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Productivity and Trophic Interactions in the Missouri River Impoundments

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Productivity and Trophic Interactions in the Missouri River Impoundments

BY

Mark J. Fincel

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Productivity and Trophic Interactions in the Missouri River Impoundments

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Steven R. Chipps
Major advisor Date

Dr. David W. Willis
Head, Department Natural Resource Management Date

DEDICATION

This dissertation is dedicated to my wife, Elizabeth, parents, Kyle and Leslie, aunt and uncle, Susie (Sue-Ann) and Dean (Duber), grandmother, Dorothy, and brother and sister, Kevin (Kev-Bo) and Maggie (Pickle). This dissertation is also dedicated to Azrael, Neo, Loki, Bartelbee, Lotic and Dutch.

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ABSTRACT

Productivity and Trophic Interactions in the Missouri River Impoundments

Mark J. Fincel

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Standardized monitoring is a vital component of fisheries assessment in Missouri River impoundments. In South Dakota, annual variation in fish growth and abundance is used to monitor changes in fish populations and develop strategies (i.e. regulations) for managing recreational fishes. Although variation in fish abundance provides important insight into the status of fish populations, it can be difficult to link these changes to environmental conditions (i.e. hydrology) without concurrent information about reservoir productivity. Measures of nutrient concentration, algal biomass, and zooplankton composition/abundance provide important insights into reservoir productivity, but standardized approaches for collecting these measures have not been developed for Missouri River impoundments in South Dakota. Furthermore, development of protocols that account for spatial and temporal variation in these parameters would enhance our ability to understand factors affecting fish populations.

Inter- and intra- reservoir variation in prey fish composition and abundance has an important effect on sport fish populations in the Missouri River. Coldwater habitat in Lake Oahe, for example, provides refuge for rainbow smelt *Osmorus mordax* --- a forage species that contributes significantly to walleye *Sander vitreus* production. In contrast,

prey fish populations in downstream impoundments are dominated by gizzard shad *Dorosoma cepedianum*, cyprinids, and age-0 recreational fishes. In the late 1990s, the decline of rainbow smelt in Lake Oahe had significant impacts on walleye production. Although the smelt population has been recovering since the early 2000s, low water levels combined with the recent expansion of gizzard shad in Lake Oahe, have resulted in a unique food web never before observed in this system. As a result, factors affecting gizzard shad abundance, distribution, and their contribution to the growth dynamics of walleyes in Lake Oahe are poorly understood.

In addition to the trophic interactions of walleye and gizzard shad, similarities/differences between foraging patterns of walleye and sauger *Sander canadenses*, two similar species found throughout the Missouri River impoundments, were examined. Sauger is of particular concern in the Missouri River reservoirs due to population decline throughout the Midwest over the past 50 years. One hypothesis that could explain this downward trend in abundance is competition with walleye, a highly sought sport fish, which is frequently stocked in waters containing sauger. Examining isotopic overlap and variability in sympatric walleye and sauger populations could provide quantitative insight into energy transfer and diet breadth of each species.

Linkages between *Sander spp.* diet and hybridization have yet to be addressed though likely important. I also wanted to develop protocols that can be used to monitor trophic linkages and energy flow using stable isotope analysis. More directly, I determined the feasibility of using nonlethal tissues for isotope analysis of walleye, and if whole fish can be substituted for muscle plugs for isotope determinations of common Missouri River prey species.

To evaluate the need to document productivity throughout the Missouri River impoundments, to reveal gizzard shad population characteristics and their contribution to walleye growth dynamics, to examine isotopic characteristics between walleye and sauger, and to better standardize tissue use in future stable isotope analysis studies, I developed six primary objectives. These include: (1) develop protocols for indexing productivity in Missouri River impoundments, (2) determine gizzard shad population characteristics (age, growth, recruitment, larval growth rates, time of spawning, spawning duration) in Lake Oahe and compare these characteristics to those of gizzard shad populations in the lower Missouri River impoundments, (3) quantify the energetic contribution of gizzard shad and rainbow smelt to walleye growth, (4) compare isotopic overlap and variability between walleye and sauger in three Missouri River impoundments, (5) enhance the protocols used in stable isotope analysis and determine the usefulness of non-lethal tissues in isotope determination of South Dakota walleye and (6) compare/contrast prey fish isotope signatures using difference tissue analysis.

For my first objective, I documented nutrient and 1^o and 2^o productivity trends in Lakes Oahe, Sharpe, Francis Case and Lewis and Clark in South Dakota. In general, nutrients and 1^o and 2^o productivity tend to be highest in the transitional zones, or middle reaches, of each of reservoir. Moreover, sample sizes required to effectively monitor these parameters were minimal, with five nutrient samples, three chlorophyll *a* samples and ten zooplankton samples per site needed to precisely describe these indices.

For my second objective, I evaluated larval gizzard shad hatch timing, growth and density in Lake Oahe, South Dakota. In 2008, I collected larval gizzard shad from six sites throughout Lake Oahe from 1 May through 31 July. Subsets of gizzard shad were aged and growth and hatch date determined. I found that Lake Oahe gizzard shad exhibit reservoir wide bimodal spawning trends during the early summer months; warming water conditions in the upper-most part of the reservoir had earlier hatch dates compared to the lower portion. Peak larval gizzard shad density ranged from 0.6 to 33.6 (#/100m^3) and was significantly different spatially ($F_{5,18}$=5.83; P=0.002). Larval gizzard shad growth ranged from 0.242 to 0.579 (mm/day) and also differed spatially within the reservoir (H_5=103.595; P<0.001). Pollock and Minneconjou site locations tended to have greater growth and density of larval gizzard shad while Spring Creek and Whitlocks tended to be lower. I found no relationship between larval gizzard shad growth or density and large or small-bodied zooplankton density (P>0.05). Because gizzard shad exhibit delayed spawning, slow growth and low densities, they should be a suitable prey option for sport fishes in Lake Oahe, South Dakota.

For objective three, I evaluated the importance of gizzard shad to walleye growth and condition in Lake Oahe. Current walleye consumption and growth rates were compared to the mid 1990s, when rainbow smelt abundance was high, and the early 2000s, when both smelt and shad abundances were low. In 2008, gizzard shad were the dominant prey item of walleye, representing 60% of the diet by weight. However, in 2009, gizzard shad declined appreciably in the diet (22%) and were absent from walleye stomach contents in 2010. Conversely, rainbow smelt abundance has increased since

2008, representing 12%, 27% and 90% of walleye diets in 2008, 2009 and 2010, respectively. Comparison of walleye growth when diets consisted of 1) primarily rainbow smelt (mid 1990s), 2) few rainbow smelt or gizzard shad (early 2000s), or 3) primarily gizzard shad (2008), revealed that growth rates of walleye preying on gizzard shad were intermediate to those feeding predominantly on rainbow smelt or few rainbow smelt and gizzard shad. Because gizzard shad only become available for consumption in August, walleye achieved approximately 50% of their yearly maintenance energy requirements during this short time period. Conversely, rainbow smelt, which are available and consumed by walleye year round, provided a continuous source to help walleye meet their yearly maintenance energy requirements. In conclusion, gizzard shad in the Missouri River system, when abundant, can provide an important subsidy to fluctuating rainbow smelt populations.

For objective four, I examined isotopic characteristics of sauger and walleye in three South Dakota Missouri River impoundments that exhibit varying levels of hybridization; 22% in Lake Lewis and Clark, 4% in Lake Francis Case and 2.6% in Lake Oahe. I found high isotopic overlap between walleye and sauger in all reservoirs, suggesting similar diet composition. However, decreasing hybridization levels corresponded to differences in isotopic variability between *Sander* spp. In Lake Lewis and Clark, isotopic variability was similar between walleye and sauger (approximately 0.5 mean absolute residuals [MAR] for both species and both isotopes ($\delta^{15}N$ and $\delta^{13}C$). However, in Francis Case, I found similar $\delta^{15}N$ variability, but $\delta^{13}C$ variability was significantly increased for sauger compared to walleye (0.76 and 0.38 MAR, respectively). In Oahe, I found increased isotopic variability in sauger, compared to walleye in both isotopes (δ^{15}N 1.56 and 0.48 MAR and δ^{13}C 0.73 and 0.28 MAR for sauger and walleye, respectively). My results suggest that in all three systems, diets of walleye and sauger were largely overlapping. However, sauger exhibit increased isotope variability, while walleye exhibited decreased isotope variability, as hybridization rates between the two species declined. Differences in isotopic variability could be the result of difference in prey availability associated with varying habitat quantity or quality between reservoirs, factors that likely influence hybridization rates in these systems.

For objective five, I compared stable isotope values of muscle (lethal) to those from fins and scales (non-lethal) in walleye from multiple systems, size classes and across a range of isotopic values. I also compared isotopic variability among tissues within populations to determine the usefulness of non-lethal tissues for diet variability analyses. Muscle-derived isotope values were enriched compared to fins and depleted relative to scales. A split-sample validation technique and linear regression was used. This method indicated that isotopic composition of walleye fins and scales were significantly related to muscle tissue for both δ^{13}C and δ^{15}N ($r^2 = 0.79$ to 0.93). However, isotopic variability was significantly different in two of the six populations for δ^{15}N and three of the six populations for δ^{13}C. Although species and population specific, these findings indicate that a large proportion of the variation in isotopic composition of muscle tissue can readily be explained by non-lethally obtained tissues.

For my last objective, I examined the differences in isotopic variation of five prey fish species using whole fish, whole fish with the gut contents removed, and dorsal

muscle only. I found significant differences in both δ^{15}N and δ^{13}C between the three tissue treatments. In most cases, muscle tissue was enriched compared to whole specimens and gut-removed specimens. Moreover, differences in mean δ^{15}N within a species were up to 2‰ among treatments. This would result in a change of over half a trophic position based on a 3.4‰ increase per trophic level. However, there was no apparent relationship between tissue isotope values in fish and gut fullness (i.e., more prey tissue present). I suggest that muscle tissue should be used as the standard tissue for determining isotope composition of prey fish or age-0 recreational fishes, especially when determining enrichment for mixing models, calculating trophic position, or constructing aquatic food webs.

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Chapter 1: Introduction and Background

Productivity in South Dakota Missouri River impoundments

Water quality attributes, such as nutrient concentration, algal biomass, and water clarity, are frequently used in lake classification systems to document the trophic status of lakes and reservoirs (Carlson 1977, Goldman 1988). The trophic state of lakes and reservoirs is typically calculated by integrating several surrogate measurements, such as chlorophyll a, Secchi disk depth, and phosphorus concentration (Carlson 1977).

In reservoir systems, longitudinal changes in trophic status arise from variation in basin morphology, water depth, flow regime, and water clarity (Carillo 1979, German 1997, Wetzel 2002). These longitudinal patterns are typically associated with three zones that include: (1) the riverine zone, (2) the transition zone and (3) the lacustrine zone. Each zone is unique with respect to productivity, with the transition zone often being the most productive zone in reservoir systems.

Use of chlorophyll a as a surrogate for algal biomass has been widely used in aquatic environments (Smith 1979, Morin et al. 1999). Despite a high correlation between measures of chlorophyll a and primary productivity, productivity estimates based on chlorophyll a concentrations generally have low precision (Morin 1999). Factors such as turbidity, nutrient concentration (i.e. N:P ratios), plant physiology and/or food web effects can effect chlorophyll a concentration independent of primary productivity (Behrenfeld and Falkowski 1997). Nonetheless, as a relative measure of trophic status, chlorophyll a is a frequently measured water quality parameter that can be easily collected in the field and processed in the laboratory (Wetzel and Likens 1991).

Nutrient concentrations (primarily phosphorus and nitrogen) are also used as surrogates to index primary productivity (Brylinksy and Mann 1973). In most cases, phosphorous has been shown to be a limiting nutrient to primary production in freshwater lakes and reservoirs (Dillon and Rigler 1974, Birch et al. 1980, Goldman 1988). In some systems, total phosphorus is a better predictor of mean daily photosynthesis than chlorophyll a, and utilization of phosphorus as a surrogate removes some biases caused by algal species composition and grazing by zooplankton and other planktivores (Smith 1979).

The use of nutrients and/or algal biomass to index productivity can be influenced by food web interactions in lakes and reservoirs. In whole lake manipulations, planktivore dominated lakes had substantially higher chlorophyll a and primary productivity than did lakes with piscivore dominated systems (Carpenter et al. 2001). Evaluating primary productivity in systems with equal nutrient loadings, but with differing food web structures have yielded results that suggests that the number of trophic levels in a system has significant effects on primary productivity (Carpenter et al. 1987).

During the filling of the Missouri River impoundments, monitoring programs were established to document chemical and biotic factors in the reservoirs. Variables measured included zooplankton community composition, as well as water quality attributes (June 1974). In 1969, Lake Oahe zooplankton communities were dominated by cladocerans, with highest densities collected at stations in the northern, riverine segment of the reservoir (Selgeby 1974). Early hypotheses were developed that with reservoir age, the more northern part of the reservoir (i.e. riverine zone) would become increasingly oligotrophic (Selgeby and Jones 1974). These surveys also found that tributary inputs had important effects on the chemistry and nature of the reservoir systems (Selgeby and Jones 1974). Spatial variation in productivity has not been documented in South Dakota's Missouri River reservoirs. Understanding longitudinal changes in trophic status is important for developing standardized sampling protocols and identifying future monitoring stations.

The highly variable nature of Lake Oahe's rainbow smelt population likely affects zooplankton communities and hence, prey availability for other zooplanktivorous fishes. Similarly, gizzard shad are known to have an important impact on zooplankton prey and can limit foraging opportunities for other fishes (e.g., centrarchids). Unfortunately, zooplankton abundance and/or biomass are not routinely collected in Missouri River reservoirs, owing to the time and cost of collection and processing. Recent advances in laser technology, however, have been used to develop instruments that significantly reduce processing time and labor costs for zooplankton analysis. One such instrument, an optical plankton counter, provides rapid assessment of size distribution and total biomass of zooplankton samples, and significantly reduces processing time compared to traditional approaches (Wieland et al. 1997, Sprules et al. 1998, Phelps et al. 2007).

Measurements of aquatic productivity are time consuming and costly. As a result, several measures are frequently used as surrogates for productivity. These surrogates include measures of nutrient concentration, chlorophyll *a*, dissolved organic carbon, water transparency, and zooplankton composition/abundance. Although these measures relay information about system productivity, no protocols exist that provide recommendations on sample sizes required, spatial variability, or seasonal variation in these parameters in Missouri River impoundments. Protocols established in this study will aid in maximizing limited resources (i.e., man hours and cost) for accurately monitoring reservoir productivity.

Lake Oahe Gizzard Shad Population Characteristics

Gizzard shad (*Dorosoma cepedianum*) are found throughout the U.S. – and range from the southeast U.S. as far north as North Dakota (Carufel and Witt 1963). Gizzard shad are native to the Missouri River but their northern distribution is believed to be limited by winter severity (Walburg 1964). They have been stocked throughout the United States in efforts to improve sport fish production (Bremigan and Stein 1999). Their abundance varies between systems from 1 to 475 kg/ha (Jenkins 1967), with estimates in two South Dakota reservoirs ranging from 0.3 to 6.0 individuals/m^3 (Ward 2005). From 1990 through 1994, gizzard shad were stocked in Angostura Reservoir, South Dakota (Ward 2005) and have since migrated downstream via the Cheyenne River to Lake Oahe, where they have been increasing in abundance (Lott 2000).

Gizzard shad are known to have concentrated periods of spawning that are correlated with rising water levels (Michaletz 1997). Females have the capacity to produce large numbers of eggs, sometimes exceeding 100,000 eggs (Kilambi and Baglin 1969). Timing of water level increases is an important factor affecting gizzard shad reproduction, because gizzard shad are more likely to spawn when water level rises in early spring (Michaletz 1997b). In the absence of rising water levels, spawning is prolonged, and larva abundance is more evenly distributed among cohorts (Michaletz 1997). Temperature also affects spawning success of gizzard shad, and has been shown to enhance year class strength in years when spring water temperatures are warm (Michaletz 1997b).

Factors affecting growth rates of age-0 gizzard shad have been documented in warm water impoundments of varying productivity (Bremigan and Stein 2001, Michaletz 1998, Michaletz 1999). The main forces driving gizzard shad growth are productivity, temperature, and larval density, with growth rates being density dependent. Gizzard shad production fluctuates with reservoir productivity and is generally higher in more productive systems (Bremigan and Stein 1999, Michaletz 1999). Factors affecting gizzard shad abundances are unclear. However, it is thought that predation and density dependent mortality play key roles (Buynak et al. 1992, Welker et al. 1994). Gizzard shad abundance has been positively correlated with nutrient loading, specifically phosphorous, with the highest gizzard shad biomass observed in hypereutrophic reservoirs (Bremigan and Stein 2001). These correlations have led to model predictions of gizzard shad biomass across reservoir systems (Bremigan and Stein 2001). At present, the influence of fluctuating water levels on gizzard shad growth and production are not known for Missouri River impoundments. In Lake Oahe, record water level lows are coincident with increases in gizzard shad abundance. Hence, baseline data on gizzard shad growth and abundance are necessary to determine the influence of increased water levels when the reservoir eventually refills.

Gizzard shad are an important prey source for many sport fishes in the United States (Noble 1981, Johnson et al. 1988, Storck 1986, Michaletz 1997, Michaletz 1998b). Predation of gizzard shad by sport fishes, such as largemouth bass (*Micropterus salmoides*), walleyes (*Sander vitreus*), white crappies (*Pomoxis annularis*), and white bass (*Morone chrysops*) is dependent on growth of age-0 gizzard shad (Michaletz 1997, Michaletz 1998b). In some systems, gizzard shad produce slow growing individuals that remain vulnerable to sport fish predation for long periods of time (Storck 1986, Michaletz 1997B, Michaletz 1998, Allen et al. 1999), thus increasing growth of large predators (Michaletz 1997b). In contrast, in systems where growth rate is high, gizzard shad quickly reach sizes that sport fishes cannot exploit (Noble 1981). Modeling approaches have been used to show how gizzard shad consumption by fish changes based on their growth (Adams and DeAngelis 1987). Hence, growth rate of age-0 gizzard shad has a strong influence on prey availability for predators.

Walleye predation on gizzard shad has received less attention than has been given other piscivorous fishes (but see Hartman and Margraf 1992, Ward 2005, Hanten 2007). In South Dakota lakes and reservoirs, walleye diets have been extensively examined, though usually in the absence of gizzard shad (Jackson et al. 1993, Bryan 1995). Nevertheless, in three western South Dakota reservoirs, delayed use of gizzard shad was shown, with gizzard shad representing an insignificant component of walleye diets until August (Ward 2005). However, once exploited, gizzard shad became the dominant prey species for walleyes in August and September. A narrow temporal window of gizzard shad use has also been documented in several studies throughout the south and midwest (Bonds 2000, Kocovsky and Carline 2001, Michaletz 1997, Wickstrom 2006). In years when age-0 gizzard shad growth was high, they became unavailable as prey to largemouth bass as early as October each year (Michaletz 1997b).

Although gizzard shad have been identified as a major food source for some sport fishes, they can have adverse effects on sport fish recruitment (Dettmers and Stein 1992, DeVries and Stein 1992, Stein et al. 1995). Competitive exclusion by age-0 gizzard shad on zooplankton has been documented with largemouth bass and bluegill (*Lepomis macrochirus*, Dettmers and Stein 1992, DeVries and Stein 1992). Consumption of zooplankton by age-0 gizzard shad has the potential to cause mid-summer zooplankton declines (Dettmers and Stein 1992, DeVries and Stein 1992). A more apparent problem with gizzard shad is the competition between larval gizzard shad and age-0 sportfish. Because of high fecundity and efficiency of grazing on zooplankton by gizzard shad, a reduction in larval bluegill has been seen in many reservoirs as gizzard shad abundance increases. Reduction in bluegill recruitment may, in turn, influence predator population dynamics that consume this species (DeVries et al. 1991, Stein et al. 1991).

Gizzard shad can positively influence sport fishes by regulating zooplankton communities through nutrient uptake and nutrient cycling (DeVries and Stein 1992, Schaus et al. 1997, Stein 1995). Gizzard shad begin to feed on organic detritus within the sediment at about 35 mm (Pierce et al. 1987, Mundahl and Wissing 1987). By feeding on benthic detritus, gizzard shad have been shown to (1) transport nutrients from the benthos into the water column and (2) convert these nutrients into forms that algal communities can use (Brabrand et al. 1990, Drenner et al. 1986, Schaus et al. 1997). Release of phosphorus by gizzard shad, in some systems, can be greater than phosphorus inputs from streams entering the reservoir, implying that adult gizzard shad, like other detritivores, supply a large amount of nutrients to the pelagic food web (Schaus et al. 1997).

Gizzard shad have generally been restricted to the lower Missouri River impoundments in South Dakota, where they serve as important prey for walleyes. The recent decline of rainbow smelt in Lake Oahe has prompted concern among biologists and anglers in South Dakota. While it is clear that an abundant rainbow smelt population contributes to a healthy walleye fishery, in recent years, gizzard shad numbers have increased in Lake Oahe potentially affecting the walleye fishery. With increased gizzard shad abundance, many questions arise about their population dynamics, how they grow relative to populations further south, where spawning takes place, and factors affecting year class strength. Results from this study will provide age, growth, and distribution data and shed light on environmental factors affecting year class strength.

Walleye Consumption, Growth and Bioenergetics

Walleye occur throughout most of North America. Walleye populations range from Quebec, across Canada to the Rocky Mountains, and as far south as the Gulf of Mexico and have been enhanced by stocking efforts in non-native habitats (Pflieger, 1997, Ross 2001). They prefer large lakes and exhibit crepuscular feeding strategies, often moving into shallow water to forage (Rawson 1956, Eddy and Underhill 1974, Ryder 1977, Schupp 1978). Age-0 walleye are planktivorous until they reach a length of >30 mm (Jackson 1992). As juveniles, walleyes generally shift from a benthic invertebrate diet to a diet dominated by fishes (Colby et al. 1979). They generally select soft-rayed species (rainbow smelt, cyprinids) but also consume smaller percids, moronids, drum and alewifes (Parsons 1971, Wahl and Nielson 1985, Davis 2006, Hanten 2007). In some systems, walleyes rely heavily on invertebrate prey throughout most of their life cycle (Johnson et al. 1988). In highly productive systems (i.e. eastern South Dakota glacial lakes), invertebrates may reach densities high enough to compose a substantial portion of adult walleye diets (Isaak et al. 1993). In earlier studies on walleye diets in Lake Oahe, Jackson et al. (1992) and Bryan (1995) noted low use of macroinvertebrates when rainbow smelt abundance was high. However, after declines in rainbow smelt populations occurred in Lake Oahe, use of invertebrate prey increased (Davis 2004, Hanten 2007).

Like other reservoir systems, Lake Oahe can be characterized by three distinct zones; riverine, transition, and lacustrine zones. During the growing season (summer months), rainbow smelt are generally restricted to the lower, stratified, lacustrine portion of the reservoir where cold water habitat exists (Jackson 1992, Davis 2004, Hanten 2007). In the 1980’s, rainbow smelt were found in the diets of walleyes collected from the lower and middle reaches (lacustrine to transition), but no smelt were found in walleyes collected from upper most portion of the reservoir (Jackson 1992). In contrast, Bryan (1995) showed that the frequency of occurrence of smelt in walleye diets was high throughout the reservoir, owing to high water levels, cooler temperatures, and coldwater habitat throughout the reservoir.

Bioenergetics models have been used extensively to quantify prey consumption by fishes. Bioenergetics modeling is a cost effective method for estimating annual forage demand by a predator population (Stewart et al. 1993). These models provide insight into factors affecting growth and consumption in free-ranging fishes and are often used to evaluate hypotheses regarding prey use (Adams and Breck 1990). The bioenergetics approach has been applied to address a variety of questions that include the influence of water temperature, prey availability, toxin loadings, and food web dynamics (Kitchell et al. 1977, Borgemann and Whittle 1992, Schindler et al. 1993). Bioenergetics models have been used most often to quantify predator energy demands (Lyons 1984, Ney 1990, Bryan 1995). The basic mass-balance model can be expressed as,

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

where C = consumption, R = respiration, S = specific dynamic action, F = egestion, U = excretion, and ΔB = change in growth. Bioenergetics models partition food energy into several fractions: 1) energy used for metabolic costs, 2) energy released as heat increment (movement, physical processes), 3) energy incorporated into body tissue (growth), and 4) energy excreted as waste (Hartman and Brandt 1993). Each model must be parameterized using species-specific physiological estimates of consumption, growth, respiration, egestion, and excretion (Kitchell et al. 1977).

Walleye bioenergetics in Lake Oahe were first studied in the early 1990's, when rainbow smelt abundance was high and walleye diets were composed primarily of rainbow smelt (~95%; Bryan 1995). During this period, consumption of rainbow smelt contributed to some of the highest growth rates reported for Lake Oahe (Figure 1). When the rainbow smelt population declined appreciably in the late 1990's, bioenergetics modeling showed that consumption of rainbow smelt by walleyes declined appreciably. During this period, Lake Oahe walleye were meeting basic energy requirements only by supplementing rainbow smelt consumption with other prey items (i.e. invertebrates and other prey fishes; Figure 2). The severe reduction in rainbow smelt use led to reduced growth rates and increased natural mortality, particularly for larger, older walleyes (>3 years of age). Given the recent expansion of the Lake Oahe gizzard shad population, it is unclear what role gizzard shad have on growth dynamics of walleyes. Linking new information (bioenergetics modeling) with past modeling efforts will provide important baseline data for understanding the effects of variable prey populations on walleye growth dynamics.

The importance of gizzard shad on growth dynamics of Lake Oahe walleyes is not known. Previous studies have shown that when rainbow smelt are abundant, walleyes obtain nearly all of their energetic requirements (>90%) from smelt – and grow at high rates (Bryan 1995). When smelt are rare, walleyes must forage on alternative prey, resulting in reduced growth and condition (Hanten 2007). In downstream impoundments (i.e. Lakes Sharpe) gizzard shad represent an important diet item for walleyes (M. R. Wuellner - personal communication). With the recent expansion of gizzard shad into Lake Oahe, information about the energetic contribution of gizzard shad to walleye growth is needed.

Specific questions that need to be addressed are 1) what is the energetic contribution of gizzard shad to annual growth rates of Lake Oahe walleyes, 2) do gizzard shad provide a subsidy to rainbow smelt (which are slowly recovering, but still well below levels seen in the mid 1990s)?, and 3) has the Lake Oahe food web become more similar to those observed downstream? This study will determine to what extent Lake Oahe walleye are foraging on gizzard shad, quantify the energetic contribution of gizzard shad to walleye growth, and evaluate temporal patterns in energy flow across Missouri River impoundments. Additionally, the timing of this study will allow us to document and compare walleye food habits to previous studies in Lake Oahe (Jackson 1992, Bryan 1995, Hanten 2007).

Use of Stable Isotope Analysis in Revealing Trophic Linkages in the South Dakota Missouri River Impounments

Stable isotope analyses (SIA) have become increasingly useful in identifying trophic relationships in aquatic and terrestrial environments. SIA does not provide direct dietary information, but can be used to quantify long-term feeding relationships of an organism. SIA is currently used to address a variety of topics, such as determining dietary shifts from pelagic to benthic prey (Vander Zanden et al. 1998), modeling contaminant bioaccumulation in piscivorous fishes (Kidd et al. 1996) and monitoring the effects of eutrophication on aquatic food webs (Cabana and Rasmussen 1996). Additionally, SIA can reveal feeding interactions not detected by traditional gut content analyses -- identifying those prey items actually assimilated by the consumer. Stable carbon ratios (^{12}C:^{13}C) and nitrogen ratios (^{14}N:^{15}N) can also provide temporal information about energy flow (Kling et al. 1992, Cabana and Rasmussen 1994).

Stable isotope signatures can provide predictable changes from food source to consumer (Johnson et al. 2002). ^{13}Carbon signatures ($\delta^{13}C$) depend upon the photosynthetic pathway used to sequester carbon. A consumer's carbon signature is similar to its food source, with an enrichment of approximately one part per thousand per trophic level, due to loss of ^{12}C during respiration (Fry and Sherr 1984, Johnson et al. 2002, Vander Zanden and Rasmussen 1997). ^{15}Nitrogen signatures ($\delta^{15}N$) are usually 3 to 4 ‰ enriched relative to diet, due to loss of ^{14}N in nitrogenous wastes (Johnson et al. 2002, Vander Zanden et al. 1997). Hence, $\delta^{13}C$ can be used to compare energy sources between consumers (e.g. benthic production vs. pelagic production) and $\delta^{15}N$ can be used to identify important trophic relationships and energy pathways.

White muscle has been the choice of isotope analyses because of low lipid content and ease of homogenation, with carbon and nitrogen values in dorsal white muscle matching closely those of the food items consumed (De Niro and Epstein 1978, Pinnegar and Polunin 1999). Liver, gonadal tissue, bone collagen, otoliths, brain and whole fish (on smaller specimens) are other tissues used for isotope determinations (Pinnegar and Polunin 1999). The problem with using these tissues, or whole fish specimens, is that fish must be sacrificed to obtain them, which can be undesirable when working on rare species, species of concern, or large, mature sport fishes.

With increased interest in using stable isotopes for food web analysis, and concerns over protecting the resource being studied, questions arise on the validity of sacrificing large numbers of specimens. While SIA generally required fewer samples compared to traditional gut content analysis, development of non-lethal protocols for isotope determinations would eliminate the need to sacrifice organisms. Using non-lethal tissues for stable isotope analyses would increase sample size without affecting population size, removing the resource from the system, or reducing the gene pool (Kelly et al. 2006).

Fins and scales have been used as surrogates for determining isotope signatures, however, little information exists on how these results compare to lethally attained tissues (Perga and Gerdeaux 2003, Kelly et al. 2006). Kelly et al. (2006) compared isotope signatures between white muscle, fins and scales in sculpin and sunfishes and found strong correlations in isotope signatures between the different tissues, with fins being indistinguishable from muscle when analyzing $\delta^{13}C$. A high correlation was also found between muscle and scales when evaluating $\delta^{15}N$, though a correction factor was needed to predict food web characteristics. The applicability of using scales for SIA extend beyond that of present diet studies -- archived scale collections, catalogued for growth studies, could provide a unique opportunity for retrospective isotope studies.

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Chapter 2: Spatial Variation of Primary and Secondary Productivity Indices in South Dakota Missouri River Impoundments

Abstract

Measures of nutrient concentration, algal biomass, and zooplankton composition/abundance provide important insight into reservoir productivity. However, standardized approaches have not been developed for Missouri River impoundments. Developing protocols that account for spatial and temporal variation in these parameters would 1) improve the cost effectiveness of reservoir sampling, 2) enhance our ability to document reservoir productivity, and 3) contribute to a better understanding of factors that affect fish populations. In this study, I quantify spatiotemporal patterns in nutrient concentration, algal biomass and primary consumers (zooplankton) in Lakes Oahe, Sharpe, Francis Case and Lewis and Clark in Central South Dakota. In general, measures of productivity were highest in the transitional zones of each reservoir (i.e. middle reaches) and decreased in downstream areas (i.e., lacustrine zones). The location of tributary inputs was associated with localized increases in reservoir productivity likely owing to increased nutrient inputs from these sources. I found that nutrient concentration and standing stock of algae and zooplankton collected during spring (April-May) were correlated to mean, summer averages and were also generally less variable. Moreover, sample sizes required to effectively monitor site-specific productivity were relatively low, with five nutrient samples, three chlorophyll a samples and ten zooplankton samples needed to reliably (±12%) quantify these parameters. Accounting for seasonal and spatial variation in reservoir productivity is important for developing cost-effective monitoring programs that could ultimately be linked to

fisheries stock assessment data to enhance management decisions in Missouri River impoundments.

Introduction

Limnological data can be important for understanding the impact of changing ecological processes and management actions in freshwater systems (Carpenter et al. 1985). Reservoir productivity can significantly affect fish production (i.e., bottom up biotic controls; Yako et al. 1996) and ultimately sport fish populations (Hokanson and Lien 1986, Peterson et al. 2006). Similarly, higher trophic levels can influence primary and secondary productivity and as a result, stocking of piscivorous fishes has often been used to improve water quality (i.e., biomanipulation; Arcifa et al. 1986; Carpenter et al. 1987, 2001; Jacobsen et al. 1997). Because of the interdependent role of primary and secondary productivity on fish production, many state agencies routinely monitor measures of productivity to better forecast sport fish production and(or) document food web changes associated with management actions.

In reservoirs, longitudinal changes in productivity arise from variation in basin morphology, water depth, flow regime, and water clarity (Carillo 1979, German 1997, Wetzel 2002). These changes can typically be classified into three distinct zones: (1) the riverine zone, (2) the transition zone and (3) the lacustrine zone (Wetzel 2002). Each zone is defined by unique in patterns in nutrient availability and productivity with the transition zone often being the most productive zone. While most reservoirs contain these three distinct zones, the length of each zone, location of each zone within the reservoir and the impact of localized nutrient inputs (through urban or tributary inputs) can vary by reservoir. Furthermore, reservoirs often contain tributaries that can have local effects on productivity (Stanford 1994). Water quality attributes, such as nutrient concentration, algal biomass, and water clarity are frequently used to document trophic status of lakes and reservoirs (Carlson 1977, Goldman 1988). One common measure of productivity is the trophic state index (TSI) that is typically calculated using surrogate measures such as chlorophyll a, Secchi disk depth, and(or) phosphorus concentration (Carlson 1977).

During the filling of the Missouri River impoundments, monitoring programs were established to document chemical and biotic changes in reservoir productivity. Variables measured include zooplankton community composition and water quality attributes (June 1974). In 1969, Lake Oahe zooplankton communities were dominated by cladocerans, with the highest densities found at stations in the northern, riverine segment of the reservoir (Selgeby 1974). These monitoring programs also found that tributary inputs greatly affected the chemistry and nature of the reservoir system (Selgeby and Jones 1974).

Spatial variation in productivity has not been documented in South Dakota's Missouri River reservoirs since the early 1970s. Understanding longitudinal changes in trophic status is important for developing standardized sampling protocols and identifying future monitoring stations. Of particular interest, is highlighting the number of samples required to effectively describe nutrient and productivity dynamics while minimizing the amount of resources used to complete the endeavor. In this study, my objectives were to document spatial and temporal patterns in reservoir productivity metrics in four South Dakota Missouri River impoundments. I also comment on the need for establishing a long term reservoir monitoring program that can be used to supplement fisheries stock assessment data.

Methods

Study Reservoirs

Lake Oahe is the second largest impoundment, out of a series of six impoundments, on the Missouri River (Figure 2-1). It extends from Bismarck, ND to Pierre, SD. At normal pool, the South Dakota portion of Lake Oahe has a surface area of approximately 145,000 ha; with a mean depth of approximately 19 m and a maximum depth of 67 m. Lake Sharpe is located in central South Dakota and extends from Oahe Dam to Big Bend Dam. At normal pool, Lake Sharpe has a surface area of approximately 25,000 ha and mean and maximum depths of 9.5 and 23.7 m, respectively. Lake Francis Case extends from Big Bend Dam to Fort Randall Dam in central South Dakota. At normal pool, Lake Francis Case has a surface area of approximately 25,000 ha and mean and maximum depths of 15.2 and 42.6 m, respectively. Lake Lewis and Clark is the furthest downstream, and the smallest Missouri River reservoir. Lake Lewis and Clark extends from Fort Randall Dam to Gavin's Point Dam in south central South Dakota. At normal pool, Lake Lewis and Clark has a surface area of 10,500 ha and mean and maximum depths of 5 and 16.7 m, respectively, which is considerably shallower than the other study reservoirs. Lake Lewis and Clark is unique in that it contains 70 km of riverine habitat and delta formation within the reservoir (Niobrara River Delta).

I chose six sites within each of the South Dakota Missouri River impoundments. All sites within each reservoir were equidistant from one another (see appendix 1 for a list of sites with geo-referenced coordinates). Primary and secondary productivity metrics and physiochemical parameters were collected from each site in April, June, and August of 2008.

Water Chemistry

At each site, I determined Secchi depth, turbidity (using a LaMotte® turbidity meter), dissolved oxygen and water temperature using a YSI® datasonde (Yellow Springs Instruments, Yellow Springs, OH). I used an integrated water sampler to collect replicate water samples from the water surface to twice the Secchi depth or at a depth not to exceed the thermocline (if present). Water samples were transferred to 1 L acid washed containers, placed on ice and transported to SDSU Northern Plains Biostress Laboratory. Determinations of total phosphorous, total kjeldahl nitrogen and total suspended solids were conducted by the Water Resource Institute at South Dakota State University. For chlorophyll *a* determination, 250 ml of water was filtered through a 0.7 μm Whatman GF/F filter in the field, wrapped in aluminum foil, placed on ice, and transported to the SDSU Northern Plains Biostress Laboratory for processing. I determined chlorophyll *a* concentration as outlined by APHA (1998). This procedure involved extracting chlorophyll *a* for 24 hours in 90% acetone and then measuring its concentration using a Turner TD-700 fluorometer.

Zooplankton Collection and Processing

Zooplankton samples were collected concurrently with water chemistry in each of the four reservoirs. Samples were obtained using a conical shaped Wisconsin net (10 cm diameter, 150 μm mesh) towed vertically from twice the Secchi depth to the surface (or from 1 m above the sediment to the surface if water depth was less than twice the Secchi depth). I preserved zooplankton samples in 10% Lugol's solution and transported to SDSU Northern Plains Biostress Laboratory. In the laboratory, approximately 10% of the original sample was used for zooplankton identification and enumeration (in increments of 2 ml sub samples). The total number of zooplankton in each sample (ZPD_{SS}) was extrapolated from the number found in the zooplankton subsamples. I then calculated zooplankton density (ZP; # of zooplankton / L) by

$$ZP = (ZPD_{SS}*VOL_{SS})*1000 / VOL_{TS}$$

where ZPD_{SS} is the number of zooplankton in the entire sample, VOL_{SS} is the volume of sample liquid (ml) and VOL_{TS} is the total water column sampled in the field (L).

Sample Size Determination

Because I wanted to develop protocols for quantifying zooplankton and physiochemical parameters in Missouri River impoundments, sample size estimators were used to determine the minimum number of samples needed to be confident that samples collected expressed the true mean. For chlorophyll *a*, total phosphorus, total Kjeldahl nitrogen, total suspended solids and zooplankton density, I calculated the minimum sample size (SS) required to be 95% confident that the sample mean was ± 12.5% the true mean. I used the equation

$$SS = [(s / X)^2]*[(t^2_{\alpha} / r^2)*100]^2$$

where s = standard deviation of the samples, *X* is the sample mean, t^2_α = Student's *t* with *n* – 1 df for 1 – α level of confidence, and *r* = desired relative error (Krebs 1999).

Statistical Analysis

Because nutrient dynamics and productivity metrics (algae and zooplankton) change seasonally, I compared these metrics between reservoirs within each season (i.e., April, June and August). When analyzing productivity metrics, tests of normality (Shapiro-Wilk test) were rarely met. Thus, I compared mean concentration and sample sizes required for chlorophyll *a*, total phosphorus, and total kjeldahl nitrogen between reservoirs using an ANOVA on ranks (α=0.05) with a Dunn's multiple comparison test to reveal significant differences. Zooplankton samples were normally distributed, so I used an ANOVA to compare cladoceran density and sample size requirements among reservoirs.

Results

Water temperature in South Dakota Missouri River impoundments generally increased from upstream to downstream sites within each reservoir (Appendix 1). However, due to hypolimnetic releases from each dam, tailrace reaches were generally cooler than surface water temperatures above the dam, causing discontinuity in river water temperatures from the upstream reaches of Lake Oahe to the most downstream site in Lewis and Clark Lake. Among the reservoirs, Secchi depth (m) ranged from 0.2 to 3.4, 0.1 to 6.0 and 0.2 to 3.9 in April, June and August, respectively, and turbidity (NTU) ranged from 0.53 to 15.50, 0.62 to 68.20 and 1.70 to 25.10 in April, June and August, respectively. Secchi depth generally exhibited an inverse bell-shaped relationship from upstream to downstream sites, with higher water clarity in the upper and lower reaches within each reservoir. Turbidity, as expected, tended to exhibit a reciprocal relationship with Secchi depth where the highest turbidity tended to be in the middle reaches of the reservoir. Conductivity (uș/cm^2) and pH were variable throughout the reservoirs systems with no discernable trends with rkm.

Mean chlorophyll *a* concentration was significantly higher in Lakes Oahe and Lewis and Clark than Lakes Sharpe in April (H_3=13.675; P=0.003; Figure 2-2). I found no differences in mean chlorophyll *a* concentration among reservoirs in June or August. Mean chlorophyll *a* concentration was highest in upstream Lake Oahe and decreased downstream (Appendix 2). Conversely, mean chlorophyll *a* concentration was lowest in Lake Lewis and Clark tailrace and increased downstream. Both Lakes Sharpe and Francis Case exhibited bell-shaped relationships with regard to rkm with peak mean chlorophyll *a* concentrations occurring in the middle of the reservoirs. Sample size requirements for chlorophyll *a* were generally low (approximately 1) for all reservoirs, seasons and sites. One exception to low sample size requirements was Lake Lewis and Clark in June and August where required chlorophyll *a* samples were increased in sites 4 and 6 (Figure 2-2). There were no significant differences in sample size requirements between reservoirs (p>0.05) seasonally.

Total phosphorus (TP) was similar between all reservoirs seasonally (p>0.05; Figure 2-3). Lakes Oahe, Sharpe and Francis Case exhibited bell-shaped relationships between TP and reservoir location with the highest TP concentration occurring in the middle of the reservoirs (Appendix 2). Conversely, Lake Lewis and Clark exhibited increased TP concentration with rkm. Sample size requirements for TP were generally low for all reservoirs, seasons and sites. However, specific sites within Lakes Oahe (Mobridge and Whitlock), Francis Case (Elk Creek) and Lewis and Clark (Gavin's Point Dam) where abnormal and exhibited high variability and subsequently, increased sample size requirements (Figure 2-3). There were no significant differences in sample size requirements between reservoirs (p>0.05) seasonally.

Total kjeldahl nitrogen (TKN) was similar between reservoirs in June and August; however, in April, Lake Lewis and Clark had significantly higher TKN concentration than Lake Sharpe (H_3=11.275; p=0.01; Figure 2-4). Lakes Oahe, Sharpe and Francis Case exhibited bell-shaped trends in TKN with the highest TKN concentrations occurring in the reservoir center (Appendix 2). Lake Lewis and Clark exhibited low TKN in the tailrace and increased TKN with rkm (similar to TP). Sample size requirements for TKN were generally low (between 2 and 4 samples) in April and June, but increased in August. No differences in sample size requirements were found among reservoirs seasonally (p>0.05). Moreover, nutrients, chlorophyll *a*, and zooplankton measured during spring (April/May) were positively correlated to mean summer values in each reservoir (Figure 2-5), implying that spring sampling provided a reasonable time frame for indexing relative productivity.

Trophic state index (TSI) values ranged from eutrophic (>60) to oligotrophic (<40) throughout the study reaches (Figure 2-6). TSI values in Lakes Oahe, Sharpe and Francis Case were lowest in the lower reservoir and tailrace locations and increased in the middle reaches of the reservoirs. Conversely, TSI values in Lake Lewis and Clark were lowest in the tailrace section of the reservoir and steadily increased with decreasing rkm. These relationships between TSI values and rkm were consistent despite season, in all reservoirs. Tributaries seemed to increase local TSI values, especially near the mouth of the Moreau, Cheyenne, Bad and White rivers (Figure 2-6).

Cladoceran density (#/L) was similar between reservoirs in April and June ($p>0.05$) but Lake Francis Case had significantly higher cladoceran density than other reservoirs in August (Figure 7; $F_{3,20}=7.114$; $p=0.002$). Within reservoirs, cladoceran density exhibited bell-shaped trends, similar to TKN, TP and chlorophyll *a*, where the center of the reservoirs had the highest cladoceran density and values declined in the upper and lower reaches (Appendix 2). Sample size requirements for cladoceran density were higher in April (approximately nine) and generally lower in June and August (approximately four). There were no differences in sample size requirements among reservoirs in April or August ($p>0.05$); however, required sample sizes in Oahe were significantly higher than the other reservoirs in June ($F_{3,19}=8.799$, $p<0.001$).

Discussion

Seasonal and spatial trends in productivity metrics for Lakes Oahe, Sharpe and Francis Case were similar to those reported for other reservoirs (Carpenter 2001). However, Lake Lewis and Clark was noteable in that nutrients, and subsequent productivity, was lowest in the tailrace above the reservoirs and increased with decreasing rkm. Lake Lewis and Clark is also unique in that it contains 70 km of riverine habitat and 25 km of delta formation within the reservoir (i.e., Niobrara River delta). As a result of this unique habitat, it is likely that nutrients remain suspended into the lacustrine zone, thus leading to the substantial increase in productivity throughout the lower reaches of Lake Lewis and Clark (Schreck 2010).

In Lakes Sharpe, Francis Case and Lewis and Clark, TSI values exhibited a bell-shaped relationship with reservoir location. In contrast, Lake Oahe exhibited the highest TSI values in the upper reaches, with values declining with decreasing rkm. This is congruent with findings from 2001 and 2002 when Bolgrien et al. (2009) documented TSI trends in Lake Oahe to be highest in the riverine section of the reservoir and lower in the transitional and lacustrine zones. Because Lake Oahe extends 140 km into North Dakota, it is likely that the bell-shaped TSI trend observed in the other reservoirs would also occur here. However, because my sampling effort started at the South Dakota border, I was unable to identify the lower TSI values associated with tailrace reaches below Garrison Dam.

Zooplankton densities in the Missouri River impoundments were intermediate to densities found in temperate lakes and reservoirs (see Pinto-Coelho et al. 2005 for review). However, spikes in June and August zooplankton samples far surpassed levels found in temperate lakes and reservoirs and were more indicative of eutrophic sub-tropical reservoirs (Havens et al. 2000). Fish production can be highly influenced by zooplankton abundance (Dai and Miner 1997; Hoxmeier et al. 2004; Bremigan and Stein 2011) and it is important that the timing of zooplankton blooms overlaps with critical periods in fish life histories (match/mismatch hypothesis; Burrow et al. 2011). Because many age-0 fishes undergo an ontogenetic feeding shift away from zooplankton early in their life stages (Graeb et al. 2004; Galarowicz, et al. 2006) it is unlikely that zooplankton spikes in August can be readily utilized by these fishes. However, zooplankton spikes in June can have far reaching benefits promoting gizzard shad growth (a primary prey resource in Lake Sharpe; Wuellner et al. 2010) and increasing growth and survival of warm water sport fishes.

In South Dakota, upstream impoundments seem to dictate downstream temperature, water clarity, TP, TKN, chlorophyll *a*, and cladoceran density, with tailrace reaches having decreased physiochemical and 1^o and 2^o productivity compared to downstream reaches. These system “breaks” have been termed serial discontinuity (Ward and Stanford 1983) and disrupt the normal progression of nutrient, productivity and biotic relationships along longitudinal gradients in lotic waters (Baldwin et al. 2010). The tailwaters of the South Dakota Missouri River reservoirs are largely depleted in nutrients and characterized by low nutrient, algae and zooplankton concentrations. However, I found that tributaries in the Missouri River appear to enhance local reservoir productivity owing to increased nutrients, warmer water, or a combination of both. These tributaries increased localized 1^o and 2^o productivity, and in the case of the Niobrara River in Lake Lewis and Clark, can have far reaching effects on reservoir productivity. Downstream tributary inputs have been shown to alleviate some of the disturbance conditions associated with dams (Selgeby and Jones 1974; Stanford 1994). Often times, streams large enough to make substantial contributions to temperature and nutrients of impaired tailwaters are far downstream or absent entirely. In some instances, 100 to 1000 km stretches of tailwaters can remain impaired and lack nutrient inputs (Stanford 1994; Stevens et al. 1997). In each of the South Dakota Missouri River impoundments, there appears to be a tributary large enough to mediate the low temperatures and reduced productivity associated with hypolimentic releases of the upstream dams.

Increases in reservoir water levels are often associated with productivity ‘pulses’, created by increased nutrient inputs and mineralization (Straskraba et al. 1993; Ostrofsky 2007). At the time of my study, Lake Oahe water levels were the lowest since the reservoir was filled in the late 1950s. By fall 2009, high water inflows resulted in the re-filling of Lake Oahe in merely a year. Thus, results reported here can serve as important baseline information to compare physiochemical and productivity metrics to those during high water years to evaluate the effects of fluctuating water levels on reservoir productivity.

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Figure 2-1. Map of the South Dakota Missouri River impoundments in central South Dakota.

Figure 2-2. Mean chlorophyll *a* (top panels; mg/l) and the number of samples required to estimate the true sample mean +/- 12.5% (bottom panels; #) by season (left panels) and site (right panels) for Missouri River impoundments (Lake Oahe - open bars; Lake Sharpe - filled bars; Lake Francis Case - large hash; Lake Lewis and Clark - small hash). Different letters represent significant differences (ANOVA of ranks; $p<0.05$) in mean chlorophyll *a* concentration seasonally. Error bars represent 1 standard error.

Figure 2-3. Mean total phosphorus (top panels; mg/l) and the number of samples required to estimate the true sample mean +/- 12.5% (bottom panels; #) by season (left panels) and site (right panels) for in the South Dakota Missouri River impoundments (Lake Oahe - open bars; Lake Sharpe - filled bars; Lake Francis Case - large hash; Lake Lewis and Clark - small hash). Error bars represent 1 unit of standard error.

Figure 2-4. Mean kjeldahl nitrogen (top panels; mg/l) and the number of samples required to estimate the true sample mean +/- 12.5% (bottom panels; #) by season (left panels) and site (right panels) for in the South Dakota Missouri River impoundments (Lake Oahe - open bars; Lake Sharpe - filled bars; Lake

Francis Case - large hash; Lake Lewis and Clark - small hash). Different letters represent significant differences (ANOVA of ranks; $p<0.05$) in mean chlorophyll *a* concentration seasonally. Error bars represent 1 unit of standard error.

Figure 2-5. Mean chlorophyll *a*, mean kjeldahl nitrogen (TKN), mean total phosphorus and mean cladoceran density collected from April/May compared to mean summer values. Filled circles represent Lake Oahe, open circles represent Lake Sharpe, filled triangles represent Lake Francis Case and open triangles represent Lake Lewis and Clark.

Figure 2-6. Trophic State Index (TSI) values for South Dakota Missouri River impoundments from upstream (left panels; starting with Lake Oahe) to downstream (right panels; ending with Lewis and Clark). Top panels represent samples collected in April, middle panels represent samples collected in June and bottom panels represent samples collected in August. Closed circles represent TSI values calculated using Secchi depth, open circles represent TSI values calculated using chlorophyll *a*, and closed triangles represented TSI values calculated using total phosphorus. Vertical dashed lines represent tributary input locations.

Figure 2-7. Mean cladoceran density (top panels; #/l) and the number of samples required to estimate the true sample mean +/- 12.5% (bottom panels; #) by season (left panels) and site (right panels) for in the South Dakota Missouri River impoundments (Lake Oahe - open bars; Lake Sharpe - filled bars; Lake Francis Case - large hash; Lake Lewis and Clark - small hash). Different letters represent significant differences (ANOVA; $p<0.05$) between reservoirs seasonally. Error bars represent 1 unit of standard error.

Figure 2-1.

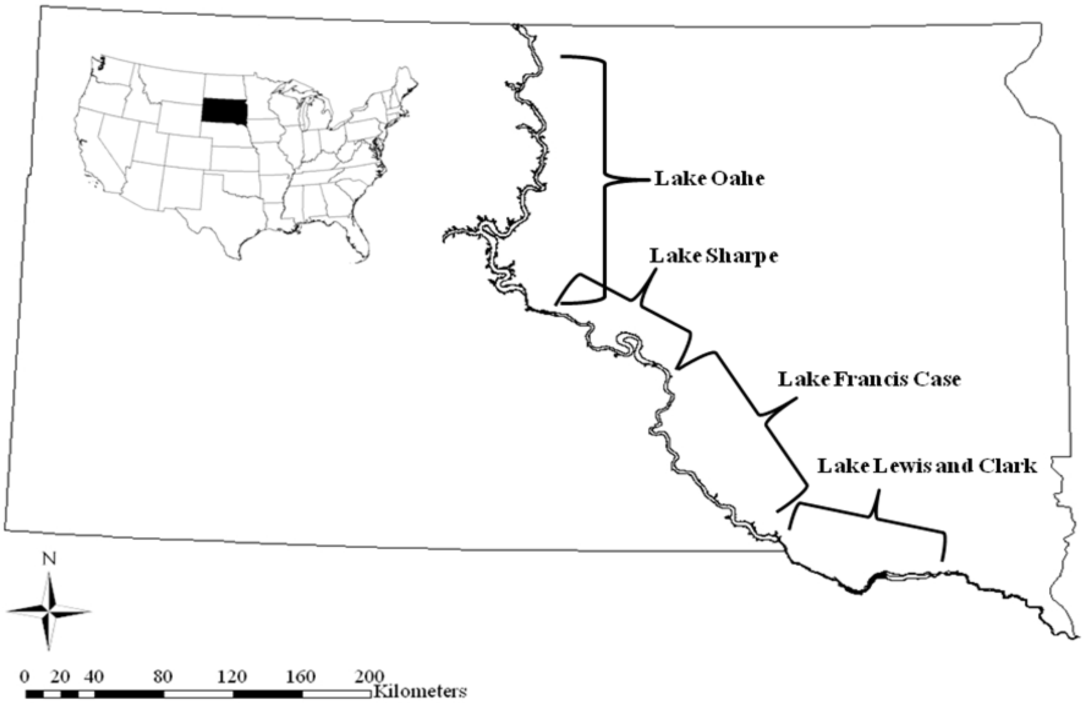

Lake Oahe
Lake Sharpe
Lake Francis Case
Lake Lewis and Clark
N
0 20 40 80 120 160 200
Kilometers

Figure 2-2.

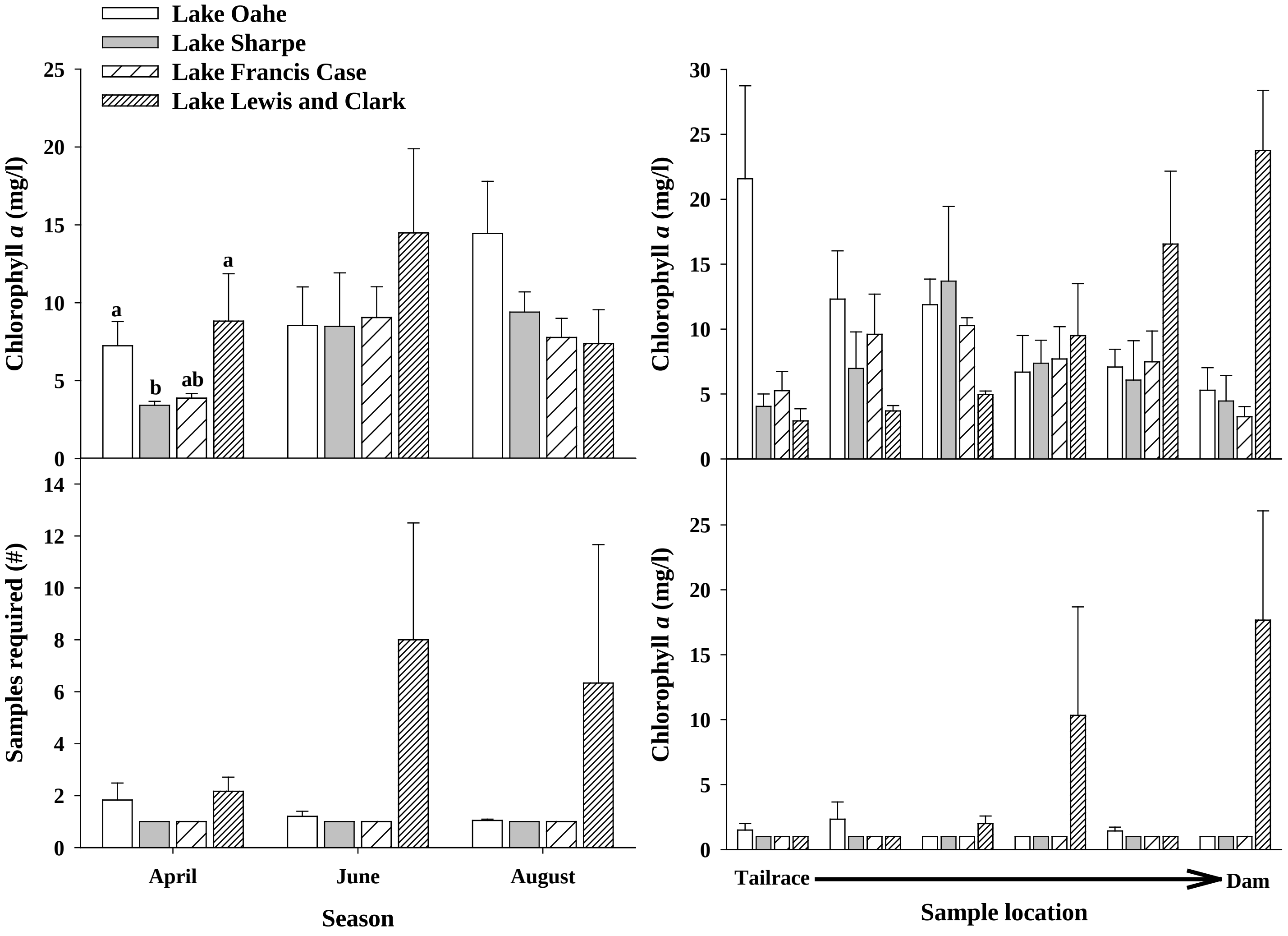
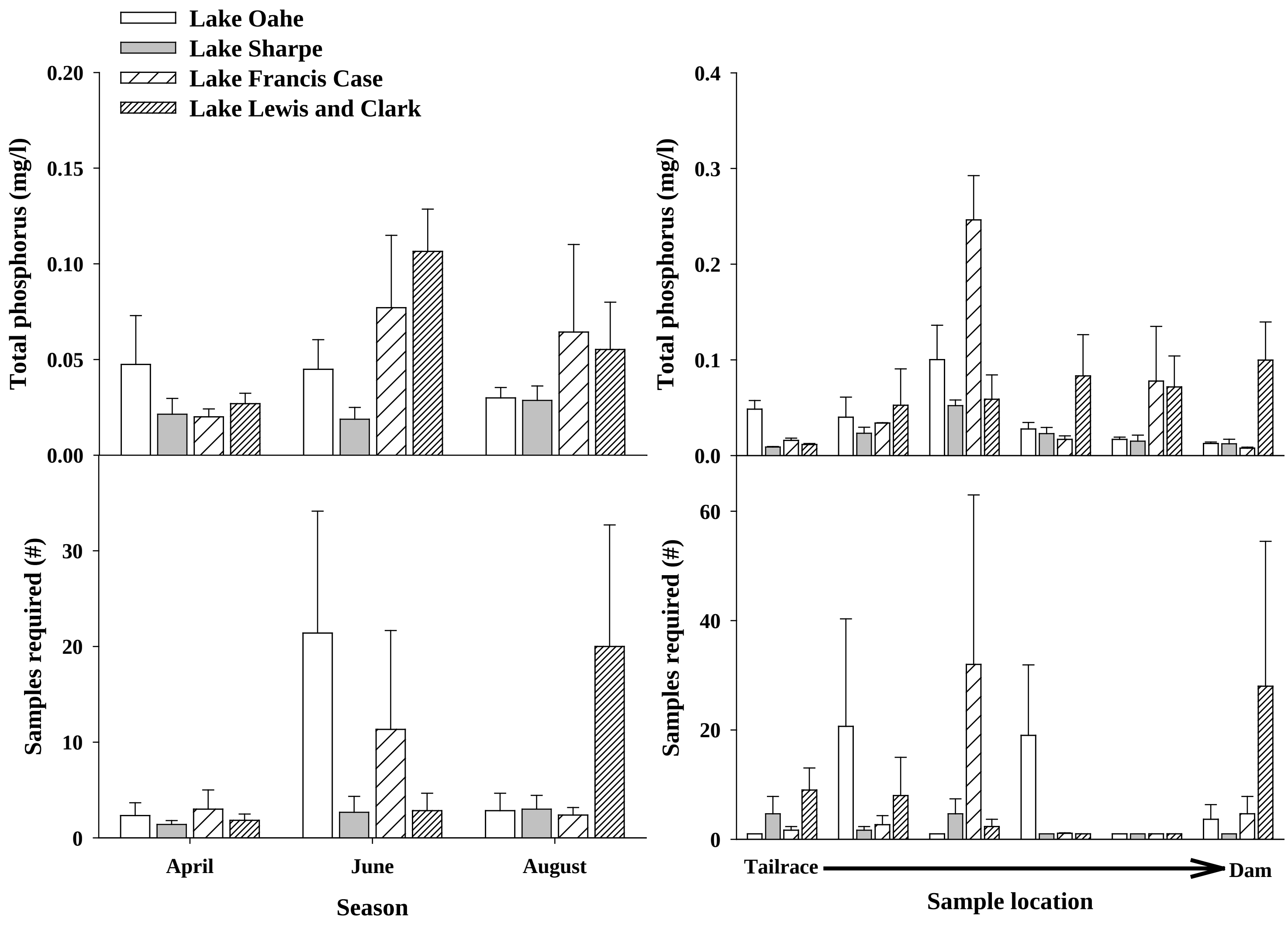
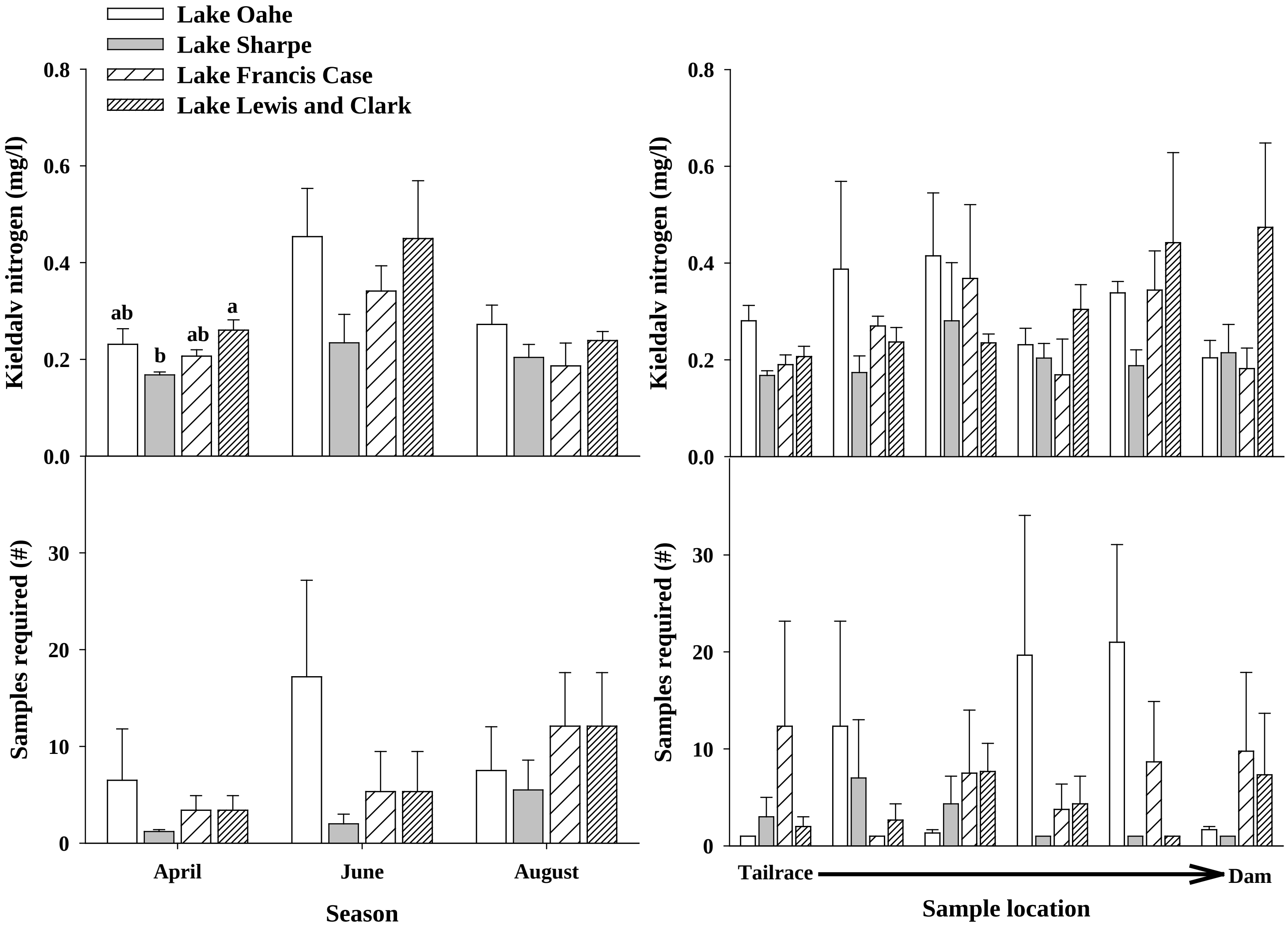

Lake Oahe
Lake Sharpe
Lake Francis Case
Lake Lewis and Clark
Chlorophyll *a* (mg/l)
0
5
10
15
20
25
a
b
ab
a
Samples required (#)
0
2
4
6
8
10
12
14
April
June
August
Season
Chlorophyll *a* (mg/l)
0
5
10
15
20
25
30
Chlorophyll *a* (mg/l)
0
5
10
15
20
25
Tailrace
Dam
Sample location

Figure 2-3.



Lake Oahe
Lake Sharpe
Lake Francis Case
Lake Lewis and Clark
Total phosphorus (mg/l)
0.20
0.15
0.10
0.05
0.00
Samples required (#)
30
20
10
0
April
June
August
Season
Total phosphorus (mg/l)
0.4
0.3
0.2
0.1
0.0
Samples required (#)
60
40
20
0
Tailrace
Dam
Sample location

Figure 2-4.



Lake Oahe
Lake Sharpe
Lake Francis Case
Lake Lewis and Clark
Kieldalv nitrogen (mg/l)
0.0
0.2
0.4
0.6
0.8
ab
b
ab
a
Samples required (#)
0
10
20
30
April
June
August
Season
Kieldalv nitrogen (mg/l)
0.0
0.2
0.4
0.6
0.8
Samples required (#)
0
10
20
30
Tailrace
Dam
Sample location

Figure 2-5

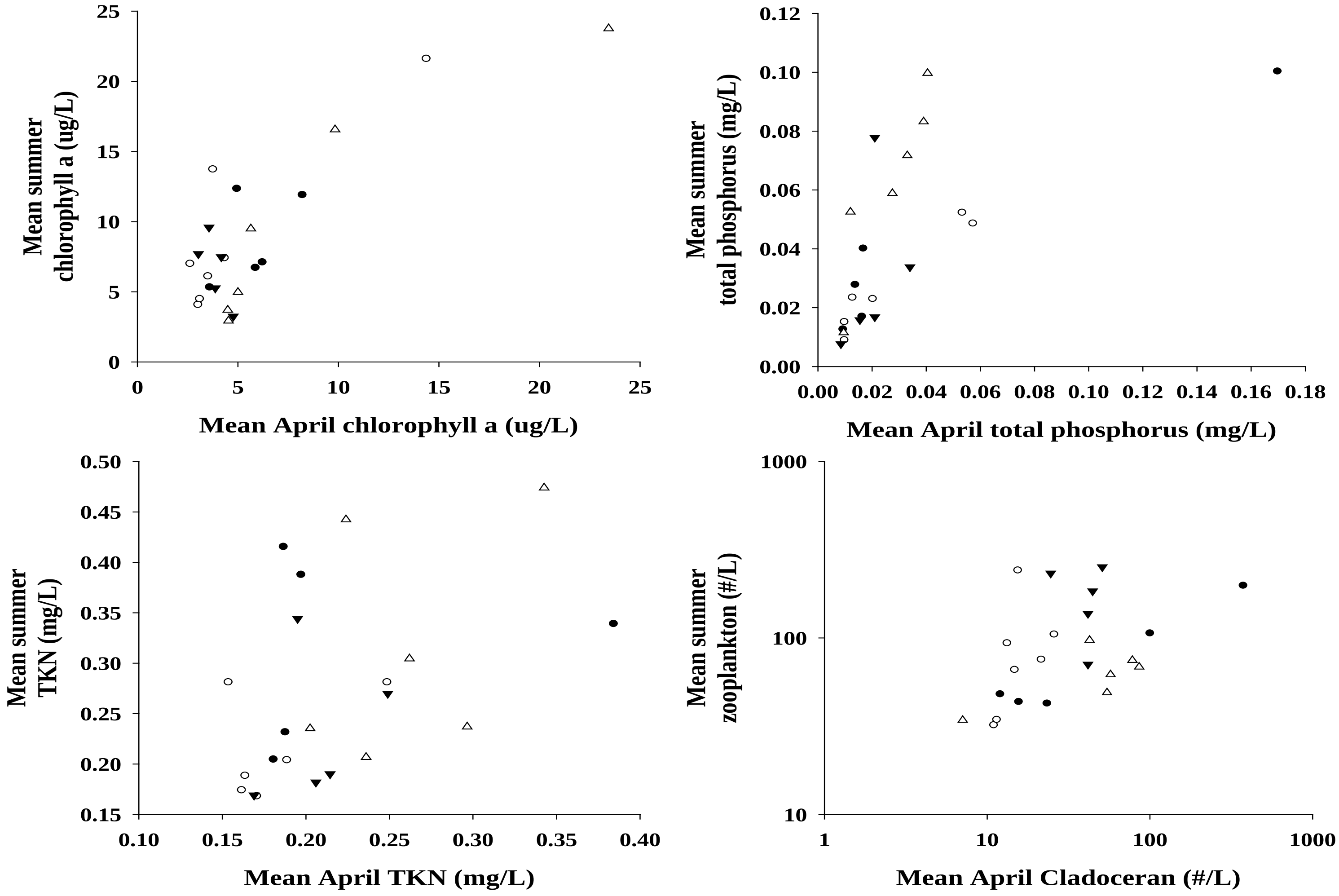

Mean summer chlorophyll a (ug/L)
25
20
15
10
5
0
0
5
10
15
20
25
Mean April chlorophyll a (ug/L)
Mean summer total phosphorus (mg/L)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
Mean April total phosphorus (mg/L)
Mean summer TKN (mg/L)
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.15
0.20
0.25
0.30
0.35
0.40
Mean April TKN (mg/L)
Mean summer zooplankton (#/L)
1000
100
10
1
10
100
1000
Mean April Cladoceran (#/L)

Figure 2-6.

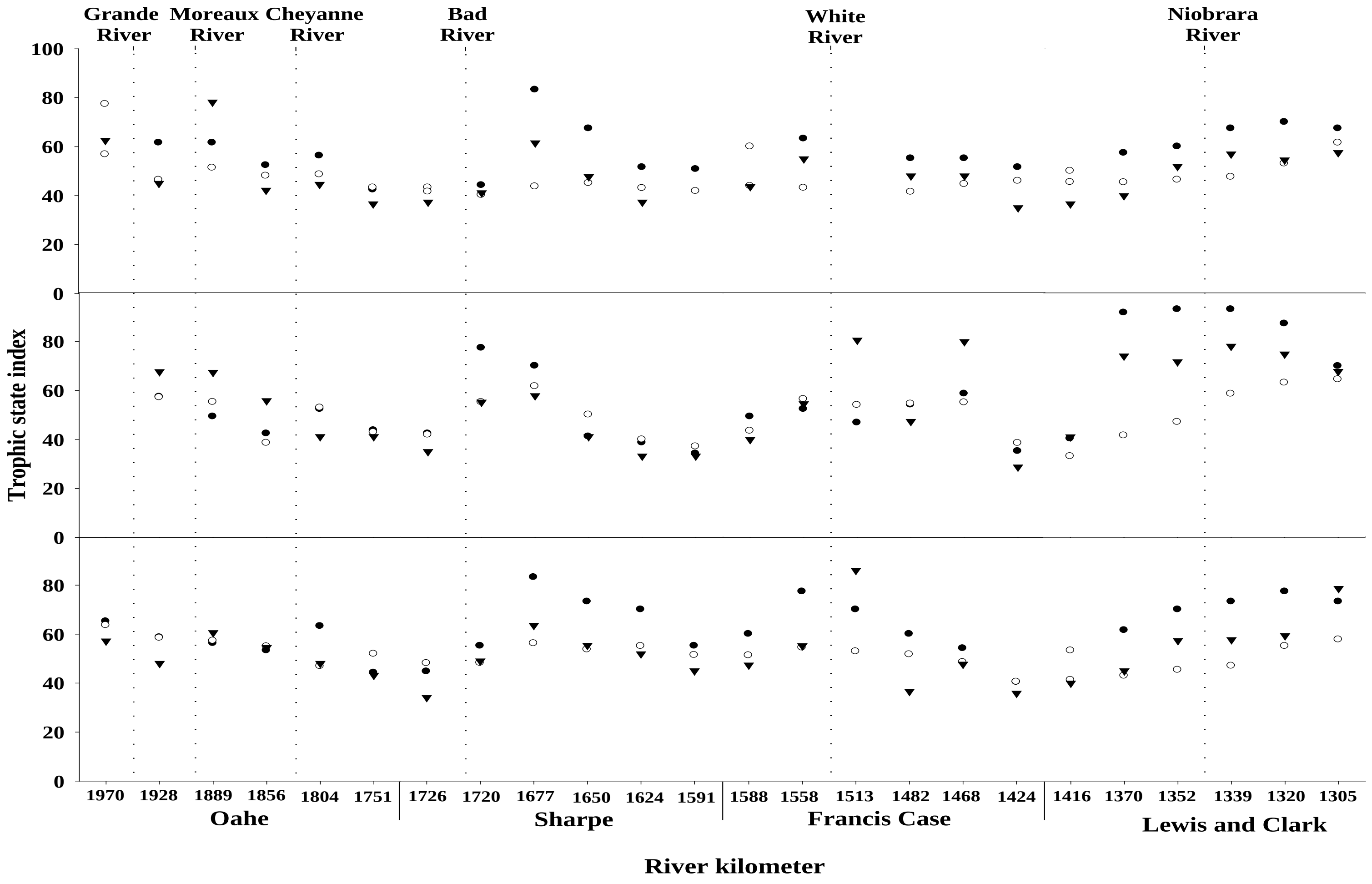
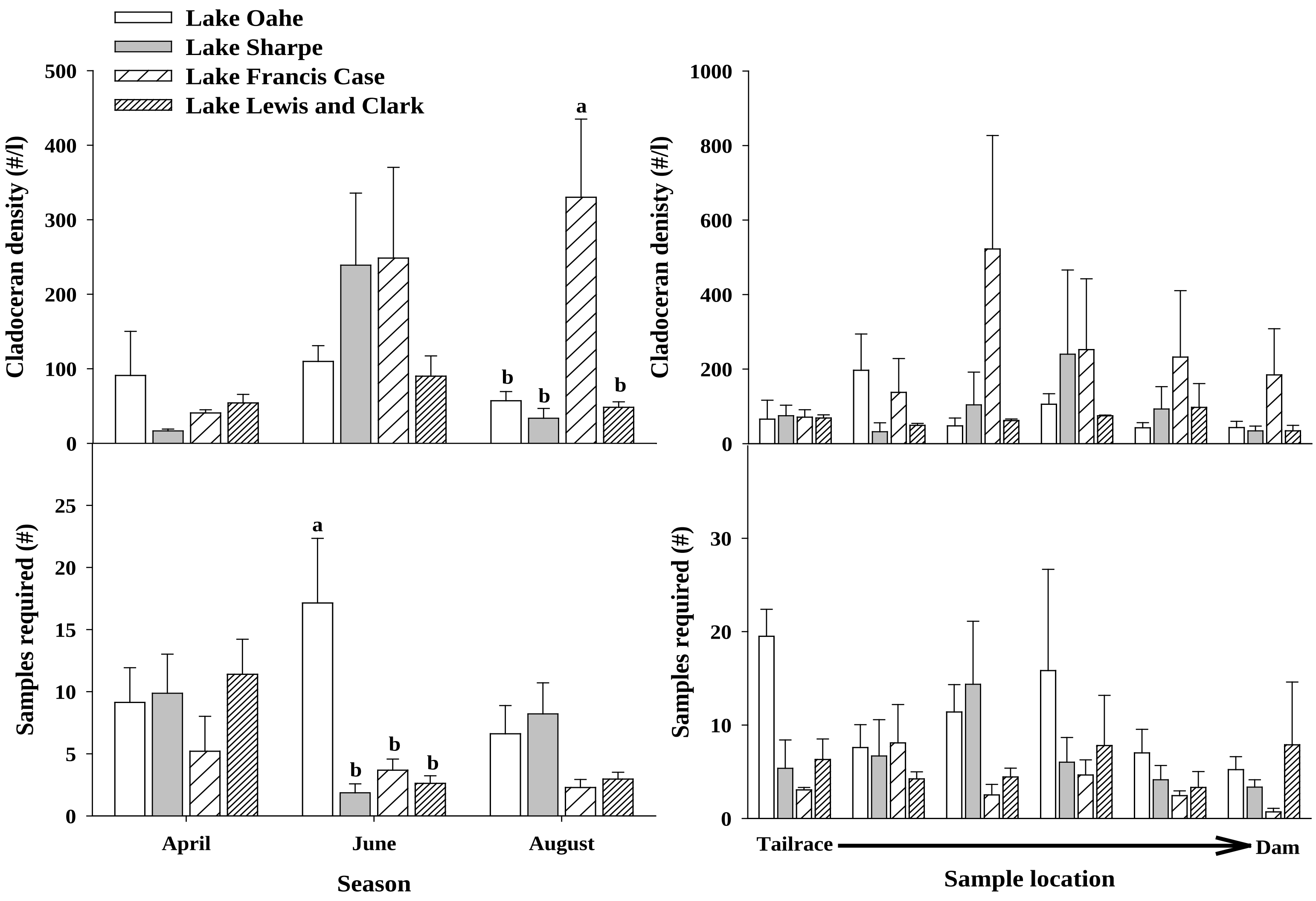

Grande River
Moreaux River
Cheyanne River
Bad River
White River
Niobrara River
100
80
60
40
20
0
Trophic state index
1970
1928
1889
1856
1804
1751
1726
1720
1677
1650
1624
1591
1588
1558
1513
1482
1468
1424
1416
1370
1352
1339
1320
1305
Oahe
Sharpe
Francis Case
Lewis and Clark
River kilometer

Figure 2-7.



Lake Oahe
Lake Sharpe
Lake Francis Case
Lake Lewis and Clark
Cladoceran density (#/l)
500
400
300
200
100
0
a
b
b
b
Cladoceran denisty (#/l)
1000
800
600
400
200
0
Samples required (#)
25
20
15
10
5
0
a
b
b
b
April
June
August
Season
Samples required (#)
30
20
10
0
Tailrace
Dam
Sample location

Chapter 3: Spatial and Temporal Variation in Larval Gizzard Shad Abundance in Lake Oahe, South Dakota: A Species at the Northern Edge of its Range

Abstract

Gizzard shad *Dorosoma cepedianum* have generally been restricted to the lower Missouri River impoundments in South Dakota. In recent years, gizzard shad numbers have increased in Lake Oahe, marking the northern most natural population and these increases could potentially affect recreational fishes. Specifically, questions arise about larval gizzard shad growth dynamics and if age-0 gizzard shad in Lake Oahe will exhibit fast or slow growth; both of which can have profound effects on piscivore populations in this reservoir. In this study, I evaluated larval gizzard shad hatch timing, growth and density in Lake Oahe, South Dakota. I collected larval gizzard shad from six sites in Lake Oahe from May through July, 2008 and used sagittal otoliths to estimate growth, and back-calculated hatch date. I found that larval gizzard shad densities exhibited bimodal peaks that were linked to water temperatures in Lake Oahe; hatching occurred earlier in the upper part of the reservoir compared to the lower portion. Peak larval gizzard shad density ranged from 0.6 to 33.6 (#/100m^3) and varied significantly among reservoir sites. Larval gizzard shad growth ranged from 0.24 to 0.57 (mm/day) and differed spatially within the reservoir. I found no relationship between larval gizzard shad growth or density and large or small bodied zooplankton density ($P>0.05$). Because this population exhibits slow growth and low densities, gizzard shad should remain a suitable forage option for recreational fishes in Lake Oahe, South Dakota.

Introduction

Gizzard shad *Dorosoma cepedianum* are an important prey resource for a suite of sport fishes (Storck 1986, Michaletz 1997, Michaletz 1998B). Gizzard shad are common in reservoirs and lakes throughout the Midwest and Southeastern U.S. and often represent a dominant component of the fish assemblage (Johnson et al. 1988; DeVries and Stein 1990). As an important prey resource, gizzard shad can strongly influence growth, recruitment and survival of predatory fishes (DeVries and Stein 1990; Garvey and Stein 1998; Bauer 2002). Predation of gizzard shad by recreational fishes, such as largemouth bass *Micropterus salmoides*, walleyes *Sander vitreus*, white crappies *Pomoxis annularis*, and white bass *Morone chrysops* is dependent on growth of age-0 gizzard shad (Michaletz 1997, Michaletz 1998). In some systems, gizzard shad produce slow growing individuals which remain vulnerable to fish predation for longer periods of time (Storck 1986, Michaletz 1997, Michaletz 1998, Allen et al. 1999), thus increasing growth of large predators (Michaletz 1997). In contrast, in systems where age-0 shad growth rates are high, shad quickly reach sizes that fishes are unable to exploit (Noble 1981). Hence, growth rate of age-0 gizzard shad has a strong influence on the quantity and timing of prey availability for predators.

One key difference in larval gizzard shad characteristics in the Northern Great Plains is the timing of gizzard shad availability. Because of colder water temperatures and subsequent delay in gizzard shad reproduction, the availability of shad is reduced compared to warmer, more southern reservoirs (see Wuellner et al. 2008 for review). Despite this late availability, gizzard shad in the Northern Great Plains show remarkable growth rates, the highest observed in North America (Wuellner et al. 2008). This high growth rate could be problematic when comparing the size of age-0 gizzard shad to the gape limitations of South Dakota piscivores. For instance, Kocovsky and Carline (2001) found that rapid growth rates of age-0 gizzard shad caused age-0 gizzard shad to be absent from walleye *Sander vitreus* diets in less than ten weeks post gizzard hatch.

In systems with slower larval gizzard shad growth, walleye exhibit increased growth rates (Santucci and Wahl 1993; Quist et al. 2002) and condition (Hartman and Margraf 2006) when foraging on shad alone. In addition, gizzard shad are particularly important when other forage species are dominated by spiny-rayed fishes (Wahl and Stein 1988; Einfalt and Wahl 1997). In Angostura Reservoir in western South Dakota, gizzard shad were stocked in 1990. In months prior to gizzard shad availability (both natural reproduction and stockings of pre-spawn adults), walleye growth is low but increases dramatically post gizzard shad stocking (Ward et al. 2007).

Recently, natural gizzard shad populations have become established in Lake Oahe in Central South Dakota and this marks the northern most range of gizzard shad in the United States. Because of the relationship between hatch timing, density and growth of larval gizzard shad to piscivore consumption and growth, I examined larval shad characteristics for this newly established population. Specifically, I examined hatch timing and related this to water temperatures throughout the reservoir. I also examined spatial differences in larval gizzard shad growth and density throughout Lake Oahe and compared these metrics to zooplankton densities.

Methods

Study area

Lake Oahe is the second largest impoundment on the Missouri River and extends from Bismarck, ND to Pierre, SD (Figure 3-1). At normal pool, the South Dakota portion of Lake Oahe has a surface area of approximately 145,000 ha, with a mean depth of approximately 19 m and a maximum depth of 67 m. The lower reservoir thermally stratifies in the summer and maintains an oxygenated hypolimnion; this coldwater habitat encompasses approximately 48,000 ha at operating pool.

I selected six equidistant sites within Lake Oahe to collect larval gizzard shad. These sites included from upstream to downstream Pollock, Mobridge, Swan Creek (Swan Crk.), Whitlock, Minneconjou and Spring Creek (Spring Crk.). Mobridge, Swan Crk., and Minneconjou sites are located directly downstream from large tributaries (i.e.,Grand, Moreau and Cheyenne Rivers, respectively; Figure 3-1). Additionally, Pollock and Whitlock sites are located adjacent to large embayments. The Spring Crk. site is novel because it has neither a local tributary nor large embayment in close proximity.

I placed temperature loggers in three locations within Lake Oahe representing upper (Pollock and Mobridge), middle (Swan Crk. and Whitlock) and lower (Minneconjou and Spring Crk.) Lake Oahe. Temperature loggers were placed one to three m below the water surface and averaged hourly water temperatures were recorded. These average temperatures were used to quantify mean daily water temperature from 14-April through 30-October.

Gizzard shad collection

I collected four ichthyoplankton samples per site every ten d from 1-May through 31-July. Samples were obtained using a 1-m conical ichthyoplankton trawl with 1,000 µg mesh (bar mesh). Surface circle trawls were towed for a minimum of 5 min, but did not exceed ten min in the open water portion of the reservoir. A flowmeter was mounted in the mouth of the trawl to estimate the volume of water filtered. I calculated larval gizzard shad density as the number of shad per 100 m^3 of water filtered.

In the laboratory, gizzard shad were enumerated and sagittal otoliths removed from ten randomly selected larval shad per sample. Hatch date for these fish was determined by counting the number of daily rings in the otoliths and adding 3.5 d to account for the first daily ring being formed 3.5 d post hatch (Davis et al. 1985). Daily growth of age-0 shad was determined by taking total length at time of capture, subtracting 5 mm for average length at hatching (Carlander 1969), and dividing by the adjusted age of the fish in days.

Zooplankton collection

I collected ten zooplankton samples at each site between 19- and 23-June. Samples were collected using a conical shaped Wisconsin net (10 cm diameter, 150 µm mesh), which was towed vertically from twice the Secchi depth to the surface (or from 1 m above the sediment to surface if water depth was less than twice the Secchi depth). I preserved zooplankton samples in 10% Lugol's solution and transported them to SDSU Northern Plains Biostress Laboratory. Zooplankton were subsampled (10%) for identification and enumeration and expressed as a volumetric density (#/L). Since larval gizzard shad exhibit differences in growth, density and survival when feeding on different size zooplankton (Bremigan and Stein 1997), I separated zooplankton samples based on relative size. The total number of large bodied zooplankton (primarily cladocerans >0.75 mm) or small bodied zooplankton (primarily copepod nauplii or calanoid copepods, <0.75 mm) was estimated for each sample.

Statistical analysis

I used a repeated measure ANOVA with a Tukey's pairwise comparison test to compare peak larval gizzard shad density between sites. Because larval gizzard shad growth rate data failed to meet normality requirements (Shapiro-Wilk Normality test $P>0.05$), I used an Kruskal-Wallis test order) to compare larval growth data with a Dunn's multiple pairwise test to test for significant differences in growth rates among sites. For all tests, I set $\alpha = 0.05$. I used a correlation matrix to examine relationships between larval gizzard shad growth and density and zooplankton density.

Results

Spring water temperatures were consistently higher in the upper reservoir, intermediate in the middle reservoir, and lowest in the lower reservoir (Figure 3-2). However, water temperatures increased at similar rates in the upper (1.3 °C/d), middle (1.2 °C/d) and lower (1.2 °C/d) sections of Lake Oahe. Larval gizzard shad hatch dates exhibited bimodal peaks in five of the six sites, which seemed to correspond to warming trends in the reservoir. Upper reservoir sections in Lake Oahe exhibited the earliest hatch dates (4-May in Pollock and 10-May in Mobridge), middle reservoir sections exhibited intermediate hatch dates (14-May in Swan Crk. and 21-May in Whitlock) and lower reservoir sections exhibited the latest hatch dates (18-May in Minneconjou and 19-May in Spring Crk.; Figure3-3).

Peak larval gizzard shad density ranged from 0.6 to 33.6 (#/100 m^3) at Spring Creek and Minneconjou, respectively, and was significantly different between sites ($F_{5,18}$=5.83; P=0.002; Figure 3-4). Peak larval gizzard shad density was significantly higher in Minneconjou compared to Spring Crk. or Whitlock. Similarly, larval gizzard shad growth ranged from 0.242 to 0.579 (mm/d) at Spring Creek and Minneconjou sites, respectively, and was significantly different among sites (H_5=103.595; P<0.001; Figure 3-5). Larval gizzard shad growth was significantly higher in Minneconjou compared to all other sites, and larval gizzard shad growth rates were higher in Pollock compared to Mobridge and Spring Crk (Figure 3-5).

Small bodied zooplankton density ranged from 201 to 1225 (#/L) in Pollock and Minneconjou, respectively. Large bodied zooplankton density ranged from 15 to 166 (#/L) in Pollock and Mobridge, respectively. Weak, non-significant positive relationships were found between small bodied zooplankton density (r = 0.39; p=0.16) and growth (r = 0.65; p = 0.57) of larval gizzard shad (Figure 3-6). I also found weak, non-significant negative relationships between both larval gizzard shad density (r = -0.62; p = 0.52) and growth (r = -0.34; p = 0.57) and large body zooplankton density (Figure 3-7). There was a strong, significant positive relationship between larval gizzard shad density and larval gizzard shad growth (r = 0.82; p = 0.046; Figure 3-8)

Discussion

Bimodal patterns in estimated hatch dates for gizzard shad revealed about a one month difference between the first hatch peak and the second peak in Lake Oahe. The exception to the bimodal hatching trend was the Spring Creek site, which is unique in that it has no associated tributary or large backwater embayment. One mechanism that could be contributing to bimodal gizzard shad spawning in Lake Oahe is that shad are exhibiting repeated spawning in this reservoir. An initial spawning takes place early with the second spawning bout a much lower magnitude. In Kansas reservoirs, gizzard shad are known to be fractional spawners (Willis 1987).

Because of the significant riverine (tributary) inputs in Lake Oahe, another plausible explanation for the bimodal peaks is that the initial spawn occurred in tributaries and(or) large embayments, that typically warm quicker than the main reservoir. Eventually, when the main lake warms to a suitable temperature-- a second, less pronounced, spawn appears to take place. Water temperature is known to be an important factor in the initiation of gizzard shad spawning (Scott and Crossman 1973), but because I did not measure water temperature in tributaries and back bays, this hypothesis needs further evaluation. Nonetheless, in other Missouri River impoundments, I have observed gizzard shad spawning first in back waters and tributaries prior to spawning in the main reservoir (Wuellner et al. 2008; B.D.S. Graeb, personal observation).

In either scenario, the bimodal spawning distribution likely increases the size variability of age-0 gizzard shad for piscivores. This prolonged spawn could have large benefits to cool water recreational fishes. For instance, in southern reservoirs, larval gizzard shad and warmwater recreational fishes often overlap in spawn timing. As a result, they compete for zooplankton as a prey source, a scenario which often has a detrimental outcome for recreational fishes (DeVries and Stein 1992; Stein et al. 1995). However, when compared to coolwater recreational fishes that spawn earlier in the spring, larval competition with gizzard shad is minimal, because they are rarely the same size classes to compete for zooplankton resources (Roseman et al. 1996).

Fast growing larval gizzard shad populations have been associated with reduced use by piscivores due to age-0 shad quickly moving past gape limitations of predators (Noble 1981; Adams and DeAngelis 1987). However, Lake Oahe shad populations have remarkably slower growth compared to other populations within South Dakota (Wuellner et al. 2008) and the Midwest (Dettmers and Stein 1992, DeVries and Stein 1992, Stein et al. 1995). For instance, larval gizzard shad growth rates in Lakes Sharpe, Francis Case and Lewis and Clark (South Dakota Missouri River impoundments) in 2003 and 2004 ranged from approximately 0.7 to 1.2 mm/d compared to the fastest growth witnessed in Lake Oahe at 0.6 mm/d. In western South Dakota reservoirs, slow growing age-0 gizzard shad are found in walleye diets as late as September (Ward et al. 2007). Despite the relatively early hatch dates, because of the slow growth that Lake Oahe shad exhibit, they appear to provide a suitable resource for piscivores in Lake Oahe. This is supported by observations of gizzard shad in Lake Oahe walleye diets as late as October in 2008 (Chapter 4).

In Lake Oahe, South Dakota, peak larval gizzard shad density exhibited a significant positive relationship to larval gizzard shad growth. This relationship is likely the result of the availability of suitable spawning areas or localized differences in adult gizzard shad population numbers, and further strengthens the argument that this is a low density population. In areas of higher peak larval densities, the habitat is suitable for adults (owing to the increased larval denisty) as well as for the fry. Essentially, in more productive areas, there are more spawners and subsequently more fry; and because it is more productive, the fry grow better.

In mesocosm experiments, larval shad growth is positively related to zooplankton density (Bremigan and Stein 1997) and results in substantial increases in larval gizzard shad survival. I found only weak non-significant relationships between growth and density of larval gizzard shad and both small and large bodied zooplankton density. However, the timing of zooplankton sampling was confounded as I collected zooplankton in late June, possibly when early hatching gizzard shad had switched foraging strategies to phytoplankton or detritus (Cramer and Marzolf 1970; Mundahl and Wissing 1987). To the contrary, back calculated larval gizzard shad growth rates in Lake Oahe were slow (i.e., < 0.6 mm/d) resulting in larvae ranging from seven to 20 mm in length at capture; therefore it is likely that these fish had not made the ontogenetic diet shift to phytoplankton or detritus.

In Lake Oahe, the slow gizzard shad growth rates make it an ideal prey resource for piscivores in this system. In more southern systems, age-0 gizzard shad have higher growth rates which allow them to quickly surpass many piscivore gape limitations. This scenario can result in depressed growth and condition of recreational fishes (Garvey and Stein 1998; Kim and DeVries 2000). In addition, *Sander spp.*, the most popular sport fish in South Dakota (Gigliotti 2007), exhibit strong positive relationships between growth and condition to gizzard shad presence (Ward et al 2007; Wuellner et al. 2010). Moreover, stockings of *Sander spp.*, are currently being conducted to coincide with peak gizzard shad densities to maximize *Sander spp.* growth and survival (Stahl and Stein 1994). Gizzard shad are also currently being stocked in small Western South Dakota reservoirs to bolster prey resources for walleye (Ward et al. 2007). In Lake Oahe, and other reservoirs in the northern Great Plains, it appears that larval gizzard shad exhibit temporal and spatial variability in abundance and growth; however, growth remains generally slow and density low compared to more southerly systems. These characteristics appear to make gizzard shad a suitable prey resource in reservoirs in South Dakota and throughout the northern Great Plains.

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Figure 3-1. Seasonal water temperature (^{o}C) from lower (solid line), middle (dottedline) and upper (hashed line) Lake Oahe, South Dakota, from 21-April through 28-July, 2008.

Figure 3-2. Mean hatching frequency (%) of gizzard shad collected from upper (Pollock and Mobridge), middle (Swan Crk. and Whitlock) and lower (Minneconjou and Spring Crk.) Lake Oahe, South Dakota, from 21-April through 14-July. Dates for peak hatching dates at each site are shown.

Figure 3-3. Peak larval gizzard shad density (#/100m^{3}) from upper (Pollock and Mobridge), middle (Swan Crk. and Whitlock) and lower (Minneconjou and Spring Crk.) Lake Oahe, South Dakota. Sampling site means with the same letter are not significantly different ($P>0.05$).

Figure 3-4. Larval gizzard shad growth (mm/day) from upper (Pollock and Mobridge), middle (Swan Crk. and Whitlock) and lower (Minneconjou and Spring Crk.) Lake Oahe, South Dakota. Sampling site means with the same letter are not significantly different ($P>0.05$).

Figure 3-5. Peak larval gizzard shad density (#/100m^{3}; top panel) and growth rate (mm/day; lower panel) in relation to small bodied zooplankton density (#/L) for upper (Pollock and Mobridge), middle (Swan Crk. and Whitlock) and lower (Minneconjou and Spring Crk.) Lake Oahe, South Dakota. Although non-significant, a weak positive relationship is observed between small bodied zooplankton density and density and growth of larval gizzard shad.

Figure 3-6. Peak larval gizzard shad density (#/100m^3; top panel) and larval gizzard shad growth (mm/day; lower panel) compared to large bodied zooplankton density (#/L) for upper (Pollock and Mobridge), middle (Swan Crk. and Whitlock) and lower (Minneconjou and Spring Crk.) Lake Oahe, South Dakota. Although non-significant, a weak positive relationship is observed between large bodied zooplankton density and growth and density of larval gizzard shad.

Figure 3-7. Peak larval gizzard shad density (#/100m^3; top panel) and larval gizzard shad growth (mm/day; lower panel) compared to larval gizzard shad growth (mm/day) at six locations from Lake Oahe, South Dakota.

Figure 3-1.

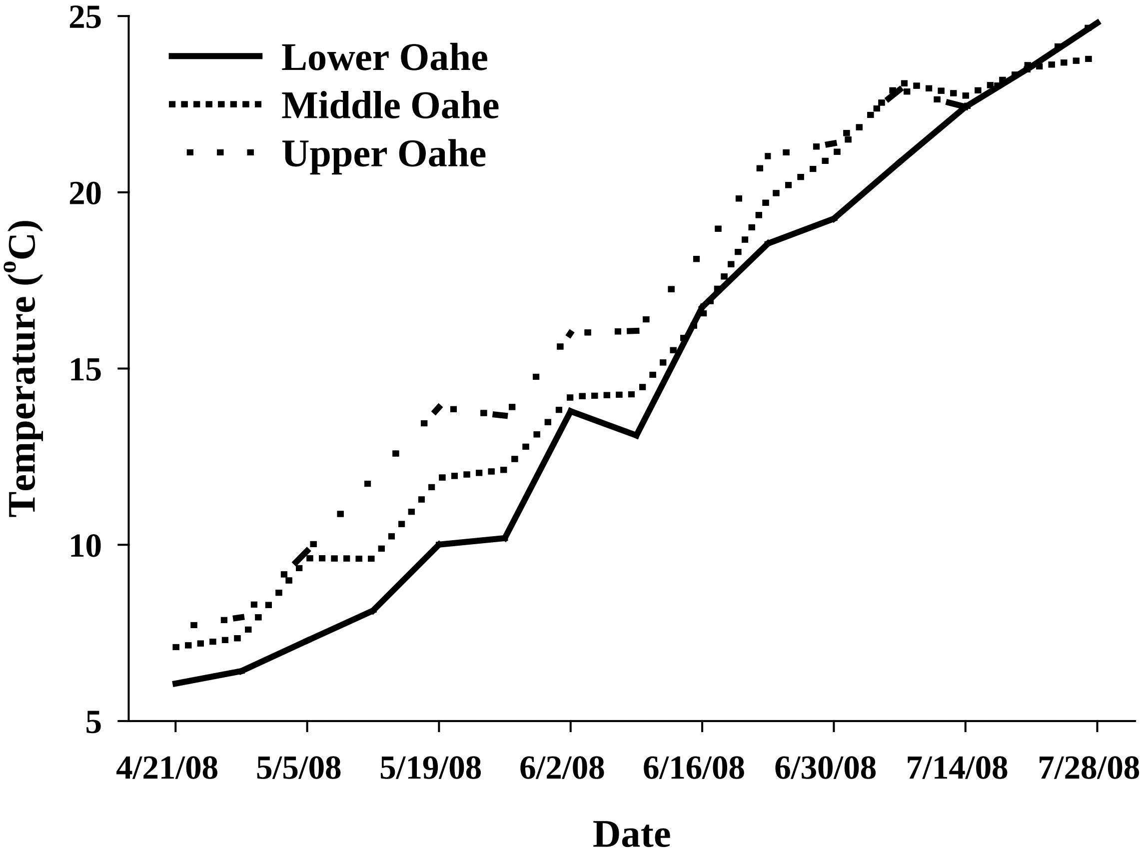

25
20
15
10
5
Lower Oahe
Middle Oahe
Upper Oahe
Temperature (^oC)
4/21/08
5/5/08
5/19/08
6/2/08
6/16/08
6/30/08
7/14/08
7/28/08
Date

Figure 3-2.

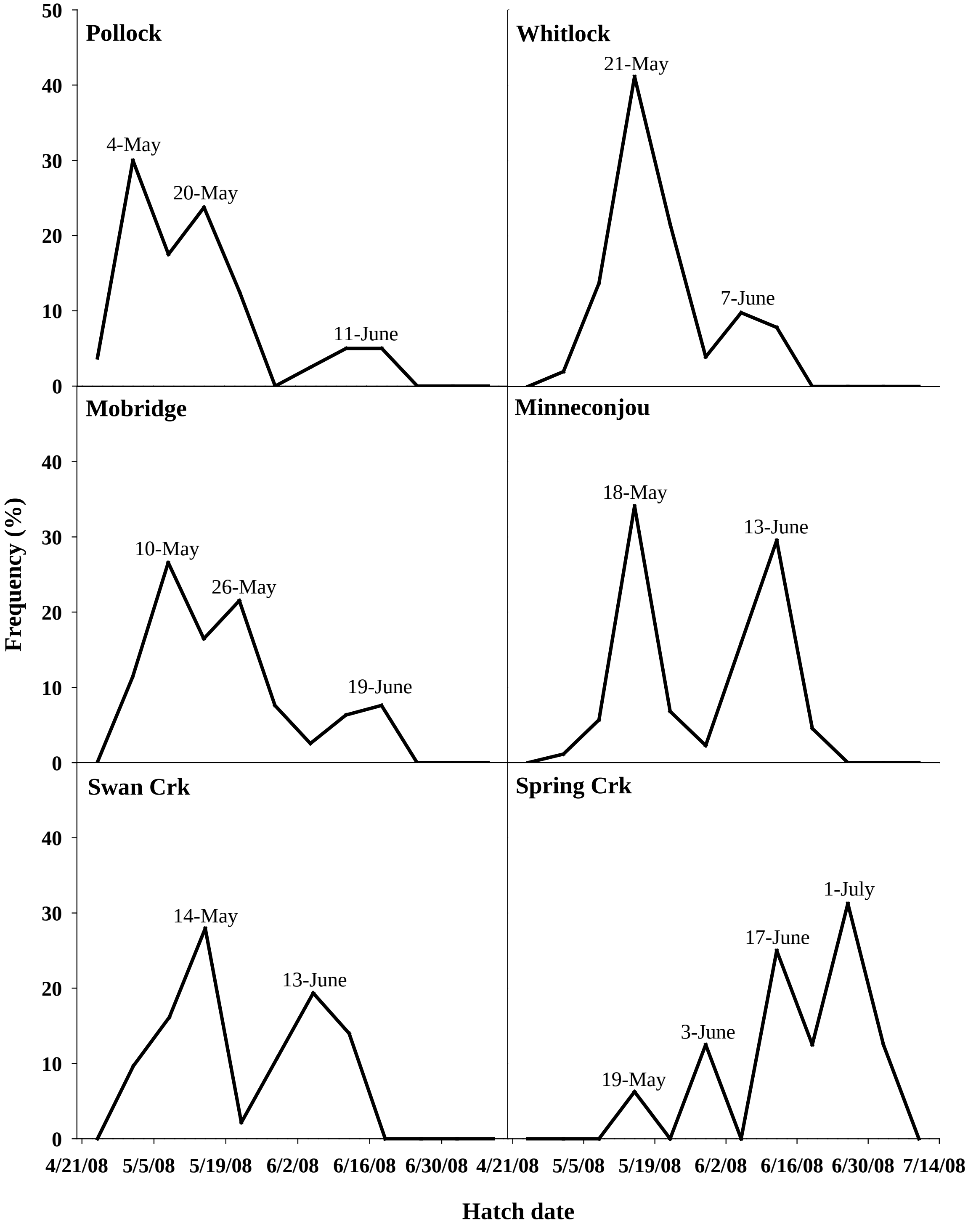

Pollock
4-May
20-May
11-June
Whitlock
21-May
7-June
Mobridge
10-May
26-May
19-June
Minneconjou
18-May
13-June
Swan Crk
14-May
13-June
Spring Crk
19-May
3-June
17-June
1-July
0
10
20
30
40
50
Frequency (%)
4/21/08
5/5/08
5/19/08
6/2/08
6/16/08
6/30/08
7/14/08
Hatch date

Figure 3-3.

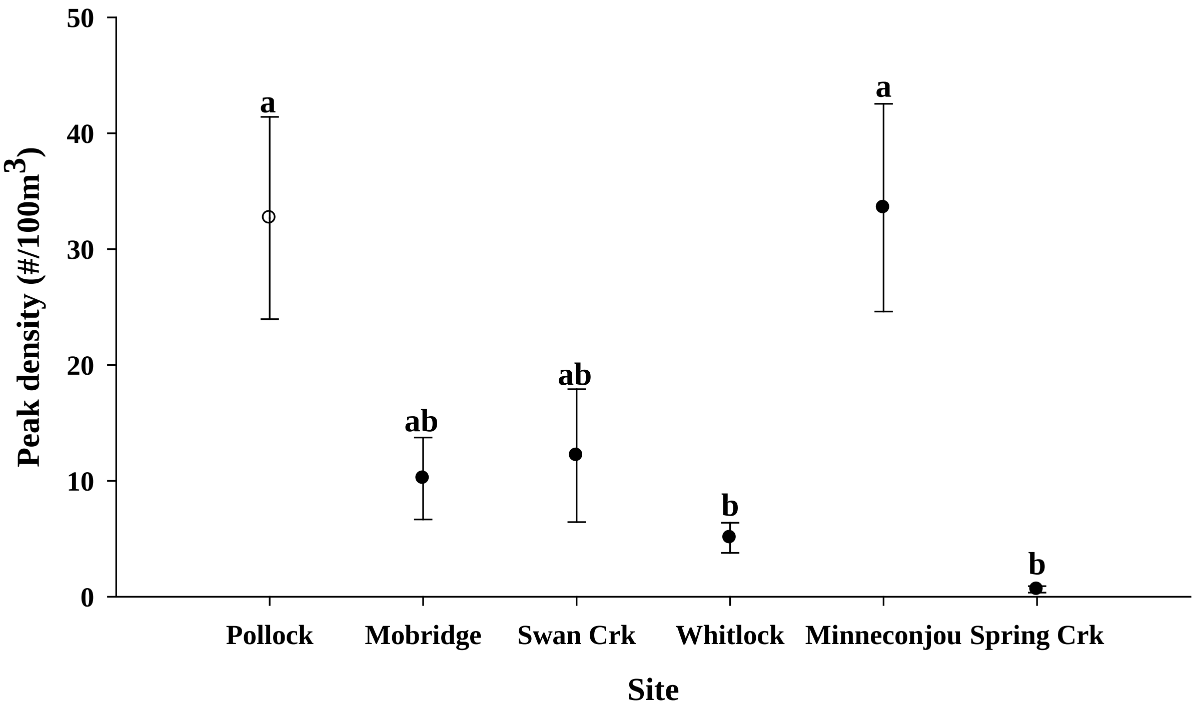

50
40
30
20
10
0
Peak density (#/100m^3)
a
ab
ab
b
a
b
Pollock
Mobridge
Swan Crk
Whitlock
Minneconjou
Spring Crk
Site

Figure 3-4.

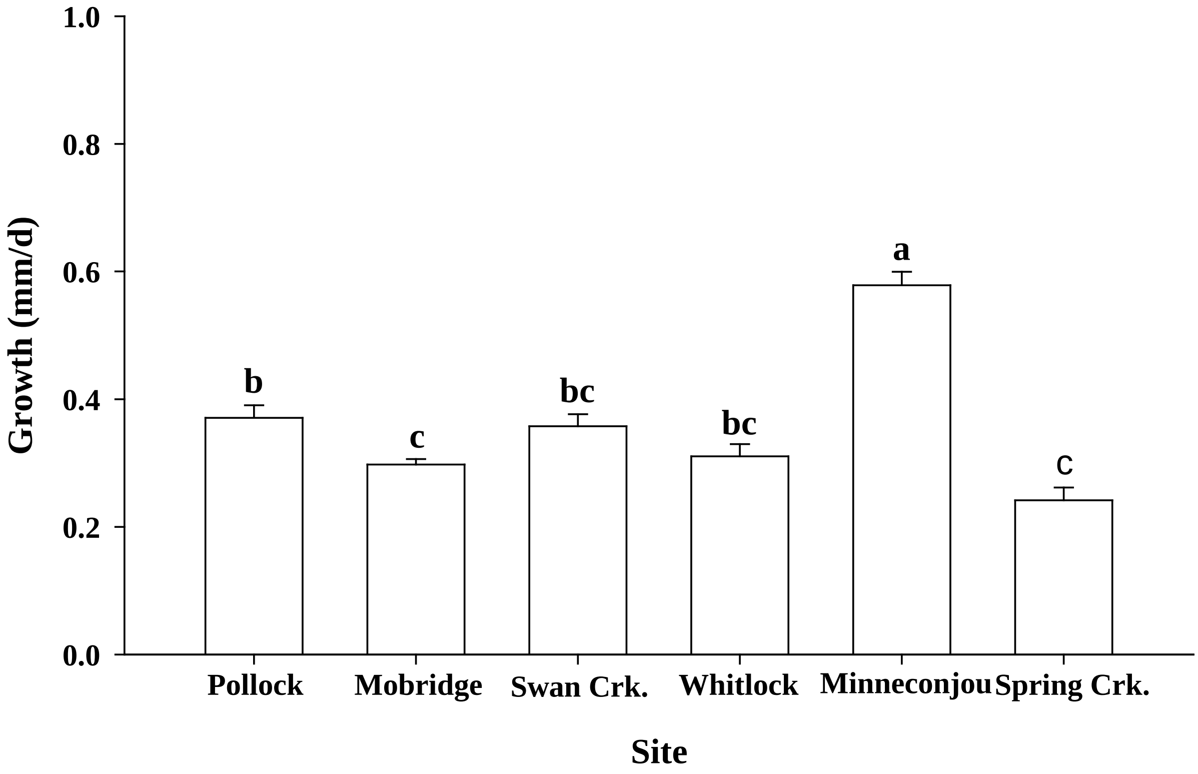

1.0
0.8
0.6
0.4
0.2
0.0
Growth (mm/d)
b
c
bc
bc
a
c
Pollock
Mobridge
Swan Crk.
Whitlock
Minneconjou
Spring Crk.
Site

Figure 3-5.

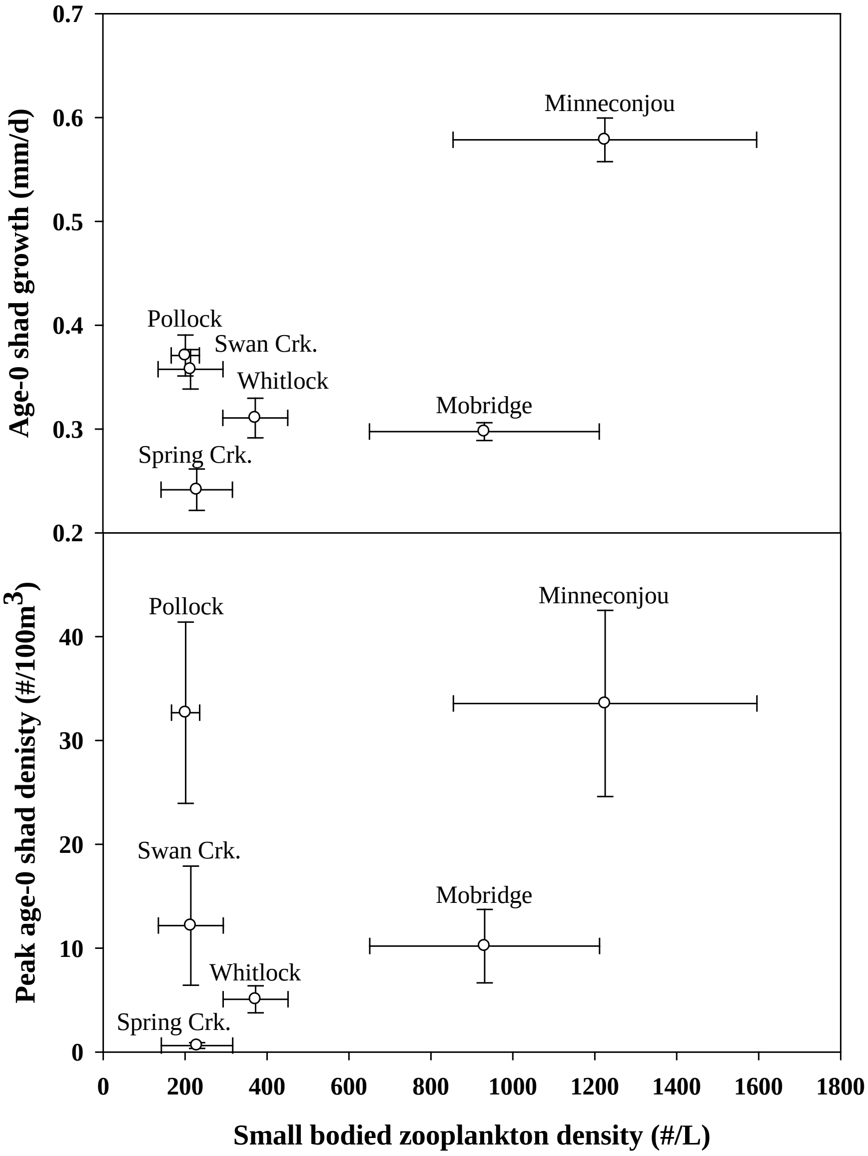
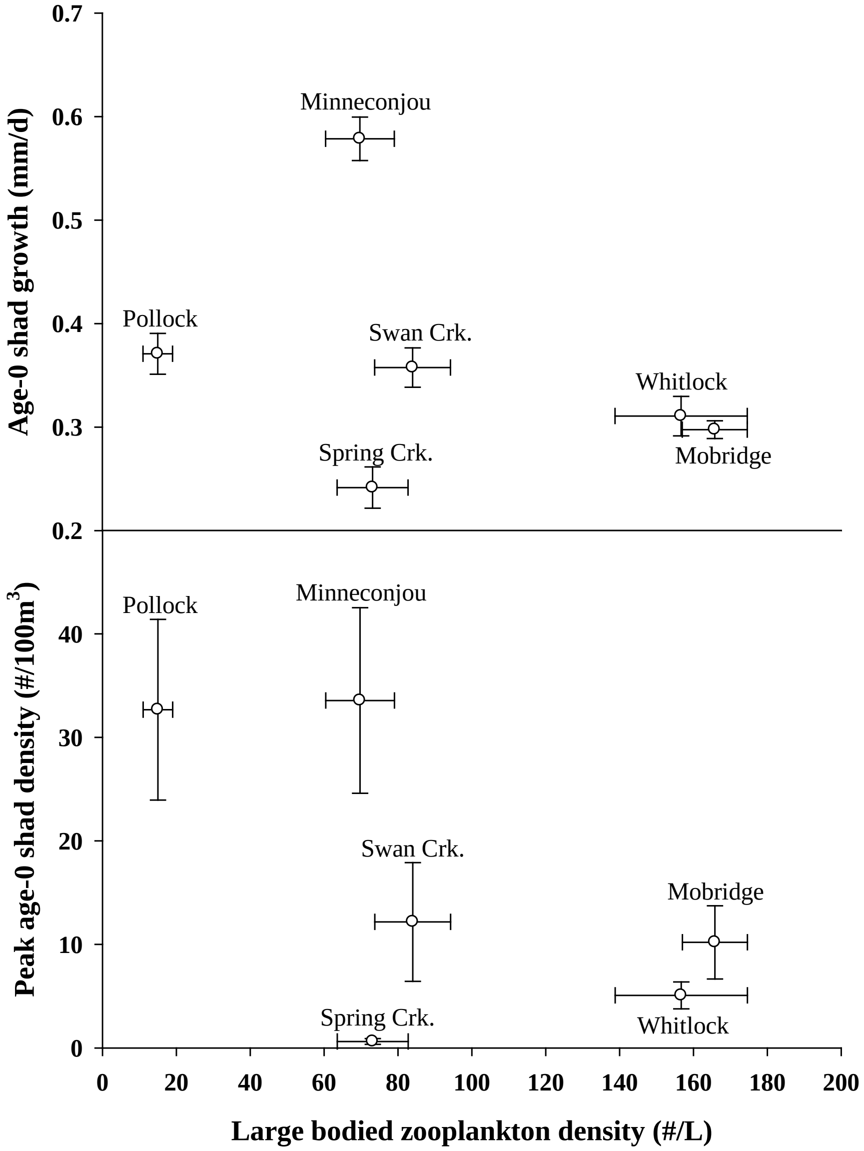
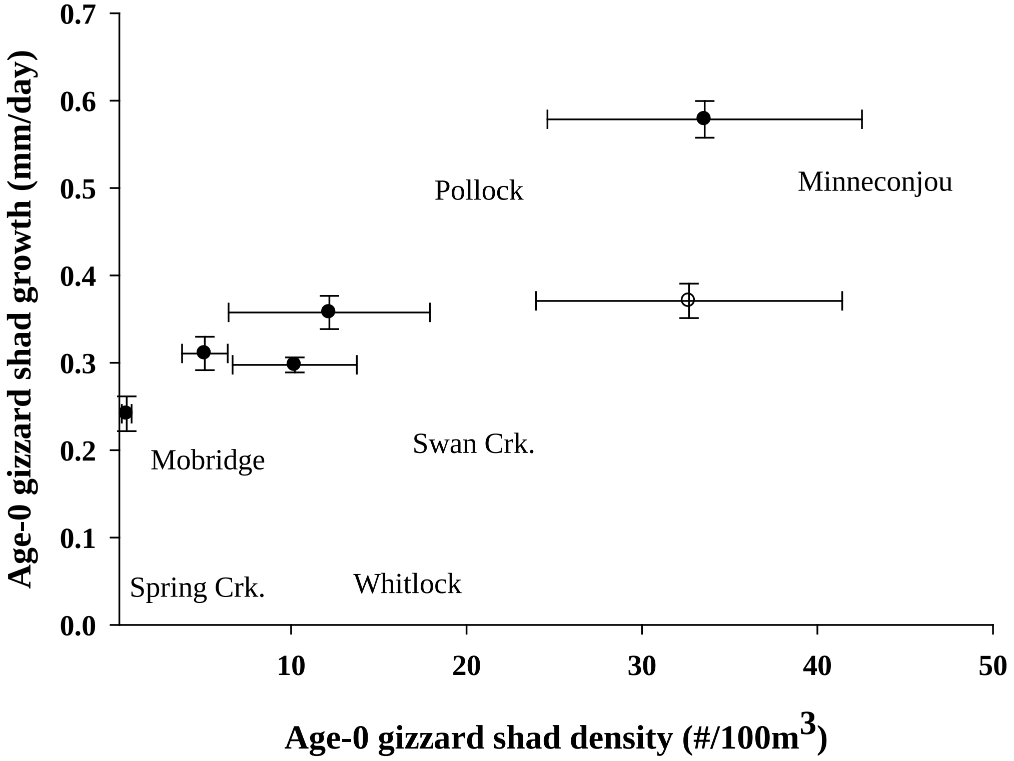

Age-0 shad growth (mm/d)
0.7
0.6
0.5
0.4
0.3
0.2
Minneconjou
Pollock
Swan Crk.
Whitlock
Mobridge
Spring Crk.
Peak age-0 shad denisty (#/100m^3)
40
30
20
10
0
Pollock
Minneconjou
Swan Crk.
Mobridge
Whitlock
Spring Crk.
0
200
400
600
800
1000
1200
1400
1600
1800
Small bodied zooplankton density (#/L)

Figure 3-6


Age-0 shad growth (mm/d)
0.7
0.6
0.5
0.4
0.3
0.2
Minneconjou
Pollock
Swan Crk.
Whitlock
Mobridge
Spring Crk.
Peak age-0 shad density (#/100m^3)
40
30
20
10
0
Pollock
Minneconjou
Swan Crk.
Mobridge
Spring Crk.
Whitlock
0
20
40
60
80
100
120
140
160
180
200
Large bodied zooplankton density (#/L)

.

Figure 3-7


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
10
20
30
40
50
Age-0 gizzard shad growth (mm/day)
Age-0 gizzard shad density (#/100m3)
Pollock
Minneconjou
Mobridge
Swan Crk.
Spring Crk.
Whitlock

Chapter 4: The Influence of Variable Prey Abundance on Walleye Growth in a Large Missouri River Reservoir

Abstract

Prey availability influences growth and condition of walleye in large reservoirs. In Lake Oahe, South Dakota, rainbow smelt are a primary prey of walleye, but their abundance varies significantly from year to year. Recently, gizzard shad have become established in Lake Oahe and their abundance has increased considerably. To evaluate the role of gizzard shad on walleye growth and condition in Lake Oahe, I compared recent estimates of walleye feeding and growth to that observed in the mid 1990s, when smelt abundance was high, and the early 2000s, when both smelt and shad abundances were low. In 2008, gizzard shad were the dominant prey item of walleye, representing about 60% of the diet by weight. However, by 2009, gizzard shad declined appreciably in the diet (22%) and were completely absent from walleye diets by 2010. Conversely, rainbow smelt abundance has increased since 2008 and represented 12%, 27% and 90% of walleye diets in 2008, 2009 and 2010, respectively. Analysis of long-term data revealed that growth rate of walleye foraging on gizzard shad (2008-2009) was intermediate to that of walleyes feeding on predominantly rainbow smelt (1993-1994) or mixed prey resources of invertebrates and fishes (2001-2002). Because gizzard shad are available during short time periods (< 2 months) in late summer, walleye can only achieve about 50% of their yearly maintenance requirements from this prey source. Conversely, rainbow smelt, which are available and consumed year round, provide a continuous energy source that contributes to high growth rates. Nonetheless, when abundant, gizzard shad can provide an important subsidy to Lake Oahe walleyes during periods of low rainbow smelt abundance.

Introduction

Prey fish availability is an important factor regulating piscivore growth and survival in large reservoirs (Ney and Orth 1986; Porath and Peters 1997; Meerbeek et al. 2002). In the absence of a dominant prey base, piscivores are often forced to consume a wide range of prey types resulting in increased energy expenditures and reduced growth and survival (Graeb et al. 2008). Thus, documenting the importance of prey availability to fish growth can have important implications for management – particularly in systems characterized by variable prey resources. Bioenergetics models (BEMs) have been used as a tool to document the importance of prey resources and the energy allocation they provide for predator growth (BEMs; Chipps and Wahl 2008).

Walleye *Sander vitreus* are a top-level piscivore that are widely distributed in North America (Henry et al. 2008). They represent a popular sport fish in the United States (Hushak et al. 1986) and are the most sought game fish in South Dakota (Gigliotti 1999). Lake Oahe, a large impoundment on the Missouri River, is nationally recognized as a trophy walleye fishery. In 1999, Lake Oahe had the largest percentage of total resident and nonresident angling trips of any body of water in South Dakota (Gigliotti 1999). During the mid-1990s,studies showed that walleye diets consisted primarily of rainbow smelt *Osmerus mordax* (~95%; Bryan 1995) and bioenergetics modeling revealed that consumption of rainbow smelt contributed to some of the fastest walleye growth rates ever reported for the Missouri River (Graeb et al. 2008).

By the early 2000s, the rainbow smelt population in Lake Oahe declined, owing to high water levels in the Missouri River and subsequent entrainment of smelt through

Lake Oahe dam (Unkenholz 1998). The reduction in consumption of rainbow smelt led to reduced growth rates and increased natural mortality of walleyes, particularly for larger, older fish (>3 years of age; Graeb et al. 2008). Angling effort for walleyes during the early 2000s was considerably lower than all previous estimates from the 1990s (Lott et al. 2000), and about 50% below the Lake Oahe Strategic Plan goal of 1 million-angler h (South Dakota Game, Fish and Parks, unpublished data). The decrease in angling pressure was due directly to the decrease in the average size of walleye caught (Lott et al. 2000).

In recent years, gizzard shad *Dorosoma cepedianum* have become established in Lake Oahe and their numbers have increased considerably (Figure 4-1). Furthermore, rainbow smelt have been increasing in abundance in Lake Oahe since the early 2000s, though their population remains below that observed in mid 1990s. Given the recent expansion of the gizzard shad population, it is unclear what role gizzard shad have on feeding and growth dynamics of walleye. Linking new information with previous bioenergetics modeling efforts will provide important data for understanding the effects of variable prey populations on walleye growth dynamics. Thus, the objective of this study was to document changes in feeding, growth and energy allocation for walleye as influenced by variable prey abundance in Lake Oahe.

Methods

Study area

Lake Oahe is the second largest impoundment on the Missouri River, and extends from Bismarck, ND to Pierre, SD (Figure 4-2). At normal pool, the South

Dakota portion of Lake Oahe has a surface area of approximately 145,000 ha, with a mean depth of approximately 19 m and a maximum depth of 67 m. The lower reservoir thermally stratifies in the summer and maintains an oxygenated hypolimnion, and this coldwater habitat encompasses about 48,000 ha at operating pool.

Walleye collection

I collected walleye seasonally (May, July and October) from 2008 through 2010 in Lake Oahe. Six sites were chosen at equal distances to encompass all reservoir zones within the South Dakota portion of the lake. Because walleye feed predominantly at night and during crepuscular periods (Forney 1977), I set experimental mesh gill nets before sunrise and retrieved them within two h. Captured walleye were measured for total length (TL; mm) and weight (g), then immediately placed on ice and stomachs removed within one hr. Stomach contents were preserved in ethanol for later identification.

In the laboratory, sagittal otoliths were removed from walleyes and used for age determination. Each otolith was aged independently by two experienced technicians. Any discrepancies in walleye age were reviewed by a third individual to finalize the age of the fish.

Walleye growth

I calculated mean monthly length at age for walleye and used these data to derive a von Bertalanffy growth function (Gallucci and Quinn 1979). Initial and final lengths for each year class were determined using the equation

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

where L_t= length (mm) at time t, and L_∞, K and t_0 are fitted parameters in the von Bertalanffy growth function (Table 4-1). Walleye length was converted to initial or final mass using weight-length regression equations derived from each year (Table 4-1). Age-specific annual growth rate (g/year) was used as input into the bioenergetics model to estimate annual consumption for Lake Oahe walleyes (see below).

Bioenergetics modeling

I used a bioenergetics model (Fish Bioenergetics 3.0; Hanson et al. 1997) to estimate age-specific consumption by walleyes collected from 2008-2010. The walleye bioenergetics model used here has been applied in a number of field and laboratory studies (Ney 1993; Whitledge 2006; Lantry et al. 2008; Madenjian et al. 2010) to quantify prey use. To evaluate the influence of gizzard shad on walleye energetics, I compared my results to those reported by Graeb et al. (2008) for two time periods: a period characterized by high rainbow smelt use (1993-1994) and a period were rainbow smelt and gizzard shad were poorly represented in the diet (2001-2002). Input data for the model included age-specific growth, mean weekly water temperature, seasonal diet composition of walleyes, prey energy density, and walleye energy density.

Data on water temperature were collected using temperature loggers (Hobo Inc.) placed 2-3 m below the water surface at three equidistant locations in Lake Oahe. Mean weekly water temperatures were averaged across the reservoir and used as input in the model. In general, seasonal patterns in water temperature were similar from 2008 through 2010; however, due to increasing water levels from above average rainfall, 2009 showed a faster warming trajectory than 2008 or 2010 (Figure 4-3).

Walleye diets

In the laboratory, stomach contents of walleyes were identified to species when possible, enumerated and weighed for wet mass. Because prey digestion was minimized by my short-term gill net sets, unidentifiable prey represented < 6% percent of total diets (by weight). Prey items found in the stomachs of walleye were assumed representative of consumption during the previous night of feeding (Lantry et al. 2008). I calculated the percent composition by weight for prey items in individual walleye stomachs and averaged this by year class to use as input in the bioenergetics model.

Prey and predator energy density

Prey fish were collected in August of 2008, 2009 and 2010 using standard seining techniques (Bonar et al. 2009). No cold water prey fish were collected during the standard prey fish collections, so 15 rainbow smelt were obtained by South Dakota Game, Fish and Parks (SDGFP) personnel and ten Chinook salmon *Oncorhynchus tshawytscha* were obtained from a SDGFP hatchery. All prey fish were measured (mm), weighed (g) and dried at 60^{o}C for 72 h. Energy density of prey fishes was then determined using bomb calorimetry.

After removing stomachs and otoliths, walleye were weighed to obtain a wet weight and then dried to a constant weight at 60°C to obtain dry weight. Dry-to-wet weight ratio of each fish was calculated and used to estimate energy density (J g wet wt^{-1}) as reported by Hartman and Brandt (1995). I then averaged walleye energy densities from all individuals within each sampling time period and used the seasonal energy densities as input parameters in the bioenergetics models.

Modeling input was based on the average individual of each year class and simulations were run from May 1 through October 31 (184 days) to encompass the typical walleye growing season in Lake Oahe (Carlander 1997; Davis 2004). I estimated age-specific, total consumption of 1) rainbow smelt, 2) gizzard shad, and 3) other prey (as combined categories) for 2008-2010 and compared these estimates to values reported by Bryan (1995) and Graeb et al. (2008).

Because water temperature, fish size, and prey quality can affect the relationship between growth and consumption, I calculated net consumption (kcal/year) by subtracting maintenance cost incurred over the year from gross annual food consumption (Hewett and Kraft 1993). A positive value for net consumption indicates the amount of surplus energy available for growth after accounting for maintenance costs. A negative value implies that fish did not obtain sufficient energy to meet minimum maintenance requirements (i.e., they lost weight over the sampling interval). To compare age-specific energy intake among years (1993-1994, 2001-2002, 2008-2010), I expressed gross annual consumption for each prey category as a percentage of total maintenance cost. This index allowed us to make relative comparisons of prey-specific consumption that were standardized to the maintenance requirement of the fish.

Results

Walleye diets and growth

I collected a total of 836 walleye from 2008-2010. Of these, the number of fish that had diet items in their stomachs was relatively high with 206 (79.5%), 208 (75.1%) and 210 (70.0%) walleye containing diet items in 2008, 2009 and 2010, respectively.

Gizzard shad were present in walleye diets in 2008 and 2009, but were only present in the summer and fall sampling periods. Gizzard shad were completely absent from walleye diets in 2010 (Table 4-2). Conversely, rainbow smelt were present in walleye diets in every sample except for spring of 2008. Invertebrates, primarily ephemeridae mayflies, were an important diet item in the spring of 2008 and 2009, but declined appreciably in 2010. Nine other fishes were observed in walleye diets and included Chinook salmon *Oncorhynchus tshawytscha,* white bass *Morone chyrsops,* channel catfish *Ictaluris punctatus,*spotail shiner *Notropis husonius,* emerald shiner *Notropis atherinoides,* yellow perch *Perca flavescens,* lake herring *Coregonus artedii,*freshwater drum *Aplodinotus grunniens,* and white crappie *Pomoxis annularis*. Annual stocking of Chinook salmon overlapped with the 2008 spring diet sampling; thus, Chinook salmon represented a large portion of the spring walleye diets in 2008. However, this is likely a localized and short lived occurrence as salmon are only stocked in one location and susceptibility likely declines appreciably after stocking. In the summer of 2009, Lake Oahe experienced a large white bass year class and these fishes were numerically dominant in the summer of 2009 walleye diets.

Growth rates of walleyes varied among years. In general, mean weight of ages 1 through 3 walleye was similar from 2008-2010, and also similar to values reported from 1993 to 1994 (Figure 4-4). However, in 2010 mean weight of age-4 and older walleye, was generally greater than other years, except when rainbow smelt were abundant in 1993-1994. In 2008 and 2009, gizzard shad represented an important component of the diet (i.e., > 40%) and walleye displayed greater growth rates compared to 2001-2002, when few shad or smelt were represented in the diet (Figure 4-4). However, growth of walleyes greater than age 4 was notably lower in 2008 and 2009 than that observed when smelt abundance was high (i.e., 1993-1994; Figure 4-4). Age 1 through 3 fish in 2008 through 2010 were larger than previous years, but growth rates and weight at age of older fish (>4) was greater for 1993-1994 compared to other periods.

Bioenergetics modeling

Bioenergetics estimates of gross annual consumption ranged from 1,453 to 3,663, 1,578 to 4,099 and 847 to 2,357 kcal/year for walleyes collected in 2008, 2009 and 2010, respectively. During this time period, gross annual consumption was generally higher compared to 2001-2002 (421 to 2857 kcal/year), but less than that reported during the high rainbow smelt period in 1993-1994 (801 to 6274 kcal/year; Graeb et al. 2008).

Although a significant part of walleye diets in 2008-2009, gizzard shad alone were not sufficient to meet maintenance energy requirements of walleye. Gizzard shad represented between 28% to 64% and 24% to 44% of their maintenance energy requirements in 2008 and 2009, respectively (Figure 4-5). Gizzard shad were not observed in walleye diets in 2010. Unlike gizzard shad, rainbow smelt where present in all years and walleye were able to exceed maintenance energy requirements in 2010 by consuming only rainbow smelt alone. Depending on walleye size (age), rainbow smelt represented between 1% to 59%, 6% to 45%, or104% to 127% of walleye maintenance requirements in 2008, 2009 and 2010 respectively. The contribution of other prey types (non- shad or smelt) to walleye energy requirements was similar in 2008 and 2009, but lower in 2010 (Figure 4-5).

Wuellner et al. (2010) documented high levels of gizzard shad consumption by walleye in Lake Sharpe (immediately downstream from Lake Oahe) starting in late July. High rates of gizzard shad consumption remained constant from August through October. In Lake Sharpe, gizzard shad hatch dates are generally earlier than Lake Oahe (Wuellner et al, 2008; M. Fincel unpublished data). Nonetheless, density of appropriate-sized gizzard shad could have peaked in Lake Oahe during August of 2008 and 2009 but not been documented by my sampling schedule. To account for this potential bias, I modeled gizzard shad consumption by applying the observed diet composition in October to August 1 (day 93 of simulation) – which likely provided a liberal estimate of gizzard shad use. Despite the potential increase of gizzard shad consumption, walleye still failed to meet maintenance energy demands by foraging on gizzard shad alone (Figure 4-6). In 2008 and 2009, the potential energetic contribution of gizzard shad, averaged by age class, was 56% and 45% of walleye yearly maintenance requirement (Figure 4-6).

Discussion

In the absence of other dominant prey types (i.e., rainbow smelt), gizzard shad are an important resource for walleye. In Lake Oahe, walleye derived between 40% and 60% of their maintenance energy requirements by consuming gizzard shad alone. Compared to the early 2000s, when overall consumption was low, this represents an important subsidy to Lake Oahe walleye when rainbow smelt abundance is reduced. Other studies report similar findings where walleye growth (Santucci and Wahl 1993; Quist et al. 2002) and condition (Hartman and Margraf 2006) are enhanced by the availability and use of gizzard shad. In addition, gizzard shad are particularly important when the forage base is dominated by spiny-rayed fishes (Wahl and Stein 1988; Einfalt and Wahl 1997). In Angostura Reservoir, South Dakota, walleye growth is slow during months prior to shad availability, but increases appreciably once walleye switch to foraging on gizzard shad (Ward et al. 2007).

The timing of gizzard shad availability in the Northern Great Plains plays a key role in walleye bioenergetics. Because of colder water temperatures and the subsequent delay in reproduction of gizzard shad, the availability of shad is reduced compared to warmer, more southern reservoirs (see Wuellner et al. 2008 for review). In Lake Sharpe, Wuellner et al. (2010) showed that gizzard shad represented 80% of walleye diets as early as June; however, this was during a drought period with unusually mild winters and earlier summers. Despite late spawning, gizzard shad in the Northern Great Plains show remarkable growth rates at these northern latitudes (Wuellner et al. 2008). Such fast growth rates could limit foraging opportunities by walleye, given the importance of gape-limitation and its effects on foraging efficiency. For instance, Kocovsky and Carline (2001) found that because of rapid growth, age-0 gizzard shad were absent from walleye diets as early as September as they grew too large for fish to consume.

Lake Oahe marks the northern range of gizzard shad in the Great Plains (Wuellner et al. 2008). Variable climactic conditions (i.e., long, harsh winters) likely constrain overwinter survival of gizzard shad and create ‘boom’ or ‘bust’ cycles in shad recruitment. Mild winters and drought conditions from 2000-2005 may have provided favorable conditions for gizzard shad in Lake Oahe. However, since 2007, South

Dakota has experience more severe winters with greater snowfall and subsequent increased water levels in Lake Oahe. Water levels rose appreciably from 2009 to 2010 leading to cooler, spring water temperatures in Lake Oahe; these conditions were associated with a reduction in gizzard shad abundance, as indicated by the absence of gizzard shad from field surveys and walleye diets in 2010.

Given the likelihood for increased warming in the Northern Great Plains (Poiani et al. 1996) gizzard shad occurrence may become more frequent in Lake Oahe and other systems throughout the Northern Great Plains. In addition, gizzard shad have recently been stocked in several lakes and reservoirs of the Dakotas where they are viewed as a benefit to piscivore growth and size structure (see Wuellner et al. 2008 for a review). Although walleye predation demand is larger than the observed gizzard shad biomass (determined by gizzard shad accounting for ~50% of maintenance energy; Cyterski et al. 2003), in the absence of a large rainbow smelt population, gizzard shad appear to be an important alternative forage resource and energetic subsidy.

Since the population increase of gizzard shad in Lake Oahe, rainbow smelt numbers have been increasing (Figure 4-7). This is likely a function of increasing reservoir productivity and/or increased coldwater habitat owing to increased water levels since 2007. However, gizzard shad likely aided in the recovery of the rainbow smelt population by acting as an alternative prey resource for walleye, thus releasing predation on rainbow smelt. In a related example, alewives appear to buffer predation of stocked brown trout by walleye by acting as an alternative prey resource (Johnson and Rakoczy 2004). As a result, Johnson et al. (2009) recommended stocking windows of brown trout to coincide with peak abundance of alewives to promote alternative predation on alewives. Future research may examine the potential to use gizzard shad as an alternative forage resource to mediate predation on declining rainbow smelt populations.

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Table 4-1.Von Bertalanffy and weight length regression parameters from Lake Oahe walleye in 1994, 2001 and 2008 through 2010.

	von Bertalanffy growth parameters			Weight length regression parameters		
Year	$L\infty$	K	t_0	intercept	slope	r^2
[a]1994	1025	0.097	-1.475	-5.5838	3.2277	0.988
[a]2001	714	0.116	-1.810	-5.4580	3.1530	0.996
2008	690	0.165	-2.155	-5.2730	3.0940	0.983
2009	718	0.146	-2.352	-5.4900	3.1770	0.970
2010	720	0.165	-1.869	-5.4410	3.1640	0.978

[a] Growth parameters obtained from Graeb et al. (2008), and length-weight regression parameters obtained from Bryan (1995) and Davis (2004)

Table 4-2. Percent composition (wet weight) of the diets of walleye collected from Lake Oahe in 1994, 2001, and 2008 through 2010.

Year	Season	[b]Invertebrates	Gizzard shad	Rainbow smelt	[a]Other fish
[c]1994	Spring	0.0	0.0	76.6	22.5
	Summer	0.0	0.0	88.3	10.6
	Fall	0.0	0.0	96.8	1.9
[d]2001	Spring	68.0	0.0	18.0	11.0
	Summer	28.0	0.0	22.0	50.0
	Fall	0.0	11.0	56.0	33.0
2008	Spring	25.0	0.0	0.0	75.0
	Summer	29.0	13.1	32.4	25.7
	Fall	0.0	80.1	16.1	3.7
2009	Spring	58.0	0.0	38.4	3.6
	Summer	7.4	16.5	13.4	62.7
	Fall	1.5	49.7	44.6	4.2
2010	Spring	3.1	0.0	95.3	1.6
	Summer	0.7	0.0	83.5	15.9
	Fall	0.1	0.0	93.4	6.5

[a] Other fish included Chinook salmon *Oncorhynchus tshawytscha*, white bass *Morone chyrsops*, channel catfish *Ictaluris punctatus*,spotail shiner *Notropis husonius*, emerald shiner *Notropis atherinoides*, yellow perch *Perca flavescens*, lake herring *Coregonus artedii*, freshwater drum *Aplodinotus grunniens*, and white crappie *Pomoxis annularis*

[b] invertebrates included ephemeridae, chironomidae, Odonataand crustacean zooplankton

[c] 1994 diet data obtained from Bryan (1995)

[d] 2001 diet data obtained from Davis (2004)

Figure 4-1. Estimated rainbow smelt density (open bars) and age-0 gizzard shad CPUE (hashed bars - catch per unit effort) in Lake Oahe, South Dakota from 1999 through 2005.

Figure 4-2.Map of Lake Oahe in Central South Dakota.

Figure 4-3. Mean daily water temperature (^{0}C) taken every two weeks in 2008 (filled circles), 2009 (open circles) and 2010 (filled triangles) collected from May 1st through October 31st in Lake Oahe, South Dakota.

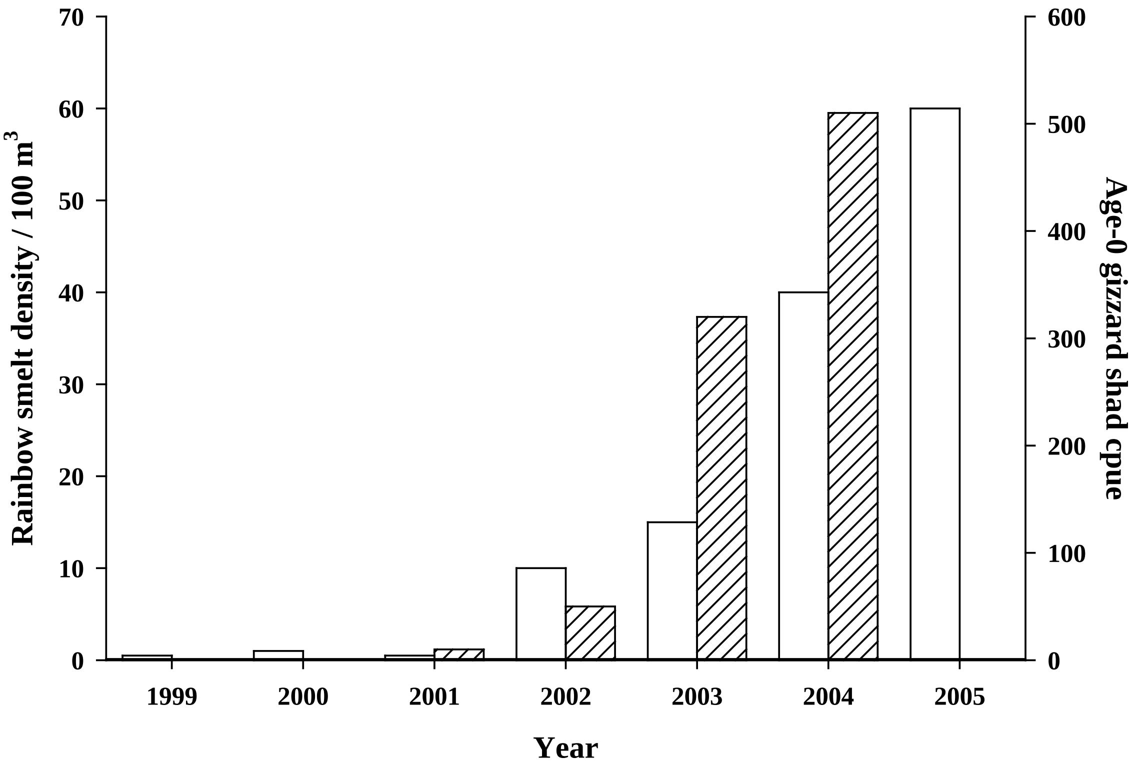
Figure 4-4. Mean mass (g) of age-1 through age-6 walleye collected from Lake Oahe, South Dakota in 1994 (open squares), 2001 (open triangles), 2008 (filled triangles), 2009 (open circles), and 2010 (filled circles).

Figure 4-5. Percent maintenance energy estimates for age 2 through 6 walleye collected from Lake Oahe, South Dakota in 1994, 2001, 2008, 2009 and 2010. Open bars represent energy derived through consumption of rainbow smelt, hashed bars represent energy derived from consumption of gizzard shad and filled bars represent energy derived from other prey resources. Horizontal hashed line represents energy required to meet 100% of minimum maintenance energy requirements.

Figure 4-6. Percent maintenance energy estimates averaged for age 2 through 6 walleye collected from Lake Oahe, South Dakota in 2008 and 2009. Filled bars represent total energy consumption, open bars represent energy obtained from observed gizzard shad consumption, and hashed bars represent potential energy obtained from gizzard shad consumption only. Horizontal hashed line represents energy required to meet 100% of minimum maintenance energy requirements.

Figure 4-7. Rainbow smelt population estimates (open bars) and gizzard shad CPUE (hashed bars) during the study period of 2008 through 2010. No gizzard shad were caught in 2010 and rainbow smelt population estimates were unreliable in 2009 (K. Edwards SDGF&P personal communication).

Figure 4-1.



Rainbow smelt density / 100 m^3
0
10
20
30
40
50
60
70
Age-0 gizzard shad cpue
0
100
200
300
400
500
600
1999
2000
2001
2002
2003
2004
2005
Year

Figure 4-2.

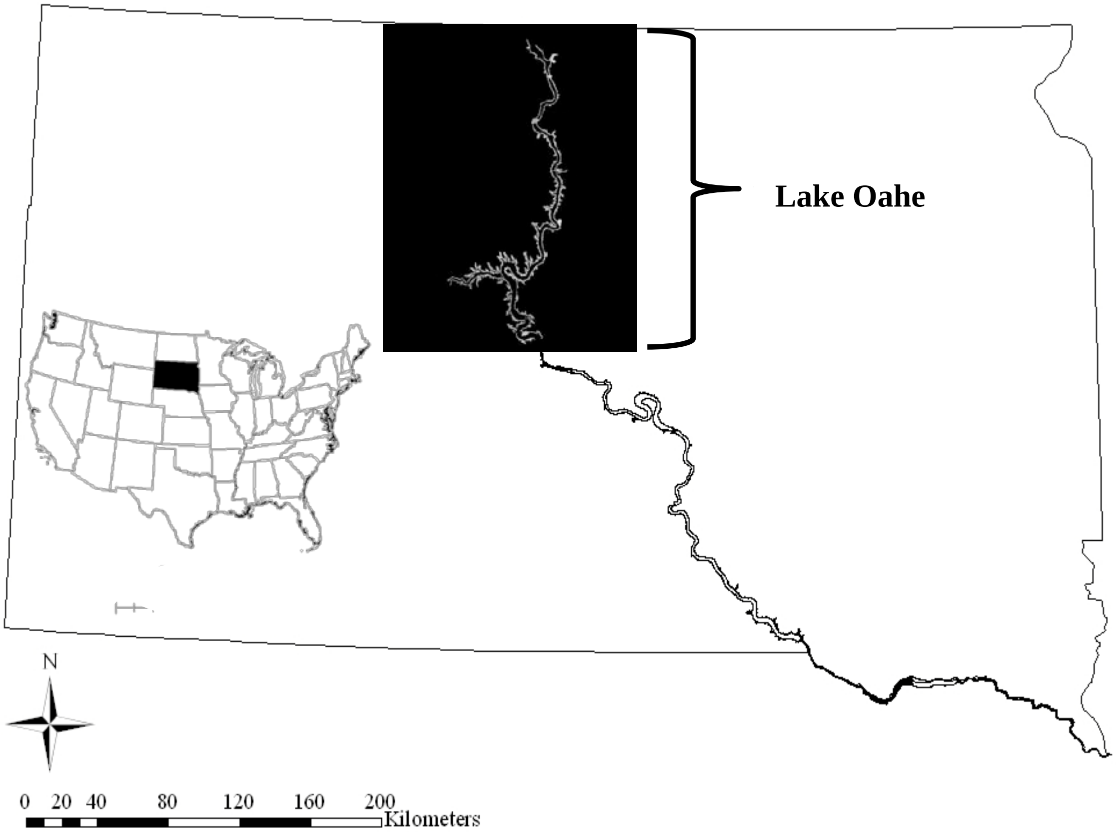


Figure 4-3.

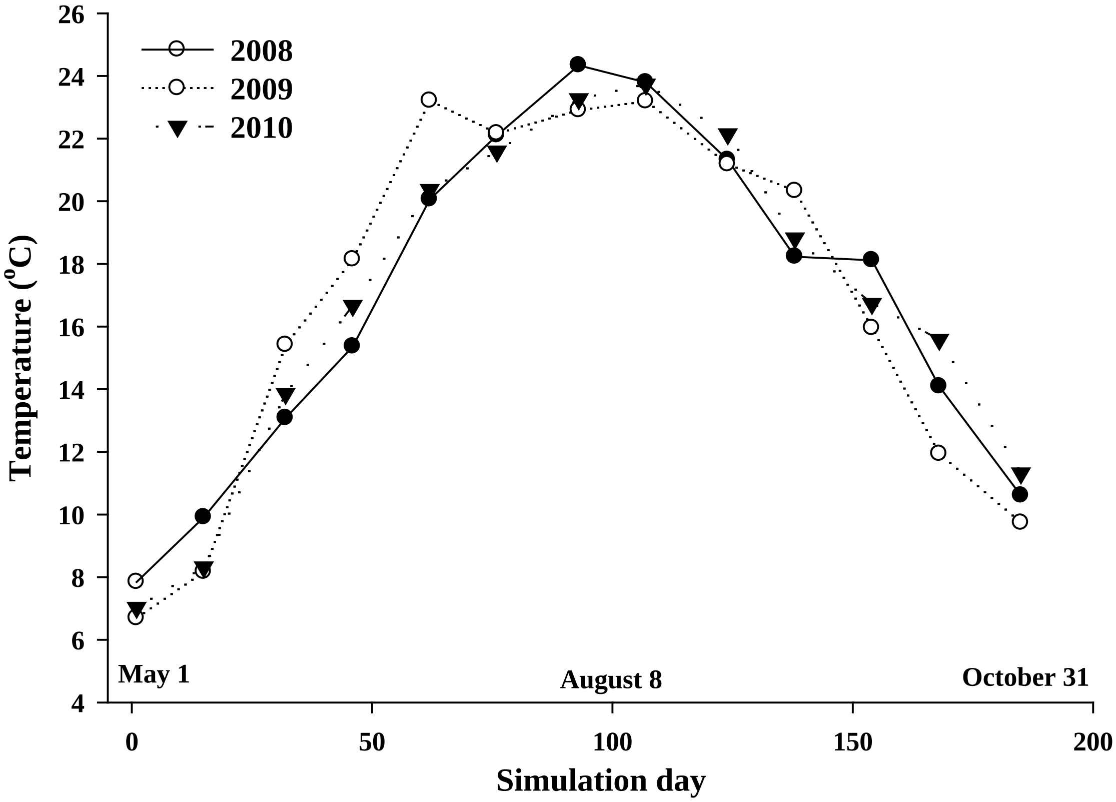

2008
2009
2010
26
24
22
20
18
16
14
12
10
8
6
4
Temperature (^{o}C)
May 1
August 8
October 31
0
50
100
150
200
Simulation day

Figure4-4.

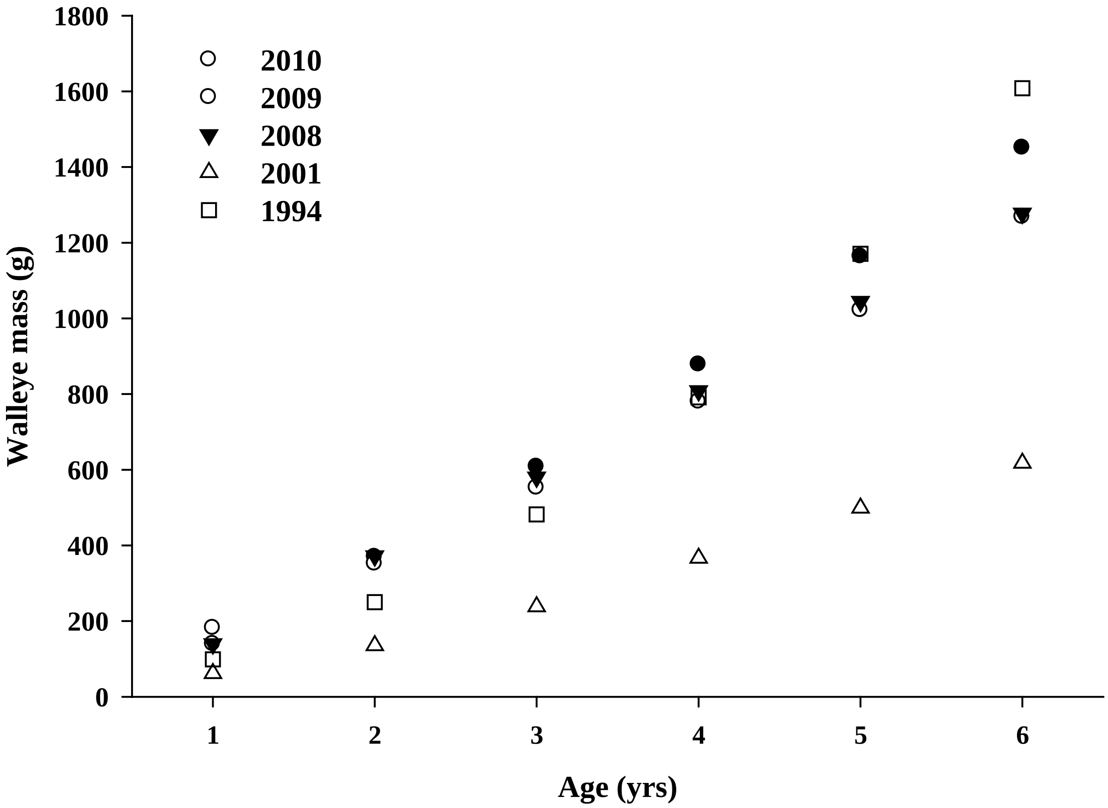

1800
1600
1400
1200
1000
800
600
400
200
0
Walleye mass (g)
○ 2010
○ 2009
▼ 2008
△ 2001
□ 1994
1
2
3
4
5
6
Age (yrs)

Figure 4-5.

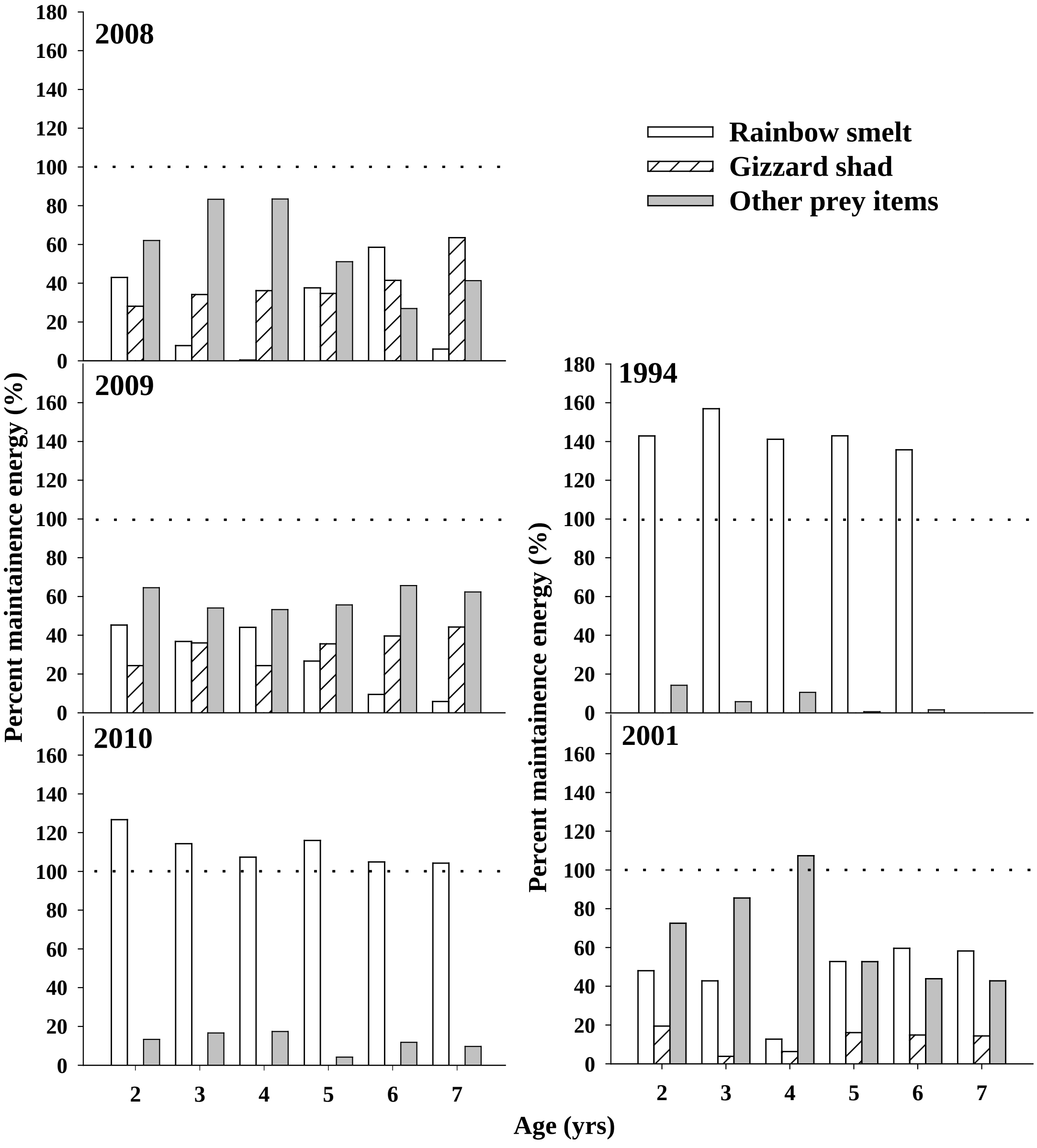

2008
2009
2010
1994
2001
Rainbow smelt
Gizzard shad
Other prey items
Percent maintainence energy (%)
Percent maintainence energy (%)
Age (yrs)
0
20
40
60
80
100
120
140
160
180
2
3
4
5
6
7

Figure 4-6.

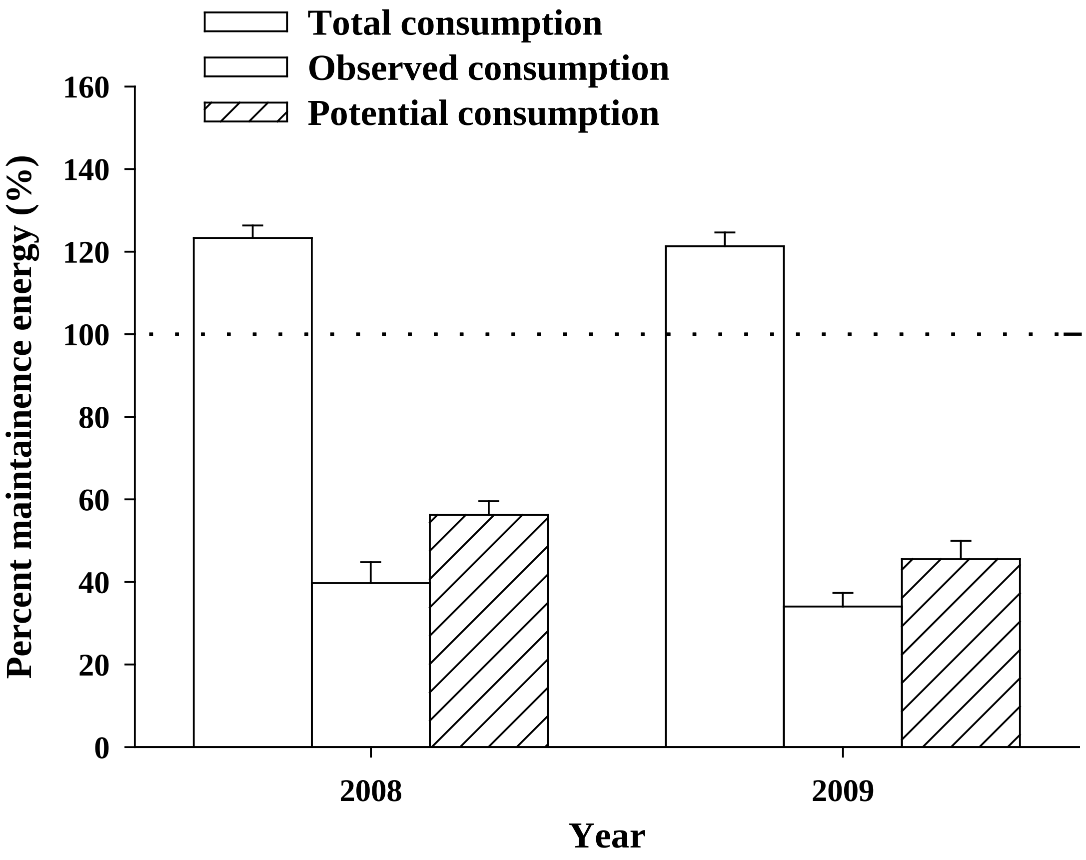
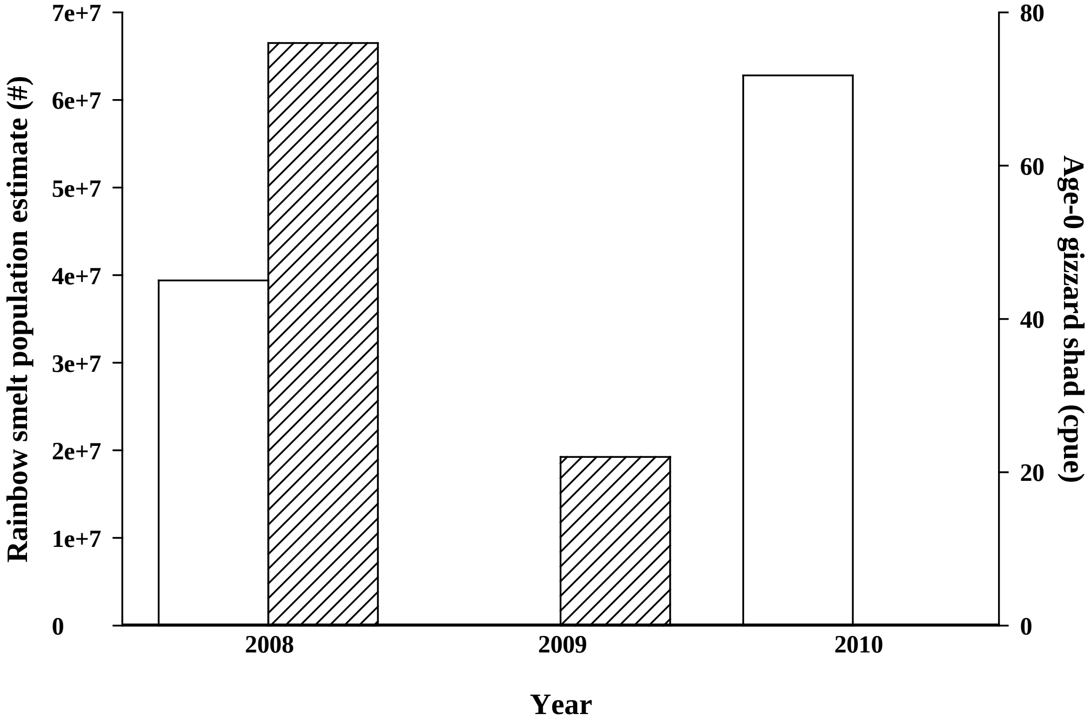

Total consumption
Observed consumption
Potential consumption
Percent maintainence energy (%)
160
140
120
100
80
60
40
20
0
2008
2009
Year

Figure 4-7.


7e+7
6e+7
5e+7
4e+7
3e+7
2e+7
1e+7
0
Rainbow smelt population estimate (#)
80
60
40
20
0
Age-0 gizzard shad (cpue)
2008
2009
2010
Year

Chapter 5: Diet Variation in Sauger and Walleye Inferred from Stable Isotope Ratios: Implications for Hybridization in Missouri River Impoundments

Abstract

Sauger populations have declined throughout the Midwest, United States over the past 50 years. One hypothesis proposed to explain declines in sauger abundance centers on potential competition with walleye that are frequently stocked in waters containing sauger. Stable isotope analysis provides a robust approach for quantifying energy acquisition by fishes and comparing measures such as diet breadth and variability among sympatric species. In this study, I examined isotopic characteristics of sauger and walleye in three Missouri River impoundments which exhibit varying levels of hybridization; 22% in Lake Lewis and Clark, 4% in Lake Francis Case and 2.6% in Lake Oahe. I found high isotopic overlap between walleye and sauger in all reservoirs, suggesting similar diet composition. However, isotopic variability (I_{VAR}), indexed from residual analysis of length versus isotope biplots, generally increased with decreasing hybridization levels. In Lake Lewis and Clark, I_{VAR} was similar between walleye and sauger (~0.5) for both $\delta^{15}N$ and$\delta^{13}C$. However, in Lake Francis Case, I_{VAR} was similar for $\delta^{15}N$ but for $\delta^{13}C$, was significantly greater for sauger (0.076) compared to walleye (0.38). In Lake Oahe, I found greater I_{VAR} in sauger compared to walleye for both $\delta^{15}N$ (sauger =1.56; walleye = 0.48) and $\delta^{13}C$ (sauger = 0.73; walleye=0.28). These findings imply that in all three systems, diets of walleye and sauger are largely overlapping. However, sauger exhibit increased isotopic variability, while walleye exhibit decreased isotope variability, as hybridization rates between the two species decline. Differences in isotopic variability could be the result of varying habitat quantity or quality between reservoirs; factors further facilitating hybridization rates in these systems.

Introduction

Sauger *Sander canadensis* are a native predator in large, turbid rivers throughout the United States and Canada (Scott and Crossman 1973) that have been declining in abundance and distribution throughout their range (Nelson and Walburg 1977; Hesse 1994; Pegg et al. 1997; McMahon and Gardner 2001). Evidence suggests that these declines may be linked to resource competition and/or hybridization with walleye *Sander vitreus* (Bellgraph et al. 2008; Graeb et al. 2010). The negative effects of walleye on sauger populations appears minimized in unaltered riverine environments (Swenson 1977; Rawson and Scholl 1978; Schlick 1978), but increases with anthropogenic disturbance (i.e., river regulation or reservoir construction; Gangl et al. 2000; Rawson and Scholl 1978; Fitz and Halbrook 1978; Mero 1992). For instance, Bellgraph (2006) found increased resource overlap between walleye and sauger in the regulated Missouri River compared to the unregulated Yellowstone River.

Sauger and walleye are native to the Missouri River, with sympatric populations found in all South Dakota Missouri River impoundments (Hoagstrom et al. 2007). Recently, Graeb et al. (2010) showed that hybridization rate varied with reservoir size and increased downstream from Lake Oahe (2%) to Lewis and Clark Lake (22%). Although specific mechanisms regulating hybridization were not studied, Graeb et al. (2010) suggested that habitat availability may be responsible for differential hybridization rates. Many studies of sympatric walleye and sauger populations have shown high diet overlap between these predators (Priegel 1963; Swenson and Smith

1976; Fitz and Holbrook 1978; Mero 1992; Bellgraph et al. 2008) although the extent of diet overlap has not been linked to hybridization rates between species.

Diet composition represents a critical component for understanding food web interactions (Bearhop et al. 2004). One key aspect generally overlooked in comparing diets of two species is the level of feeding variability, or the degree of specialization or generalization each species exhibits. Criteria defining a useful and robust measure of feeding variability should allow direct comparison among individuals, populations and species. Criteria should also combine information on richness and evenness of diet composition that permit integration of dietary information over spatial and temporal scales (Bearhop et al. 2004). Traditional diet studies have been used to reveal diet overlap within and among species (Wiens and Rotenberry 1979; Svanback and Persson 2004). However, several practical problems arise when using diet analysis. Diet studies only represent a snapshot of diet composition and do not offer time-dependent integration of dietary information. Additionally, gut content analysis can be misleading since it is difficult to assess assimilation of prey and their energetic contribution to the consumer (Kling et al. 1992). In large and species rich systems, labor and costs are often too prohibitive to allow successful examination of large-scale spatial and temporal variation, especially when predator diets and prey resources are variable (Rybczynski et al. 2008).

Stable isotope analysis is a common tool used to monitor energy sources and trophic linkages in aquatic systems. Stable isotope analysis (SIA) offers time-integrated analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), which is reflective of the energy assimilated by consumers. Further, SIA offers the ability to assess energy flow and feeding relationships within aquatic food webs (Minagawa and Wada 1984, Kling et al. 1992, Cabana and Rasmussen 1996, Vander Zanden et al. 1997, Vander Zanden et al. 2000, Lake et al. 2001). Stable isotope analysis is used to address a variety of topics including diet shifts from pelagic to benthic prey (Vander Zanden et al. 1998), contaminant bioaccumulation in fishes (Kidd et al. 1996) and effects of eutrophication on aquatic food webs (Cabana and Rasmussen 1996). Only recently has stable isotope analysis been used to determine differences in isotopic variability between populations and species (Bootsma et al. 1996; Vander Zanden 2000; Limen et al. 2005; Paterson et al. 2006). Stable isotope analysis provides a means for determining diet variability that allows for direct comparison among individuals, populations and species. Stable isotope analysis also allows for temporal integration of dietary information over different time scales using minimal sampling.

In this study, I quantified isotopic overlap and diet variability of walleye and sauger in three South Dakota Missouri River impoundments where these species co-occur. Using data on isotopic composition, I address two questions: (1) does diet overlap vary between populations with different hybridization rates and (2) does feeding variability vary with hybridization rate?

Methods

Study area

Lake Oahe is the second largest of a series of six impoundments on the Missouri River and extends from Bismarck, ND to Pierre, SD (Figure 5-1). At normal pool, the

South Dakota portion of Lake Oahe has a surface area of approximately 145,000 ha with a mean depth of approximately 19 m and a maximum depth of 67 m. Lake Oahe has little riverine habitat and no established delta formations within South Dakota.

Lake Oahe has a diverse fish assemblage. Sport fishes include walleye, sauger, rainbow trout *Oncorhynchus mykiss*, chinook salmon *Oncorhynchus tshawytscha*, northern pike *Esox lucius*, channel catfish *Ictalurus punctatus*, and smallmouth bass *Micropterus dolomieui*. Primary prey resources include rainbow smelt *Osmorus mordax*, spottail shiners *Notropis hudsonius*, lake herring *Coregonus artedi*, white bass *Morone chrysops*, yellow perch *Perca flavescens*, freshwater drum *Aplodinotus grunniens*, emerald shiners *Notropis atherinoides*, white crappie *Pomoxis annularis*, gizzard shad *Dorosoma cepedianum*, age-0 sport fish, and various invertebrates. The sauger population in Lake Oahe is relatively small, averaging less than 0.5 fish per net night (gill net catch per unit effort; Figure 5-2) compared to 5 to 7.5 fish per net night in downstream impoundments (see below).

Lake Francis Case is the fifth most upstream reservoir on the Missouri River and extends from Big Bend Dam to Fort Randall Dam in central South Dakota. At normal pool, Lake Francis Case has a surface area of approximately 25,000 ha, with mean and maximum depths of 15.2 and 42.6 m, respectively. Sport fishes in Lake Francis Case include walleye, sauger, northern pike, channel catfish, and smallmouth bass. Primary prey resources include spottail shiners, white bass, yellow perch, freshwater drum, emerald shiners, white crappie, gizzard shad, age-0 sport fish, and various invertebrates. Lake Francis Case contains superficially similar fish species as Lake Oahe but differs in that it contains common riverine species within the small delta region of the reservoir (i.e., lateral delta of the White river). These riverine species include river carpsucker *Carpiodes carpio,* flathead chub *Platygobio gracilis,* creek chub *Semotilus atromaculatus,* etc. Lake Francis Case also has more species present within the delta-system (>30 spp. collected in 2010) than Lake Oahe (Schreck 2010). The Lake Francis Case sauger population is generally more abundant than Lake Oahe, averaging 4.95 fish per gillnet night (Figure 2).

Lake Lewis and Clark is the smallest and furthest downstream reservoir on the Missouri River. Lake Lewis and Clark extends from Fort Randall Dam to Gavin's Point Dam in south central South Dakota. At normal pool, Lake Lewis and Clark has a surface area of 10,500 ha, and is considerably shallower than the other two study lakes with mean and maximum depths of 5and 16.7 m, respectively. Lake Lewis and Clark is unique in that it contains 70 km of riverine habitat and a large delta region formed by sediment inputs from the Niobrara River. As a result of the extensive delta habitat (>25km), Lake Lewis and Clark contains similar species as Lake Francis Case although much more delta habitat is available compared to Lake Francis Case (Schreck 2010). Lake Lewis and Clark's sauger population is greater than both lakes Oahe and Francis Case with an average catch per unit effort of 7.52 fish per gillnet night (Figure 5-2). During standardized surveys, however, gill nets are generally not set in the delta region which is likely the optimal habitat for sauger in Lake Lewis and Clark (Scott and Crossman 1973; Graeb et al. 2009). Thus, reported CPUE of sauger in Lake Lewis and Clark is probably a conservative estimate.

Fish collection

Walleye and sauger were collected from Lakes Oahe, Francis Case and Lewis and Clark in August of 2007 using experimental mesh gill nets. Fish were identified to species by common phenotypic characteristics and potential hybrids were excluded from the study. I used phenotypic metrics described by Ward and Berry (1995), to characterize sauger, walleye and their potential hybrids. Using this approach, Ward and Berry (1995) showed that approximately 90% of fish were correctly identified as parental types or hybrids. All fish collected were placed on ice and transported to South Dakota State University for processing. In the laboratory, white muscle samples (~2 g) were removed from the dorsal region of each fish, above the lateral line and anterior to the dorsal fin. Skin was then removed from each muscle sample using a fillet knife and all samples were rinsed with deionized water and frozen at -20 °C prior to analysis.

Stable isotope analysis

Samples were thawed, rinsed, and dried at 70°C for 72 h before being pulverized with a mortar and pestle. Ground muscle samples (2.4-2.6 mg) were then placed into 4x6 mm tin capsules for isotopic analysis. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were determined using a Europa 20-20 mass spectrometer. Isotope values were reported in δ notation, as per mille (‰) deviations from a standard material (Pee Dee Belemnite carbon or atmospheric nitrogen) using the equation

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample} - R_{std}\right) \big/ R_{std} \right] * 1000 \tag{1}$$

where $R_{sample}$is the isotopic ratio of the sample and R_{std} is the isotopic ratio of the standard. Carbon-to-nitrogen (C:N) ratios for all tissue types were less than four, indicative of non-fatty tissue (Gray et al. 2004; Sanderson et al. 2009). Thus, I did not perform lipid extraction on tissue samples prior to analysis (Sanderson et al. 2009).

Statistical analysis

I used a randomization test to examine differences in mean $\delta^{13}C$ and $\delta^{15}N$ between sauger and walleye (Peres-Neto and Olden 2001; Manly 2007). To accomplish this, I calculated the observed difference (MeanDiff) between mean $\delta^{13}C$ or $\delta^{15}N$ for sauger and walleye within each reservoir. I then randomly sorted data into two new samples (n_1 and n_2) equal in size to the original data and calculated the difference between mean values ($MeanDiff_{random}$) for $\delta^{13}C$ or $\delta^{15}N$. I repeated the latter process until I reached n=5000 permutations. I then compared the observed mean difference (MeanDiff) between walleye and sauger to the normal distribution of randomized values ($MeanDiff_{random}$). If observed MeanDiff values were located outside the 2.5 or 97.5 percentiles of the normal distribution for randomized values (i.e., α=0.05 of two tailed test), I considered the difference to be significantly different (Manly 2007; Chipps and Garvey 2007). Estimated p-values based on the randomization test were calculated from a frequency distribution of $MeanDiff_{random}$ values as,

$$\frac{\text{Number of } MeanDiff_{random} \text{values} > \text{(or <) observed mean difference}}{5{,}000.}$$

To test for differences in isotopic variability between species, I used regression analysis to examine the relationship between isotopic values and total length (mm) of walleye or sauger from each reservoir. The regression analysis allowed us to take into account any length-related bias in isotope signatures (Vander Zanden and Rasmussen 1999). Using the fitted regression line, I then calculated the mean, residual value for each species (i.e., the absolute distance each individual's isotopic signature was from the population mean; Fincel et al. 2011) and used this as an index of isotopic variability (I_{VAR}). I used the same randomization procedure previously described to compare I_{VAR} values ($\delta^{13}C$ and $\delta^{15}N$) between species within each reservoir (Vander Zanden and Rasmussen 1999).

Because I did not have baseline isotope data for each reservoir, I only compared mean isotope values ($\delta^{13}C$ and $\delta^{15}N$) of walleye and sauger within each reservoir (Post 2002). However, variability in isotopic composition (i.e.,I_{VAR}) can be compared between systems as baseline corrections are not needed. Thus, I compared isotope variability of each species *between* reservoirs using the randomization procedure described above.

Results

I collected a total of 103 walleye from Lakes Lewis and Clark (n=47), Francis Case (n=21), and Oahe (n=35) in 2007. Total length of walleye ranged from173 to 565 mm in Lake Lewis and Clark, 232 to 449 mm in Lake Francis Case, and 219 to 619 mm in Lake Oahe. Because of low sauger abundance in Lakes Oahe and Francis Case, I collected few sauger that could be reliably identified as non-hybrids. Only 42 total sauger were caught, ranging in length from 180 to 525 mm in Lake Lewis and Clark (n=32), 232 to 411 mm in Lake Francis Case (n=5), and 343 to 399 mm in Lake Oahe (n=5). There were no significant differences in TL (ANOVA; $F_{5,136}$=0.789; p=0.56) or mass (ANOVA; $F_{5,136}$=1.495; p=0.19) between walleye and sauger.

In general, I found poor relationships between isotope signatures and total length of walleye and sauger (Table 5-1). On average, total length explained between 18 to 32% of the variability in δ^{15}N values of walleyes and sauger, respectively. Similarly, total length explained 11 to 45% of the variability inδ^{13}C values of walleye and sauger. For saugers in Lake Oahe, however, total length explained 92 and 89% of the variation in δ^{13}Cand δ^{15}N values, implying that variation in isotopic signatures was length-dependent ($P<0.10$; Table 5-1).

Within each reservoir, mean δ^{15}N was similar for sauger and walleye ranging from 15.7 to 17.8 for sauger and 15.2 to 17.7 for walleye (Figure 5-3). Mean δ^{13}C values were similar for sauger and walleye in Lewis and Clark and Francis Case reservoirs, but differed significantly between these species in Lake Oahe. Mean δ^{13}C was significantly greater for sauger than for walleye in Lake Oahe (randomization test p=0.003; Figure 5-3). Variation in δ^{15}N signatures, as indexed by I_{VAR}, ranged from 0.02 to 2.05 for sauger and 0.01 to 1.96for walleye. Similarly, variation in mean δ^{13}C isotope values ranged from 0.01 to 1.99 for sauger and 0.00 to 1.76 for walleye.

Isotope variability for both δ^{13}C and δ^{15}N was similar between walleye and sauger in Lewis and Clark reservoir (Table 5-2); however, δ^{13}C variability was greater for sauger in Francis Case and both δ^{13}C and δ^{15}N variability was greater for sauger than for walleye in Lake Oahe (Table 5-2). Comparison of species-specific variation in isotope values showed that walleye δ^{15}N variability was similar among reservoirs whereas $\delta^{13}C$ variability increased from Lake Oahe downstream to Lewis and Clark Lake (Figure 5-4). Conversely, isotopic variability for sauger generally decreased from Lake Oahe downstream to Lewis and Clark Lake for both $\delta^{15}N$ and $\delta^{13}C$.

Discussion

Isotopic overlap was high for walleye and sauger in Lakes Lewis and Clark and Francis Case but differences in mean $\delta^{13}C$ in Lake Oahe suggest possible diet partitioning of *Sander* spp. in this reservoir. Lake Lewis and Clark has a diverse fish assemblage, due to its large riverine and delta habitats promoting the potential for specialization and likely allowing for increased diet divergence between *Sander spp*. However, $\delta^{15}N$ and $\delta^{13}C$ were similar, with minimal variability, between sauger and walleye in Lake Lewis and Clark suggesting common foraging strategies between these two species. Although walleye and sauger have similar isotopic composition, they may not necessarily be feeding on similar prey. Different prey items, with similar isotope signatures, could be consumed by each species resulting in similar isotope signatures for walleye and sauger (Bootsma et al. 1996). However, most literature to date confirms high overlap in foraging behavior between walleye and sauger (Priegel 1963; Swenson and Smith 1976; Fitz and Holbrook 1978; Mero 1992; Belgraph et al. 2008). Due to the high isotopic overlap of these two species in Missouri River impoundments the potential for competition between walleye and sauger is likely high (Swenson and Smith 1976; Bellgraph et al. 2008).

Although many studies have revealed high diet overlap of sauger and walleye (see Chipps and Graeb 2011 for a review), no studies have examined differences in diet variability of sympatric walleye and sauger populations. In the present study, I found that diet variability was similar between walleye and sauger in Lewis and Clark, but diverged as hybridization rate decreased (i.e., moving upstream). This was expected: as resources are shared between species, hybridization potential likely increases. Conversely, as interactions between the two species decline (i.e. greater diet breadth of one or both species); it is likely that hybridization rates will decrease (Johannesson 2001).

The species composition in Lake Oahe is generally less variable compared to Lake Lewis and Clark; thus, I thought diet variability would be lowest in Lake Oahe (which was true for walleye). However, Lake Oahe sauger exhibited the greatest $\delta^{15}N$ variability compared to Lakes Francis Case and Lewis and Clark, and increased $\delta^{13}C$ variability compared to Lake Lewis and Clark. These results suggest that sauger in Lake Oahe were feeding on a wider range of prey types compared to sauger in Lake Lewis and Clark and to a lesser extent, sauger in Lake Francis Case. Conversely, walleye were feeding on a relatively narrow range of prey types in all reservoirs (i.e., no difference in $\delta^{15}N$ variability and a slight decrease in $\delta^{13}C$ variability among reservoirs). A larger isotopic variance in Lake Oahe sauger suggest a larger diet breadth or reduced diet consistency (Vander Zanden et al. 2000).

Bellgraph (2006) examined trophic position (TP) of walleye and sauger in the Missouri and Yellowstone Rivers (Montana) using stable isotopes. Sauger in the Missouri River had a higher variation in TP compared to walleye, whereas sauger had a lower variation in TP compared to walleye in the Yellowstone river. These comparisons are notable because the Missouri River sites were described as having increased anthropogenic disturbances compared to the Yellowstone River sites, suggesting diet variability is connected to habitat quality. It appears that in unaltered systems, sauger feed on a narrow range of prey types, but as habitat is altered they broaden their forage base (Bellgraph 2006).

Sauger are adapted to large river systems (Scott and Crossman 1973) and are known to decline in systems after human alteration (Nelson and Walburg 1977; St John 1990; Hesse 1994). Although no data exist on sauger population parameters in the Missouri River in South Dakota prior to dam construction, the extensive delta development in Lake Lewis and Clark (and to a lesser extent Lake Francis Case) in many ways mirrors pre-impoundment habitats (Schreck 2010). Previous diet studies have shown considerable diet overlap between sauger and walleye; however, all of these studies were conducted in lentic and reservoir habitats (Priegel 1963; Swenson and Smith 1976; Fitz and Holbrook 1978; Mero 1992). In more natural lotic habitats, sauger appear to consume a narrower range of prey types, compared to lentic environments (Bellgraph 2006).

The use of stable isotopes provides important insight into feeding behavior (i.e., diet specialist or generalist) of species cohabitating similar aquatic ecosystem compartments (Paterson et al. 2006). In this study, I found that isotopic variability of sauger was lowest in Lake Lewis and Clark and highest in Lake Oahe. This suggests that in Lake Lewis and Clark sauger display a more specialist feeding behavior. Conversely, in Lake Oahe, which has a reduced forage base, sauger exhibit a generalist feeding behavior. These differences in foraging behavior correspond to observed trends in *Sander* spp. hybridization. Hybridization rates are lowest in Lake Oahe (estimated ~ 2.6 %) and increase downstream (4% in Lake Francis Case and 21% in Lake Lewis and Clark; Graeb et al. 2010). In Lake Oahe, walleye and sauger apparently forage on a different range of prey, thus reducing potential dietary overlap of these two species. This is supported by my observation that isotopic differences (mean and variability) between these species were generally greatest in Lake Oahe compared to downstream reservoirs. Conversely, in Lake Lewis and Clark, resource overlap may be relatively high (Bellgraph et al. 2008) as indicated by similar isotopic composition and reduced variation in sauger isotope values.

One mechanism that could be driving observed isotopic trends in *Sander* spp. is the occurrence of suitable habitat for sauger. In Lake Lewis and Clark, the delta region provides suitable habitat for sauger yet diet variability is reduced in this system. Decreased diet variability could explain why sauger are specialist in Lake Lewis and Clark. Being a specialist enables them to reduce foraging energy expenditure and could explain the increased sauger abundance in this reservoir (SDGF&P 2000B). Perhaps, in South Dakota impoundments, sauger exhibit a connected relationship to habitat, feeding behavior, degree of hybridization and subsequent population size. In this theoretical model, feeding strategy and subsequent population size and hybridization rates are dependent on the quantity of suitable habitat (i.e., the riverine and delta habitats found throughout Lake Lewis and Clark and to a lesser extent, Lake Francis Case). Therefore, the detrimental effects of walleye on sauger may be less severe than hypothesized where sauger abundance is less dependent on walleye presence and abundance, but linked to suitable habitat. In other words, habitat that benefits walleye production may be detrimental to sauger, and vice versa, however, this needs to be studied in more detail.

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Table 5-1.Regression parameters of the relationships of total length (mm) and isotopic composition ($\delta^{15}N$ and $\delta^{13}C$) for walleye or sauger collected from three South Dakota Missouri River reservoirs.

Species	Lake	Isotope	n	Intercept	Slope	P	r^2
Walleye	Lewis and Clark	$\delta^{15}N$	47	15.60	0.0004	0.611	0.01
		$\delta^{13}C$	47	-23.40	0.0028	<0.001	0.22
	Francis Case	$\delta^{15}N$	21	13.17	0.0055	0.107	0.13
		$\delta^{13}C$	21	-22.28	-0.0007	0.731	0.01
	Oahe	$\delta^{15}N$	35	14.31	0.0058	<0.001	0.42
		$\delta^{13}C$	35	-24.48	-0.0014	0.510	0.11
Sauger	Lewis and Clark	$\delta^{15}N$	32	15.41	0.0005	0.722	0.00
		$\delta^{13}C$	32	-23.75	0.0044	<0.001	0.42
	Francis Case	$\delta^{15}N$	5	14.97	0.0010	0.715	0.05
		$\delta^{13}C$	5	-22.86	0.0020	0.689	0.06
	Oahe	$\delta^{15}N$	5	42.41	0.0718	0.100	0.92
		$\delta^{13}C$	5	-36.26	0.0330	0.016	0.89

Table 5-2.Isotopic variability ($\delta^{15}N$ and $\delta^{13}C$) compared between sauger and walleye collected from three Missouri River impoundments. MeanDiff represents the observed difference in mean isotope variability (MAR) between species. All comparisons p<0.05 represent significant differences in isotopic variability between species.

			Randomization test
Reservoir	Isotope	MeanDiff	Estimated p
Oahe	$\delta^{15}N$	1.08	<0.001
	$\delta^{13}C$	0.45	0.002
Francis Case	$\delta^{15}N$	-0.17	0.439
	$\delta^{13}C$	0.37	0.025
Lewis and Clark	$\delta^{15}N$	0.11	0.273
	$\delta^{13}C$	-0.01	0.892

Figure 5-1. Map of three South Dakota Missouri River impoundments: from downstream -- Lakes Lewis and Clark, Francis Case and Oahe.

Figure 5-2. Gillnet catch per unit effort (number of fish collected / net night) of sauger collected in Lakes Oahe (solid bars), Francis Case (open bars) and Lewis and Clark (hashed bars) in 1996 through 2000. Lake Francis Case was not sampled in 1996. Insufficient sauger were collected from Lake Oahe in 2000 to create summary statistics. Error bars represent one unit of standard error. Caution must be taken when interpreting catch rates because gill nets were set in open water habitats, and evidence suggests that sauger may use back waters, riverine area and deltas in greater occurrence than open water habitat. Data recreated from SDGF&P (2000a; 2000b; 2001).

Figure 5-3.Mean $\delta^{15}N$ (top panel) and $\delta^{13}C$ (bottom panel) values from walleye (white bars) and sauger (grey bars) collected from three South Dakota Missouri River impoundments. Isotopic overlap was compared between walleye and sauger within each reservoir using a randomization test and asterisks denote significant differences found in mean isotopic composition at $p<0.05$. Error bars represent one unit of standard error.

Figure 5-4.Mean isotopic variation (I_{var}) for$\delta^{15}N$ (top panel) and $\delta^{13}C$ (bottom panel) of walleye (white bars) and sauger (grey bars) collected from three South Dakota Missouri River impoundments. Isotopic variability was compared between reservoirs for walleye or sauger using a randomization test (see text for details).Groupings with different letters (‘a’ and ‘b’ for walleye and ‘y’ and ‘z’ for sauger) represent significantly different mean residual values at the $P<0.05$ level. Error bars represent one standard error.

Figure 5-1.

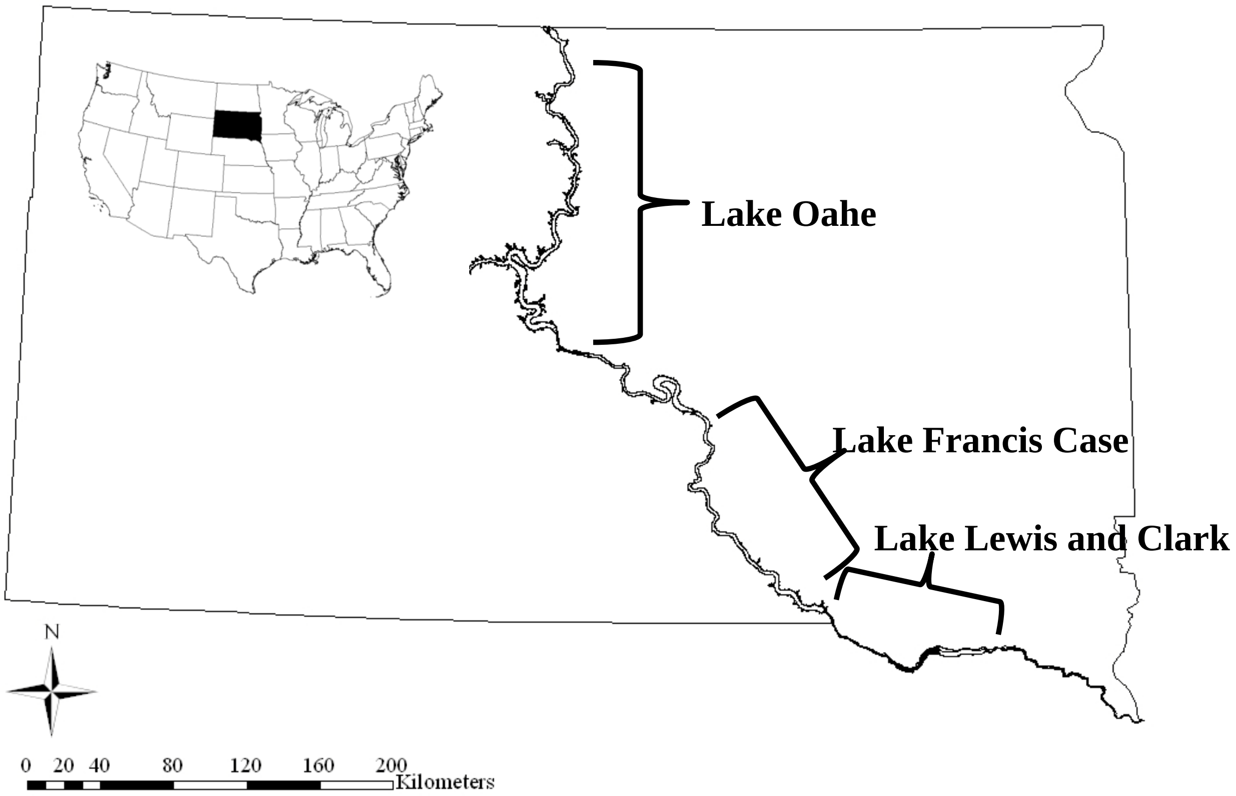

Lake Oahe
Lake Francis Case
Lake Lewis and Clark
N
0 20 40 80 120 160 200
Kilometers

Figure 5-2.

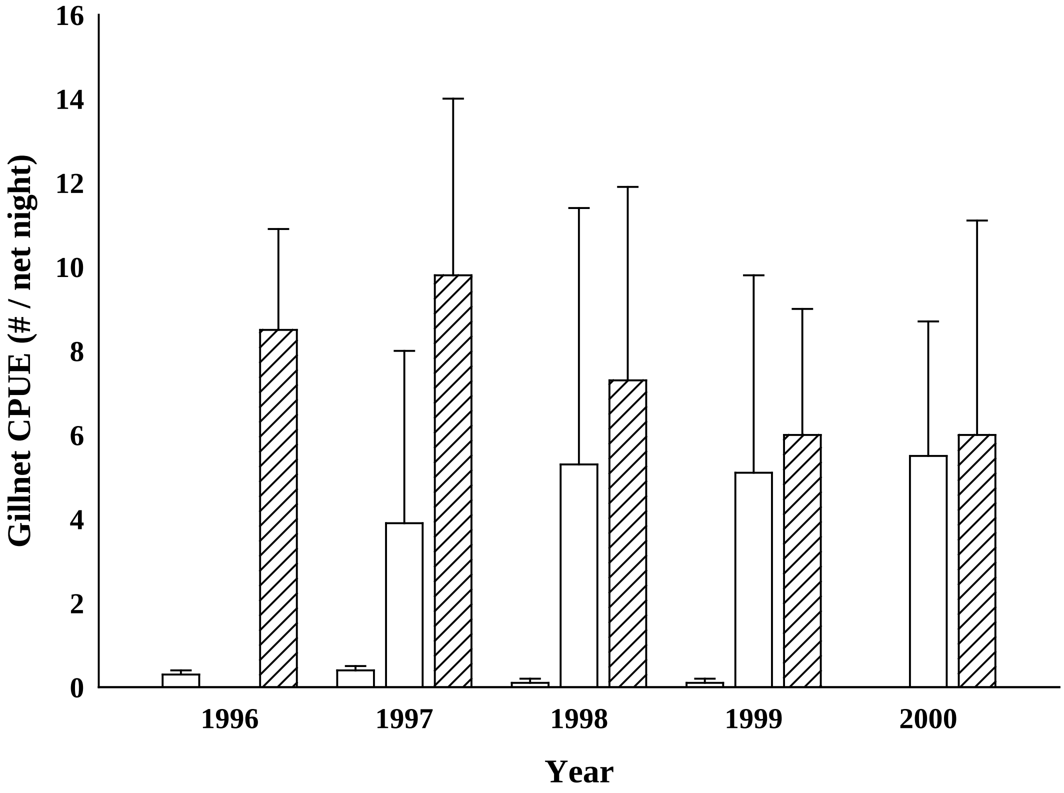

16
14
12
10
8
6
4
2
0
Gillnet CPUE (# / net night)
1996
1997
1998
1999
2000
Year

Figure 5-3.

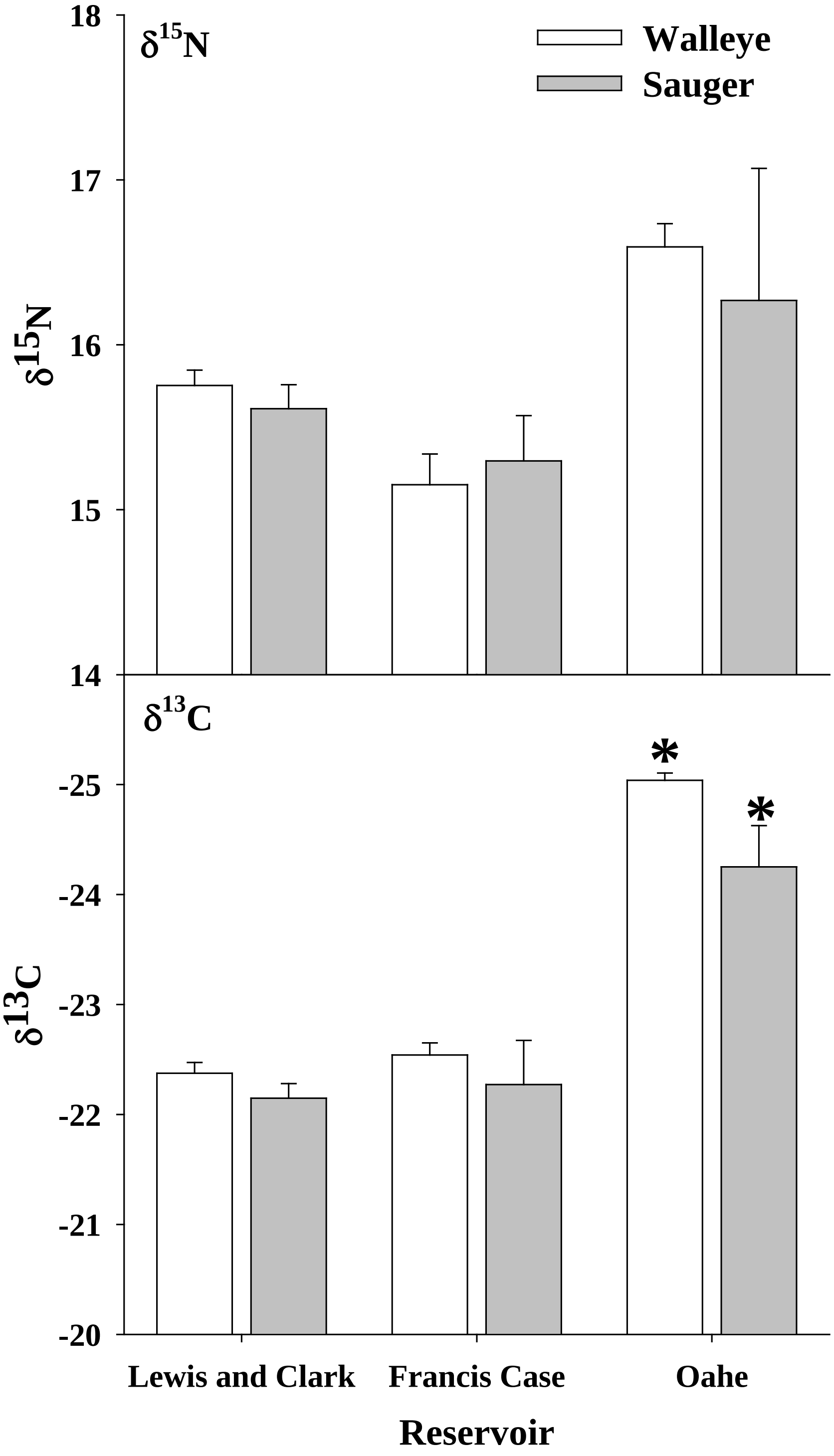
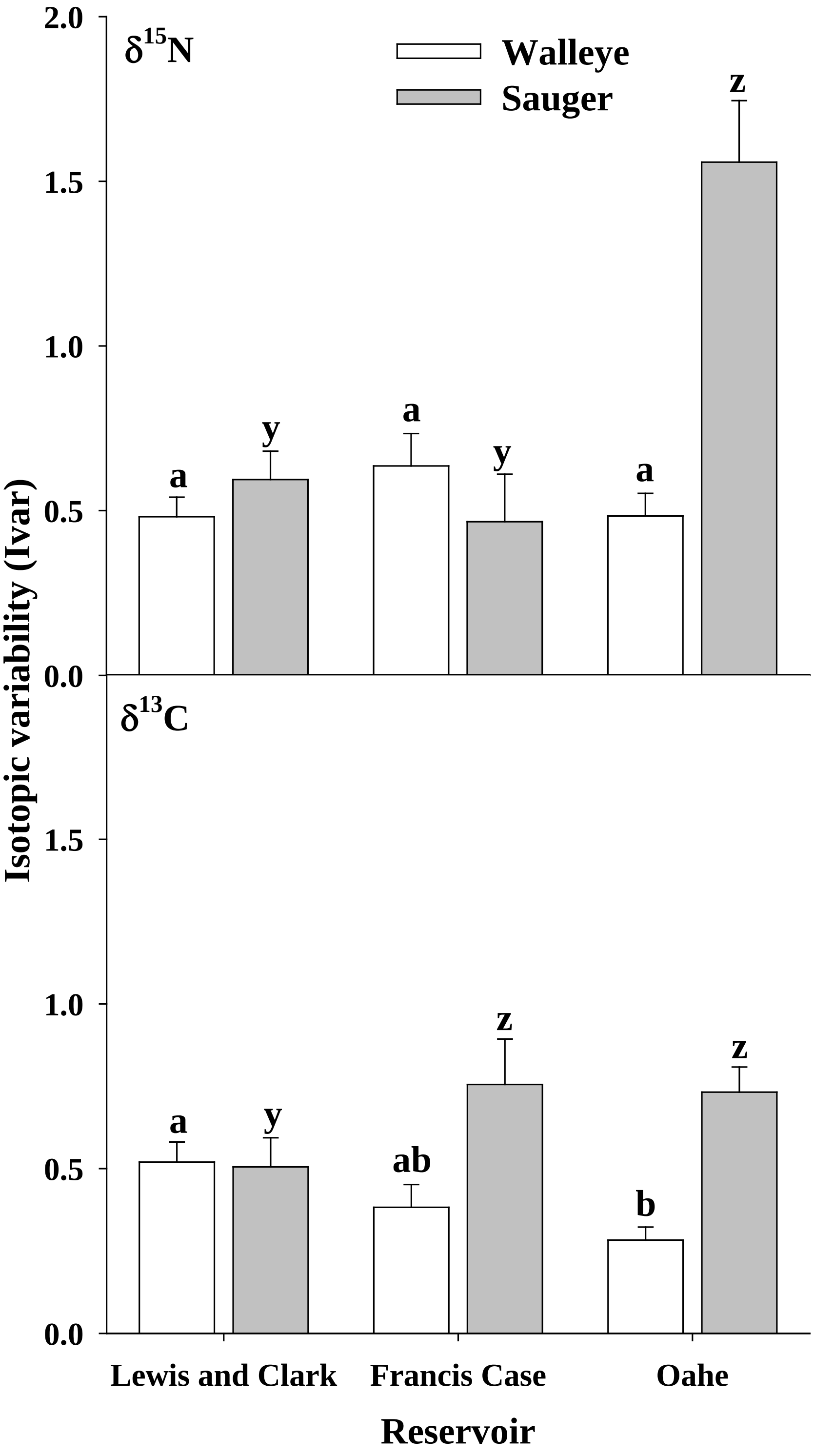

δ15N
Walleye
Sauger
18
17
16
15
14
δ15N
δ13C
-25
-24
-23
-22
-21
-20
δ13C
*
*
Lewis and Clark
Francis Case
Oahe
Reservoir

Figure 5-4.


δ15N
δ13C
Walleye
Sauger
Isotopic variability (Ivar)
2.0
1.5
1.0
0.5
0.0
a
y
a
y
a
z
a
y
ab
z
b
z
Lewis and Clark
Francis Case
Oahe
Reservoir

Chapter 6: Non-lethal Sampling of Walleye for Stable Isotope Analysis: A Comparison of Three Tissues

Abstract

Stable isotope analysis of fishes is often performed using muscle or organ tissues that require sacrificing animals. Non-lethal sampling provides an alternative for evaluating isotopic composition for species of concern or individuals of exceptional value. Stable isotope values of white muscle (lethal) were compared to those from fins and scales (non-lethal) in walleye, *Sander vitreus* (Mitchill), from multiple systems, size classes and across a range of isotopic values. Isotopic variability was also compared among populations to determine the potential of non-lethal tissues for diet-variability analyses. Muscle-derived isotope values where enriched compared to fins, and depleted relative to scales. A split-sample validation technique and linear regression found that isotopic composition of walleye fins and scales were significantly related to that in muscle tissue for both $\delta^{13}C$ and $\delta^{15}N$ ($r^2 = 0.79$ to 0.93). However, isotopic variability was significantly different between tissue types in two of six populations for $\delta^{15}N$ and three of six populations for $\delta^{13}C$. Although species and population specific, these findings indicate that isotopic measures obtained from non-lethal tissues are indicative of those obtained from muscle.

Introduction

Stable isotope analysis (SIA) is a useful approach for quantifying energy flow and trophic relationships in aquatic and terrestrial ecosystems (Kling *et al.* 1992; Cabana & Rasmussen 1994). Stable isotope values in fish tissue have been used to address a variety of questions that include quantifying diet shifts (Vander Zanden *et al.* 1998), modeling contaminant accumulation (Kidd *et al.* 1998) and monitoring the effects of eutrophication (Cabana & Rasmussen 1996). Although diet composition is difficult to assess using SIA, it offers time-integrated information about important energy sources assimilated by consumers. Further, unlike traditional gut content analysis, SIA is not hampered by empty stomachs and allows more efficient use of specimens collected for analysis (Vander Zanden *et al.* 1998). In most SIA applications, tissue samples from white muscle, liver, gonads, bone, otoliths, brain or entire fish are used for isotope determinations (De Niro & Epstein 1977; Pinnegar & Polunin 1999). One drawback with using these tissues is that fish generally are sacrificed to obtain them, which can be undesirable when working with species of special concern or large, mature individuals of recreational value (Sanderson *et al*. 2009).

The use of non-lethal tissues in SIA has received increased attention in food web studies (Jardine *et al*. 2005; Kelly *et al.* 2006b; Sanderson *et al.* 2009). Comparative studies have shown that isotopic values for $\delta^{13}C$ or $\delta^{15}N$ derived from lethal and non-lethal sampling are strongly correlated for a variety of fishes (Perga & Gerdeaux 2003; Jardine *et al*. 2005; Kelly *et al.* 2006b; Sanderson *et al.* 2009); however, because turnover rates differ among tissue types (Fry 2006), isotope values derived from lethal and non-lethal sampling may not be equally informative (Kelly *et al.* 2006b; Sanderson *et al.* 2009). Sanderson et al. (2009) demonstrated that simple regression models can be used to estimate muscle stable isotope values from non-lethally obtained fins and scales for a variety of fishes.

The ability to estimate muscle $\delta^{13}C$ or $\delta^{15}N$ values from fins or scales has several advantages: it allows for comparability between studies that use muscle tissue versus those that use fin or scale tissue. One limitation to estimating muscle isotope values from non-lethally obtained tissues is that predictive models are often species and life-stage specific (Kelly *et al.* 2006b; Sinnatamby *et al.* 2008). Moreover, it is important that models are developed across multiple populations and fish sizes to account for variability in diet composition, growth rate or system productivity.

A novel but increasing application of SIA is the use of a population's isotope variability to determine trophic niche width or feeding variability within and between populations (Bearhop *et al*. 2004). As a measure of trophic niche width, greater isotope variability is indicative of greater diet breadth and consistency, whereas low variability can be attributed to either high population diet breadth with little consistency or low population diet breadth (Vander Zanden *et al*. 2000). Although few studies have used SIA for analyzing feeding variability within and between populations, recent results suggest that change in isotopic variability offer a promising tool to study population-level diet variation (Paterson *et al.* 2006; Syvaranta & Jones 2008). In addition to direct comparisons using non-lethal and lethal tissues for SIA, non-lethal tissues have never been examined for determining trophic breadth based on isotopic variability.

The objectives of this study were 1) to quantify and compare isotope values from muscle, fins and scales in walleye, *Sander vitreus* (Mitchill), from six populations encompassing differences in lake productivity and walleye size classes, 2) to develop and evaluate a model for predicting muscle-derived $\delta^{13}C$ or $\delta^{15}N$ from non-lethal samples across six walleye populations, 3) to determine whether non-lethal tissues can be used as surrogates for white muscle tissue when analyzing diet variability using SIA and 4) to assess relationships between fish length and $\delta^{15}N$.

Methods

Study site

Walleye were collected from six populations that included three natural, glacial lakes (Lardy, East Krause, Middle Lynn lakes) and three Missouri River reservoirs (Lake Oahe, Lake Sharpe, Lake Francis Case) in South Dakota, USA. Natural lakes were located in the Glaciated Plains ecoregion and ranged in surface area from 70 ha (East Krause Lake) to 280 ha (Middle Lynn Lake). Glacial lakes are classified as mesotrophic to eutrophic based on July trophic state index (TSI; Carlson 1977) values (53.9 to 60.1; VanDeHey et al. *In Press*). Walleye diets in the Glaciated Plains ecoregion are dominated by yellow perch, *Perca flavescens* (Mitchill), fathead minnows, *Pimephales promelas* (Rafinesque), and various invertebrates (VanDeHey 2011). Missouri River reservoirs were located in the Northwestern Glaciated Plains ecoregion and ranged in surface area from 22,600 ha (Lake Sharpe) to 202,000 ha (Lake Oahe), with summer TSI values ranging from eutrophic in the riverine and transitional zones to oligotrophic in the lacustrine zones (Lake Francis Case = 56.4 to 28.7; Lake Oahe = 64.6 to 38.5; Lake

Sharpe = 61.7 to 37.0; M.J. Fincel, unpublished data). Walleyes diets in Lake Oahe are generally dominated by rainbow smelt, *Osmerus mordax* (Mitchill), white bass, *Morone chrysops* (Rafinesque), freshwater drum, *Aplodinotus grunniens* (Rafinesque), gizzard shad, *Dorosoma cepedianum* (Lesueur), and invertebrates (Davis 2004). Gizzard shad and rainbow smelt are dominant prey items in Lake Sharpe (Wuellner *et al.* 2010), and walleye diets are largely unknown in Lake Francis Case.

Sample collection

Walleye were collected from August to September 2007 using experimental mesh gill nets set for 2-4 h. In the Missouri River impoundments, walleye were collected from all reservoir zones. A total of 95 fish ranging from 178- to 682-mm total length were collected from the six populations. Because of the limited amount of tissue obtained from smaller fish, specimens smaller than 175 mm were not included in the study. Captured fish were placed on ice for up to 2 h until tissue samples were obtained. White muscle samples (~2 g) were removed from the dorsal region of each fish above the lateral line and anterior to the dorsal fin. Scales were obtained from the dorsal region of each fish above the lateral line, and whole pelvic fins were excised. Tissue samples were then frozen and stored at -20 °C until analysis. Although some previous studies acid washed scales to remove carbonates in preparation for SIA (Perga & Gerdeaux 2003), scales were not acid washed in this study because of poor support in favor of the technique and possible increased variability in δ^{15}N caused by scale acidification (Bunn *et al.* 1995; Blanco *et al.* 2009; Rennie *et al*. 2009).

Stable isotope analysis

All samples were dried at 70°C for 72 h. Dried muscle and fin tissue were pulverized using a mortar and pestle. Due to the difficulty of manually grinding scales, scale samples were processed using a Wig-L-Bug® grinding mill (Dentsply-Rinn Inc. Elgin, IL). Ground tissues (0.4-0.6 mg) were then placed into 4x6 mm tin capsules for isotopic analysis. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were determined using a Europa 20-20 mass spectrometer. Isotope values were reported in δ notation, as per mille (‰) deviations from a standard material (Pee Dee Belemnite carbon or atmospheric nitrogen) using the equation

$$\delta^{13}C \ or \ \delta^{15}N = \left[\left(R_{sample} - R_{std} \right) \big/ R_{std} \right] * 1000 , \tag{1}$$

where R_{sample} is the isotopic ratio of the sample and R_{std} is the isotopic ratio of the standard. Lipid extraction on tissue samples was not performed prior to analysis; carbon-to-nitrogen (C:N) ratios for all tissue types were less than four, indicative of non-fatty tissue (Sanderson *et al.* 2009).

Data analysis

Muscle-derived $\delta^{15}N$, and hence trophic position, generally increases with walleye body size as fish prey become more important in the diet (Overman & Parrish 2001). Thus, the influence of body size on muscle-derived $\delta^{15}N$ values was explored for each population using correlation analysis. Paired t-tests were used to test the hypothesis that muscle isotope values did not differ from those of fins or scales. When differences between muscle isotope values and those from fins or scales were significant at $P<0.10$, a linear regression analysis was used to develop a predictive model for estimating muscle isotope values. To evaluate the reliability of model predictions, a split-sample validation approach was used where data were randomly divided into two groups of equal sample size (i.e. development and evaluation data sets; Steyerberg 2001). This resulted in a total of 43 fish being used for the muscle:fin comparison and 33 fish being used for the muscle:scale comparison from the development data set. Linear regression analysis was applied to one group of data (development data set) to generate predictive models for estimating muscle isotope values ($Muscle_{(Pred)}$) as,

$$Muscle_{(\mathrm{Pr}ed)} = a + Nonlethal_{(value)} * b \tag{2}$$

where $Nonlethal_{(value)}$ is the observed isotope value obtained from the non-lethal tissue sample (fin or scale), b = slope and a = intercept parameter. The model was then used to predict muscle isotope values from the evaluation data set. Sources of error between predicted and observed muscle isotope values were evaluated by decomposition of mean square error (MSE) as

$$MSE = \left(\frac{1}{n}\right) n \sum i = 1 (P_i - A_i)^2 = (P - A)^2 + (S_p - rS_A)^2 - (1 + r^2) S_A{}^2 \tag{3}$$

where n is the number of paired observations, P_i and A_i are predicted and observed muscle isotope values, P and A are the means of P_i and A_i, S_p and S_A are the standard deviations of P_i and A_i, and r is the correlation coefficient (Theil 1961). The MSE, obtained from least-squares regression of predicted values on observed values, represents the variance around the 1:1 line (i.e. unity) and is expressed by

$$1 = Z + S + E;$$

where Z is the error due to differences in the mean values, *S* is the slope component or error due to deviations of the slope from unity and *E* is the residual component due to random error (and Z<S; Theil 1961).

Differences in the isotopic variability in each tissue type were assessed by comparing mean absolute residuals (MAR; i.e., the magnitude of variability around the mean) for $\delta^{15}N$ and $\delta^{13}C$ among the six walleye populations. An ANOVA with a Tukey's test was used to determine which tissue types had significantly different absolute isotopic variability within each population. Because there were multiple comparisons (*n*=12), a Bonferroni correction was used to adjust *P* (α=0.008).

To estimate the minimum sample size required for developing accurate isotopic relationships between lethal and non-lethal tissues, a re-sampling with replacement protocol was used to identify at what sample size r^2 was maximized and the sample size at which the slope and intercept values were similar to those observed in the full model. To accomplish this, 10% of the observations from the development data set were randomly removed and a linear regression analysis used to develop a predictive model for estimating muscle isotope values from fin and scale values. The r^2 slope and intercept were recorded, and data points returned to original data set. This was repeated 10 times at increasing intervals of 10% (e.g., 10-100% of the data used). The mean of the r^2, slope and intercept were then plotted against sample size to estimate the minimal sample sizes required to have a similar r^2 and regression parameters to those in the full development data model.

Results

Muscle $\delta^{15}N$ values ranged from 14.7 to 20.9 and, in general, were positively related to walleye total length (Table 6-1). Bi-plots of $\delta^{15}N$ versus $\delta^{13}C$ revealed that walleye populations grouped similarly based on muscle and fin values (Figure 6-1). Scale-derived isotope bi-plots were less similar to muscle- and fin-derived plots, but groupings within populations were tighter compared to muscle- and fin-derived isotope bi-plots. Mean muscle, fin and scale $\delta^{15}N$ was 17.7 (±1.40), 17.3 (±1.7) and 17.8 (±2.0), respectively. Additionally, mean muscle, fin and scale $\delta^{13}C$ was -23.3 (±1.6), -23.1 (±1.9), and -20.6 (±1.6) respectively. Isotope values for muscle and fin tissue differed significantly for both $\delta^{15}N$ ($t_{88} = 4.00$; $P<0.001$) and $\delta^{13}C$ ($t_{88} = -3.42$, $P<0.001$). Isotope values for muscle and scale tissue differed significantly for $\delta^{13}C$ ($t_{66} = -47.30$, $P<0.001$) but not for $\delta^{15}N$ ($t_{66} = 1.50$; $P<0.138$). No trend of differences in isotope values between muscle and fin or muscle and scale with walleye size was evident.

Linear regression of developmental data showed that muscle-derived $\delta^{15}N$ or $\delta^{13}C$ measures were significantly related to those measured from fin or scale tissue (Figure 6-2). Comparison of observed muscle isotope values to those predicted by applying the developmental data models to the evaluation data set showed that 83-99% of the variability in the models could be attributable to random error (Table 6-2). The MAR of scales tended to be larger compared to fins, especially for $\delta^{13}C$, mostly due to differences between mean values of scales and muscle tissue (Figure 6-3).

Isotopic variability was significantly different in two of the six walleye populations for $\delta^{15}N$ and three of the six walleye populations for $\delta^{13}C$ (Figure 6-4).

Other than Lake Francis Case, in those populations with significantly different $\delta^{15}N$ variability, both fins and scales tended to have increased isotopic variability compared to muscle. East Krause was the only walleye population that showed significantly decreased isotopic variability ($\delta^{13}C$) in scales. Conversely, fins had increased variability relative to muscle for $\delta^{13}C$ in East Krause, Lardy and Lake Sharpe.

Required sample sizes for developing accurate isotopic relationships between lethal and non-lethal tissues were smaller for $\delta^{13}C$ than $\delta^{15}N$ and generally smaller when using fins as the non-lethal tissue type. The r^2, slope and intercept values were similar to those of the overall model variability at a sample size of approximately 20 fish for $\delta^{13}C$ (Figure 6-5). These parameters were more variable for $\delta^{15}N$, and a larger sample size of approximately 25 fish would be needed to develop a r^2, slope and intercept similar to those developed in the full model (Figure 6-6).

Discussion

The isotopic signatures obtained from lethal and non-lethal tissues of walleye were significantly related in six diverse, South Dakota lakes. Results suggest that stable isotope measures from fin tissue can be reasonably substituted for walleye muscle tissue; scale stable isotope measures, although significantly related to muscle, tended to be more enriched, especially for $\delta^{13}C$, and caution should be made when interpreting isotope results based on scale tissue. On average, muscle-derived $\delta^{15}N$ values were higher than those measured from scales or fins, but the magnitude of these differences was small (0.2-0.4 ‰). Conversely, $\delta^{13}C$ values varied significantly between muscle and scale tissue and on average were 2.4‰ higher in scales. The regression-based corrective equation effectively provided an adjustment to better account for the variability found between muscle and scale isotope values in walleye. These results build upon previous research that documented correlations between fish tissues within a species (Satterfield & Finney 2002; Perga & Gerdeaux 2003; Kelly *et al*. 2006b; Sanderson *et al.* 2009).

The significant positive correlations of fins and scales with muscle tissue for both δ^{13}C and δ^{15}N values from walleye are notable because of the range in fish sizes, ages and locations from which these fish were collected. Walleye were collected from systems with varying morphology, limnological conditions, productivity and primary diet items (Davis 2004; Wuellner *et al.* 2010). Moreover, fish from 178 to 682 mm TL were used to evaluate relationships in tissue isotope composition revealing these relationships remained similar despite likely changes in diets both spatially (i.e. large oligotrophic reservoirs vs. small eutrophic glacial lakes) and ontogenetically (i.e. size and age differences). Including the wide array of fish sizes and geographic locations into regression analysis incorporated a large degree of the isotopic variability of walleye from lakes and reservoirs throughout the Great Plains (Davis 2004; Wuellner *et al.* 2010) and supports the use of predictive equations developed in this study for estimating muscle-tissue isotope levels from fins and scales for walleye collected in other systems that exhibit similar trophic status and physical and biotic conditions.

Walleye scales have enriched δ^{13}C signatures and depleted δ^{15}N signatures relative to muscle values, which may be attributed to the lack of lipids in the scales (DeNiro & Epstein 1977; Blanco et al. 2009) but higher concentrations of lipid in muscle (DeNiro & Epstein 1977; Jobling *et al.* 1998). Lipid content was not assessed in any tissues, so this speculation remains unresolved. Additionally, differences in isotope signatures between scale and muscle tissue could be caused by the differences in turnover rates in each tissue (Tiesszen *et al.* 1983; Pinnegar and Polunin 1999). Although scales grow continuously throughout life, they are rather stable chemical reservoirs (Pruell *et al.* 2003). Conversely, metabolic turnover and rapid growth can change the chemical composition of muscle over shorter time periods.

In addition to using non-lethal tissues for food web reconstruction, tracking energy flow or determining trophic position, non-lethal tissues may be a suitable replacement for comparing diet variability within and between populations. Isotopic variability was generally consistent between tissues, but both fins and scales do not equally predict muscle δ^{15}N and δ^{13}C. Only one of six walleye populations had statistically different δ^{15}N variability between fins and muscle. Additionally, two of six walleye populations had statistically different δ^{15}N variability between fins and scales suggesting that fins, and to a lesser extent scales, may be a useful non-lethal surrogate for assessing δ^{15}N variability. Conversely, three of size walleye populations had significantly different muscle and fin δ^{13}C variability, and only one walleye population had significantly different muscle and scale δ^{13}C variability; thus, scales may be the tissue of choice when estimating δ^{13}C variability. This suggests that determining the required isotopic signatures should dictate non-lethal tissue use.

The ability to use fin and scale tissue as surrogates for lethally obtained muscle tissue in fishes is important when performing SIA on rare species or popular recreational fishes (Jardine *et al.* 2005). Muscle tissue removal can be non-lethal in large animals

(Shannon *et al*. 2001); and, while there is some evidence that muscle biopsy might be a non-lethal means of collecting fish tissue for SIA (Osmundson *et al*. 2000, Hamilton *et al*. 2002), limited research has been done to evaluate survival of fishes following the biopsy, especially in wild populations (Baker *et al*. 2004). Additionally, demonstrating the ability to use calcified structures (i.e. scales) for SIA allows the use of archived tissue samples for historic food web reconstruction. Many state, federal and non-governmental agencies collect calcified structures during annual surveys (often used for age determination). Although the use of SIA to assess long-term temporal variability in diets has become more common, especially in mammals, its use in fisheries remains limited (see Dalerum & Angerbjörn 2005 for a review). The majority of fisheries research using SIA for analyzing changes in food habits over time have used lethally obtained tissues (muscle, whole fish and otoliths; Dalerum & Angerbjörn 2005). However, archived scale samples have been used successfully to assess temporal diet patterns (up to 30 years) in several Pacific salmonid species (Satterfield & Finney 2002). In addition, archived scale samples have been used to identify shifts in δ^{13}C signatures of striped bass, *Morone saxatilis* (Walbaum), in Chesapeake Bay (Pruell *et al.* 2003); and the use of archived scales to identify temporal changes in food webs and assess the impacts of species introductions and invasions *post hoc* is in its infancy.

Although use of non-lethal tissues for SIA has merit and provides useful estimates of isotopic signatures, care must be taken when determining which tissues will be most informative, taking into account the volume of tissue required for isotope analysis. In the present study, sufficient scale tissue (i.e., approximately one gram dried tissue) was removed from only 33 of approximately 97 captured walleye. Walleye greater than 175 mm long were used in this study. Using smaller specimens for isotope analysis may be problematic as more scales will need to be removed, and the lethality of removing this quantity of tissue is unknown. Although prior research has revealed little impacts of pelvic fin removal on most species (Zymonas & McMahon 2006; Wagner *et al.* 2009), the effects of fin removal on survival and swimming or feeding behavior vary by fin and species, and the potential negative consequences should be assessed prior to selecting a non-lethal tissue. Second, when possible, a subset of fish should be sacrificed to produce predictive equations for estimating muscle-tissue isotope ratios. For walleye in this study, the samples sizes required to develop predictive equations were relatively small ($n<25$). Given the strong correlations found between tissues in other species (see Kelly *et al*. 2006b), it is likely that required sample sizes will be similar for other species. However, the required sample size may vary with species and systems, and the results presented in this study only apply directly to walleye in similar systems. Third, using archived scale samples provides a unique opportunity to examine foraging patterns of fishes throughout time. However, mixed results in scales compared to muscle tissue were found for both mean isotope signatures and isotope variability. When performing retrospective studies, care must be taken in the interpretation of the data as some substantial differences were found in walleye scales, especially when analyzing variability in isotopic signatures between scales and muscle. Moreover, in this study scale-envelopes were not used. However, this is a common practice when removing and cataloging scales for aging purposes. Different storage methods may alter the isotopic signatures of the scale tissue, necessitating the need to identify the impacts of preservation techniques (Kelly *et al.* 2006a; Andvik *et al.* 2010).

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Table 6-1. Correlation (r = Pearson's correlation coefficient) between muscle δ^{15}N values and total length (TL; mm) for six walleye populations in South Dakota.

Population	*n*	TL (mm)	δ^{15}N range	r	*P*
East Krause Lake	17	178-682	15.8-20.9	0.91	<0.01
Lardy Lake	17	371-532	17.8-19.6	0.91	<0.01
Middle Lynn Lake	15	368-591	17.7-19.5	0.37	0.15
Lake Oahe	25	259-619	14.9-18.1	0.76	<0.01
Lake Sharpe	12	251-429	14.7-17.1	0.93	<0.01
Lake Francis Case	9	289-449	14.8-16.0	0.75	0.01

Table 6-2. Mean (SE) observed and predicted muscle stable isotope values for walleyes from six South Dakota populations. Predicted values were obtained using regression parameters in Figure 2 for fin or scale isotope measurements. Sources of error, calculated from decomposition of mean square error, are given for comparisons of observed and predicted values.

			Predicted muscle value		Sources of error		
Isotope	*n*	Observed muscle	From fin isotope	From scale isotope	Mean	Slope	Residual
$\delta^{15}N$	44	17.8 (0.21)	17.6 (0.22)		0.05	0.10	0.85
	33	18.0 (0.24)		18.0 (0.23)	<0.01	0.04	0.95
$\delta^{13}C$	44	-23.5 (0.23)	-23.5 (0.22)		<0.01	<0.01	0.98
	33	-22.9 (0.30)		-22.7 (0.29)	0.16	<0.01	0.83

Figure 6-1. Bi-plot of $\delta^{15}N$ versus $\delta^{13}C$ values for six walleye populations in South Dakota.

Figure 6-2. Residual differences between observed $\delta^{15}N$ and $\delta^{13}C$ values obtained from white dorsal muscle tissue and fin and scale tissues from walleyes collected from six populations in South Dakota.

Figure 6-3. Comparison of observed muscle $\delta^{15}N$ and $\delta^{13}C$ with muscle $\delta^{15}N$ and $\delta^{13}C$ predicted from fins and scales for walleye from six populations in South Dakota.

Figure 6-4. Differences in mean absolute residuals for $\delta^{15}N$ and $\delta^{13}C$ between the tissue types of walleyes collected from six populations in South Dakota. Open bars represent muscle tissue, large hatched bars represent fin tissue, and small hatched bars represent scale tissue. Means with the same letters were not significantly different by ANOVA with Bonferroni correction for multiple comparisons α=0.004.

Figure 6-5. Sample sizes (number of fish) required to obtain similar estimates of linear regression parameters (r^2, slope and intercept) to those parameters generated using all data points (horizontal dashed line; *n*= 43 fish muscle:fin and *n*=33 muscle:scale) for $\delta^{13}C$ values when using fins (left panels) or scales (right panels) for walleye from six South Dakota populations. Error bars represent mean standard error from the 10 simulations at each sample size.

Figure 6-6. Sample sizes (number of fish) required to obtain similar estimates of linear regression parameters (r^2, slope and intercept) to those parameters generated using all data points (horizontal dashed line; *n*= 43 fish muscle:fin and *n*=33 muscle:scale)for $\delta^{15}N$ values when using fins (left panels) or scales (right panels) for walleye from six South Dakota populations. Error bars represent mean standard error from the 10 simulations at each sample size.

Figure 6-1.

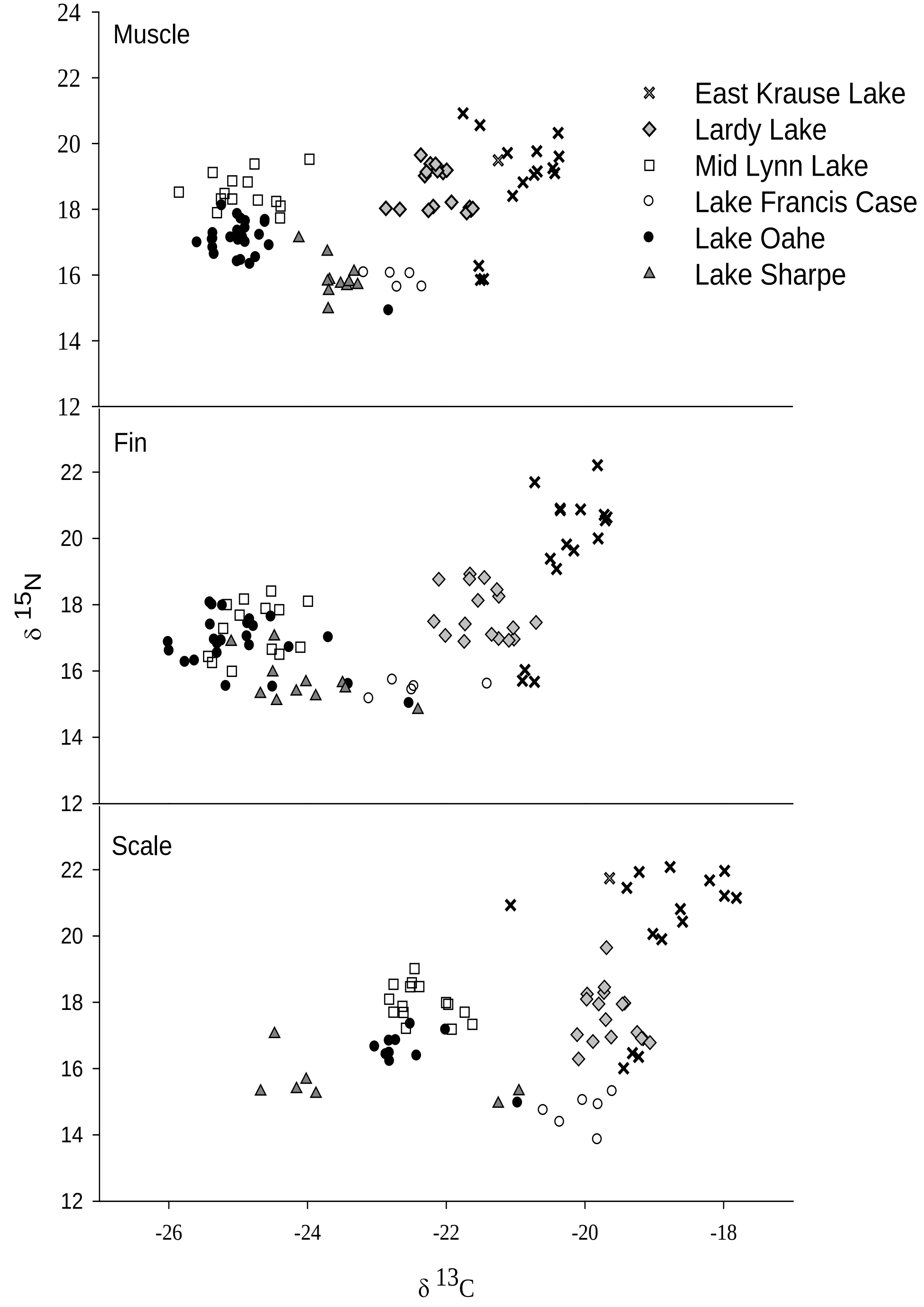

Muscle
Fin
Scale
East Krause Lake
Lardy Lake
Mid Lynn Lake
Lake Francis Case
Lake Oahe
Lake Sharpe
24
22
20
18
16
14
12
-26
-24
-22
-20
-18
δ 15N
δ 13C

Figure 6-2.

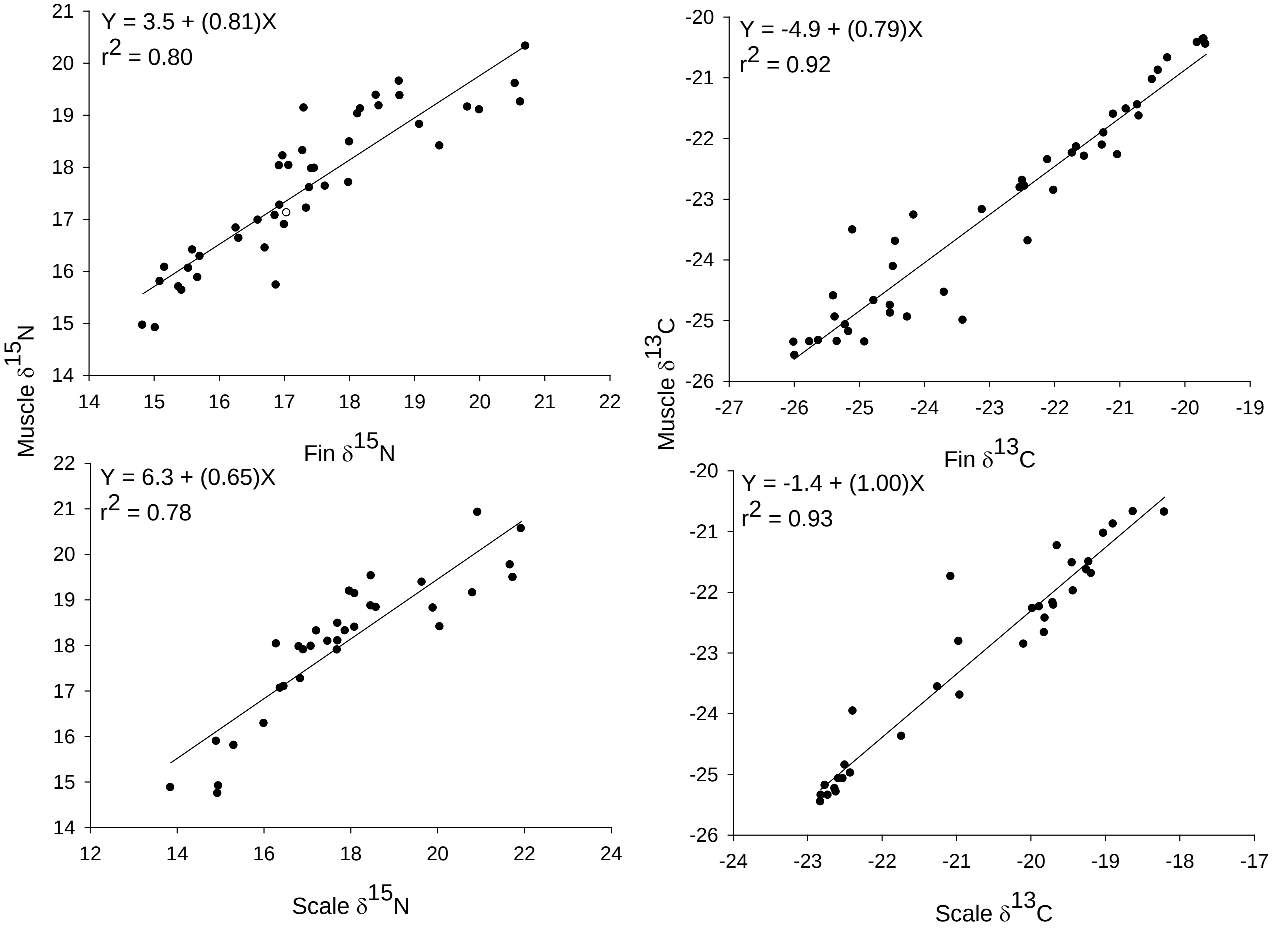

Y = 3.5 + (0.81)X
r2 = 0.80
Muscle δ15N
Fin δ15N
21
20
19
18
17
16
15
14
14
15
16
17
18
19
20
21
22
Y = -4.9 + (0.79)X
r2 = 0.92
Muscle δ13C
Fin δ13C
-20
-21
-22
-23
-24
-25
-26
-27
-26
-25
-24
-23
-22
-21
-20
-19
Y = 6.3 + (0.65)X
r2 = 0.78
Scale δ15N
22
21
20
19
18
17
16
15
14
12
14
16
18
20
22
24
Y = -1.4 + (1.00)X
r2 = 0.93
Scale δ13C
-20
-21
-22
-23
-24
-25
-26
-24
-23
-22
-21
-20
-19
-18
-17

Figure 6-3.

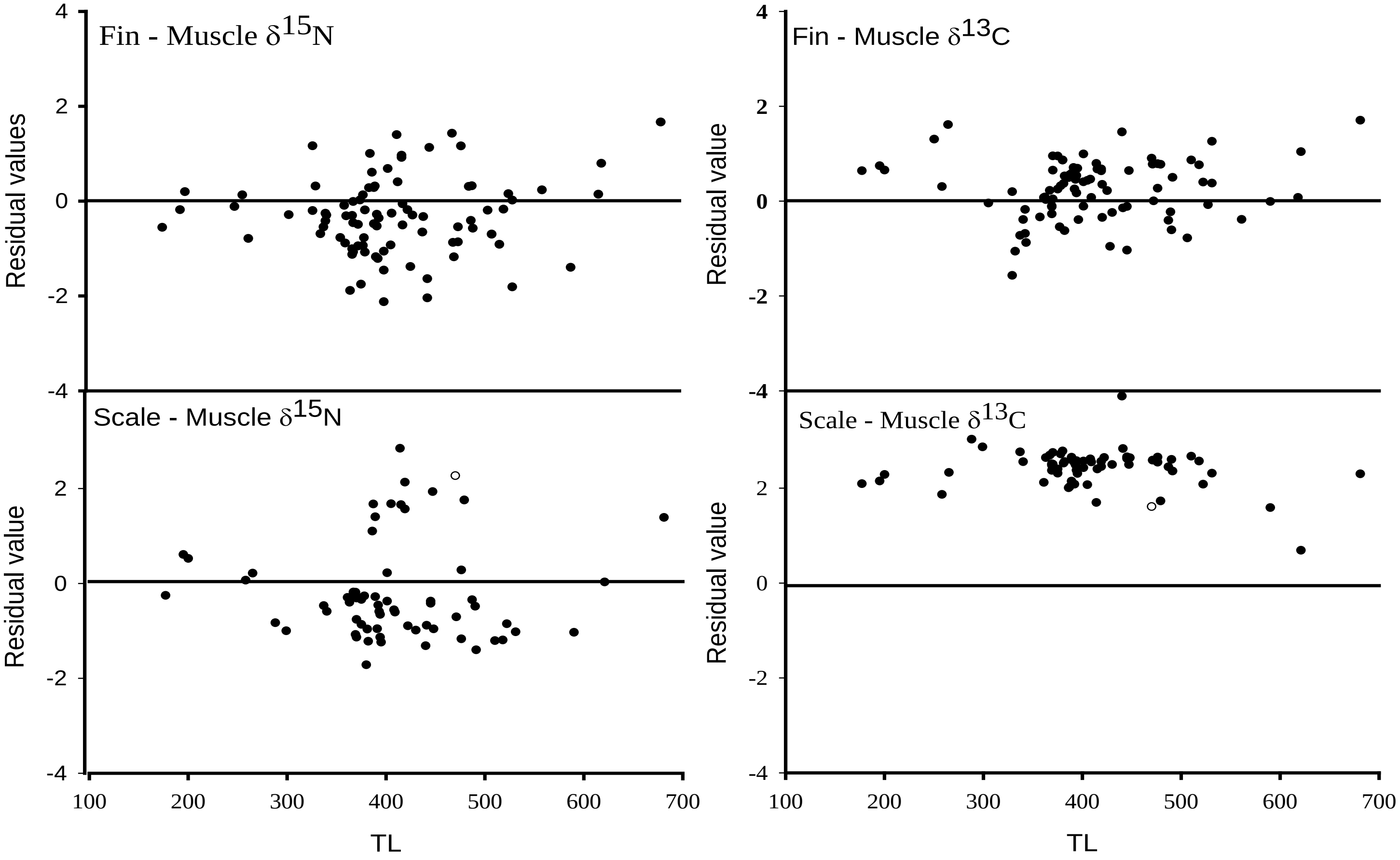

Fin - Muscle δ^{15}N
Fin - Muscle δ^{13}C
Scale - Muscle δ^{15}N
Scale - Muscle δ^{13}C
Residual values
Residual value
Residual value
Residual value
4
2
0
-2
-4
100
200
300
400
500
600
700
TL
TL

Figure 6-4.

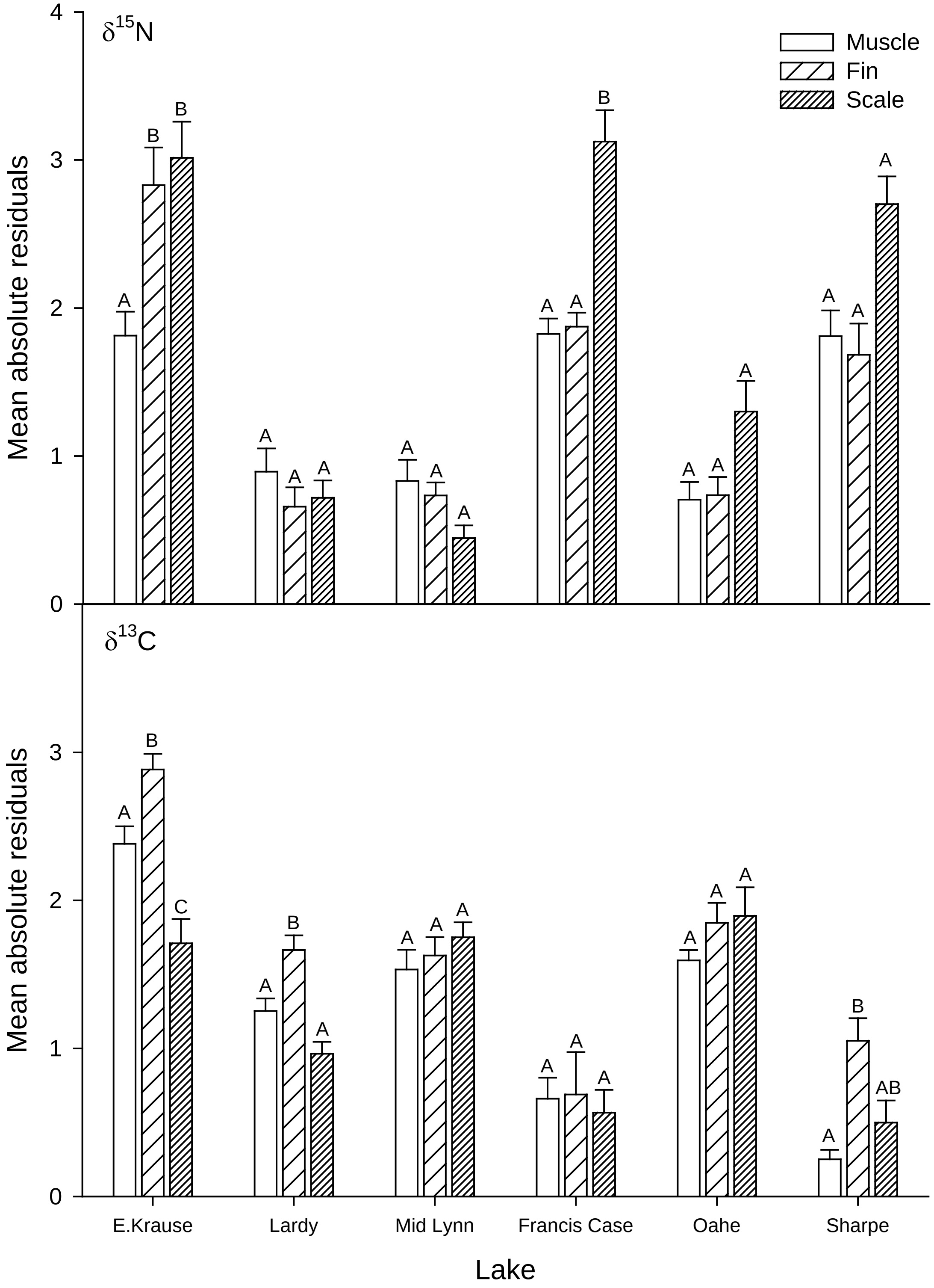

δ15N
δ13C
Muscle
Fin
Scale
Mean absolute residuals
Mean absolute residuals
0
1
2
3
4
0
1
2
3
A B B
A A A
A A A
A A B
A A A
A A A
A B C
A B A
A A A
A A A
A A A
A B AB
E.Krause
Lardy
Mid Lynn
Francis Case
Oahe
Sharpe
Lake

Figure 6-5.

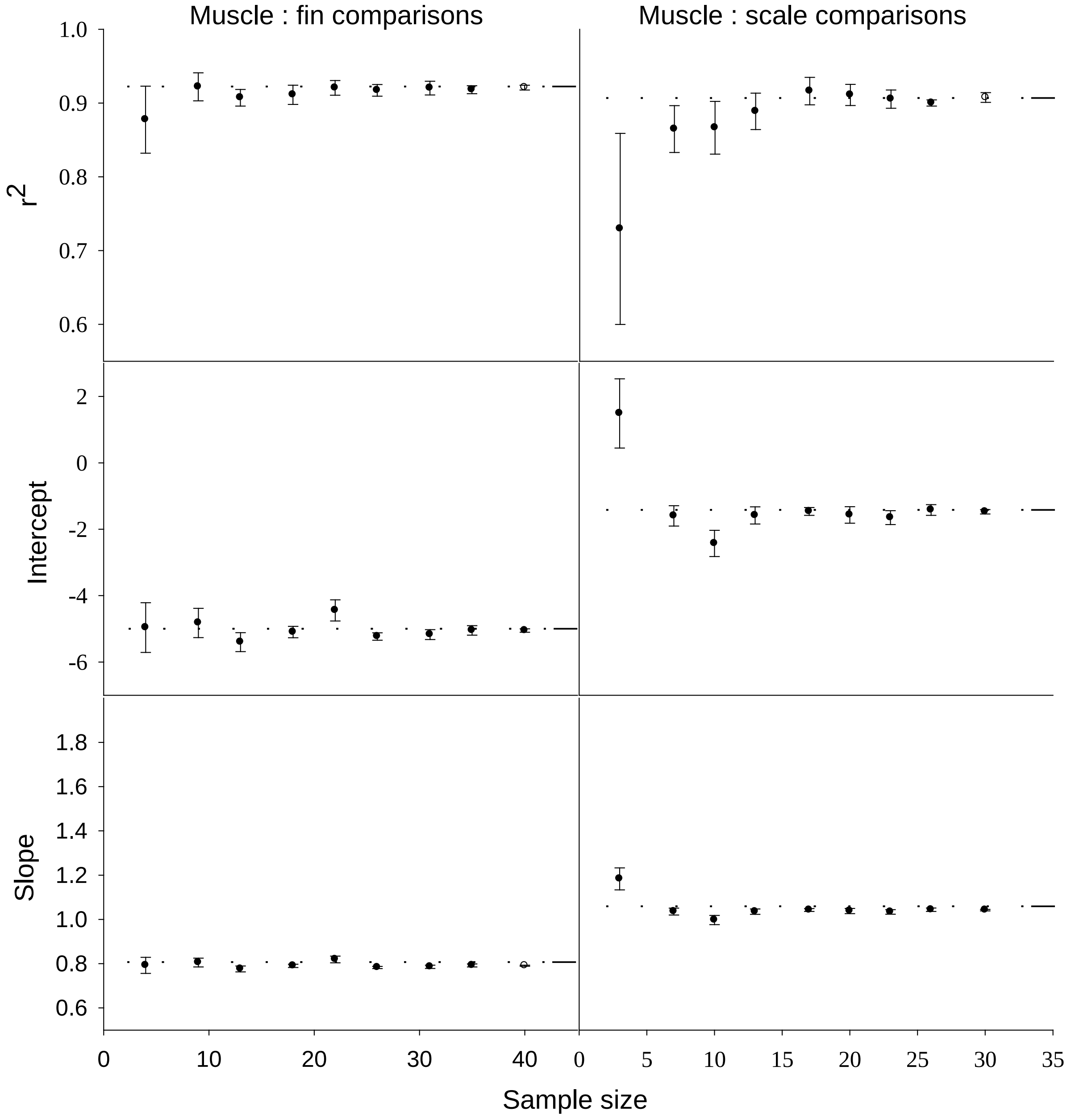
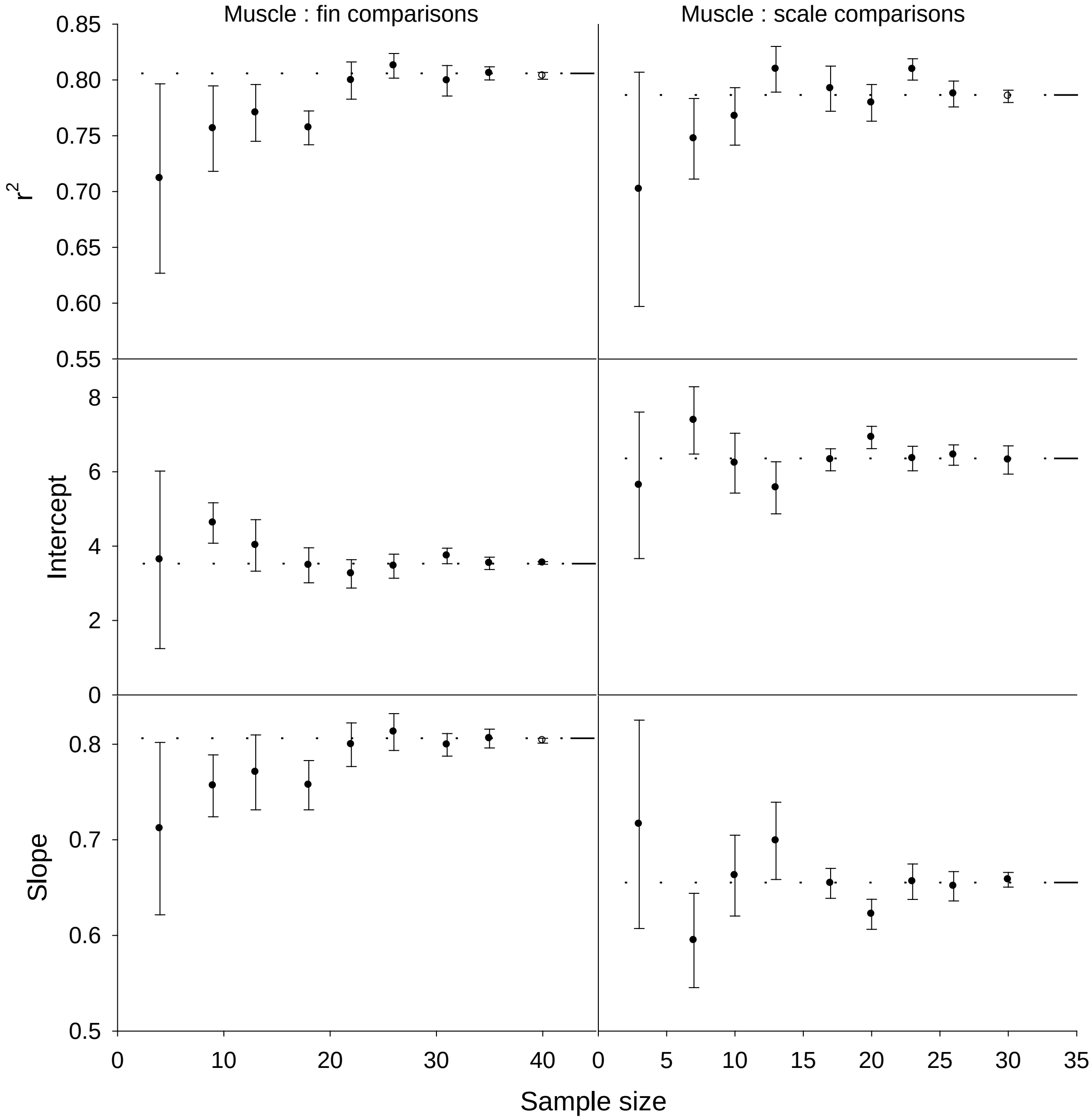

Muscle : fin comparisons
Muscle : scale comparisons
r^2
1.0
0.9
0.8
0.7
0.6
Intercept
2
0
-2
-4
-6
Slope
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0
10
20
30
40
0
5
10
15
20
25
30
35
Sample size

Figure 6-6.


Muscle : fin comparisons
Muscle : scale comparisons
r2
0.85
0.80
0.75
0.70
0.65
0.60
0.55
Intercept
8
6
4
2
0
Slope
0.8
0.7
0.6
0.5
0
10
20
30
40
0
5
10
15
20
25
30
35
Sample size

Chapter 7: Comparing Isotope Signatures of Prey Fish: Does Gut Removal Affect $\delta^{13}C$ or $\delta^{15}N$?

Abstract

Stable isotope analysis is a quick and inexpensive method to monitor effects of food web changes on aquatic communities. Traditionally, whole specimens have been used when determining isotope composition of prey fish or age-0 recreational fishes. However, gut contents of prey fish could potentially alter isotope composition of the specimen especially when recent foraging has taken place or when the gut contains non-assimilated material that would normally pass through fishes undigested. To assess the impacts of gut content on prey fish isotope signatures, I examined the differences in isotopic variation of five prey fish species using whole fish, whole fish with the gut contents removed, and dorsal muscle only. I found significant differences in both $\delta^{15}N$ and $\delta^{13}C$ between the three tissue treatments. In most cases, muscle tissue was enriched compared to whole specimens or gut-removed specimens. Moreover, differences in mean $\delta^{15}N$ within a species were up to 2‰ among treatments. This would result in a change of over half a trophic position based on a 3.4‰ increase per trophic level. However, there were no apparent relationships between tissue isotope values in fish with increased gut fullness (more prey tissue present). I suggest that muscle tissue should be used as the standard tissue for determining isotope composition of prey fish or age-0 recreational fishes especially when determining enrichment for mixing models, calculating trophic position, or constructing aquatic food webs.

Introduction

Stable isotope analysis (SIA) offers a useful approach for quantifying energy flow within food webs (Kling et al. 1992, Cabana and Rasmussen 1994). Stable isotope analysis offers time-integrated analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) reflective of energy assimilated by consumers and provides an analytical approach for determining trophic position (TP; Kling et al. 1992, Cabana and Rasmussen 1996, Vander Zanden et al. 1999). Trophic position is a continuous variable that accounts for omnivory and better quantifies matter and energy flow within a food web (Kling et al. 1992, Vander Zanden and Rasmussen 1996, Post 2002). One key assumption in developing food web models and calculating TP is developing a known measure of enrichment (Δ), or the magnitude of increase of a predator's isotopic value relative to the isotopic value of its prey (i.e., $\Delta = \delta^{15}N_{consumer} - \delta^{15}N_{diet}$; Vanderklift and Ponsard 2003). Many studies have attempted to incorporate Δ variability to improve the efficiency of mixing models; however, these models are contingent on accurate estimates of Δ and further emphasize the need to develop accurate Δ estimates when using SIA in food web and energy flow studies (Phillips and Koch 2002).

Many variables affect Δ; these variables include but are not limited to the biochemical form of nitrogenous waste, feeding behaviors of the species, taxonomic classes, and the type of ecosystem under consideration (see Vanderklift and Ponsard 2003 for a review). One variable shown to influence Δ is the type of tissue used; however, results of these studies were conflicting (Yoneyama et al. 1983, Hobson and Clark 1992, Vanderklift and Ponsard 2003). For example, in a review by Vanderklift and Ponsard (2003), Δ was examined using both whole fish and dorsal muscle, but no clear evidence was established regarding the effect of using whole fish on Δ, likely because of small sample sizes of whole fish (n=1, Δ=3.2).

The use of whole fish in SIA studies has many potential benefits to that of dorsal muscle as prey fish vulnerable to predation by larger fish or age-0 recreational fishes are generally small, making removal of enough dorsal muscle tissue for isotope analysis difficult. However, isotopic signatures derived from whole fish or pooled muscle tissue from multiple small specimens may alter inherent isotopic variability found in prey fish or age-0 recreational fish samples (Yoshioka et al. 1994, Mitchell et al. 1996, Vander Zanden et al. 1998, Johnson et al. 2002, McIntyre et al. 2006). Moreover, no information exists on the isotopic differences found between whole fish and dorsal muscle and the impacts of removing gut contents of prey fish on their isotopic signatures. Additionally, small variations in Δ may produce significant differences in the output of isotopic mixing models (Ben-David and Schell 2001). Due to the growing use of SIA in food web reconstruction and the limited information that exists on isotopic differences between whole fish and dorsal muscle, the objective of our study was to determine if differences exist in $\delta^{13}C$ and $\delta^{15}N$ between whole fish, whole fish with the gastrointestinal tract (i.e, gut) removed, and dorsal muscle in five prey fish species and to determine if gut fullness had an effect on isotopic signatures.

Methods

Thirty specimens from five different prey species [rainbow smelt (*Osmerus mordax*), gizzard shad (*Dorosoma cepedianum*), yellow perch (*Perca flavescens*), white bass (*Morone chrysops*), and spottail shiner (*Notropis hudsonius*)] were collected from Lake Oahe, South Dakota, in late August 2008 using standard shoreline seining procedures. All specimens of a single species were collected within a single location to minimize potential isotopic disparities caused by differences in feeding patterns or isotopic baselines spatially (McKinney et al. 1999). Upon capture, all fish were placed on ice and transported to the laboratory. All specimens were rinsed with distilled water to remove external matter, and total length and mass were recorded. I excised and weighed the gastrointestinal tract from all individuals. Ten individuals of each species were then randomly assigned to each of the three groups for isotopic analysis. Groups included whole fish (WF – the entire fish used), whole fish with the gut removed (GR), and dorsal muscle tissue (DM – only dorsal muscle used). Samples were placed in individually labeled aluminum trays, dried for 72 h, then ground and homogenized using a mortar and pestle. Samples were analyzed for $\delta^{15}N$ and $\delta^{13}C$ using a Europa 20-20 mass spectrometer.

I tested for differences in $\delta^{15}N$ and $\delta^{13}C$ between tissue treatments using an analysis of variance (ANOVA) with a Tukey's significance test to determine if significant differences existed between treatments. In addition, since total length may affect isotopic signatures due to ontogenetic diet shifts and isotopic ratios of $\delta^{15}N$ tend to increase at higher trophic levels (Kling et al. 1992), $\delta^{15}N$ values should be positively correlated with total length (Vander Zandenet al. 1998, Fincel et al. 2011). To account for potential differences in size or feeding patterns between groups, I used an ANOVA with a Tukey's significance test to examine differences in total length between treatment groups. Because gut fullness could also alter isotope signatures of treatment groups, I used an ANOVA with a Tukey's significance test to examine differences in gut weight to total weight ratios between the treatment groups of each species. For all comparisons, I used a Bonferroni correction for multiple comparisons and set the significance level at α=0.001.

Results

In general, the DM treatment tended to have higher δ^{15}N and δ^{13}C compared to both WF and GR groups for three of the five species studied (i.e., yellow perch, gizzard shad, and white bass; Figure 7-1). Spottail shiner and rainbow smelt were the only species that had similar isotopic values (both δ^{15}N and δ^{13}C) between the DM and GR treatments. Significant differences in δ^{13}C were found between tissue types for white bass and spottail shiner (Table 7-1). White bass was the only species that showed consistent enrichment in DM for both the δ^{13}C and δ^{15}N between treatments. Other than the DM and GR comparisons for spottail shiner and rainbow smelt, in all other significant pair-wise comparisons, the DM treatments were enriched compared to WF or GR groups.

No significant differences were observed in total length between any tissue groups (Table 7-2; Figure 7-2). Two of the five species showed significant differences in gut weight to total weight (GW/TW). Yellow perch in the DM treatment group had greater GW/TW compared to the WF or GR treatments. For white bass GW/TW ratios were significantly different among all three tissue treatments. However, no relationships were found relating differences in isotope signatures between tissues to differences in GW/TW in any species.

Discussion

I found significant differences in isotopic values between DM, WF and GR prey fish samples in three of five species, suggesting that substantial error can be accrued when analyzing different tissue types for stable isotope analyses and subsequent Δ calculation. For instance, the use of WF yellow perch for Δ estimates of $\delta^{15}N$ on a Lake Oahe food web study would result in a difference of 2‰ [i.e., over half a trophic position based on 3.4‰ Δ by Post (2002)] compared to the DM of yellow perch. This could significantly alter mixing models and estimation of trophic position using this species and tissue type. Similarly, if white bass were an important component in the food web, the significant differences in signatures of both isotopes between treatment types could dramatically impact interpretation of energy flow, food webs and mixing models (Vander Zanden and Rasmussen 2001). Therefore, when trying to minimize error associated with Δ, a standard tissue type should be used.

Across species, the WF treatment was depleted in $\delta^{13}C$ for four of five species compared to both DM and GR treatments. Additionally, the WF treatment was depleted in $\delta^{15}N$ for four of five species relative to DM treatments. Several potential explanations may exist for WF treatments being depleted in $\delta^{15}N$ and $\delta^{13}C$

compared to DM or GR. One reason could be that food items or undigested waste product altered whole prey fish isotopic signatures relative to the DM or GR treatments. However, this comparison was only statistically significant in five (of 10) WF to DM comparisons and one WF to GR comparison. Another reason for the consistent isotopic depletion in WF could be related to the gut weight to fish weight ratios. However, in our study GW/TW ratios did not appear to significantly alter isotopic signatures.

I saw no differences in TL between tissue groups for any species, which was expected. However, I did find significant differences in gut fullness (GW/TW). White bass showed significant differences in gut fullness, as the DM treatment had greater GW/TW compared to the WF treatment and the GR treatment had at least twice the ratio as that of the other two treatment groups. However, due to the randomization process, the fullest guts were in DM and GR treatments and not in the WF treatment. Some of the isotope signature of the whole fish is likely undigested waste (explaining the lower signature of whole fish relative to other treatment groups), which would not likely be incorporated into predators' diets (Vanderklift and Ponsard 2003, Jardine et al. 2005, Caut et al. 2009). If gut contents did in fact decrease specimen isotope values, I did not reveal this scenario, because the WF treatment had the lowest GW/TW compared to the other treatments. Including individuals with full stomachs in WF treatments should be considered in future studies. In addition, gut evacuation rates vary among species (Brooke et al. 1996, Irigoien 1998, Miyasaka and Genkai-Kato 2009) by water temperature (Chipps

1998) and by diet (Targett and Targett 1990). Though I did not quantify gut evacuation rates, I collected specimens in August when warmer water temperature likely facilitated high gut evacuation rates. This coupled with differences in gut evacuation rates between species could aid in the non-significant isotopic depletion in the WF treatments relative to other tissues.

Another explanation for the observed differences between WF, GR, and DM treatments may be the incorporation of lipid-rich tissues into the isotopic signatures of WF and GR groups. Generally, white muscle is more δ^{15}N-enriched compared to the heart, liver, and red muscle, a likely result of increased tuarine or other amino acids in white muscle tissue (Wilson and Poe 1974, Pinnegar and Polunin 1999). By simply removing the gastrointestinal tract, I left those tissues with decreased lipids and potentially lowered the δ^{15}N signature of the specimen compared to muscle alone. Moreover, lipids are relatively depleted in δ^{13}C (DeNiro and Epstein 1977), which could explain the relative similarities in δ^{13}C between WF, GR, and DM treatments compared to the differences observed in δ^{15}N. The DM group was only significantly enriched in δ^{13}C for two of five species. In spottail shiners, the DM group was not significantly different than GR, which may be a function of gut contents being assimilated into the δ^{13}C signature of the specimen. Future research may focus on removing liver, heart, and other lipid-depleted tissues to determine whether differences are still observed between treatments.

Acknowledgements

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Table 7-1. ANOVA results for differences between whole fish (WF), gut removed whole fish (GR) and dorsal muscle (DM) treatments in δ^{15}N and δ^{13}C for gizzard shad, rainbow smelt, spottail shiner, white bass, and yellow perch collected from Lake Oahe, South Dakota. Due to multiple comparisons, α=0.001.

		δ^{15}N		δ^{13}C	
Species	df	F-Value	P-value	F-Value	P-value
gizzard shad	2,27	6.12	0.006	2.51	0.100
rainbow smelt	2,27	2.96	0.069	0.19	0.830
spottail shiner	2,27	5.54	0.010	5.947	0.007
white bass	2,27	8.29	0.002	10.33	<0.001
yellow perch	2,27	19.28	<0.001	1.82	0.181

Table 7-2. ANOVA results for differences between whole fish (WF), gut removed whole fish (GR) and dorsal muscle (DM) treatments for total length and gut weight to total weight for gizzard shad, rainbow smelt, spottail shiner, white bass, and yellow perch collected from Lake Oahe, South Dakota. Due to multiple comparisons α was set at 0.001.

		Total Length		Gut weight / Total weight	
Species	df	F-Value	P-value	F-Value	P-value
gizzard shad	2,27	1.21	0.315	1.15	0.332
rainbow smelt	2,27	0.60	0.556	3.80	0.035
spottail shiner	2,27	1.09	0.349	2.65	0.089
white bass	2,27	0.38	0.687	62.05	<0.001
yellow perch	2,27	0.40	0.671	13.20	<0.001

Figure 7-1. ANOVA results for differences among tissues (whole fish [WF] – dark bars, gut removed whole fish [GR] – hashed bars, and dorsal muscle tissue [DM] – open bars) in A) δ^{15}N and B) δ^{13}C. Those tissues with different letters are significantly different ($p<0.01$). Species include gizzard shad (GZD), rainbow smelt (RBS), spottail shiner (STS), white bass (WTB), and yellow perch (YLP)collected from Lake Oahe, South Dakota. Error bars represent one unit of standard error.

Figure 7-2. ANOVA results for differences among tissues (whole fish [WF] – dark bars, gut removed whole fish [GR] – hashed bars, and dorsal muscle tissue [DM] – open bars) in A) total length and B) the ratio of gut weight to total weight (GW/TW). Those tissues with different letters are significantly different ($p<0.01$). Species include gizzard shad (GZD), rainbow smelt (RBS), spottail shiner (STS), white bass (WTB), and yellow perch (YLP) collected from Lake Oahe, South Dakota. Error bars represent one unit of standard error.

Figure 7-1.

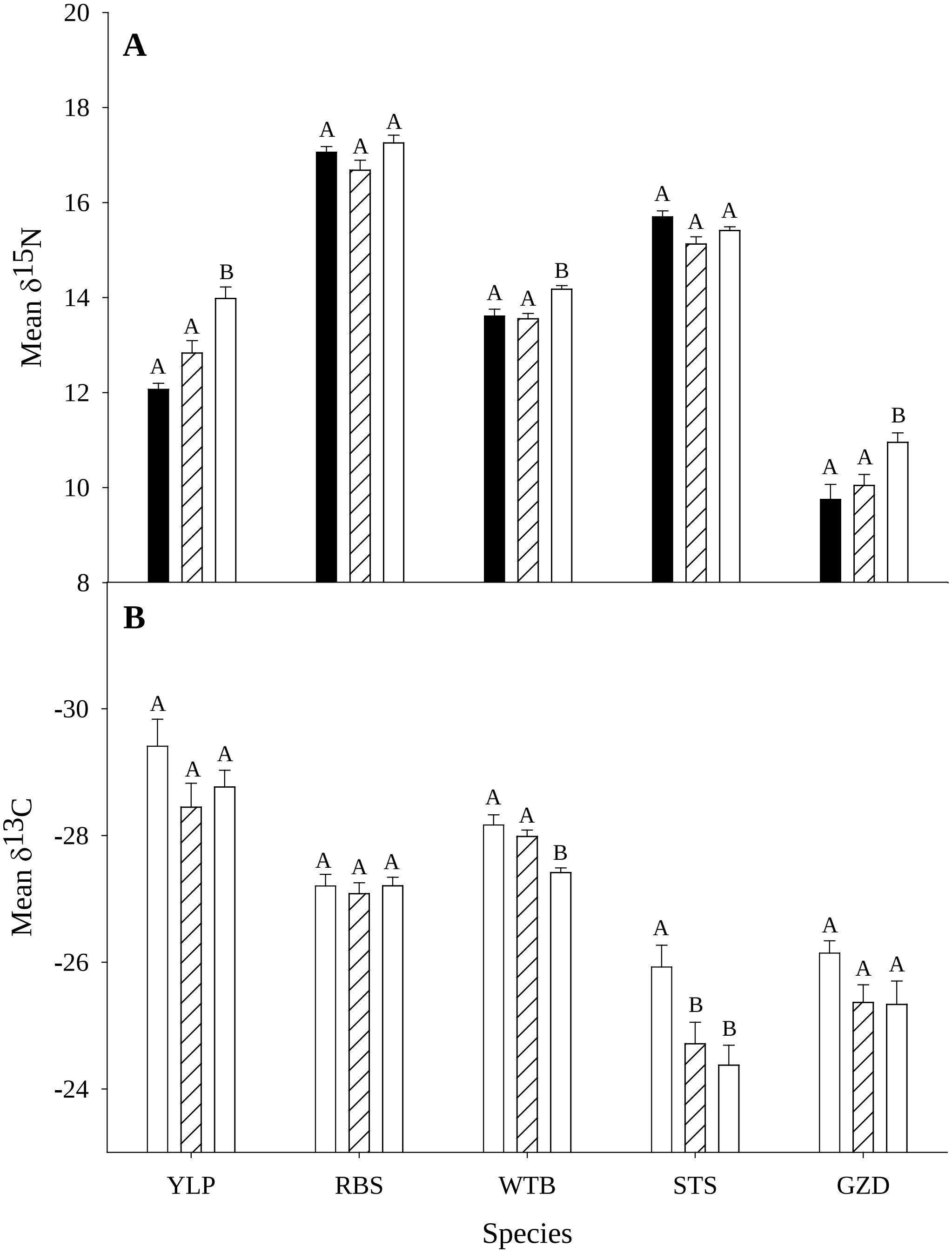
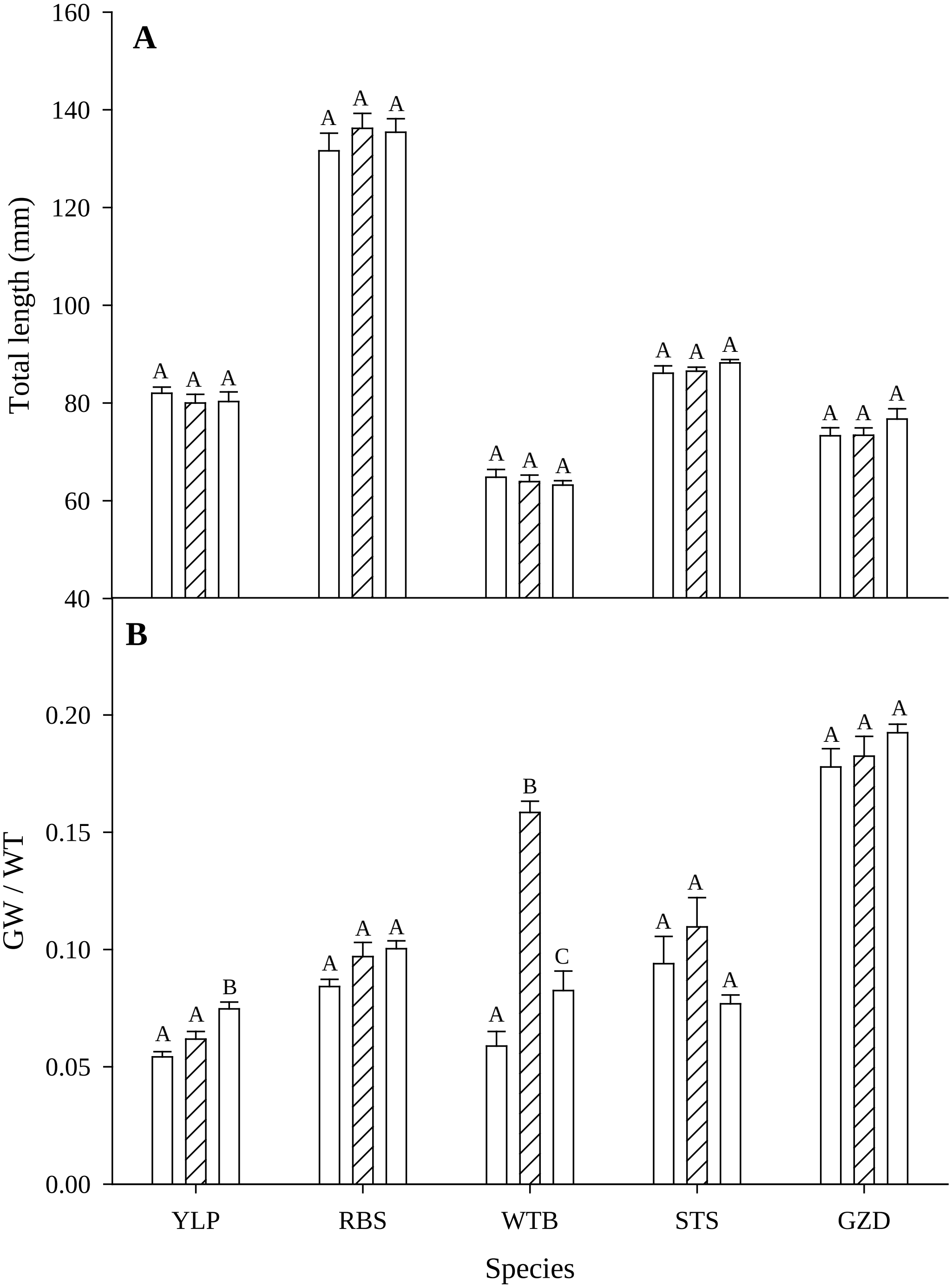


Figure 7-2.


A
B
Total length (mm)
160
140
120
100
80
60
40
GW / WT
0.20
0.15
0.10
0.05
0.00
YLP
RBS
WTB
STS
GZD
Species
A A A
A A A
A A A
A A A
A A A
A A B
A A A
A B C
A A A
A A A

Chapter 8: Management Recommendations

Productivity Attributes in South Dakota Missouri River Reservoirs

Monitoring of physiochemical characteristics and productivity are vital for addressing local water quality problems, environmental processes and productivity forecasting (Yako et al. 1996; Popovičová 2009). Post hoc analyses of water quality and productivity estimates are informative, but can suffer from limited sample sizes (Bolgrien et al. 2009). One goal of this project was to develop protocols to monitor physiochemical and productivity estimates in the Missouri River impoundments. These protocols sought to maximize the information, while minimizing the sampling time and effort. For nutrients and chlorophyll *a*, minimal samples were found to be needed for monitoring programs. Although spikes in these parameters occurred, sample size requirements were generally uniform and a suite of recommendations can be made from the data. For TKN and TP, three 1 L integrated water samples (not to exceed twice the Secchi depth) can be collected in April, from the lower lacustrine zone of each reservoir and these samples will accurately describe nutrient dynamics. Three chlorophyll *a* samples should also be collected simultaneously with the April nutrient collections. Moreover, ten zooplankton samples using a conical shaped Wisconsin net (10 cm diameter, 150 μm mesh) towed vertically from twice the Secchi depth to the surface (or from 1 m above the sediment to the surface if water depth was less than twice the Secchi depth) would be sufficient to account for the variability observed in South Dakota Missouri River impoundments. These could be collected at any time, but to improve efficiency, April zooplankton collections would be optimal.

Larval Gizzard Shad Characteristics in Lake Oahe, South Dakota

In Lake Oahe, slow gizzard shad growth rates make this species an ideal prey resource for piscivores. In this system, and other reservoirs in the northern Great Plains, larval gizzard shad appear to exhibit temporal and spatial variability in abundance and growth; however, growth remains generally slow and density low, compared to more southerly systems. These characteristics appear to make gizzard shad a suitable prey resource in reservoirs in South Dakota and throughout the northern Great Plains. When examining the relationship between gizzard shad and walleye, the most popular sport fish in South Dakota (Gigliotti 2007), there exists a strong positive relationship where walleye growth and condition is positively related to gizzard shad presence (Ward et al 2007; Wuellner et al. 2010). Thus, gizzard shad are frequently stocked in small Western South Dakota reservoirs to bolster walleye prey resources (Ward et al. 2007). Future work should evaluate the potential for this practice in Lake Oahe, South Dakota.

Walleye Consumption and Growth in Lake Oahe, South Dakota

In Lake Oahe, South Dakota, walleye can attain between 40% and 60% of their maintenance energy requirements from gizzard shad, when abundant. During times of low rainbow smelt abundance, shad can be an important subsidy to Lake Oahe walleye consumption and subsequent growth. Despite a limited window of availability and high age-0 growth rates, this resource provides a significant energy source to Lake Oahe walleye. Additionally, gizzard shad may act as an alternative prey resource to buffer predation effects on recovering rainbow smelt populations. Because of the observed use of gizzard shad by walleye in Lake Oahe, South Dakota Game, Fish and Parks will begin a gizzard shad stocking strategy to manipulate prey resources for Lake Oahe piscivores. This strategy will hopefully provide an alternative prey resource for Lake Oahe piscivores and lower predation rates on other prey resources.

Isotopic Variability of Sauger and Walleye in South Dakota Missouri River Impoundments

In three South Dakota Missouri River impoundments, differences in isotope variability between sauger and walleye, with varying levels of hybridization and potential habitat quality (i.e., level of anthropogenic disturbance), were documented. Previous studies have demonstrated high diet overlap of these two species (Priegel 1963; Swenson and Smith 1976; Fitz and Holbrook 1978; Mero 1992; Bellgraph et al. 2008); however, diet variability has never been examined. In systems where isotopic composition (i.e., mean and variability) between walleye and sauger are similar (i.e., relatively greater resource overlap), increased hybridization rates were found. Conversely, in Lake Oahe, where walleye and sauger exhibit differences in isotopic composition, hybridization rates are relatively low. Thus, there seems to be a strong correlation between the degree of *Sander spp.* hybridization and the overlap in habitat and/or resource use. Future research should focus on identifying those specific resources or habitats that promote cohabitation of niche compartments likely facilitating higher hybridization between the two species.

Non-Lethal Sampling of Walleye for Stable Isotope Analysis

Because of the disparities in isotopic signatures between muscle, fins and scales, muscle tissue should be utilized whenever available. If performing SIA on special species of concern (i.e., rare or endangered, large sport fish of recreational value), a small subset of organisms can be sacrificed to develop corrective equations to produce more accurate isotope estimates for tissue comparisons. When muscle tissue is not available, fins tend to be the next best alternative. However, if examining dietary niche partitioning (through absolute population variability in isotope signatures), researchers should use scales instead of fins, since the variability in this tissue best matches that of muscle. When performing retrospective studies using catalogued scales (collected for age determination), care must be taken with data interpretation as some substantial differences were found in walleye scales, especially when analyzing variability in isotopic signatures between scales and muscle.

Comparing Isotope Signatures of Prey Fish

Comparing isotopic signatures of various organ systems within an individual solidify the need to standardize tissue use in stable isotope analysis for food web reconstruction, calculating trophic position, and the development of mixing models. Small differences in Δ can reflect large changes in mixing models (Caut et al. 2009), and one method to reduce Δ variability is through the use of muscle tissue (or creating a standardized tissue). Although I recognize that prey fish and age-0 recreational fishes are often too small for SIA, researchers should try to use muscle tissue when possible. If whole fish are to be used, I recommend caution when interpreting the effects on food webs, trophic position estimates or mixing models.

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Appendix 1.

Water chemistry estimates from South Dakota Missouri River impoundments in April (Table 1), June (Table 2) and August (Table 3) in 2008. River kilometer (RKM) is the distance upstream (in km) from the confluence of the Missouri and Mississippi Rivers, and site coordinates (N and W) where each sample was collected. Dashes represent parameters that were not taken during sampling events.

Table 1.

Lake	RKM	N	W	Secchi (m)	Turbidity (NTU)	Temperature (°C)	Dissolved Oxygen (mg/l)	pH	Water Depth (m)	Conductivity (ms/cm^2)	Total Suspended Solids (g/l)
Oahe	1970	45°51.656'	100°23.004'	0.3	13.30	9.91	--	8.63	4.0	677	66.00
	1928	45°34.037'	100°28.575'	0.9	4.20	6.30	--	8.55	10.0	598	39.00
	1889	45°17.535'	100°18.125'	0.9	4.51	6.16	--	8.57	10.0	618	36.20
	1856	45°01.923	100°16.963'	1.7	2.24	5.76	--	8.53	20.0	653	34.65
	1804	44°45.172'	100°40.502'	1.3	2.96	7.91	--	8.59	13.0	728	33.40
	1751	44°32.271'	100°31.431'	3.4	0.53	5.09	--	8.57	41.0	706	23.40
Sharpe	1726	44°26.199'	100°23.243'	3.2	1.71	4.32	--	8.57	4.0	710	24.60
	1720	44°20.692'	100°20.330'	3.0	1.78	4.32	--	8.56	5.0	713	45.80
	1677	44°15.597'	99°55.819'	0.2	15.50	8.35	--	8.53	2.5	713	67.60
	1650	44°08.096'	99°47.479'	0.6	7.21	9.94	--	8.55	8.0	719	46.40
	1624	44°11.478'	99°41.471'	1.8	3.81	7.98	--	8.54	5.0	711	35.75
	1591	44°03.803'	99°31.068'	1.9	1.23	5.94	--	8.56	18.0	682	--
Francis Case	1588	44°02.264	99°25.429'	1.0	4.97	6.08	--	8.56	7.0	681	31.35
	1558	43°49.789'	99°20.251'	0.8	14.10	9.40	--	8.47	5.0	689	54.65
	1513	43°33.965'	99°19.321'	--	--	--	--	--	--	--	--
	1482	43°23.316'	99°08.012'	1.4	4.33	7.81	--	8.54	15.0	712	21.25
	1468	43°17.219'	99°01.304'	1.4	3.56	6.02	--	8.53	22.0	701	24.05
	1424	43°04.591'	98°40.088'	1.8	1.98	4.86	--	8.50	30.0	736	39.25
Lewis and Clark	1416	43°03.250'	98°33.375'	2.0	1.87	4.71	--	8.56	2.7	737	13.80
	1370	42°49.844'	98°09.287'	1.2	5.50	7.60	--	8.48	2.4	735	13.30
	1352	42°46.300'	97°58.561'	1.0	5.11	9.26	--	8.46	2.5	749	23.25
	1339	42°51.348'	97°53.029'	0.6	9.01	8.60	--	8.45	2.3	858	20.60
	1320	42°51.282'	97°41.636'	0.5	8.87	9.07	--	8.52	3.0	773	27.85
	1305	42°51.314'	97°32.332'	0.6	9.13	8.16	--	8.56	12.0	694	11.00

Table 2.

Lake	RKM	N	W	Secchi (m)	Turbidity (NTU)	Temperature (°C)	Dissolved Oxygen (mg/l)	pH	Water Depth (m)	Conductivity (ms/cm^2)	Total Suspended Solids (g/l)
Oahe	1970	45°51.656'	100°23.004'	--	--	--	--	--	--	--	--
	1928	45°34.037'	100°28.575'	1.2	5.59	20.02	9.83	8.68	6.0	674	31.50
	1889	45°17.535'	100°18.125'	2.1	2.14	20.82	10.12	8.72	13.0	669	17.30
	1856	45°01.923	100°16.963'	3.4	1.87	20.87	9.43	8.61	10.0	629	13.65
	1804	44°45.172'	100°40.502'	1.7	2.05	22.22	10.70	8.74	13.0	1065	17.80
	1751	44°32.271'	100°31.431'	3.1	0.51	20.06	11.13	8.73	27.0	712	31.85
Sharpe	1726	44°26.199'	100°23.243'	>3.4	0.78	14.42	10.90	8.60	3.4	700	25.40
	1720	44°20.692'	100°20.330'	0.3	10.49	19.31	10.76	8.60	3.4	753	31.90
	1677	44°15.597'	99°55.819'	0.5	10.95	23.21	9.83	8.82	3.5	872	27.65
	1650	44°08.096'	99°47.479'	3.7	2.20	21.30	9.23	8.69	7.0	733	18.40
	1624	44°11.478'	99°41.471'	4.4	1.25	21.75	9.11	8.70	8.0	723	16.05
	1591	44°03.803'	99°31.068'	6.0	0.62	19.84	9.57	8.72	18.0	727	22.65
Francis Case	1588	44°02.264	99°25.429'	2.1	3.56	19.41	9.12	8.62	8.0	718	18.60
	1558	43°49.789'	99°20.251'	1.7	3.91	21.28	10.15	8.89	8.4	637	32.35
	1513	43°33.965'	99°19.321'	2.5	3.51	21.15	8.86	8.65	5.0	694	25.55
	1482	43°23.316'	99°08.012'	1.5	2.30	20.87	10.15	8.80	16.0	724	22.45
	1468	43°17.219'	99°01.304'	1.1	3.53	21.42	10.07	8.77	20.0	707	32.50
	1424	43°04.591'	98°40.088'	5.6	0.93	18.98	9.00	8.57	21.0	724	15.85
Lewis and Clark	1416	43°03.250'	98°33.375'	3.9	2.14	11.69	10.23	8.42	4.0	739	18.65
	1370	42°49.844'	98°09.287'	0.1	49.60	15.15	9.23	8.45	6.0	733	86.55
	1352	42°46.300'	97°58.561'	0.1	43.40	17.86	9.42	8.43	0.9	755	71.25
	1339	42°51.348'	97°53.029'	0.1	68.20	18.69	8.78	8.37	2.0	744	81.50
	1320	42°51.282'	97°41.636'	0.2	17.00	22.56	6.90	8.40	3.0	690	28.53
	1305	42°51.314'	97°32.332'	0.5	14.70	22.38	8.89	8.48	8.0	659	26.85

Table 3.

Lake	RKM	N	W	Secchi (m)	Turbidity (NTU)	Temperature (°C)	Dissolved Oxygen (mg/l)	pH	Water Depth (m)	Conductivity (ms/cm^2)	Total Suspended Solids (g/l)
Oahe	1970	45°51.656'	100°23.004'	0.7	6.70	21.18	8.78	8.85	9.0	679	44.55
	1928	45°34.037'	100°28.575'	1.1	5.16	21.91	7.59	8.74	12.0	700	38.40
	1889	45°17.535'	100°18.125'	1.3	3.72	21.67	7.47	8.72	13.0	694	13.60
	1856	45°01.923	100°16.963'	1.6	2.92	21.33	7.56	8.74	18.0	679	23.95
	1804	44°45.172'	100°40.502'	0.8	6.06	22.19	7.15	8.76	17.0	909	27.20
	1751	44°32.271'	100°31.431'	3.0	1.97	20.09	7.89	8.78	26.0	728	27.00
Sharpe	1726	44°26.199'	100°23.243'	2.9	2.47	18.50	8.17	8.76	4.0	725	21.05
	1720	44°20.692'	100°20.330'	1.4	3.77	19.28	8.31	8.72	6.0	724	30.15
	1677	44°15.597'	99°55.819'	0.2	25.10	19.80	8.12	8.76	3.0	733	67.30
	1650	44°08.096'	99°47.479'	0.4	13.50	20.88	7.76	8.73	6.0	729	52.40
	1624	44°11.478'	99°41.471'	0.5	9.94	22.17	7.34	8.74	5.0	734	50.70
	1591	44°03.803'	99°31.068'	1.4	4.65	23.18	7.69	8.78	4.0	737	31.15
Francis Case	1588	44°02.264	99°25.429'	1.0	7.38	22.93	7.2	8.75	5.0	736	29.55
	1558	43°49.789'	99°20.251'	0.3	17.90	22.12	7.24	8.78	4.0	743	29.15
	1513	43°33.965'	99°19.321'	0.5	9.28	21.47	7.34	8.78	3.0	751	26.15
	1482	43°23.316'	99°08.012'	1.0	6.38	24.46	7.34	8.77	16.0	738	9.65
	1468	43°17.219'	99°01.304'	1.5	3.82	24.62	7.13	8.74	23.0	735	12.50
	1424	43°04.591'	98°40.088'	3.9	1.70	24.62	7.25	8.75	20.0	737	12.50
Lewis and Clark	1416	43°03.250'	98°33.375'	1.6	3.49	23.30	6.65	8.61	3.0	736	8.34
	1370	42°49.844'	98°09.287'	0.9	9.22	22.69	6.91	8.62	8.0	737	11.65
	1352	42°46.300'	97°58.561'	0.5	14.90	22.41	6.13	8.34	1.6	747	29.85
	1339	42°51.348'	97°53.029'	0.4	15.80	21.89	6.06	8.33	2.0	752	33.50
	1320	42°51.282'	97°41.636'	0.3	19.30	22.43	7.12	8.62	7.0	751	24.85
	1305	42°51.314'	97°32.332'	0.4	15.10	22.90	8.06	8.73	9.0	739	14.20

Appendix 2.

Spatially explicit maps of Lakes Oahe (Figure 1.), Sharpe (Figure 2), Francis Case (Figure 3) and Lewis and Clark (Figure 4) describing total phosphorus (upper left; blue; mg/L), total kjeldahl nitrogen concentration (lower left; yellow; mg/L), chlorophyll *a* concentration (upper right; green; µg/l), and total cladoceran density (lower right; red; #/L) averaged throughout 2008.

Figure 1

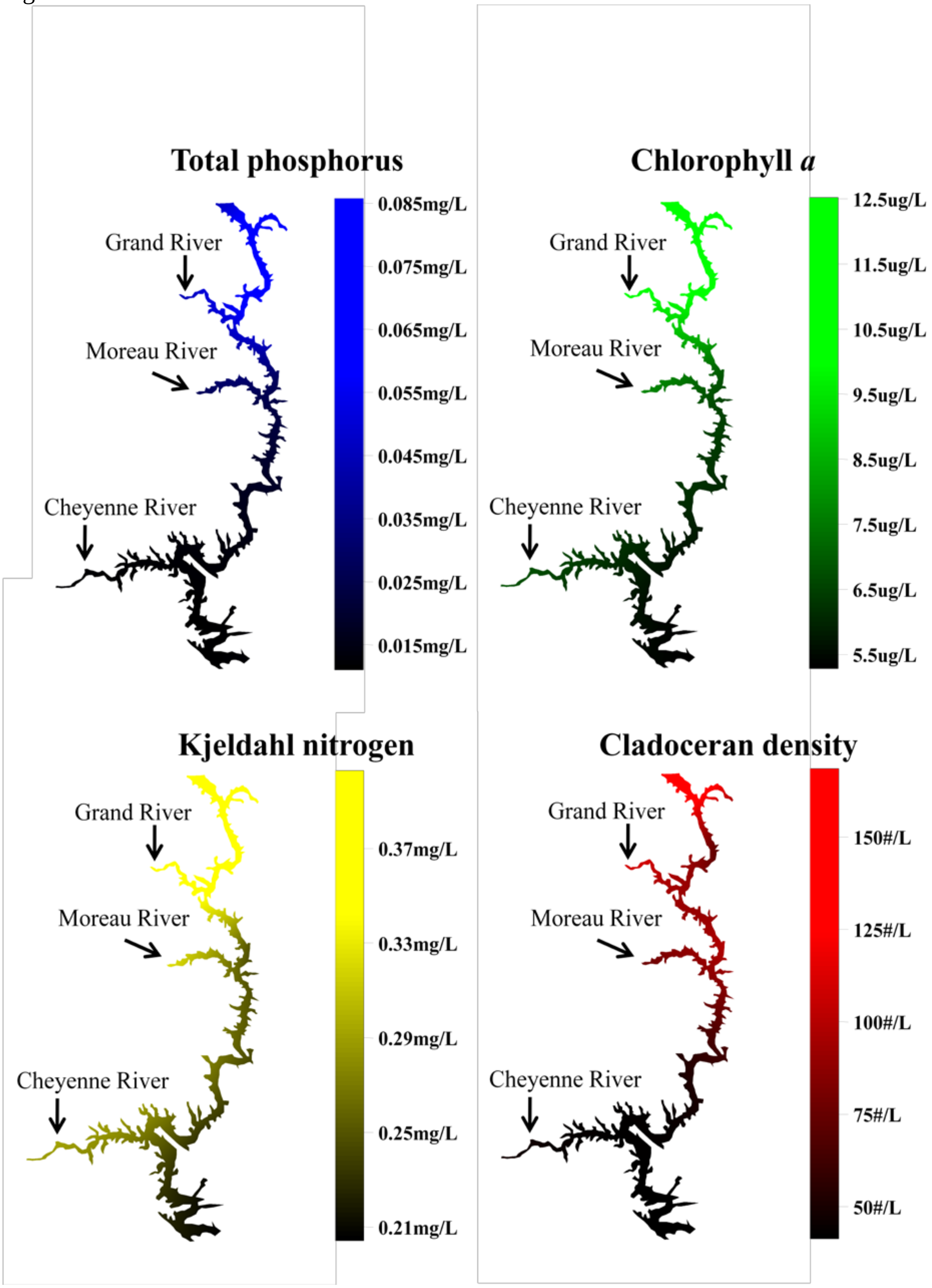

Total phosphorus
Grand River
Moreau River
Cheyenne River
0.085mg/L
0.075mg/L
0.065mg/L
0.055mg/L
0.045mg/L
0.035mg/L
0.025mg/L
0.015mg/L
Chlorophyll a
Grand River
Moreau River
Cheyenne River
12.5ug/L
11.5ug/L
10.5ug/L
9.5ug/L
8.5ug/L
7.5ug/L
6.5ug/L
5.5ug/L
Kjeldahl nitrogen
Grand River
Moreau River
Cheyenne River
0.37mg/L
0.33mg/L
0.29mg/L
0.25mg/L
0.21mg/L
Cladoceran density
Grand River
Moreau River
Cheyenne River
150#/L
125#/L
100#/L
75#/L
50#/L

Figure 2.

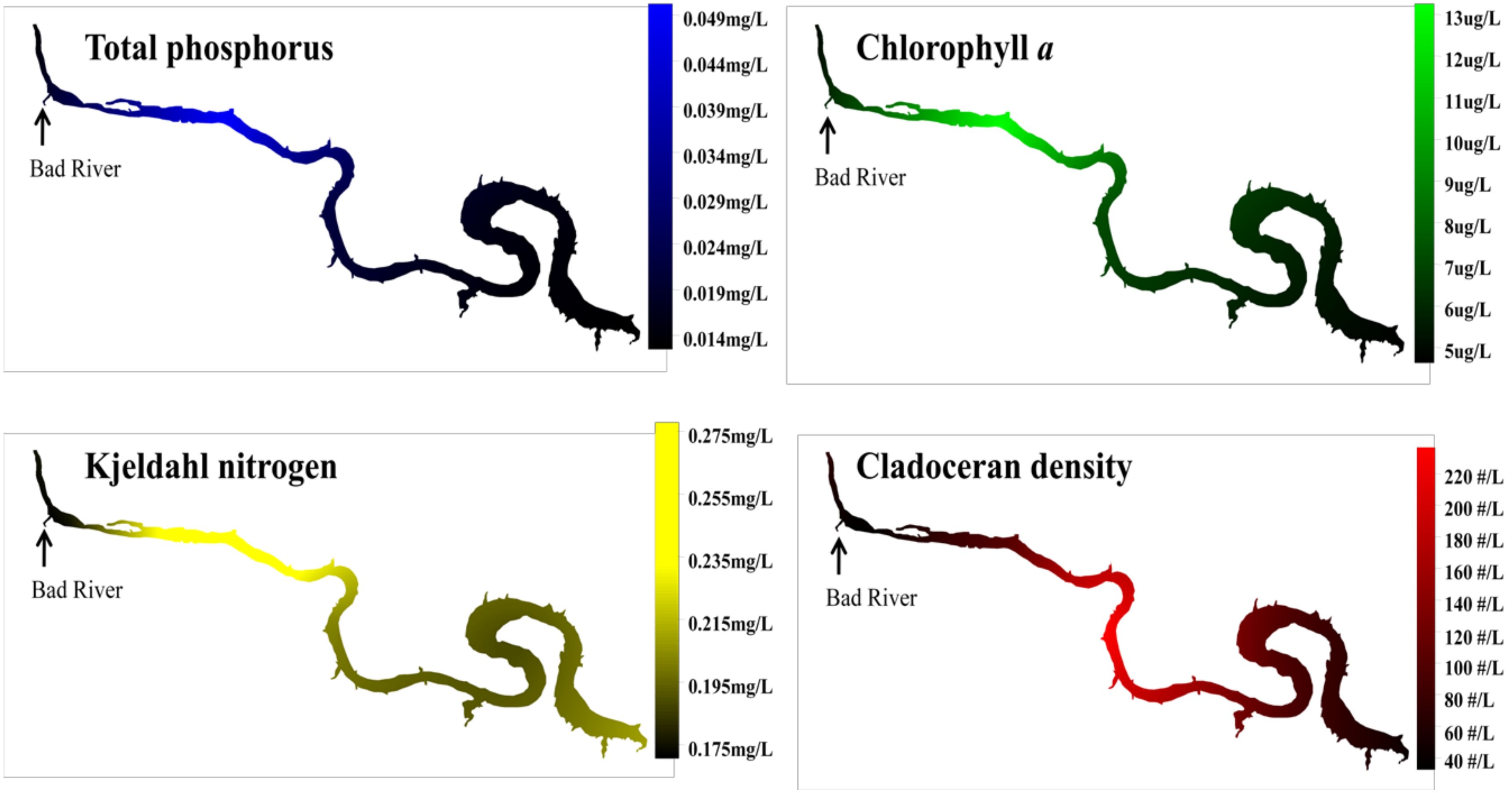

Total phosphorus
0.049mg/L
0.044mg/L
0.039mg/L
0.034mg/L
0.029mg/L
0.024mg/L
0.019mg/L
0.014mg/L
Bad River
Chlorophyll *a*
13ug/L
12ug/L
11ug/L
10ug/L
9ug/L
8ug/L
7ug/L
6ug/L
5ug/L
Bad River
Kjeldahl nitrogen
0.275mg/L
0.255mg/L
0.235mg/L
0.215mg/L
0.195mg/L
0.175mg/L
Bad River
Cladoceran density
220 #/L
200 #/L
180 #/L
160 #/L
140 #/L
120 #/L
100 #/L
80 #/L
60 #/L
40 #/L
Bad River

Figure 3.

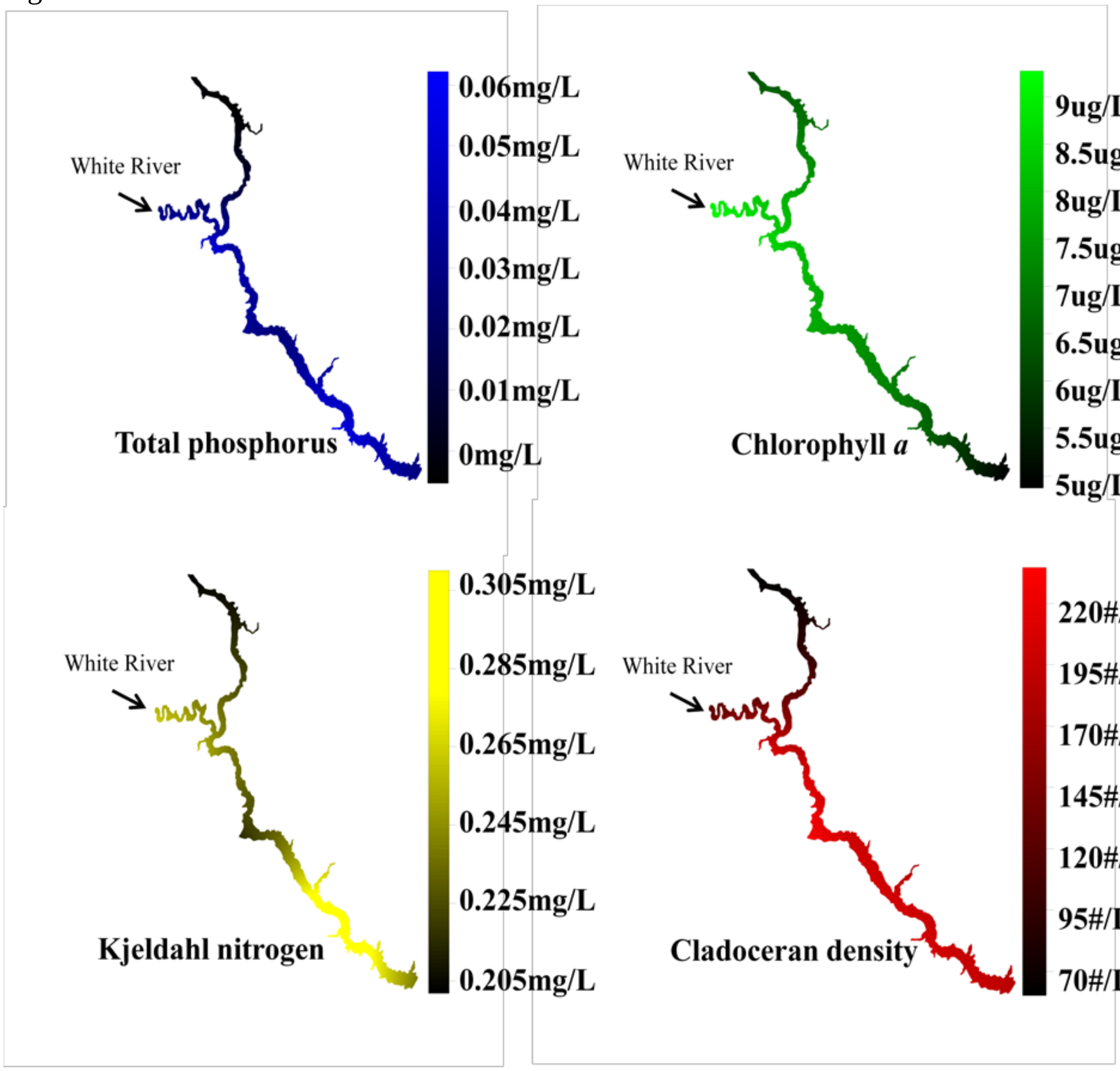
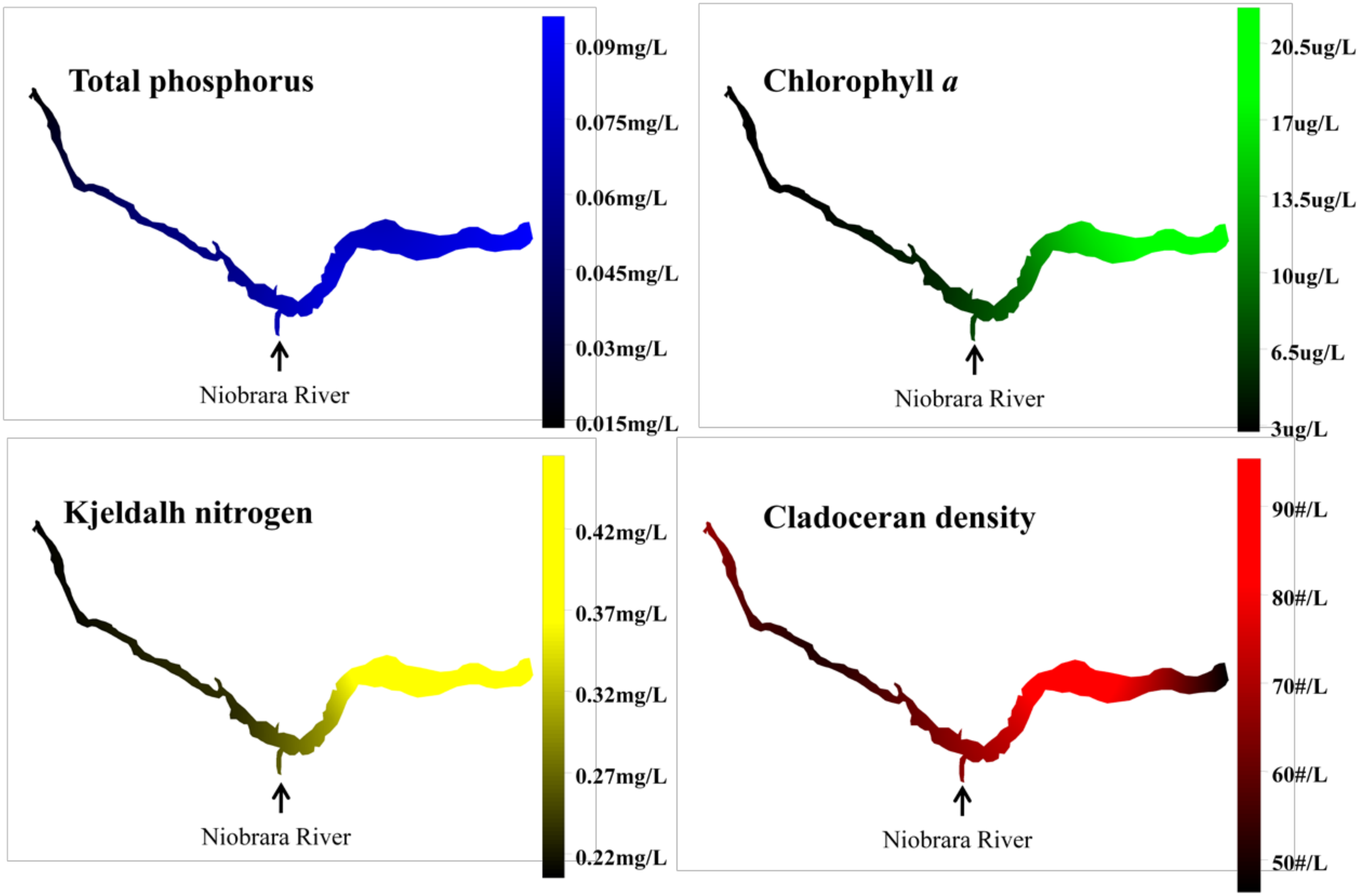

White River
Total phosphorus
0.06mg/L
0.05mg/L
0.04mg/L
0.03mg/L
0.02mg/L
0.01mg/L
0mg/L
White River
Chlorophyll *a*
9ug/L
8.5ug/L
8ug/L
7.5ug/L
7ug/L
6.5ug/L
6ug/L
5.5ug/L
5ug/L
White River
Kjeldahl nitrogen
0.305mg/L
0.285mg/L
0.265mg/L
0.245mg/L
0.225mg/L
0.205mg/L
White River
Cladoceran density
220#/L
195#/L
170#/L
145#/L
120#/L
95#/L
70#/L

Figure 4.


Total phosphorus
0.09mg/L
0.075mg/L
0.06mg/L
0.045mg/L
0.03mg/L
0.015mg/L
Niobrara River
Chlorophyll *a*
20.5ug/L
17ug/L
13.5ug/L
10ug/L
6.5ug/L
3ug/L
Niobrara River
Kjeldalh nitrogen
0.42mg/L
0.37mg/L
0.32mg/L
0.27mg/L
0.22mg/L
Niobrara River
Cladoceran density
90#/L
80#/L
70#/L
60#/L
50#/L
Niobrara River