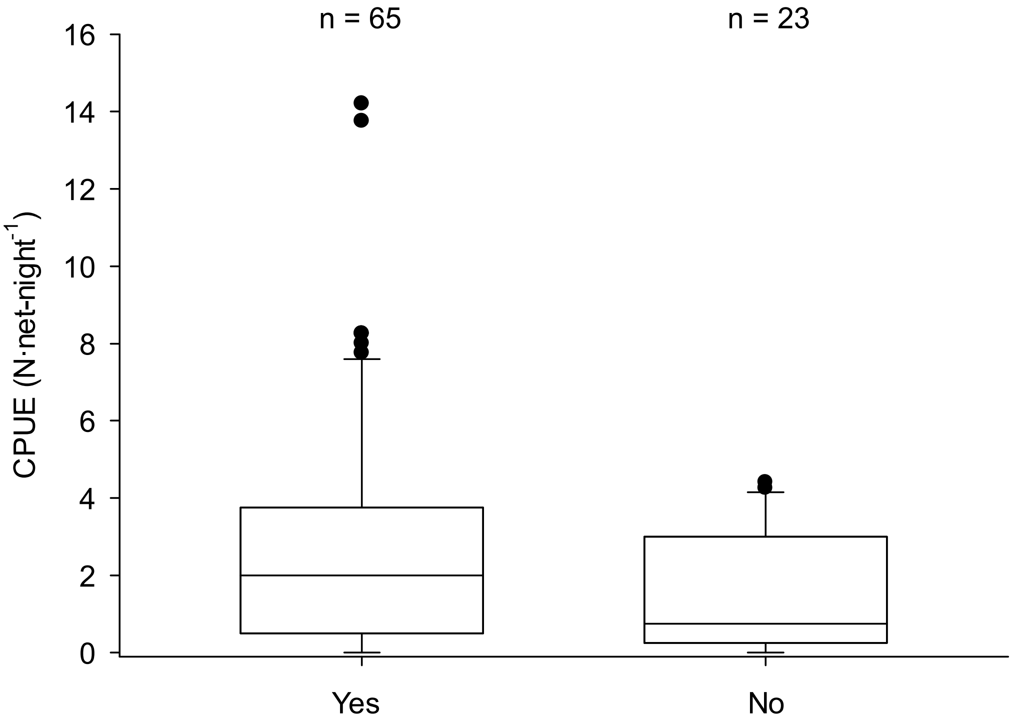

Figure 4.1. Catch per unit effort (CPUE, number per net-night) of age-1 walleye as a function of walleye stocking (yes versus no) during the previous year. Whiskers indicate 5th and 95th percentiles, box lines indicate 25th, 50th, and 75th percentiles, and ● indicates outliers. Data were from Enders, Swanson, Red Willow, Medicine Creek, and Harlan County reservoirs in the Republican River basin, NE from 1994-2012.

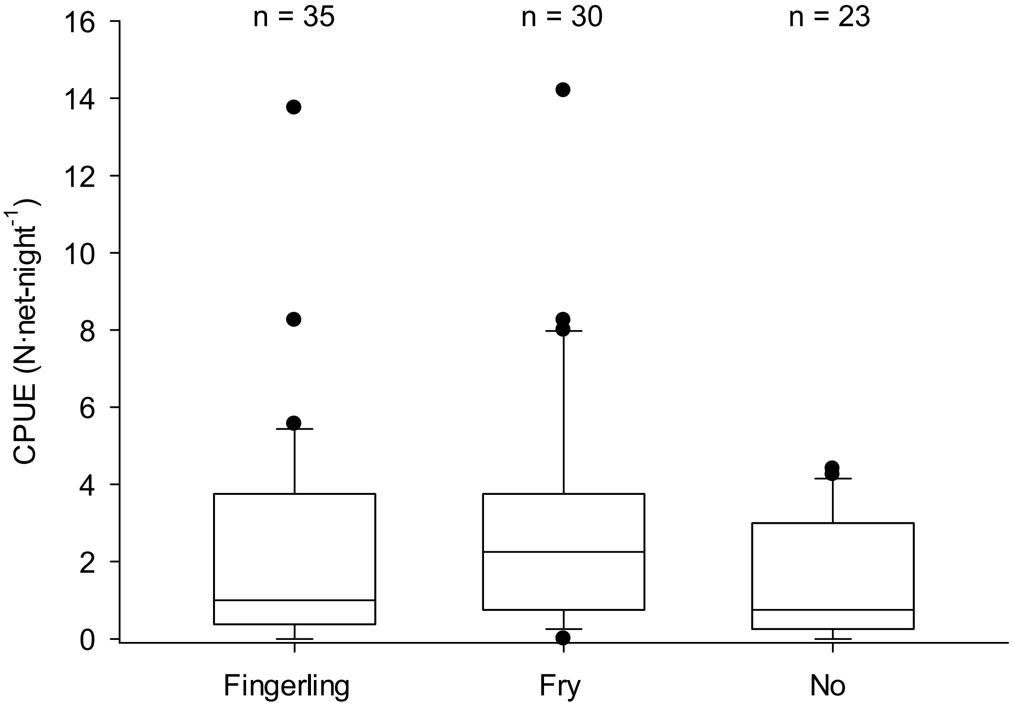

Figure 4.2. Catch per unit effort (CPUE, number per net-night) of age-1 walleye as a function of walleye stocking (fingerling versus fry versus no) during the previous year. Whiskers indicate 5th and 95th percentiles, box lines indicate 25th, 50th, and 75th percentiles, and ● indicates outliers. Data were from Enders, Swanson, Red Willow, Medicine Creek, and Harlan County reservoirs in the Republican River basin, NE from 1994-2012.

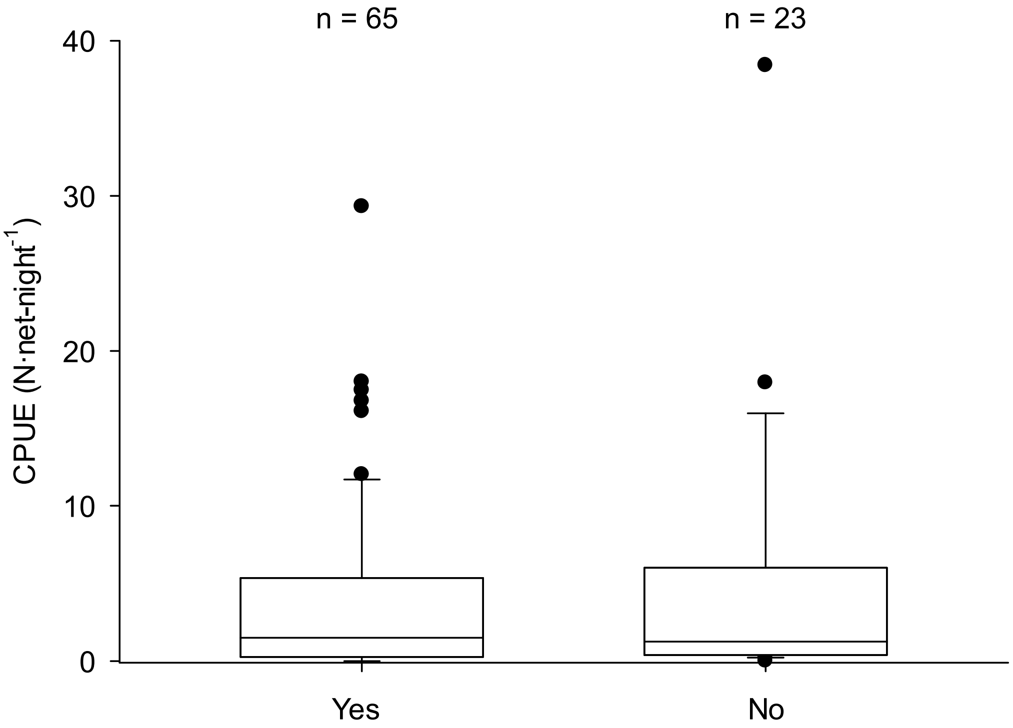

Figure 4.3. Catch per unit effort (CPUE, number per net-night) of age-1 white bass as a function of walleye stocking (yes versus no) during the previous year. Whiskers indicate 5th and 95th percentiles, box lines indicate 25th, 50th, and 75th percentiles, and ● indicates outliers. Data were from Enders, Swanson, Red Willow, Medicine Creek, and Harlan County reservoirs in the Republican River basin, NE from 1994-2012.

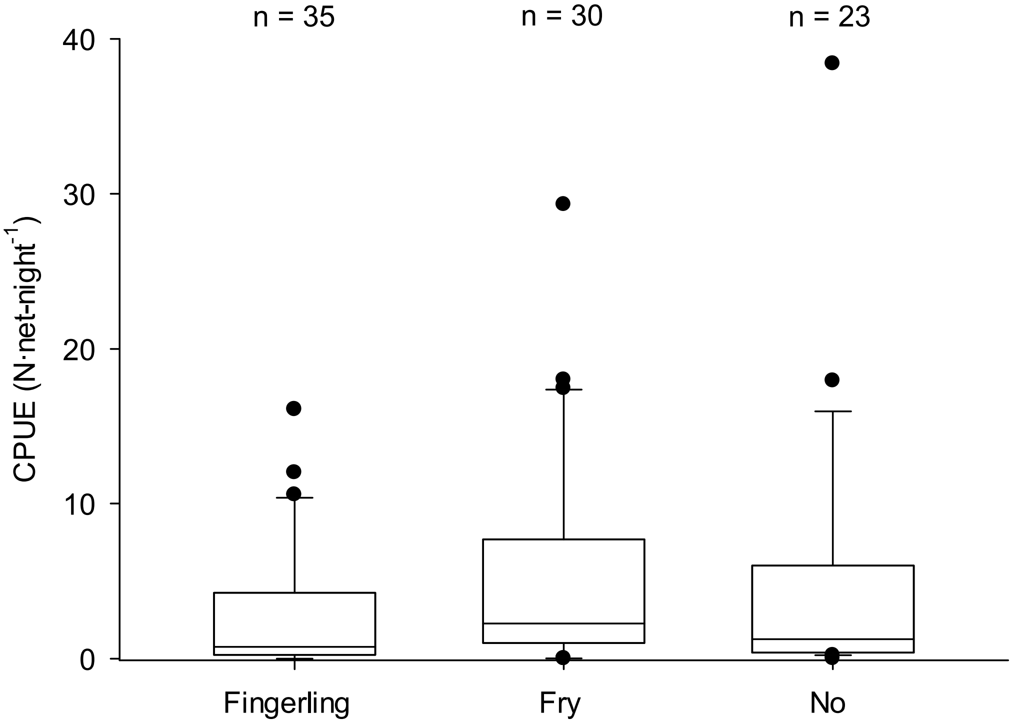

Figure 4.4. Catch per unit effort (CPUE, number per net-night) of age-1 white bass as a function of walleye stocking (fingerling versus fry versus no) during the previous year. Whiskers indicate 5th and 95th percentiles, box lines indicate 25th, 50th, and 75th percentiles, and ● indicates outliers. Data were from Enders, Swanson, Red Willow, Medicine Creek, and Harlan County reservoirs in the Republican River basin, NE from 1994-2012.

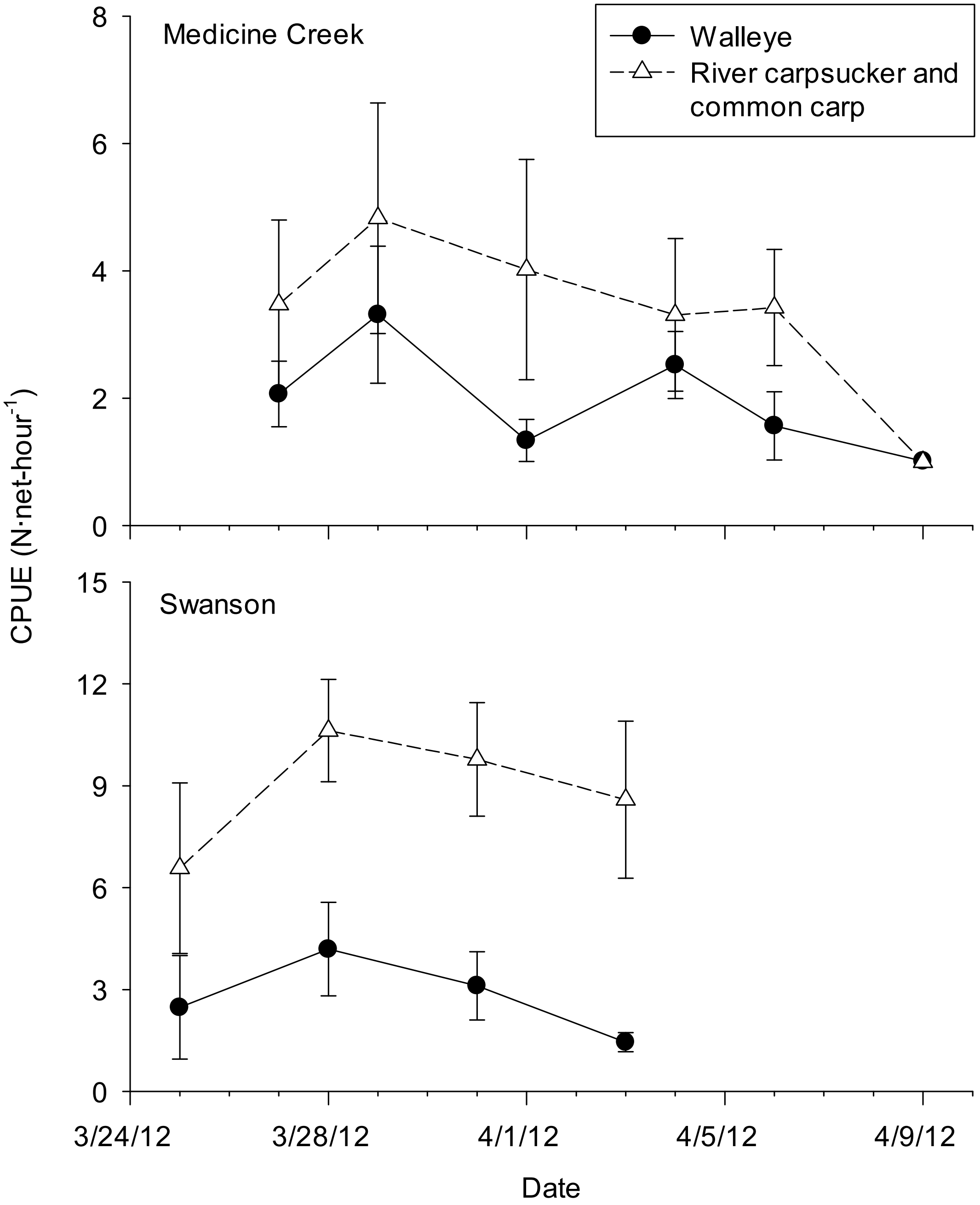

Figure 4.5. Catch per unit effort (CPUE, catch per net hour, mean ± SE) of walleye and combined CPUE of river carpsucker and common carp by date during peak walleye spawning activity (i.e., CPUE ≥ 10% of maximum walleye CPUE by reservoir). Data were from the Republican River basin, NE during spring 2012.

# APPENDIX A: BIOLOGICAL DATA FROM FEMALE WALLEYE

Table A.1. Biological data from female walleye collected from Medicine Creek (MC) and Swanson (SW) reservoirs during spring 2012. Spawning condition indexed as green (G), ripe (R), and spent (S). Egg sizes from subsamples processed in the laboratory. An asterisk in the age column denotes the fish was a recapture and already had its dorsal spine removed for aging.

| Reservoir | Sample date | Sex (M, F) | Spawning Condition (G, R, S) | Age | Length (mm) | Field weight (g) | Laboratory weight (g) | Liver weight (g) | Left ovary weight (g) | Right ovary weight (g) | Estimated fecundity | Egg sample weight (g) | Minimum egg size (mm) | Maximum egg size (mm) | Mean (± SE) egg size (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MC | 3/27/2012 | F | G | 7 | 581 | 2500 | | | | | | | | | |
| MC | 3/27/2012 | F | G | 6 | 589 | 2100 | | | | | | | | | |
| MC | 3/27/2012 | F | G | 7 | 609 | 2700 | | | | | | | | | |
| MC | 3/27/2012 | F | G | 7 | 620 | 2800 | | | | | | | | | |
| MC | 3/27/2012 | F | G | 8 | 629 | 3000 | | | | | | | | | |
| MC | 3/27/2012 | F | G | 8 | 631 | 2800 | | | | | | | | | |
| MC | 3/27/2012 | F | G | 8 | 654 | 3200 | | | | | | | | | |
| MC | 3/27/2012 | F | R | 9 | 625 | 2200 | 2466.0 | 29.8 | 220.0 | 259.1 | 163821 | 21.7 | 1.6 | 2.4 | 1.8 ± 0.02 |
| MC | 3/27/2012 | F | R | 8 | 625 | 3000 | 2955.5 | 33.2 | 314.3 | 359.6 | 247097 | 10.5 | 1.6 | 2.7 | 1.8 ± 0.03 |
| MC | 3/27/2012 | F | R | 8 | 636 | 2900 | 2924.8 | 32.9 | 227.2 | 335.8 | 183808 | 12.5 | 1.7 | 2.4 | 1.9 ± 0.03 |
| MC | 3/27/2012 | F | R | 5 | 638 | 3100 | 3057.2 | 30.9 | 281.4 | 349.0 | 190665 | 10.2 | 1.6 | 2.6 | 1.8 ± 0.03 |
| MC | 3/29/2012 | F | G | 6 | 585 | 2400 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 7 | 591 | 2400 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 8 | 595 | 2400 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 8 | 596 | 2600 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 5 | 599 | 2800 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 7 | 606 | 2700 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 7 | 614 | 3000 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 6 | 617 | 2700 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 7 | 618 | 2600 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 7 | 631 | 2700 | | | | | | | | | |
| MC | 3/29/2012 | F | G | 9 | 635 | 3200 | | | | | | | | | |
| MC | 3/29/2012 | F | G | * | | | | | | | | | | | |
| MC | 3/29/2012 | F | R | 8 | 646 | 3200 | 3254.4 | 36.1 | 308.8 | 412.8 | 253495 | 10.8 | 1.7 | 2.0 | 1.8 ± 0.02 |
| MC | 4/1/2012 | F | G | 8 | 615 | 2900 | | | | | | | | | |
| MC | 4/1/2012 | F | G | 8 | 618 | 2800 | | | | | | | | | |
| MC | 4/1/2012 | F | G | 9 | 649 | 2800 | | | | | | | | | |
| MC | 4/1/2012 | F | G | * | | | | | | | | | | | |
| MC | 4/4/2012 | F | G | 7 | 596 | 2500 | | | | | | | | | |

Table A.1. continued.

| Reservoir | Sample date | Sex (M, F) | Spawning Condition (G, R, S) | Age | Length (mm) | Field weight (g) | Laboratory weight (g) | Liver weight (g) | Left ovary weight (g) | Right ovary weight (g) | Estimated fecundity | Egg sample weight (g) | Minimum egg size (mm) | Maximum egg size (mm) | Mean (± SE) egg size (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MC | 4/4/2012 | F | G | 6 | 599 | 2600 | | | | | | | | | |
| MC | 4/4/2012 | F | G | 8 | 646 | 2100 | | | | | | | | | |
| MC | 4/4/2012 | F | G | * | | | | | | | | | | | |
| MC | 4/4/2012 | F | R | 7 | 615 | 2500 | 2501.0 | 33.2 | 231.6 | 277.4 | 143384 | 10.6 | 1.7 | 2.0 | 1.9 ± 0.02 |
| MC | 4/6/2012 | F | G | 7 | 603 | 2800 | | | | | | | | | |
| MC | 4/6/2012 | F | G | 9 | 634 | 2700 | | | | | | | | | |
| MC | 4/6/2012 | F | R | 8 | 616 | 3100 | 3057.0 | 48.6 | 248.0 | 315.1 | 193957 | 9.9 | 1.7 | 2.4 | 1.8 ± 0.03 |
| MC | 4/9/2012 | F | S | 9 | 626 | 2300 | | | | | | | | | |
| SW | 3/25/2012 | F | G | 6 | 513 | 1646 | | | | | | | | | |
| SW | 3/25/2012 | F | G | 4 | 552 | 2200 | | | | | | | | | |
| SW | 3/25/2012 | F | G | 6 | 585 | 2500 | | | | | | | | | |
| SW | 3/25/2012 | F | G | 7 | 615 | 2468 | | | | | | | | | |
| SW | 3/25/2012 | F | G | 8 | 687 | 5686 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 523 | 1400 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 5 | 525 | 1500 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 536 | 1900 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 543 | 2200 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 545 | 2000 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 546 | 2200 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 554 | 2200 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 562 | 2800 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 566 | 2400 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 569 | 2400 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 574 | 2500 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 576 | 2300 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 579 | 2500 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 581 | 2300 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 594 | 2500 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 594 | 2400 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 599 | 2600 | | | | | | | | | |

Table A.1. continued.

| Reservoir | Sample date | Sex (M, F) | Spawning Condition (G, R, S) | Age | Length (mm) | Field weight (g) | Laboratory weight (g) | Liver weight (g) | Left ovary weight (g) | Right ovary weight (g) | Estimated fecundity | Egg sample weight (g) | Minimum egg size (mm) | Maximum egg size (mm) | Mean (± SE) egg size (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SW | 3/28/2012 | F | G | 8 | 601 | 2800 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 604 | 2800 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 5 | 611 | 2900 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 616 | 2600 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 626 | 2700 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 626 | 3000 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 628 | 2900 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 629 | 3000 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 630 | 3100 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 9 | 636 | 3000 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 636 | 3300 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 637 | 3500 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 637 | 3300 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 638 | 3200 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 654 | 3100 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 9 | 666 | 3400 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 6 | 675 | 3300 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 676 | 3600 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 8 | 688 | 2800 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 7 | 694 | 3800 | | | | | | | | | |
| SW | 3/28/2012 | F | G | 5 | 546 | 2200 | | | | | | | | | |
| SW | 3/28/2012 | F | R | 9 | 579 | 2600 | 2495.8 | 47.3 | 223.4 | 205.8 | 164512 | 9.7 | 1.5 | 2.5 | 1.8 ± 0.05 |
| SW | 3/28/2012 | F | R | 9 | 656 | 3300 | 3248.5 | 63.8 | 198.9 | 262.2 | 163047 | 11.1 | 1.7 | 2.7 | 1.9 ± 0.04 |
| SW | 3/28/2012 | F | R | 10 | 696 | 3800 | 3836.5 | 64.5 | 213.1 | 283.7 | 181935 | 10.3 | 1.7 | 3.3 | 1.9 ± 0.04 |
| SW | 3/28/2012 | F | R | 10 | 705 | 3800 | 3857.9 | 66.1 | 335.0 | 420.8 | 234514 | 10.5 | 1.7 | 2.8 | 1.8 ± 0.02 |
| SW | 3/28/2012 | M | | - | 415 | 700 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 6 | 526 | 1900 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 5 | 551 | 2100 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 5 | 555 | 1900 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 4 | 566 | 2200 | | | | | | | | | |

Table A.1. continued.

| Reservoir | Sample date | Sex (M, F) | Spawning Condition (G, R, S) | Age | Length (mm) | Field weight (g) | Laboratory weight (g) | Liver weight (g) | Left ovary weight (g) | Right ovary weight (g) | Estimated fecundity | Egg sample weight (g) | Minimum egg size (mm) | Maximum egg size (mm) | Mean (± SE) egg size (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SW | 3/31/2012 | F | G | 8 | 574 | 2200 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 7 | 592 | 2700 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 7 | 597 | 2500 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 9 | 603 | 2800 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 8 | 603 | 2600 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 7 | 606 | 2600 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 10 | 612 | 2700 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 10 | 613 | 2700 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 8 | 618 | 3000 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 7 | 618 | 2800 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 8 | 621 | 2900 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 7 | 626 | 3000 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 8 | 627 | 2800 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 8 | 630 | 3000 | | | | | | | | | |
| SW | 3/31/2012 | F | G | 8 | 640 | 3200 | | | | | | | | | |
| SW | 3/31/2012 | F | G | * | | | | | | | | | | | |
| SW | 3/31/2012 | F | G | * | | | | | | | | | | | |
| SW | 3/31/2012 | F | R | 7 | 555 | 2200 | 2195.8 | 32.1 | 175.3 | 233.3 | 154247 | 10.8 | 1.6 | 2.0 | 1.8 ± 0.03 |
| SW | 3/31/2012 | F | R | 8 | 584 | 2400 | 2366.9 | 36.0 | 180 | 242.3 | 163590 | 10.3 | 1.7 | 1.9 | 1.8 ± 0.01 |
| SW | 4/3/2012 | F | G | 7 | 548 | 2000 | | | | | | | | | |
| SW | 4/3/2012 | F | G | 8 | 585 | 2200 | | | | | | | | | |
| SW | 4/3/2012 | F | G | 9 | 611 | 2900 | | | | | | | | | |
| SW | 4/3/2012 | F | G | 9 | 654 | 2800 | | | | | | | | | |
| SW | 4/3/2012 | F | R | 8 | 617 | 2700 | 2703.0 | 40.8 | 253.9 | 315.7 | 138956 | 11.2 | 1.5 | 2.9 | 1.9 ± 0.03 |
| SW | 4/7/2012 | F | G | 8 | 602 | 2600 | | | | | | | | | |
| SW | 4/7/2012 | F | R | 7 | 620 | 2900 | 2903.0 | 40.3 | 253.9 | 315.7 | 186896 | 10.1 | 1.7 | 2.1 | 1.8 ± 0.02 |
| SW | 4/10/2012 | F | R | 6 | 520 | 1600 | 1716.3 | 32.8 | 147.5 | 154.5 | 110230 | 11.2 | 1.7 | 2.5 | 1.9 ± 0.05 |
| SW | 4/13/2012 | F | R | 7 | 623 | 2600 | 2603.5 | 48.6 | 217.5 | 248.4 | 166271 | 10.9 | 1.7 | 2.5 | 1.9 ± 0.03 |
| SW | 4/13/2012 | F | R | 8 | 656 | 3100 | 3175.3 | 50.6 | 340.2 | 376.4 | 269009 | 12.6 | 1.5 | 2.5 | 1.8 ± 0.05 |