Masked Expression of Life-History Traits in a Highly Variable Environment

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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 often inherent in phenotypic and evolved responses to anthropogenic change. Alternatively, if there are environmental cues that predict reproductive potential, differential expression of life-history strategies may represent differences in the adaptive capacity to optimize current reproductive value given variation in environmental conditions. 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. 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 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.

Key Words: environmental variability, irrigation reservoir, life-history expression, *Sander vitreus*, walleye

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 fre-

quency 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; Kieffer and Colgan 1992; Laland et al. 2003 and references therein; Brown et al. 2011). 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 ben-

efits of current reproductive investment (Forbes 1991; Bårdsen et al. 2008). In fishes, learning plays an important role in the development of numerous skills and behaviors (Kieffer and Colgan 1992; Laland et al. 2003 and references therein), including foraging (Warburton 2003), antipredator behavior (Kelley and Magurran 2003; Kelley and Magurran 2006), and reproductive behavior (Witte and Nöbel 2011).

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 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, that 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 increasing with age—older walleye should modify their reproductive output more than younger walleye, given the same environmental conditions (*sensu* Bunce et al. 2005; Baran and Adkins-Regan 2014).

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 timing and (2) female condition, size, and reproductive investment in environments that differ in the degree of annual variation in water level. We knew larger—and ostensibly 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 fish 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, and thus walleye in southwest Nebraska likely are at the upper thermal limit at which they can thrive (Colby et al. 1979).

We obtained reservoir water-level data for 2003–2012 from the US 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-
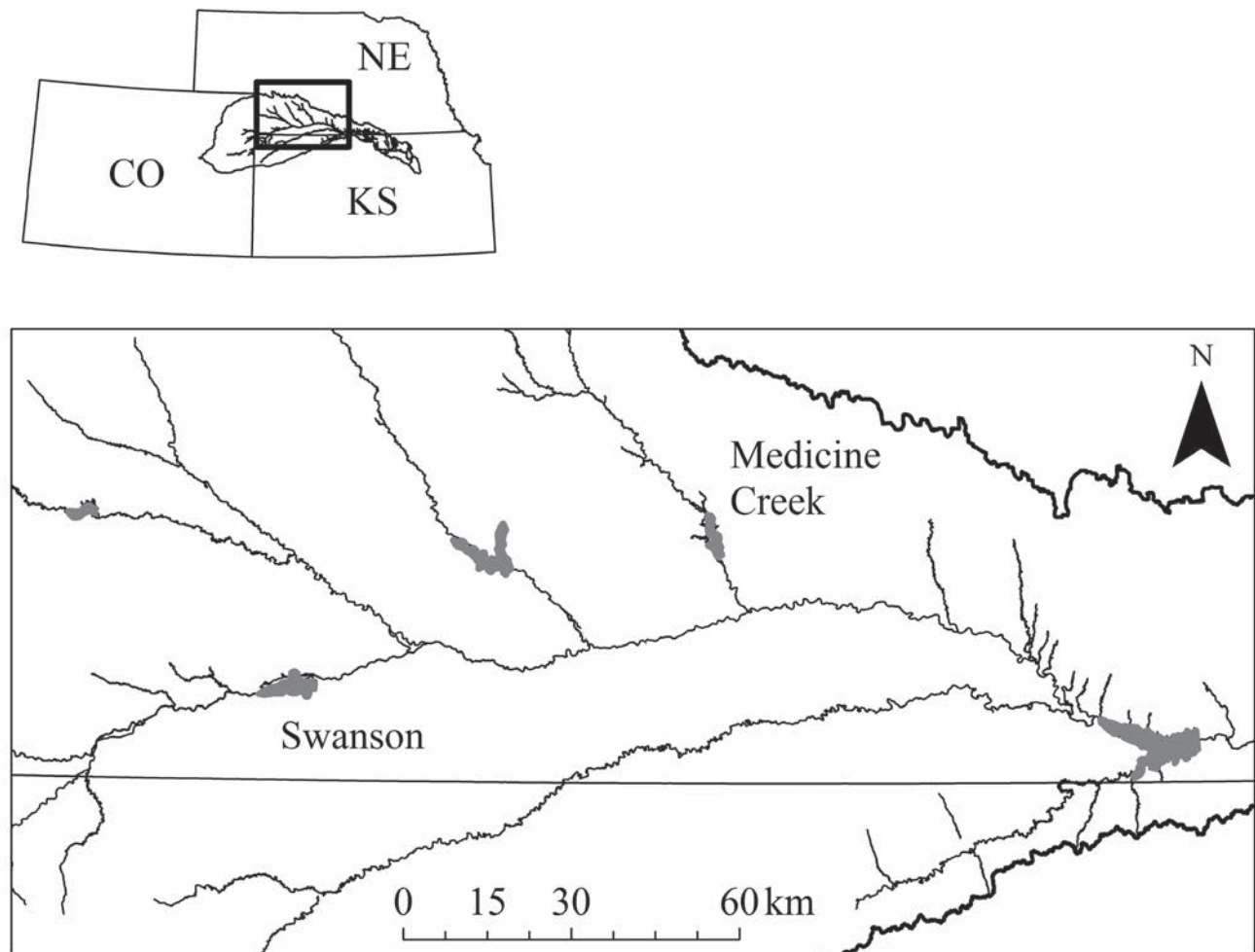
Figure 1. Map of the Republican River basin in Colorado, Kansas, and Nebraska, and the two irrigation reservoirs we studied in Nebraska.

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%; Fig. 1). The majority of the water-level variability at these reservoirs occurs during June–September (irrigation season) of each year, though the specific timing, duration, and intensity of the irrigation drawdown is predicated on precipitation patterns and the nuances of agricultural demands. 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. Although the source population of stocked walleye has changed throughout the history of these reservoirs, Medicine Creek and Swanson Reservoirs have nearly always received stocked fish from the same source population in a given year (Nebraska Game and Parks Commission, unpublished data). We collected walleye on alternate nights from March 25

to April 13, 2012, but because of weather conditions, the actual number of sampling nights at each reservoir differed. We set two to three 100 m by 1.8 m monofilament gillnets with 7.6 cm bar mesh 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 nets after approximately a one-hour deployment. We measured water temperature at a depth of 1 m at the start of every net deployment. Upon capture, we released males and measured each female for total length (mm) and weight (g), and removed her second dorsal spine for aging (DeVries and Frie 1996). We later prepared and aged each dorsal spine in the laboratory following standard protocol (Logsdon 2007). Individual females usually spawn in one night (Ellis and Giles 1965); therefore, we assumed all female walleye captured to be in breeding condition. We euthanized all ripe females (i.e., those with distended abdomens that exuded eggs when gentle pressure was ap-
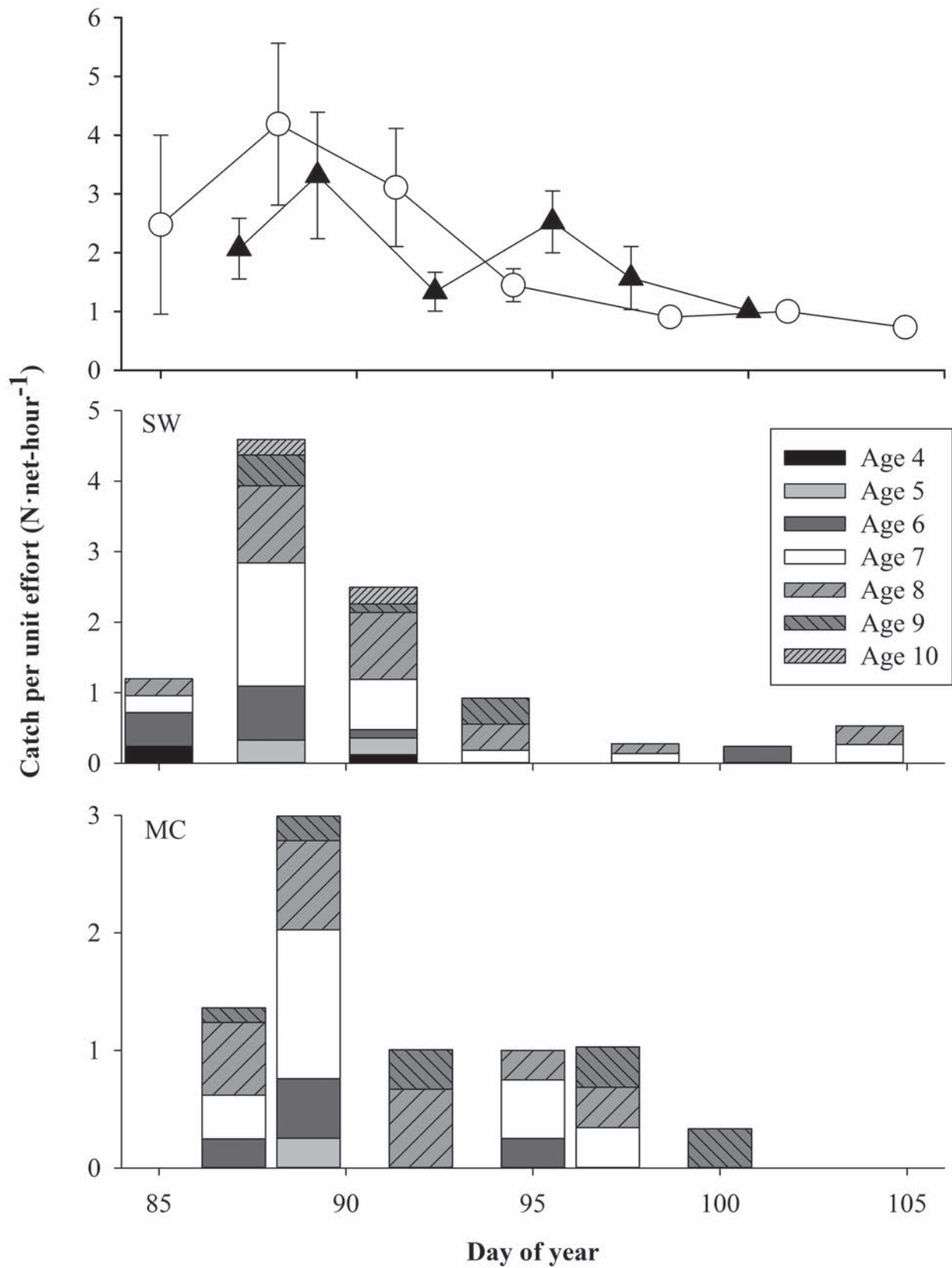
Figure 2. Mean ± SE catch per unit effort of female walleye during spring 2012 at Swanson Reservoir (○) and Medicine Creek Reservoir (▲), Nebraska (top panel). Composition of catch per unit effort by age for female walleye collected at Swanson (SW) and Medicine Creek (MC) during spring 2012 (bottom panels). Day 85 was March 25; day 105 was April 14.
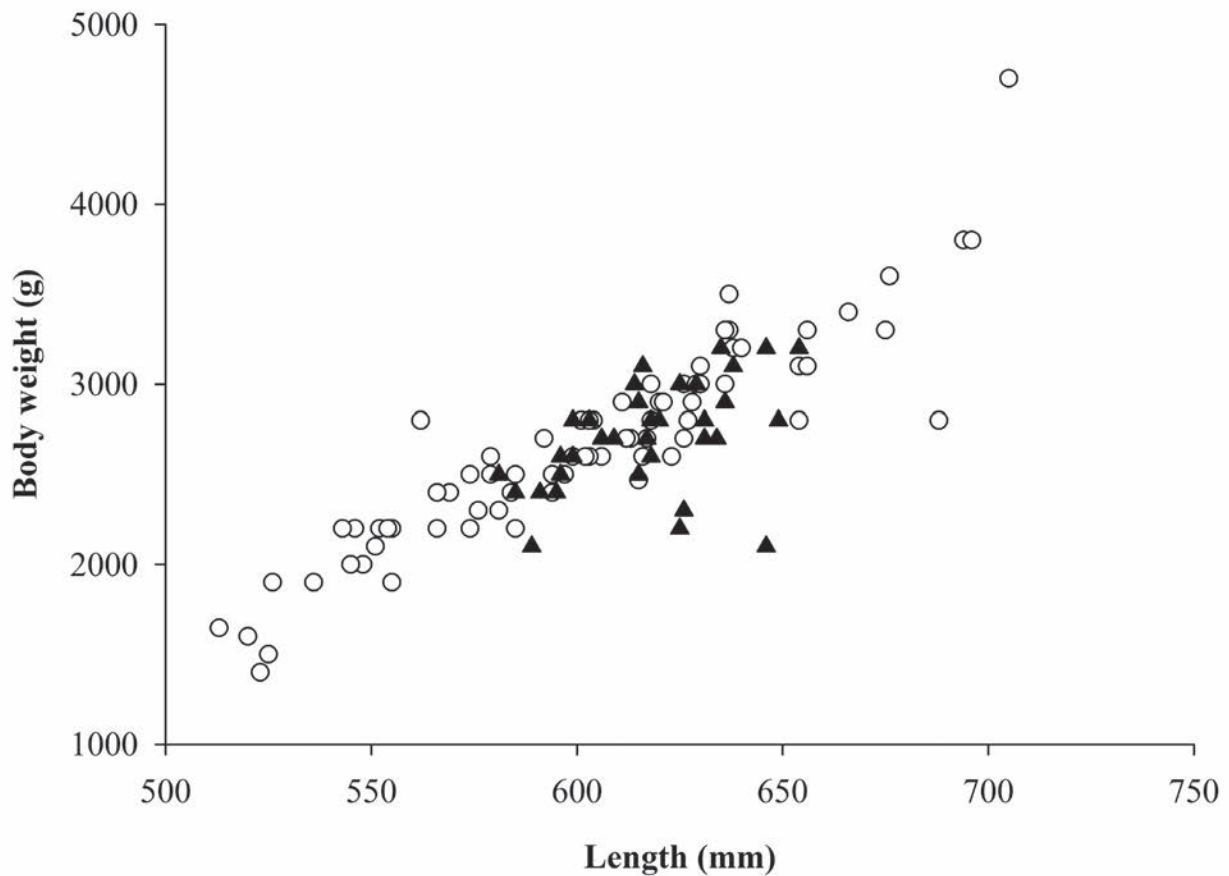
Figure 3. Body weight as a function of length for female walleye collected during spring 2012 from Swanson Reservoir (○) and Medicine Creek Reservoir (▲), Nebraska.

plied) and extracted and weighed the ovaries and the liver individually (0.1 g). Walleye exhibit group synchronous ovarian development (Malison and Held 1996); therefore, we collected a ~5 mL sample of eggs from the posterior third of the right ovary from each euthanized fish to ensure eggs of the same developmental stage were sampled. We preserved the egg samples with 10% buffered formalin phosphate. We later measured egg diameter (0.01 mm) of the first 25 eggs encountered from each sample in the laboratory using an ocular micrometer on a dissecting microscope; we counted the remaining eggs in each sample. We performed this study under the auspices of UNL Institutional Animal Care and Use Committee (protocol #778).

Data Analyses

We excluded from analysis females that had already released their eggs (only one such fish was captured).

We estimated female age structure 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 differences existed between reservoirs, we modeled (using Analysis of Covariance, or ANCOVA) several dependent variables as a function of a continuous independent variable (i.e., day of year, length, somatic weight) and reservoir, which was a fixed, categorical, dependent variable in all models. We modeled catch per unit effort as a function of day of year (fixed) and reservoir. To determine if any relationship existed between age and spawning phenology (i.e., timing and duration) within a season and between reservoirs, we modeled female age as a function of day of year (fixed) and reservoir. We compared body condition between reservoirs by (1) modeling body weight as a function of length (random) and reservoir, and by (2) modeling liver weight as a function of somatic weight (random)

and reservoir. We indexed reproductive investment as fecundity, egg size, and gonad weight, all of which we modeled independently as a function of somatic weight (random) and reservoir. We estimated fecundity by multiplying the number of eggs in each sample by the ratio between total combined ovary weight and egg sample weight. We indexed egg size as the mean diameter (0.1 mm) of 25 eggs from each sample. To determine if any relationship existed between water temperature and day of year between reservoirs, we modeled mean water temperature (calculated for each sampling date) as a function of day of year (fixed) and reservoir. We used SAS (Version 9.2, SAS Institute Inc., Cary NC) for all analyses, with α = 0.05. In all analyses, a significant reservoir model term indicated a difference in the dependent variable 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 (Fig. 2). 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 (Fig. 2), 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; Fig. 3).

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; Fig. 4A) or between egg size and reservoir (F = 2.14; df = 1, 357; P = 0.1; Fig. 4A); however, liver weight (F = 47.7; df = 1, 15; P < 0.0001; Fig. 4B), fecundity (F = 7.1; df = 1, 15; P = 0.02; Fig. 4C), and gonad weight (F = 10.8; df = 1, 15; P = 0.005; Fig. 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; Fig. 4B), there

was no difference between reservoirs in fecundity (F = 1.53; df = 1, 15; P = 0.2; Fig. 4C) or gonad weight (F = 4.04; df = 1, 15; P = 0.06; Fig. 4D). 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 the prediction of condition, though not of reproductive investment; despite significant differences in female body mass and liver mass between reservoirs (Figs. 3, 4B), we found no difference in reproductive investment as measured by either egg size or fecundity (Figs. 4A, 4C). This evidence is not only counter to life-history theory but also 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 in fish (Hutchings 1991; Johnston and Leggett 2002; Wang et al. 2012), turtles (Rowe 1994), and amphipods (Glazier 1999) that when individuals inhabit
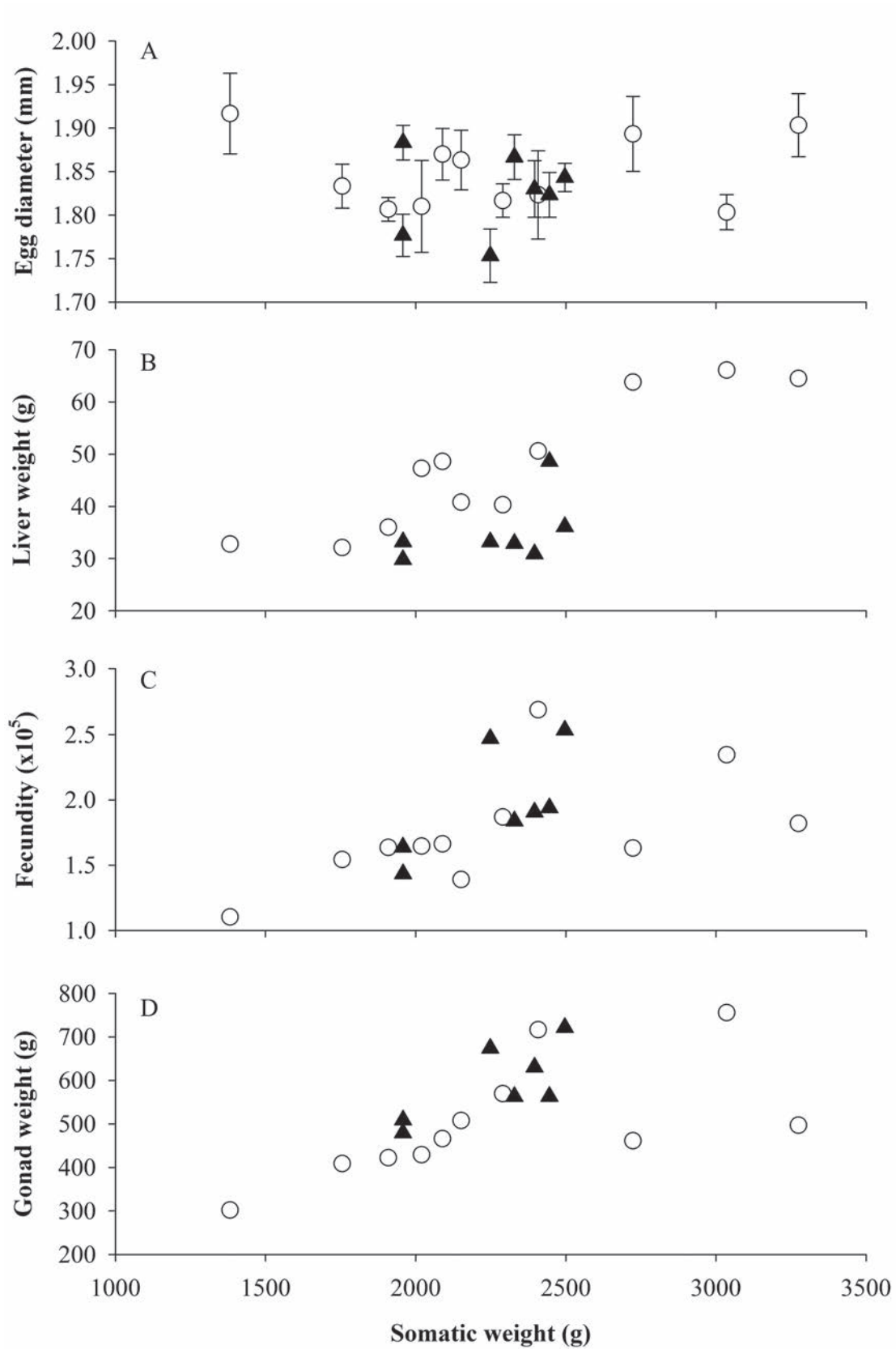
Figure 4. *A*, Mean ± sᴇ egg diameter; *B*, liver weight; *C*, fecundity; and *D*, gonad weight as a function of somatic weight for female walleye collected during spring 2012 from Swanson Reservoir (○) and Medicine Creek Reservoir (▲), Nebraska.

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 (Figs. 4A, 4C), despite differences in water-level variability and suspected differences in environmental conditions (e.g., turbidity, zooplankton assemblage; J. DeBoer, unpublished data). 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 trade-off 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 (e.g., zooplankton and larval gizzard shad densities; J. DeBoer, unpublished data) 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 postbreeding (Clutton-Brock et al. 1987; Miranda and Muncy 1987; Sydeman et al. 1991; Schultz 1993; Sinervo and Doughty 1996; Cargnelli and Neff 2006; Donelson et al. 2008). 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). We found no difference in breeding phenology among age groups or reservoirs as the overwhelming majority of

females spawned in a two- or three-day period, which is also counter to previous studies (Miranda and Muncy 1987 and references therein). 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; the youngest spawning female walleyes at Medicine Creek were age 5, compared to age 4 at Swanson (Fig. 2). However, in addition to coping with abiotic variability, walleye in irrigation reservoirs also experience significant harvest mortality (and perhaps catch-and-release 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). Given the substantially greater angling pressure at Medicine Creek, if catch-and-release angling is occurring for walleye at Medicine Creek, walleye could not only be learning to avoid recapture (thus explaining lower harvest versus Swanson; *sensu* Askey et al. 2006) but also be perceiving angling as a survival constraint. 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 not only reducing 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). Although the source population of stocked walleye has changed throughout the history of these reservoirs, Medicine Creek and Swanson have nearly always received stocked fish from the same source population in a given year (Nebraska Game and Parks Commission, unpublished data). 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 un-

intentionally select for walleye that spawn during the same two- or three-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 likely 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 (Quinn et al. 2000; Otterå et al. 2006), 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, even to those outside of fisheries. 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. These reproductive traits may be resultant from the interaction of several factors, including environmental and anthropogenic pressures, which could be affecting walleye population dynamics (Hansen et al. 1998). Walleye in Medicine Creek could perceive this harsher 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. Outside the realm of fisheries science, counterintuitive reproductive traits—although not commonly described in the literature—have recently been documented in birds (Gunness et al. 2001), insects (Leimar et al. 1994; Rosenheim 2011), and lizards (Angilletta et al. 2000), often in response to environmental variability. When considered with our research, these studies emphasize the need to understand the degree to which life-history expression represents physiological constraints versus ecological optimization, particularly as anthropogenic change continues to alter environmental conditions.

Acknowledgments

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