

5-2010

Introduced Sport Fish and Fish Conservation in a Novel Food Web: Evidence of Predatory Impact

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INTRODUCED SPORT FISH AND FISH CONSERVATION IN A NOVEL
FOOD WEB: EVIDENCE OF PREDATORY IMPACT

by

Kevin Landom

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2010

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ABSTRACT

Introduced Sport Fish and Fish Conservation in a Novel Food Web:

Evidence of Predatory Impact

by

Kevin Landom, Master of Science

Utah State University, 2010

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Department: Watershed Sciences

This study addressed a fundamental question in applied ecology and conservation; what is the predatory impact of introduced piscivorous sport fish on imperiled native fish populations? More specifically, which of many introduced species and size-classes represent the greatest threats and should be targeted for control? In order to explore this important question, an integrated analysis of stable isotopes, quantified observed diet analysis, and stable isotope mass-balance models were used to quantify trophic interactions. These tools were used to construct food web models that were then compared to draw inferences regarding the relative contribution of prey fish, including rare native fish, to the diet of introduced sport fish. The stable isotope-derived food web illustrated a slight decoupling in energy flow between a pelagic and a benthic-littoral sub-web. The quantified diet analysis suggested piscivory was low overall, and that the introduced sport fish assemblage relied heavily on zooplankton and aquatic insect prey. The integrated stable isotope and quantified diet analysis demonstrated that the

consumption of prey fish, particularly pelagic prey fish, was typically underestimated using stomach content analyses. From the evaluation, comparison, and integration of food web models, I suggest that substantial predation was occurring on the early life stages of Utah Lake fishes, including native fishes, and it was not being observed using stomach content analysis. My comparative modeling demonstrated that introduced sport fish are an impediment to native fish conservation and identified the small size-class of white bass as the most immediate threat.

(69 pages)

ACKNOWLEDGMENTS

Funding for this study was provided by the June Sucker Recovery Implementation Program through the Central Utah Water Conservancy District. Administrative assistance was provided by the Utah State Ecology Center and Watershed Sciences Department. I would like to thank my major advisor, Todd A. Crowl, and my committee members, Phaedra Budy and Eric Gese, for their guidance and comments, and Leigh C. Latta IV for his editorial suggestions. I would like to thank the Utah Division of Wildlife Resources, Utah State Parks, and Loy Fisheries for their field support. I am grateful to the Crowl Aquatic Ecology Lab graduate students, Kris Buelow, Dave Cole, Brian Hines, and Stephanie Kraft, and technicians, Kirk Bagley, Laura Hines, Levi Rose, Andy Dean, Laura Buelow, Kevin Groot, Jessie Larsen, and Shilah Morley, for their invaluable field and lab assistance.

Kevin Landom

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INTRODUCTION

The human induced spread of nonnative species (a species that occurs outside of its native range) is a primary threat to ecosystem function and biodiversity (Mooney and Cleland 2001, Rahel 2002, Crowl et al. 2008). Nonnative species introductions can be particularly detrimental to island ecosystems (MacArthur and Wilson 1963, Simberloff 1974), such as freshwater lakes. In the United States, most freshwater lakes are significantly altered by nonnative species, particularly as a result of nonnative fishes (Benson 1999, Fuller 2003), as no other country has endured more fish introductions (Dextrase and Coscarelli 1999). The most common vector for nonnative fishes in North America is recreational fishing (sport fishing) where in most cases, nonnative sport fish were introduced intentionally by government agencies to develop or improve recreational fisheries (Courtenay 1993, Crossman and Cudmore 1999). Unfortunately, what has happened in the United States has been repeated in many other countries (e.g., Maezono and Miyashita 2003, Baxter et al. 2004, Ebner et al. 2007, Fugi et al. 2008), where these introductions involve top-level predators; their aggressive piscivorous feeding habits and large individual body size make them desirable sport fish (Dextrase and Coscarelli 1999). Native aquatic species are exceptionally vulnerable to introduced carnivorous predators, because they lack anti-predator traits necessary to escape predation from the novel predators (Cox and Lima 2006). Consequently, introduced sport fish (nonnative fishes intentionally introduced for recreational purposes) represent a primary threat to native aquatic species (Courtenay 1993, Dextrase and Coscarelli 1999, Cambray 2003).

Successful introductions of nonnative piscivorous sport fish have caused obvious ecological (Helfman 2007) and social (Clarkson et al. 2005) impediments to fish

conservation. Although nonnative piscivores may alter native biota through competitive interactions, a direct effect of predation is the most probable cause for decline or extirpation of many native fish populations (Moyle et al. 1986, Ross 1991, Townsend and Crowl 1991). As such, re-establishment and augmentation efforts for threatened native fish populations are often hindered by the predatory affect of nonnative sport fish (Marsh and Brooks 1989, McMahon and Bennett 1996). The recreational angling public has developed expectations and demands that sport fish will continuously be available (Dextrase and Coscarelli 1999), and some management organizations have responded to this social expectation by providing and managing aquatic ecosystems for sport fishing. These same organizations are often responsible for the protection and recovery of imperiled native fishes. The dual responsibilities are often incompatible and result in a conflict of interest between conservationists, sport fish managers, and the public (Courtenay 1993, McMahon and Bennett 1996, Dextrase and Coscarelli 1999, Cambray 2003, Clarkson et al. 2005). In the end, removal of nonnative sport fish is not always a socially acceptable management strategy for fish conservation, and in some instances successful removal is potentially unfeasible (e.g., Mueller 2005).

Most evidence for the impact of introduced sport fish on native fish communities is anecdotal because pre-introduction data are usually insufficient and the interactions between introduced species and native biota are difficult to observe (Taylor et al. 1984, Moyle et al. 1986, Ross 1991). Fish conservationists are often faced with the task of quantifying predatory impact by introduced sport fish, well after the strongest effects have occurred. Ideally, predatory impact is quantified using empirically-derived observations of predation on native species (e.g. Ruzycki et al. 2003) or by modeling

native species population rates of change in response to recently introduced predators (e.g. Sinclair et al. 1998). However, as organisms warranting conservation are typically rare (due to the already felt impacts of the introduced predators often in combination with other factors), the effects of predation on native species are usually not well understood, and empirical evidence is difficult to obtain (Taylor et al. 1984, Moyle et al. 1986, Ebner et al. 2007). Consequently, population statistics for rare species are often insufficient to model rates of change in response to introduced predators (e.g. Maxwell and Jennings 2005). In many instances, decline in native fish populations is falsely attributed to factors other than predation, as the impact occurs on the very early life stages of native fish when it is difficult to observe and quantify (Crowder 1980, Moyle et al. 1986, Marsh and Brooks 1989, Carpenter and Mueller 2008, Schooley et al. 2008). Given the detrimental effects of introduced piscivores, it is critical that we identify the niche they fill in their new food web, and build empirical evidence toward quantifying predatory impact on native fishes.

Food webs are descriptions of trophic interactions in biological communities (de Ruiter et al. 2005), and food web analyses have become a central component of population, community, and ecosystem ecology (de Ruiter et al. 2005, Begon et al. 2006). In addition, food web analyses contribute greatly to applied ecological endeavors such as restoration or conservation-based management (Power 2001, Vander Zanden et al. 2006, Helfman 2007). Food web models are useful in initially framing energy flow pathways and resource management issues, and they promote the hypothesis development and falsification process central to hypothetico-deductive science and adaptive management (Power 2001). Food web analyses can act as a form of passive adaptive management in

which predictive modeling can help inform management decisions (Power 2001).

Initiating a food web analysis entails understanding and quantifying trophic interactions in order to construct a food web model. This first step can be challenging and is best achieved by integrating multiple ecological tools aimed at quantifying trophic interactions (e.g., Pazzia et al. 2002, Clarke et al. 2005, Keyse et al. 2005, Caut et al. 2006).

The tools ecologists use to understand trophic interactions have progressed from skilled observational deductions (Elton 1927), theoretical niche models (Hutchinson and MacArthur 1959), and simple trophic efficiency models (Lindeman 1942), to more systematic observational techniques (quantitative diet analyses), and stoichiometric and stable isotope analyses (Belgrano et al. 2005). Quantified diet analyses provide taxon-specific dietary estimates, but can be biased because they only represent a temporal snapshot, and digestibility and evacuation rates can vary greatly among prey species (Custer and Pitelka 1975, Jackson et al. 1987), and among predator habitat-based thermal experience (Smith et al. 1989, Bromley 1994). Consequently, the dietary contribution of rapidly-digested prey can be underestimated, especially larval fish prey (Schooley et al. 2008). Stable isotopes provide information on assimilated diet, rather than the recently ingested diet, and reflect long-term feeding behavior (Tieszen et al. 1983, Peterson and Fry 1987). However, unaccompanied stable isotopes do not provide taxon-specific dietary information (Vinson and Budy 2009, *in press*). An integrated quantified diet and stable isotope analysis provides two levels of temporal resolution, as well as a framework for identifying or evaluating taxon-specific trophic interactions (e.g., Clarke et al. 2005, McIntyre et al. 2006).

This study represents one component of a food web modeling approach to adaptive management that supports fish conservation and aquatic ecosystem restoration. In this study, I addressed a fundamental question in applied ecology and conservation; what is the predatory impact of introduced sport fish on native fish populations? More specifically, I attempted to determine which of many introduced species and size-classes represent the greatest threat and should be targeted for control. I faced a difficult, yet extremely common obstacle; a lack of directly-observable empirical evidence of predation on native fish populations. Therefore, in order to explore this question, I used an integrated analysis of stable isotopes, quantified diet, and stable isotope mass-balance models to quantify trophic interactions in a complex novel food web. I used these tools to first construct food web models, which I then used to draw inferences regarding the relative contribution of prey fish, including rare imperiled native fish, to the diet of introduced sport fish. In this study, I illustrate how to integrate empirical data, as well as biology and ecology to evaluate the predatory impact of introduced sport fish on native fish populations.

UTAH LAKE HISTORY AND STUDY SITE DESCRIPTION

Retreat of Lake Bonneville during the Pleistocene epoch left Utah Lake as one of the largest natural freshwater bodies in the Western Continental United States. Located in North-Central Utah, Utah Lake is a eutrophic, shallow lake ecosystem lacking thermal stratification, that experiences frequent water column mixing and intense sediment-water interactions (Schaffer 2004). As the largest freshwater body in the Great Basin Desert, Utah Lake has been a focal point for human settlement. Consequently, it has endured nearly two centuries of severe anthropogenic disturbance (Janetski 1990), and can now be characterized as a novel ecosystem composed of new combinations of species that interact in a completely altered physical setting (Hobbs et al. 2006, Seastedt et al. 2008).

The native Utah Lake food web has been significantly impacted by habitat degradation, over-fishing, pollution and nonnative fish introductions. Historically, Bonneville cutthroat trout (*Onchorhynchus clarkii utah*) was the top-level piscivore, with native scuplin (*Cottus echinatus*), juvenile suckers (*Chasmistes and Catostomus*), Utah chub (*Gila atraria*) and redbside shiner (*Gila balteata*) being the primary piscine prey. From 1871 through 1983, 24 nonnative fish species were intentionally introduced into Utah Lake, 12 of these species now have established populations (SWCA 2002), six of which are piscivorous sport fish. The introduction of the omnivorous common carp (*Cyprinus carpio*) in 1881 quickly resulted in a complete transformation of the lake flora (Cottam 1926) and severe reduction in macrophytes (Miller and Crowl 2006), an essential refuge for small fish. Cutthroat trout and native forage fishes are no longer found in the lake, and the aquatic food web is deficient in both forage fish diversity and abundance (Radant and Sakaguchi 1980, Radant and Shirley 1987), a presumed effect of

intense predation due to an overabundance of piscivores and lack of macrophyte refuge. In fact, the only native fishes that remain are the Utah sucker (*Catostomus ardens*), and the endemic and federally endangered June sucker (*Chasmistes liorus*) (SWCA 2002); the latter is the focus of intense conservation efforts. Although Utah sucker and June sucker are similar genetically and in general body morphology, their mouth morphologies have pronounced differences (Mock et al. 2006, Cole et al. 2008). In addition, intermediate mouth morphologies occur in Utah Lake as an apparent result of hybridization between Utah and June sucker. Despite morphological differences, there is currently no evidence to suggest vulnerability to predation by introduced sport fish differs among the three sucker morphologies. Consequently, as I am unable to differentiate potential predatory impact among these three morphologies, hereafter the Utah sucker, June sucker, and intermediate morphologies will be referred to collectively as Utah Lake suckers.

Currently in Utah Lake, commercial fishing is restricted to harvest of some nonnative species (some introduced sport fish are currently protected) and pollution is believed to be minimal. Nevertheless, introduced sport fish and habitat alteration are primary threats to the persistence of Utah Lake suckers (Radant and Hickman 1984). Very few wild Utah Lake sucker exist, and the population is supplemented by hatchery and translocation programs, where suckers necessarily must be introduced at a size that exceeds the gape limit of most introduced sport fish (Petersen 1996, Andersen et al. 2007). These larger individuals of the Utah Lake sucker population appear healthy and are reproductively active; however, although these native fish have proven successful at producing larval progeny each year, recruitment into the adult populations has not been

observed (Figure 1). The apparent recruitment failure of Utah Lake suckers is hypothesized to be a compounded effect of intense predation by introduced sport fish, working in combination with the absence of macrophyte refuge (Miller and Crowl 2006). Successful conservation of Utah Lake native fishes depends heavily on understanding the niche introduced sport fish fill in their new food web, and on quantifying their predatory impact on native fish progeny.

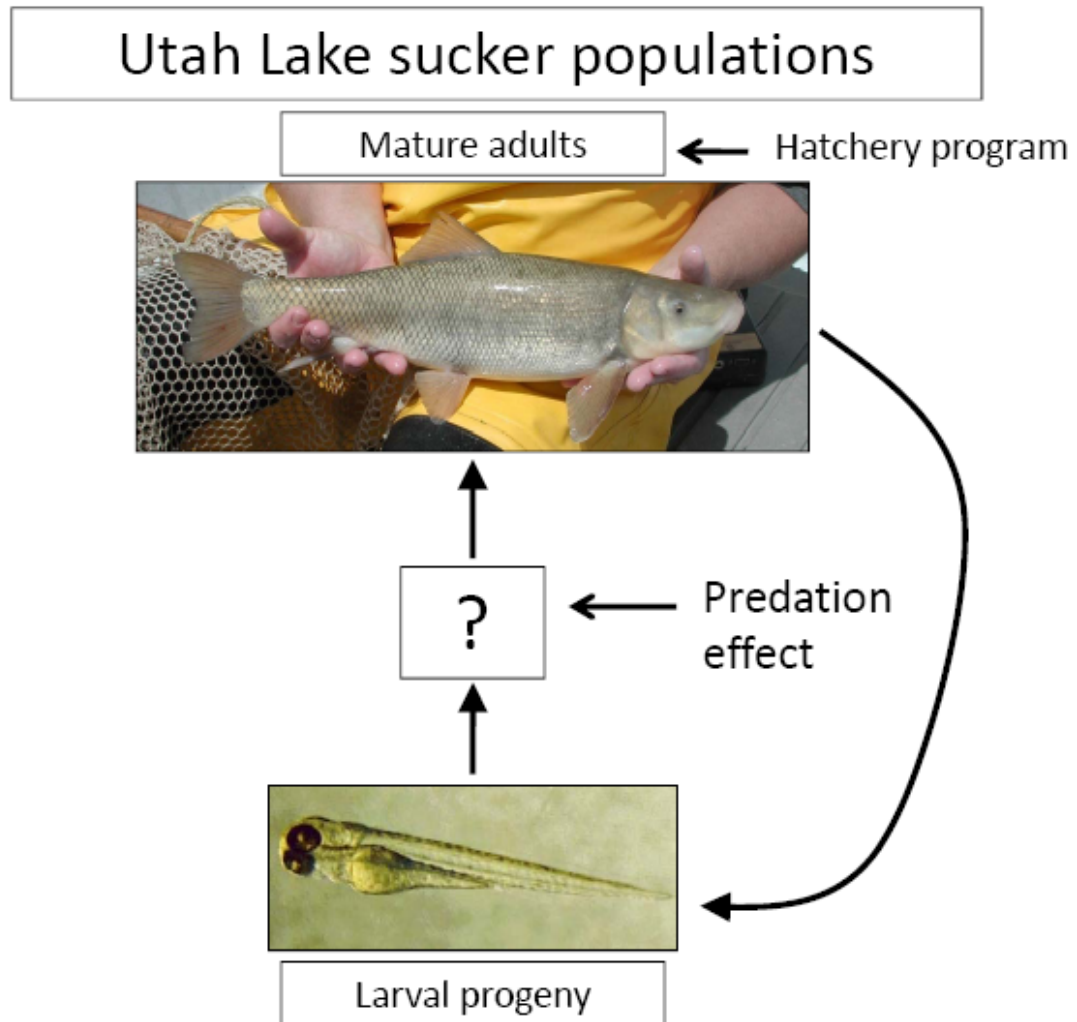


Figure 1. Current knowledge of Utah Lake native sucker populations.

METHODS

Food web sampling

Utah Lake fishes were collected from May 2006 through August 2007 by means of trammel-nets, small beach seines, commercial beach seines, minnow-traps, and fyke-nets of three different mesh sizes ($\frac{1}{8}$ ", $\frac{1}{4}$ ", and 1"). Categorical size-classes (small, medium, large) were defined for fishes *a priori* using Utah Lake length frequency histograms from 2003 and 2004 (Landom et al. 2006). Six fixed sampling locations, capturing the range in variation in within-lake location (north, south, east, and west) and substrate morphology (rock, mud, sand, and combinations) were selected as the primary sampling sites. Additional fish specimens were obtained from the Utah Division of Wildlife Resources and the local commercial fishing operation, Loy Fisheries, from various locations. Most fish specimens were obtained directly from, or near the littoral zone as the sampling gear available proved most efficient when employed near shore. Fish were taken directly to an on-site dissection station after capture, measured to the nearest millimeter, weighed to the nearest gram, and then whole stomachs were removed and preserved in 90% ethyl alcohol for future analysis. A muscle plug was taken from the anterior dorsal area of selected fishes, encapsulated in a centrifuge tube and immediately frozen in an on-site freezer to preserve for stable isotope analysis preparation.

Invertebrate specimens were collected from August 2006 through September 2007 using minnow traps, Eckman dredges, dip nets, and vertical plankton tows. Invertebrate sampling occurred at the fixed sampling locations, approximately 1km or less from the shoreline. Individuals from the same collection event and within-lake

location were combined when necessary to obtain an adequate sample weight for invertebrate stable isotope analysis. All invertebrate specimens were immediately preserved in an on-site freezer after collection. Whole individual bodies were used for all invertebrate stable isotope analysis preparation.

Muscle plugs and invertebrates were dried for 24 h in a 65 °C drying oven. Each dried sample was ground to a fine powder using a porcelain mortar and pestle, and then 1.00±0.02 mg of the fine powder was rolled in a tin capsule and inventoried in a 96-well plate.

Stable isotope analysis

The stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) are powerful tools for evaluating trophic interactions in food webs (Post 2002). The premise of this methodology is that an organisms stable isotope values reflect that of its prey, and consumers become enriched (trophic shift) in stable isotopes at a predictable rate. Stable isotope values are reported as δ (delta) and ‰ (per mil) deviations from international reference standards (Pee Dee Belemite carbon and atmospheric nitrogen):

$$^{13}\text{C} \text{ or } ^{15}\text{N} = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1,000 \quad (1)$$

where R_{sample} is the ratio of the heavy isotope to the light isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) and R_{standard} is the ratio of the heavy to the light isotope for the standard. The carbon stable isotope ratio of a consumer $\delta^{13}\text{C}$ (‰) is typically slightly enriched (0-1‰) relative to its prey (Vander Zanden and Rasmussen 2001, Post 2002, McCutchan et al. 2003), and can be used to determine the ultimate sources of organic matter. In lakes, ^{13}C ratios can be

used to differentiate between benthic-littoral and pelagic energy sources, as benthic-littoral food webs are generally more enriched in ^{13}C than plankton driven pelagic food webs (France 1995). The nitrogen stable isotope ratio of a consumer is enriched at a much higher rate (2.4-4 ‰) than carbon (Peterson and Fry 1987, Vander Zanden and Rasmussen 2001, Post 2002, Vanderklift and Ponsard 2003), and provides estimates of relative trophic position.

Carbon and nitrogen isotope compositions were analyzed at the Stable Isotope/Soil Biology Laboratory at the University of Georgia. Quality control standards used were bovine (n=34, $\delta^{13}\text{C}=-21.1$, SD=0.07, $\delta^{15}\text{N}=7.5$, SD=0.12) and poplar (n=33, $\delta^{13}\text{C}=-27.2$, SD=0.26, $\delta^{15}\text{N}=-2.4$, SD=0.22). Since ^{13}C -depletion of lipids can lead to ecological misinterpretation in stable isotope analyses, lipids were normalized for fish following the method developed by Kiljunen et al. (2006). An accurate normalization technique has not yet been developed for invertebrate species (Kiljunen et al. 2006) so lipid normalization was not applied to those samples. In order to illustrate the flow of carbon from prey to consumer, the source of carbon (pelagic vs. benthic-littoral), and the relative trophic positions of organisms in the Utah Lake food web, a bi-plot was constructed with ^{13}C on the x-axis (energy source) and ^{15}N on the y-axis (trophic level).

Isosource mixing model

The distinct stable isotope signatures of prey species, together with the stable isotope signatures of the consumer can be used to estimate the relative contributions of each prey item to the consumer's diet using mathematical mixing models (Phillips 2001). A fully constrained mixing model is limited to n+1 sources (prey stable isotope values) when there are n mixtures (predator stable isotope values, usually separate elements)

(Phillips 2001, Phillips and Gregg 2003). In this study, two mixtures were used (^{13}C and ^{15}N), such that a fully constrained mixing model was limited to three prey sources. However, all piscivorous fish in this study were found to rely on more than three prey sources. Therefore, in order to further evaluate the relative contribution of prey items to the piscivores diet, I used the stable isotope mixing model program Isosource (Phillips and Gregg 2003). Isosource executes a mixing model procedure where the range of feasible source (prey isotope values) contributions to the mixture (predator isotope values) are estimated when there are too many sources to allow for a unique mixing model solution. All combinations of each source contribution (0-100%) are examined in selected increments (1% used in this study), and all combinations that sum to the mixture isotopic signatures within a selected tolerance (0.10 used in this study) are considered feasible solutions. Mean discrimination factors ($\delta^{15}\text{N}=2.7$, $\delta^{13}\text{C}=1.0$ ‰, discussed below) were added to each source signature to account for the trophic shift in stable isotopes. The inclusion of seven prey sources in the Isosource mixing model program proved to exceed computational capabilities. Consequently, the number of source signatures was restricted to six of the most prominent prey species. As recommended by Phillips and Gregg (2003), mixing model results were presented as the range of feasible contributions (min %-max %) for each prey species isotope composition to the predator's isotope composition.

Diet analysis

The diet data represents a combination of stomach samples obtained from two collection protocols. First, quantified samples, in which all prey were quantified, were collected from the first 10 individuals caught from each species and size-class

combination, during any given sampling event. The quantified sampling protocol allowed for potential collection of 150 samples (15 sport fish species and size-class combinations), following any given sampling event. Second, prey fish identification samples, in which the goal was to enhance species-specific piscivore-prey relationship estimates, represent data from a much larger sample size. All piscivore species and size-classes captured during a given sampling event were collected for prey fish identification samples.

All prey identification procedures were conducted in the laboratory. Invertebrate prey species were identified to the lowest reasonable taxonomic level using a dissecting microscope (MEIJI, EMZ-TR). Invertebrate prey consumption was quantified by counting the total number of each prey species, and measuring a subsample of individuals (maximum of 20) using an eyepiece micrometer. Partially digested prey fish were identified using species-specific bone characteristics of Utah Lake fishes, and measured in length to the nearest millimeter when possible. If bone characteristics were indistinguishable, the prey was categorized as unidentifiable.

Mean percent biomass (MW_i) was estimated for each invertebrate prey species by applying species-specific dry weight regressions (Eckblad 1971, Dumont et al. 1975, Sage 1982, Benke et al. 1999) to the average length of each prey species within each individual stomach, and multiplying the estimated weight by the total number of each prey species within each individual stomach. Dry weight estimates for prey fish ≤ 2 g wet weight were based on a regression that I developed from wet weight=dry weight values for bay anchovy in Hartman and Brandt (1995, Table 2). Dry weights for all prey fish greater than 2 g wet weight were estimated by applying the mean % dry weight (dry

weight = wet weight x 0.24, SD=0.02) estimated from yellow perch (*Perca flavescens*) 58-100 g wet weight evaluated in Hartman and Brandt (1995, Table 2). When prey fish could be identified to species but not measured, an average intraspecific prey weight estimated within the piscivore species and size-class in question was assigned to the unmeasurable prey. When prey fish were unidentifiable to species and unmeasurable, the average seasonal (winter, spring, summer) weight of measurable prey fish found in the diet of the piscivore species, size-class, and season in question was assigned to the prey.

The prey biomass estimates were weighted so that only prey items from which stable isotope signatures were obtained were used (total biomass=100%) in subsequent analyses. The removal of biomass estimates for relatively uncommon prey was accounted for by increasing biomass estimates for the principal prey, yet maintaining estimated proportional contributions. For example, if dietary contributions of prey x=49%, y=49%, and z=2%, removal of prey z results in prey x=50%, and prey y=50% dietary contributions. Results from the prey fish identification samples were also weighted to match the quantified diet estimates of prey fish contribution to the total diet biomass. Since stable isotope values of unidentifiable prey fish are unknown, dietary contributions of identifiable prey fish were weighted in subsequent analyses to ensure prey fish contribution to the total diet biomass was accounted for appropriately.

Integrated diet and stable isotopes

One of the most difficult parameters to account for in a stable isotope-derived food web analysis is the trophic shift in stable isotopes via enrichment (trophic shift, Δ). Meta-analyses have provided mean values for the trophic shift of carbon and nitrogen that can be applied to stable isotope-derived food web models (Vander Zanden and

Rasmussen 2001, Post 2002, McCutchan et al. 2003, Vanderklift and Ponsard 2003); however, the rate of stable isotope enrichment appears to be affected by many factors, including tissue, diet, and species (Gannes et al. 1997, Caut et al. 2008, Martinez del Rio et al. 2009). In addition, meta-analyses have evaluated the effect of diet on the trophic shift of stable isotopes for various consumer categories (carnivores, herbivores, and mixed diet), and discrepancies exist among meta-analysis conclusions (Vander Zanden and Rasmussen 2001, Post 2002, McCutchan et al. 2003, Vanderklift and Ponsard 2003). Furthermore, Vanderklift and Ponsard (2003) found the consumers biological mode of excretion, which can be taxon-specific, had a significant effect on trophic shift values, and they were the first to demonstrate the importance of choosing taxon-specific values when applying a mean trophic shift value. In order to evaluate stable isotope-derived trophic interactions in this study, the application of mean trophic shift values was necessary. Taxon-specific mean trophic shift values were obtained from a variety of meta-analysis papers (Vander Zanden and Rasmussen 2001, McCutchan et al. 2003, Vanderklift and Ponsard 2003), from Sweeting et al. (2007), and were restricted to studies that used fish fed controlled diets ($\Delta \delta^{15}\text{N}$, $N=13$, $\text{mean}=2.7 \pm 1.3 \text{ SD}$; $\Delta \delta^{13}\text{C}$, $N=14$, $\text{mean}=1.0 \pm 1.1 \text{ SD}$).

For each piscivore size-class and species I compared the $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of the piscivores muscle tissue (observed) with values estimated from the diet (predicted) using a weighted average equation (e.g. ^{15}N):

$$\left(\sum_{i=1}^k \delta^{15} N_i + f \right) \times \frac{b_i}{b_t} \quad \text{and} \quad b_t = \sum_{i=1}^k b_i \quad (2)$$

where $\delta^{15}N_i$ is the isotope signature of the i th prey item, f is the trophic shift, and b_i/b_t is the proportion of the total diet biomass observed for the i th prey item (e.g., Clarke et al. 2005). To complement model evaluation, I estimated the trophic shift value necessary for the predicted to be similar to the observed for each size-class and species of introduced sport fish, and then compared these results with values from the literature.

Statistical analyses

In order to test model predictions, regressions of observed stable isotope signatures versus predicted stable isotope signatures were applied following the methodology proposed by Pineiro et al. (2008). The significance of the slope and intercept regression parameters were tested using $\alpha=0.05$. If the null hypothesis (slope=1) was rejected, the model predictions were presumed to have no consistency with the observed data, and the statistical tests were concluded. If the null hypothesis (slope=1) was not rejected, then the null hypothesis (intercept=0) was tested. If the (intercept=0) hypothesis was then rejected, the model was considered biased. If the intercept was not significantly different from zero, the differences between observed and predicted data were considered due entirely to unexplained variance. The root mean squared deviation (RSMD) (see Pineiro et al. 2008, for formula) and Theil's partial inequality coefficients (see Paruelo et al. 1998, for formulas) were calculated to complement the assessment of model performance. The RSMD represents the mean deviation of predicted values with respect to the observed values, and results are in the same units as the model under evaluation. Theil's coefficients partition the variance of observed values not explained by predicted values, and are the squared sum of predictive error. Theil's coefficients include the proportion of error associated with the mean

differences between observed and predicted values (U_{bias}), the proportion associated with the difference between the slope of the predictive model and the 1:1 line (U_{slope}), and the proportion associated with unexplained variance (U_{error}).

RESULTS

Stable isotope-derived food web

The stable isotope results indicated the presence of two primary sub-webs: a pelagic and a benthic/littoral sub-web. As the trophic shift in stable isotopes can only flow one direction (+1 ^{13}C , and +2.7 ^{15}N assumed in this study) and benthic/littoral food webs are generally more enriched in $\delta^{13}\text{C}$ than plankton driven pelagic food webs (France 1995), a slight decoupling of energy flow between the sub-webs was apparent (Figure 2). There was a distinct separation within the small size-class of white bass (*Morone chrysops*) in $\delta^{13}\text{C}$ between those <63 mm (pelagic sub-web), and those 105-131 mm (benthic/littoral sub-web). White bass 64-104 mm total length were not collected for stable isotope analysis. Accordingly, the small size-class of white bass was partitioned into “Small” and “PR” (Provo River) white bass *post hoc* to account for this distinction in stable isotope composition (Table 1) and in the quantified diet results (discussed below).

Introduced sport fish diet

Overall, very few piscivore stomachs were found to contain prey fish remains; out of 2,199 piscivores harvested, only 305 (14%) individuals contained fish remains in their digestive tracts. Quantified diet estimates showed considerable variation in prey fish dietary contributions among species and size-classes, with a general increase in piscivory following an increase in predator size (Table 2). The medium and large size-classes of walleye (*Sander vitreus*) were found to be almost exclusively piscivorous (hereafter referred to as “exclusive” piscivores). On average, only 29% of the prey biomass

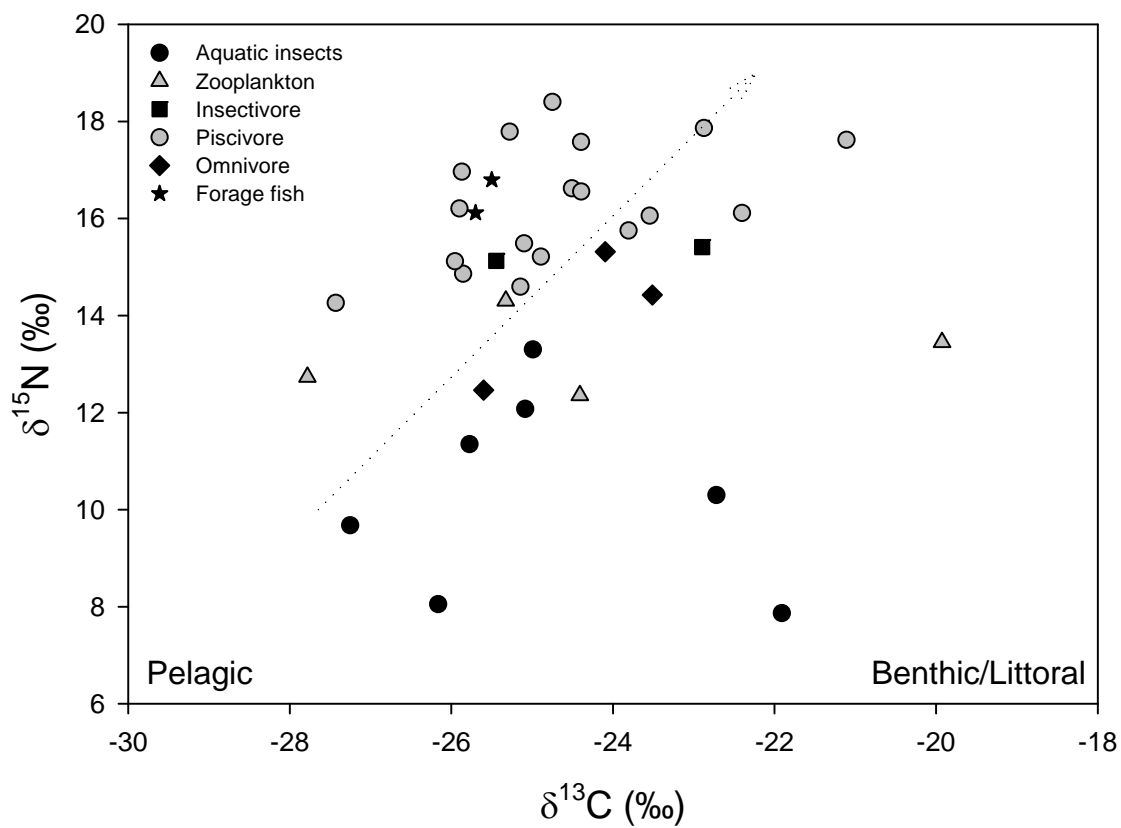


Figure 2. The mean $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) of Utah Lake biota, illustrating the energy flow and slight decoupling (dotted arrow) between the pelagic and benthic-littoral sub-webs.

Table 1. The stable isotope signatures of Utah Lake biota and the sub-webs each organism occupies (P=pelagic, B=benthic/littoral). Size-ranges for fish are provided in mm total length.

Species	Size-class, life-stage	Size-range	N	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)		Sub-web
				Mean	SD	Mean	SD	
Black bullhead	Large	209-324	23	16.6	1.8	-24.5	1.2	P
	Small	31-168	11	14.6	1.1	-25.1	1.3	P
Black crappie	Large	136-291	23	16.2	1.2	-25.9	1.6	P
	Small	30-127	11	15.5	1.6	-25.1	2.2	P
Bluegill	Large	137-201	11	15.1	0.9	-25.4	1.3	P
	Small	25-135	15	15.4	0.8	-22.9	1.6	B
Common carp	Large	614-781	11	15.3	0.8	-24.1	0.3	B
	Medium	175-457	24	12.5	1.6	-25.6	2.6	B
	Small	27-66	6	14.4	0.5	-23.5	4.0	B
Channel catfish	Large	545-754	20	16.1	0.9	-22.4	0.8	B
	Medium	208-473	23	16.1	0.6	-23.5	0.6	B
	Small	24-194	11	15.9	0.6	-23.8	2.8	B
Fathead minnow	Large	51-72	15	16.8	1.1	-25.5	0.7	P
	Small	30-47	13	16.1	1.3	-25.7	2.0	P
Green sunfish	Large	104-161	10	14.9	1.6	-25.9	2.2	P
	Small	77-96	3	14.3	2.3	-27.4	2.4	P
Walleye	Large	468-707	24	17.9	0.7	-22.9	0.7	P/B
	Medium	251-441	16	17.6	0.9	-24.4	1.8	P
	Small	77-234	14	16.6	1.9	-24.4	1.3	P
White bass	Large	312-363	26	18.4	0.8	-24.7	0.6	P
	Medium	165-289	23	17.8	0.9	-25.3	1.0	P
	PR	105-131	7	17.6	0.4	-21.1	0.4	B
	Small	33-63	6	17.0	2.0	-25.9	0.8	P
Yellow perch	Large	160-251	11	15.2	1.6	-24.9	1.3	P
	Small	38-56	10	15.1	2.3	-26.0	0.4	P
Amphipoda	Adult		5	10.3	2.0	-22.7	0.4	B
<i>Calanoid</i> spp.	Adult		4	14.3	2.9	-25.3	5.2	P
<i>Chironomidae</i> spp.	Adult		5	11.3	3.2	-25.8	0.2	B
	Larvae		15	7.9	1.6	-21.9	2.7	B
	Pupae		3	8.1	2.3	-26.2	2.6	B
Corixidae	Adult		3	9.7	2.1	-27.3	1.7	B
<i>Cyclopoid</i> spp.	Adult		4	12.4	1.3	-24.4	1.8	B
<i>Daphnia</i> spp.	Adult		3	12.7	1.6	-27.8	1.5	P
<i>Leptodora</i> spp.	Adult		3	13.5	0.2	-19.9	0.1	B
<i>Hydracarina</i> spp.	Adult		3	12.1	2.9	-25.1	0.7	B
<i>Odonata</i> spp.	Nymph		3	13.3	1.4	-25.0	5.5	B

Table 2. Quantified diet results for each sport fish size-class and species (mean percent biomass), and the percent biomass accounted for by stable isotopes from the total diet biomass (% Isotopes).

Species	Size-class	n	% Empty	% Zooplankton	% Aquatic insects	% Fish	% Isotopes
Black bullhead	Large	127	32	32	27	41	94
	Small	14	14	38	37	25	66
Black crappie	Large	185	2	42	49	9	96
	Small	27	0	77	23	0	92
Channel catfish	Large	63	10	7	30	63	89
	Medium	30	20	20	76	4	94
	Small	14	21	16	84	0	90
Walleye	Large	50	60	5	6	89	90
	Medium	63	46	0	13	87	97
	Small	14	36	22	22	56	100
White bass	Large	92	23	25	53	22	97
	Medium	222	19	56	34	10	98
	PR	11	27	49	14	37	100
	Small	40	15	90	7	3	95
Yellow perch	Large	48	33	27	48	25	99
	Small	11	0	63	37	0	95
Mean				36	35	29	93

consumed by Utah Lake sport fish was comprised of fish prey. Collectively, the prey species I selected for stable isotope analyses contributed over 90% of the total diet walleye (*Sander vitreus*) were found to be almost exclusively piscivorous (hereafter referred to as “exclusive” piscivores). On average, only 29% of the prey biomass consumed by Utah Lake sport fish was comprised of fish prey. Collectively, the prey species I selected for stable isotope analyses contributed over 90% of the total diet biomass for most sport fish size-classes and species. However, the small size-class of black bullhead (*Ameiurus melas*) was found to rely heavily on the relatively uncommon zooplankton species, diaphanosoma, of which I did not obtain stable isotope signatures. Consequently, the small size-class of black bullhead was excluded from subsequent analyses. Nearly half of the total biomass of prey fish consumed by Utah Lake piscivores was comprised of small piscivores, while forage fish species represented only 3% (Figure 3).

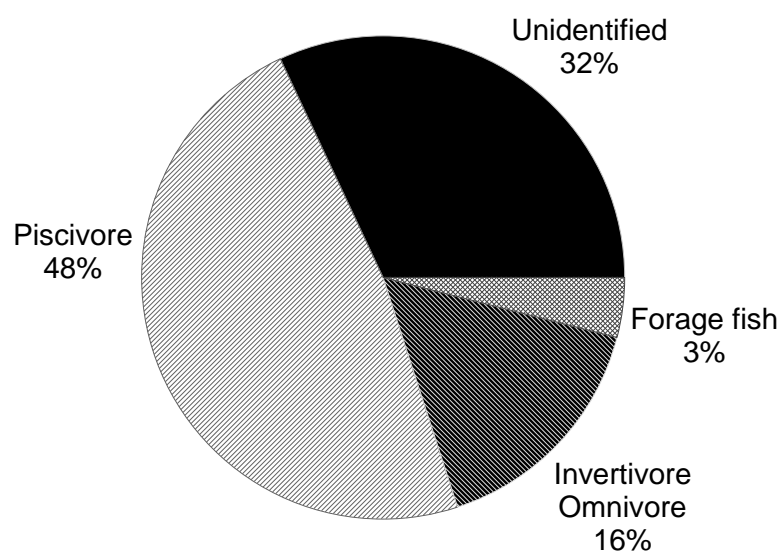


Figure 3. The contribution of prey fish categories to the total biomass of prey fish consumed by Utah Lake sport fish.

Integrated diet and stable isotopes

There was considerable disagreement between observed and predicted stable isotope values for both ^{15}N and ^{13}C (Figure 4). Model predictions based on quantified diet generally underestimated ^{15}N (trophic level), and overestimated ^{13}C stable isotope signatures (energy source), which indicated the dietary contribution of littoral prey had been overestimated. The model predictions for ^{15}N demonstrated no consistency with observed data as the slope=1 hypothesis was rejected. Based on regression analyses, differences between observed and predicted ^{13}C stable isotope values appeared to be due primarily to unexplained variance, since the slope and intercept were not significantly different than the null hypothesis. The RMSD for the ^{15}N model was substantial, and Theil's coefficients suggested most of the error in the model was associated with differences between the observed and predicted values (Table 3). Theil's coefficients for the ^{13}C model indicated there was no error associated with the slope, and all error was partitioned between unexplained variance and differences between observed and predicted values.

The piscivore-specific trophic shift values required for the predicted stable isotope signatures to be similar to the observed values were substantial (Table 4). The values for ^{15}N were comparatively high, as six of the fifteen size-classes and species of piscivores (40%) exceeded the mean \pm SD estimated from controlled fish diet studies (2.7 ± 1.3). The overall mean ^{15}N trophic shift for the piscivore assemblage also exceeded the values obtained from the literature. The required trophic shift values for ^{13}C were relatively lower, as seven of the 15 size-classes and species of piscivores (47%) exceeded the lower bounds estimated from controlled fish diet studies (1.0 ± 1.0). The overall mean required

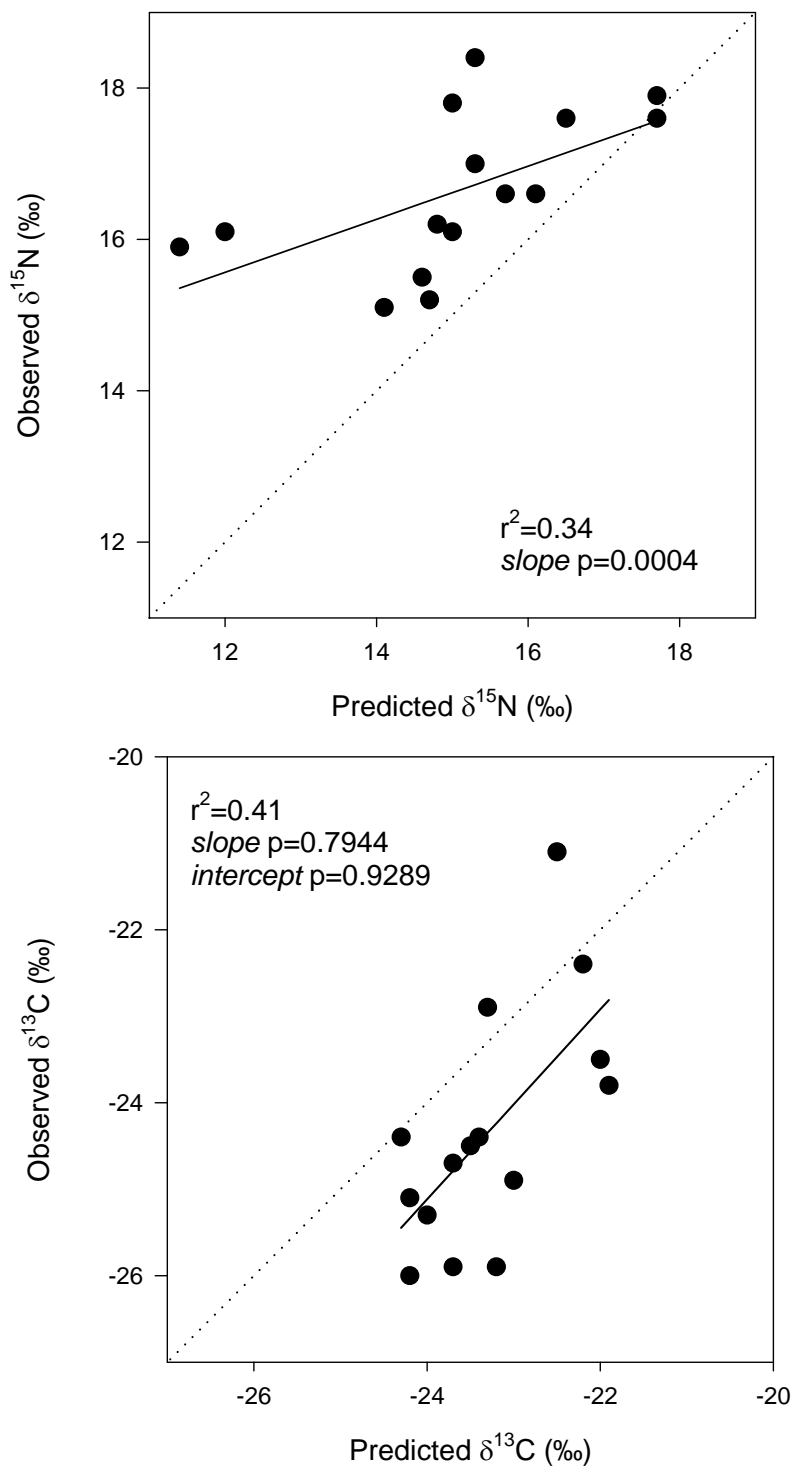


Figure 4. Observed stable isotope signatures for Utah Lake sport fish vs. those predicted based on the mean contribution of each prey species to the total diet biomass.

Table 3. The error associated with observed vs. predicted regression models for $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) stable isotope signatures of Utah Lake sport fish. (RSMD) is the mean deviation of predicted values with respect to the observed values, and is presented in the same units as the model under evaluation, (U_{bias})= the proportion of error associated with the mean differences between observed and predicted values, ($U_{\beta=1}$)= the proportion associated with the difference between the slope of the predictive model and the 1:1 line, and (U_{error})= the proportion associated with unexplained variance.

	^{15}N	^{13}C
RSMD	65.0	32.5
U_{bias}	0.58	0.51
$U_{\beta=1}$	0.27	0.00
U_{error}	0.16	0.49

^{13}C trophic value for the piscivore assemblage did not exceed the mean \pm SD literature values, but was near the lower bounds of estimated error.

The predicted stable isotope values were very similar to the observed for those size-classes and species that were exclusive piscivores, but dissimilar for the generalist piscivores (e.g. large white bass; Table 4). Overall, there was a significant relationship between the differences between observed and predicted values and prey fish dietary contribution estimated from stomach content (Figure 5). The differences between observed and predicted stable isotope values decreased significantly as the level of piscivory estimated from stomach content increased for both ^{15}N and ^{13}C .

Based on comparisons between quantified diet and the Isosource mixing model results among prey identified in stomach content, failure to correctly quantify the dietary contribution of pelagic prey fish appeared to be the primary reason for dissimilarity between observed and predicted values (Figure 6). For sport fish estimated to have low

Table 4. The mean $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) values observed in the muscle tissue of each sport fish size-class and species, the predicted values based on the contribution of each prey species to the total diet biomass, and the trophic shift value (Δ) necessary for the predicted values to be similar to the observed values. The numbers in bold indicate values that exceed the mean \pm SD of values obtained from the primary literature for comparisons.

Species	Size-class	O ^{15}N	P ^{15}N	Δ ^{15}N	O ^{13}C	P ^{13}C	Δ $\delta^{13}\text{C}$
Black bullhead	Large	16.6	15.7	3.6	-24.5	-23.5	0.1
Black crappie	Large	16.2	14.8	4.1	-25.9	-23.7	-1.3
	Small	15.5	14.6	3.6	-25.1	-24.2	0.1
Channel catfish	Large	16.1	15.0	3.8	-22.4	-22.2	1.1
	Medium	16.1	12.0	6.8	-23.5	-22.0	-0.5
	Small	15.9	11.4	7.2	-23.8	-21.9	-0.9
Walleye	Large	17.9	17.7	2.9	-22.9	-23.3	1.4
	Medium	17.6	17.7	2.6	-24.4	-24.3	0.9
	Small	16.6	16.1	3.2	-24.4	-23.4	0.0
White bass	Large	18.4	15.3	5.8	-24.7	-23.7	0.0
	Medium	17.8	15.0	5.5	-25.3	-24.0	-0.3
	PR	17.6	16.5	3.8	-21.1	-22.5	2.4
	Small	17.0	15.3	4.4	-25.9	-23.2	-1.7
Yellow perch	Large	15.2	14.7	3.2	-24.9	-24.9	-0.9
	Small	15.1	14.1	3.7	-26.0	-24.2	-0.8
Mean				4.3			0.0
SD				1.4			1.1

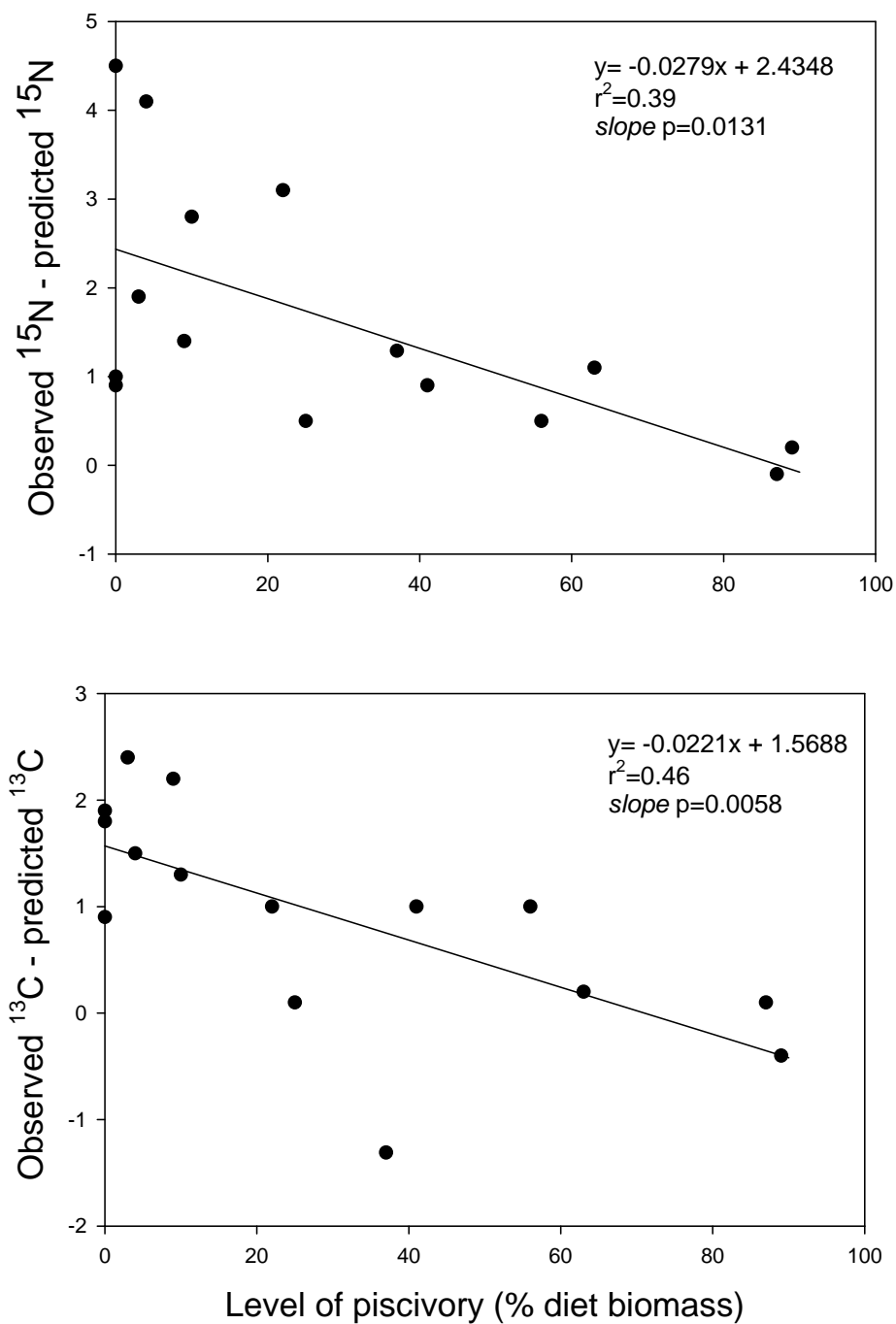


Figure 5. The relationship between the level of piscivory estimated from stomach content, and the difference between observed stable isotope values and those predicted based on the mean contribution of each prey species to the total diet biomass.

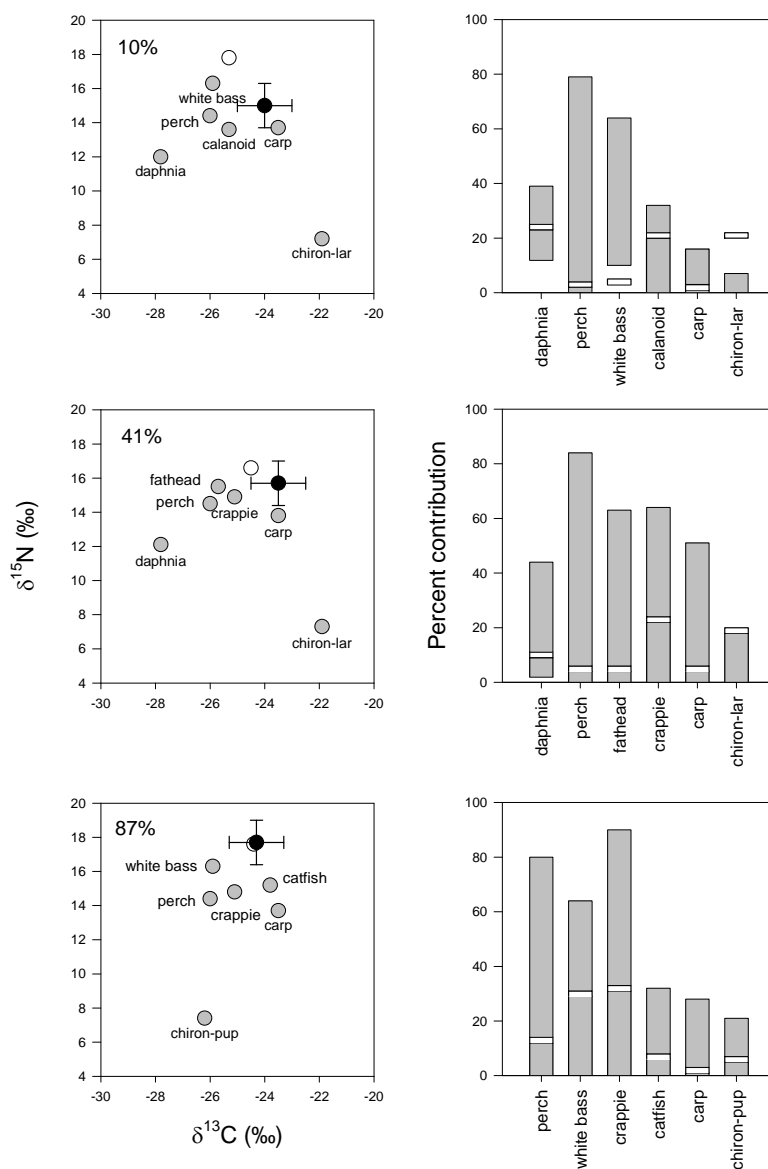


Figure 6. Comparison of observed and predicted stable isotope values, quantified diet and stable isotope mixing model results for sport fish estimated to have a low (10%, medium white bass), moderate (41%, large black bullhead) and high (87%, medium walleye) prey fish dietary contribution. (Left panels) Mean $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) values observed in sport fish muscle tissue (white circle) and the primary prey species (grey circles), compared with the predicted predator values (black circle) based on the mean contribution of each prey species to the total diet biomass. Error bars depict the possible errors associated with applying a mean discrimination factor ($\pm\text{SD}$ estimated from controlled fish diet studies). (Right panels) Isosource range of feasible solutions (grey bars) for the percent contribution of each prey species isotope composition to the piscivores isotope composition, and the mean percent biomass of each prey species estimated from quantified diet (white bars).

and moderate levels of piscivory, the mixing models indicated the dietary contribution of benthic-littoral invertebrate prey such as chironomid, was overestimated in the quantified diet. While this disparity helped explain the disagreement between ^{13}C observed and predicted values, the disagreement between observed and predicted ^{15}N values was best explained by a failure to correctly quantify the dietary contribution of prey with relatively high ^{15}N values. The Isosource mixing model results suggested pelagic prey fish were the dietary component with relatively high ^{15}N values that were typically underestimated in the quantified diet. There was exceptional agreement between mixing model results and quantified diet for exclusive piscivores.

DISCUSSION

This study addressed a fundamental question in applied ecology and conservation; what is the predatory impact of introduced sport fish on native fish populations? More explicitly, which species and size-classes pose the greatest threats to native fish survival? I addressed this in face of a common obstacle, a lack of directly-observable empirical evidence of predation on native fish. I constructed three food web models to address this important question; a stable isotope-derived food web, a quantified diet-derived food web, and finally, an integrated stable isotope and quantified diet food web. I evaluated and compared food web models, then drew inferences from the comparisons. The stable isotope-derived food web illustrated a slight decoupling in energy flow between a pelagic and benthic-littoral sub-web. The quantified diet suggested piscivory was quite low overall and that the sport fish assemblage relied heavily on zooplankton and aquatic insect prey. The integrated stable isotope and quantified diet analysis indicated the quantified diet results were inaccurate, and that the consumption of prey fish, particularly pelagic prey fish, was typically underestimated in the stomach content. From the evaluation, comparison, and integration of food web models, I conclude that predation on the early life stages of Utah Lake fishes was significant, included imperiled native fishes, and was not being observed using stomach content analyses.

The stable isotope-derived food web depicted pelagic and benthic-littoral energy pathways that were very closely coupled; however, this represents an energy flow relationship that may be severely disrupted during drought years. This study was conducted during a high water year; yet, drought is a relatively common natural

environmental disturbance in the Great Basin Desert. During low water years, the littoral zone of Utah Lake is severely reduced, and during prolonged drought coupled with irrigation drawdown, the littoral zone has been essentially departed from the aquatic ecosystem (see Buelow 2006). Furey et al. (2006) compared benthic macroinvertebrate communities between a reservoir that experiences seasonal drawdown and a natural lake that experiences little water level variation. Furey et al. (2006) concluded that variable water levels (which could result from drought and/or drawdown) could have substantial impacts on benthic food webs and the transfer of energy from the littoral to the pelagic habitat. In a stable isotope evaluation of the aquatic food web in Lake Roosevelt, Washington, a reservoir that experiences seasonal drawdown, Black et al. (2003) found that fishes typically considered to be obligate benthivores had pelagic oriented carbon stable isotope signatures. Black et al. (2003) attributed these results to decoupling of the benthic-littoral and pelagic habitats from seasonal drawdown, which resulted in an aquatic food web that was deficient in benthic carbon. Decoupling the pelagic and benthic-littoral sub-webs, a likely consequence of prolonged drought and/or drawdown, could result in a complete rearrangement of the structure and function of the Utah Lake aquatic food web.

The distinct ^{13}C values found within the small size-class of white bass suggested individuals within the same sport fish species and size-class could rely on prey from completely different habitats. However, clear separation in stable isotope signatures was not observed in any of the other fish size-classes. Although all white bass specimens were collected from the main lake habitat, those that demonstrated benthic-littoral ^{13}C values (PR white bass) were collected near the confluence of the largest inflow tributary,

the Provo River. Thus, it is possible those individuals previously inhabited the Provo River, and assimilated a littoral stable isotope signature from that habitat type. The Provo River is the primary spawning area for Utah Lake suckers. Consequently, the confluence of the Provo River and respective littoral habitat is essential for larval sucker survival. The stable isotope-derived food web illustrated that small white bass (YOY size-classes 33-63 mm, and 105-131 mm total length), were among the highest relative trophic position (^{15}N). Olson et al. (2007) also found small size-classes of white bass (60-79 mm, and 80-99 mm total length) to be among the highest relative trophic position (^{15}N) in a shallow Nebraska reservoir. The stable isotope signatures of white bass 105-131 mm total length evaluated in this study suggested they may have relied on prey that inhabited the Provo River confluence; an unsurprising result as white bass commonly inhabit river ecosystems in North America (Scott and Crossman 1973, Herwig et al. 2007). The onset of piscivory for white bass typically occurs during the very early life stages (Mittelbach and Persson 1998); an attribute that my stomach content analysis confirmed. Quist et al. (2002) reviewed food habit studies of larval white bass (4-25 mm long) and concluded they exhibited piscivory, however, zooplankton were the prominent food item overall. Conversely, Clark and Pearson (1978) found prolarval carp were the primary food item of larval white bass (7-12 mm standard length) in the Ohio River. Certainly, the level of piscivory exhibited by young white bass would be dictated by the size-structure of available prey fish (Rudolf 2008). Collectively, results from previous studies and my study suggest schools of small white bass may pose a primary threat to larval sucker survival and should be targeted for management.

The disagreement between observed and predicted stable isotope values may have reflected a littoral bias in stomach sample collection. Most sport fish size-classes and species demonstrated pelagic-oriented stable isotope signatures (Figure 2). The integrated stable isotope and quantified diet analysis suggested the dietary contributions of benthic-littoral invertebrate prey were typically overestimated in the quantified diet. Likewise, the dietary contributions of pelagic prey fish were typically underestimated in the quantified diet. As most sport fish specimens were collected near the littoral zone, the stomach content may have reflected a snapshot of relatively irregular predation events that occurred somewhat recently in the littoral zone. Consequently, pelagic predation events, such as the consumption of pelagic prey fish, may have been more common than stomach content suggested; but, note that Radant and Sakaguchi (1980) observed no difference between pelagic and littoral diet of white bass in Utah Lake, and concluded white bass relied heavily on zooplankton and aquatic insects in both habitats.

Variation in the consumer's diet affected my ability to predict stable isotope values from quantified diet. The observed and predicted stable isotope values were in congruence for the exclusive piscivores, but dissimilar for some of the generalist feeding piscivores. Clarke et al. (2005) also found observed and predicted values (equation 2) for the piscivorous size-classes and species of fish to be very similar, and the generalist feeding fish to be more dissimilar in an oligotrophic lake. A diet effect on the trophic shift of stable isotopes is one factor that could explain the dissimilarity between observed and predicted values for generalist predators. Several others have compared the trophic shift of stable isotopes among consumers relying on different diets using meta-analyses, yet results from these comparisons are inconsistent. Vander Zanden and Rasmussen

(2001) found the $\delta^{15}\text{N}$ trophic shift to be less variable and significantly higher among carnivores than in herbivores (3.41 ± 0.20 ‰ vs. 2.69 ± 2.11 ‰ respectively). In contrast, Post (2002) found no significant difference in mean or variance between herbivore and carnivore $\delta^{15}\text{N}$ trophic shifts (mean 3.35 vs. 3.45, $p=0.85$, variance 0.99 vs. 1.48, respectively). McCutchan et al. (2003) concluded that animals raised on high-protein diets had higher $\delta^{15}\text{N}$ trophic shift values than animals raised on invertebrate diets (3.3 ± 0.26 ‰ vs. 1.4 ± 0.21 ‰ respectively). Vanderklift and Ponsard (2003) found organisms with carnivorous, herbivorous, and mixed diets had similar $\delta^{15}\text{N}$ trophic shifts (2.69, 2.98, and 2.56 respectively). Meta-analyses results suggest the trophic shift of low protein diet (e.g. zooplankton) should either have been similar to or lower than the trophic shift of high protein diet (e.g. prey fish) for Utah Lake sport fish. Consequently, it is unlikely that variation in the trophic shift of prey items caused the disagreement between observed and predicted stable isotope values. Rather, it is more likely the quantified diet underestimated consumption of prey that were truly enriched in ^{15}N .

A failure to discover larval fish in the diet of larger sport fish is thus my leading hypothesis for the disagreement between the observed and predicted stable isotope values. Laboratory studies have concluded that many nonnative fishes consume native larval fish (Carpenter and Mueller 2008), and that the use of stomach content to find evidence of larval fish consumption is unreliable due to rapid chemical and mechanical digestion of these fragile tissues (Schooley et al. 2008). In addition, small food particles, such as larval fish, consumed at high water temperatures have the most rapid gut evacuation rates among food items consumed by fishes (He and Wurtsbaugh 1993). Based on typical spawning characteristics of Utah Lake fishes (Trautman 1981), most

larval fish should have emerged from early-spring through late-summer when peak annual water temperatures occur (mean 21.6°C, min 15.2°C, max 26.7°C, Buelow 2006), further hindering the ability to detect predation on this early life stage using stomach content analysis. Age-0 cohorts (post-larval) of yellow perch (*Perca flavescens*), white bass, channel catfish (*Ictalurus punctatus*), walleye, bluegill (*Lepomis macrochirus*) and common carp clearly emerged in both the sampling gear and sport fish stomach content during this study. Certainly larval individuals preceded these cohorts, and certainly these larval fish experienced intense predation pressure, as predation on the early life stages of fish is likely the leading cause of mortality (Houde 2002). Vander Zanden et al. (1998) found that smallmouth bass (*Micropterus dolomieu*) post-hatch embryos had elevated ¹⁵N values, which was attributed to a maternal effect. Thus, a failure to observe predation on ¹⁵N enriched embryos appears to explain a large portion of the disagreement between observed and predicted stable isotopes for some of the generalist feeding sport fish; an overall result of my study that has obvious implications for native fish conservation.

Application to fish conservation

Although clearly documented evidence demonstrating the impact of introduced sport fish on native biota are rare (Taylor et al. 1984, Moyle et al. 1986, Ross 1991), the existing evidence, primarily local extinction or reduction of native populations subsequent to introductions, is substantial (e.g., Courtenay 1993, Dextrase and Coscarelli 1999, Cambray 2003). In Utah Lake, local extinction of native forage fish species and reduction in native sucker populations clearly followed introductions of nonnative sport fish (Radant and Hickman 1984). However, no evidence of predation on Utah Lake

suckers has been observed in previous stomach content analyses, leading to the conclusion that Utah Lake sport fish subsist primarily on YOY sport fish, zooplankton and aquatic insects, and that the food web was deficient in forage fish diversity and abundance (Radant and Sakaguchi 1980, Radant and Shirley 1987). In this study, predation on Utah Lake suckers was not observed, which is somewhat unsurprising given that rare native fish are by definition, rare. My stomach content analyses also suggested zooplankton and aquatic insects were prominent dietary items, and that prey fish were a relatively rare commodity. However, the integrated quantified diet and stable isotope analysis demonstrated that the quantified diet was inaccurate, and piscivory by introduced sport fish was clearly underestimated from stomach content in this study and likely in preceding studies as well. Collectively, my results highlight the need for integrated food web analyses as demonstrated here, particularly when the fate of an imperiled native species is under evaluation.

An increasing body of evidence suggests native fish populations are declining in part due to predation on the early life stages by introduced fishes (Crowder 1980, Moyle et al. 1986, Marsh and Brooks 1989, Hrabik et al. 1998, Carpenter and Mueller 2008). Generally, the sizes of prey increase with increasing piscivore size (Mittelbach and Persson 1998); a generality that was also observed during this study. Consequently, it is more likely that relatively small predators would consume larval native fish than relatively large predators. Typically, top-level predators are larger in individual body size yet fewer in numbers than predators who feed at lower trophic levels (Elton 1927, Jennings and Mackinson 2003). In Utah Lake, exclusive piscivores were larger in body size yet fewer in numbers than the generalist feeding piscivores. From an immediate

conservation standpoint, the predatory impact of many generalist piscivores, especially white bass, on the very early life stages of native fishes may be preventing recruitment in Utah Lake native fish populations. A complementary study focused on stable isotope signatures of native larval fish and their potential predators may help test this hypothesis. However, native larval fish are relatively low in abundance, and consequently, all existing native larvae in Utah Lake could be consumed by only one species and size-class of introduced sport fish representing only a minimal long-term dietary contribution and contribution to the stable isotope signatures of the consumer. A more informative extension of this study would be to explicitly quantify introduced sport fish consumption of juvenile Utah Lake suckers by coupling reliable population size-structure and abundance data for both predator and prey.

By integrating empirical data, as well as biology and ecology, this study brought forth strong empirical evidence that suggested introduced sport fish negatively impact native fish populations. By applying a food web approach to conservation, hypotheses were developed and the foundation was established for evaluating management scenarios that would support fish conservation and ecosystem restoration.

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APPENDICES

APPENDIX A

Stable isotope signatures obtained during this study yet not included in the primary analyses include seston ($n=4$, $^{15}\text{N}=2.28 \pm 0.4$ SD, $^{13}\text{C}= -24.42 \pm 0.11$ SD), littoral algae ($n=4$, $^{15}\text{N}=12.35 \pm 1.4$ SD, $^{13}\text{C}= -21.36 \pm 2.3$ SD), and periphyton ($n=3$, $^{15}\text{N}=9.66 \pm 0.6$ SD, $^{13}\text{C}= -9.49 \pm 1.1$ SD). Seston samples were obtained by filtering water samples (collected ~ 1 m depth) first through an 80 μm sieve, and then through a GF/F filter. My leading hypothesis regarding the seston stable isotope results is that the samples were contaminated with blue-green algae, thus had a littoral-oriented signature.

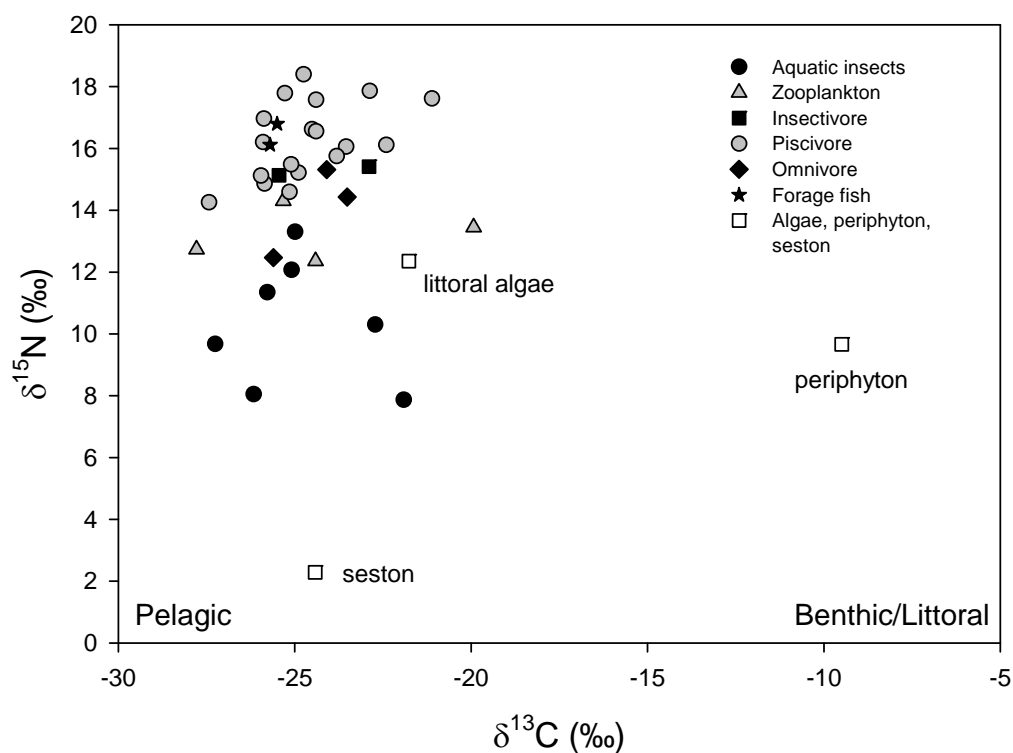


Figure 7. The stable isotope-derived Utah Lake food web, illustrating the mean stable isotope signatures of samples not included in the primary analyses (algae, seston, and periphyton).

Appendix B

Table 5. Mean percent prey biomass (MW_i) and frequency of occurrence (O_i , shown in parentheses), for all common prey items found in the stomach content of each sport fish size-class and species.

Species	Size-class	Index	% Zooplankton							
			calanoid	Cyclopoid	daphnia	ceriodaphnia	other cladocera	diaphanosoma	leptodora	
Black bullhead	Large	MW_i	6	4	9	<1	1	3	6	
		O_i	24	26	26	4	4	16	12	
	Small	MW_i	15	10	<1	8	7	18	<1	
		O_i	42	50	17	8	17	25	8	
Black crappie	Large	MW_i	10	7	16	4	2	<1	7	
		O_i	46	68	68	36	18	23	12	
	Small	MW_i	4	44	16	4	3	<1	5	
		O_i	41	100	70	44	52	19	15	
Channel catfish	Large	MW_i	<1	5	<1	0	<1	0	2	
		O_i	5	23	2	0	2	0	4	
	Medium	MW_i	<1	9	5	0	<1	0	4	
		O_i	4	29	8	0	4	0	13	
	Small	MW_i	1	<1	0	0	0	9	0	
		O_i	18	27	0	0	0	9	0	
	Walleye	Large	MW_i	0	<1	5	0	0	5	0
			O_i	0	5	5	0	0	5	0
Medium		MW_i	0	<1	0	0	<1	0	0	
		O_i	0	9	3	0	3	0	0	
Small		MW_i	0	22	0	0	0	0	0	
		O_i	0	33	0	0	0	0	0	
White bass	Large	MW_i	6	2	11	0	<1	<1	5	
		O_i	17	17	32	0	1	3	11	
	Medium	MW_i	20	4	24	<1	<1	<1	6	
		O_i	51	24	48	1	1	7	14	
	Small	MW_i	5	61	1	5	0	0	10	
		O_i	19	81	5	10	0	0	12	
Yellow perch	Large	MW_i	0	<1	11	0	0	1	14	
		O_i	0	3	23	0	0	10	20	
	Small	MW_i	8	39	10	5	0	0	5	
		O_i	15	70	15	5	0	0	5	

Table 5. Continued

Species	Size-class	Index	% Aquatic insects					
			chironomid larvae	chironomid pupa	chironomid adult	coleoptera	odonata	corixidae
Black bullhead	Large	MW						
		i	19	2	0	<1	1	0
	Small	O _i	31	9	0	1	2	0
		MW						
Black crappie	Large	i	17	0	0	0	0	0
		O _i	8	0	0	0	0	0
	Small	MW						
		i	9	6	<1	1	15	3
Channel catfish	Large	O _i	40	29	15	5	24	25
		MW						
	Small	i	6	10	<1	<1	3	2
		O _i	26	22	4	4	4	11
Walleye	Large	MW						
		i	18	3	0	2	1	1
	Medium	O _i	39	26	0	2	4	4
		MW						
White bass	Small	i	57	11	0	3	0	<1
		O _i	79	46	0	4	0	8
	Large	MW						
		i	58	12	0	0	1	0
Yellow perch	Large	O _i	82	18	0	0	18	0
		MW						
	Medium	i	5	0	<1	0	0	0
		O _i	5	0	5	0	0	0
Black crappie	Small	MW						
		i	3	6	<1	0	0	0
	Large	O _i	9	12	3	0	0	0
		MW						
Black bullhead	Small	i	0	22	0	0	0	0
		O _i	0	22	0	0	0	0
	Large	MW						
		i	19	6	1	1	22	<1
Black crappie	Medium	O _i	52	21	1	1	24	7
		MW						
	Small	i	21	4	1	0	5	1
		O _i	31	11	2	0	9	4
Black crappie	Small	MW						
		i	3	5	0	0	0	0
	Large	O _i	5	10	0	0	0	0
		MW						
Black crappie	Large	i	19	10	<1	0	15	0
		O _i	43	17	7	0	20	0
	Small	MW						
		i	0	28	0	0	5	0
Black crappie	Small	O _i	0	30	0	0	5	0

Table 5. Continued

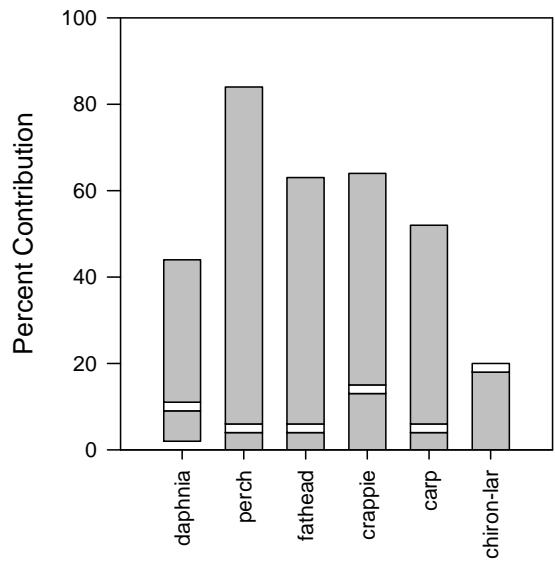
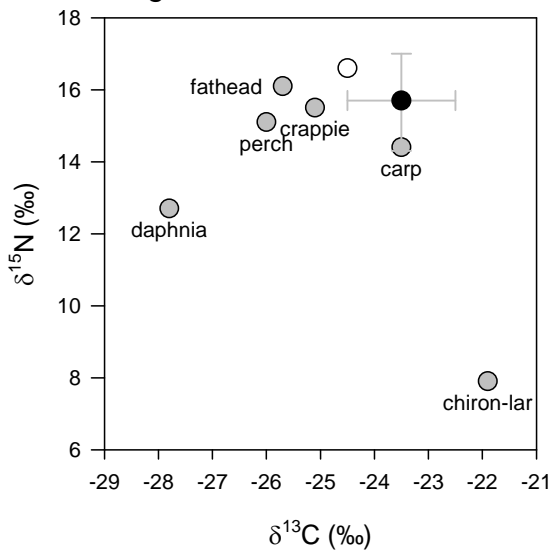
Species	Size-class	Index	% Other		
			amphipoda	hydracarina	other
Black bullhead	Large	MW _i	4	4	2
		O _i	11	26	6
	Small	MW _i	8	0	0
		O _i	8	0	0
Black crappie	Large	MW _i	14	<1	2
		O _i	22	10	8
	Small	MW _i	2	<1	<1
		O _i	7	11	7
Channel catfish	Large	MW _i	3	0	8
		O _i	5	0	16
	Medium	MW _i	4	<1	2
		O _i	4	8	21
	Small	MW _i	10	9	0
		O _i	18	9	0
Walleye	Large	MW _i	0	0	5
		O _i	0	0	5
	Medium	MW _i	3	0	3
		O _i	3	0	6
	Small	MW _i	0	0	0
		O _i	0	0	0
White bass	Large	MW _i	2	1	2
		O _i	4	8	4
	Medium	MW _i	2	<1	2
		O _i	4	1	5
	Small	MW _i	0	<1	0
		O _i	0	2	0
Yellow perch	Large	MW _i	5	0	0
		O _i	20	0	0
	Small	MW _i	0	0	<1
		O _i	0	0	5

Table 5. Continued.

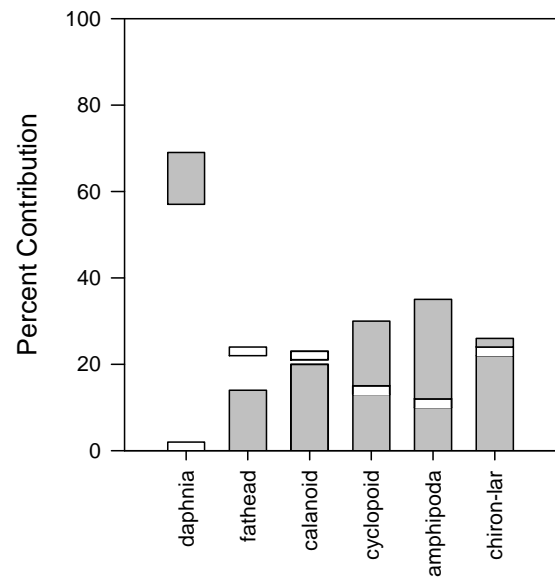
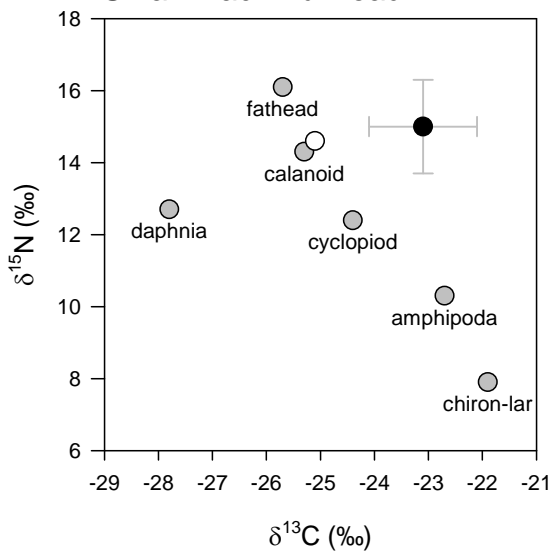
Species	Size-class	%Fish									
		unidentified	bullhead	crappie	bluegill	carp	catfish	fathead	white bass	walleye	perch
Black bullhead	Large	21	0	10	0	2	0	2	2	0	2
	Small	17	0	0	0	0	0	0	0	0	0
Black crappie	Large	5	0	0	1	1	0	2	0	0	0
	Small	0	0	0	0	0	0	0	0	0	0
Channel catfish	Large	12	0	7	1	30	1	0	6	0	1
	Medium	4	0	0	0	0	0	0	0	0	0
	Small	0	0	0	0	0	0	0	0	0	0
Walleye	Large	9	7	0	0	6	6	0	17	0	35
	Medium	38	0	18	0	1	4	1	16	0	7
	Small	42	0	0	11	0	0	0	3	0	0
White bass	Large	5	0	1	0	1	0	0	13	0	1
	Medium	7	0	1	0	1	0	0	1	0	1
	Small	3	0	0	0	0	0	6	0	0	0
Yellow perch	Large	15	0	4	0	3	0	3	0	0	0
	Small	0	0	0	0	0	0	0	0	0	0

APPENDIX C

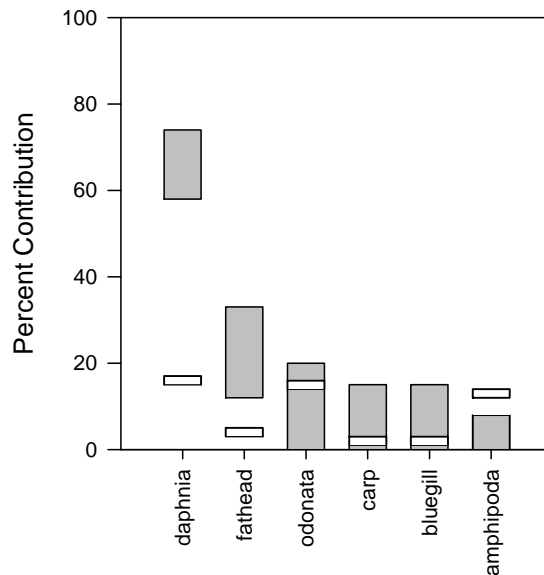
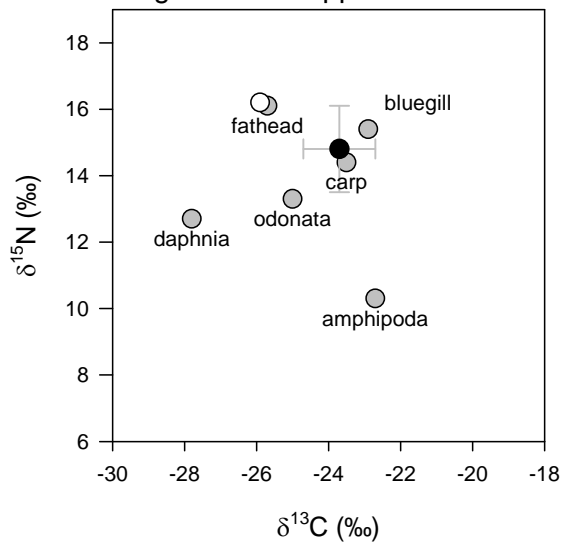
Large Black Bullhead



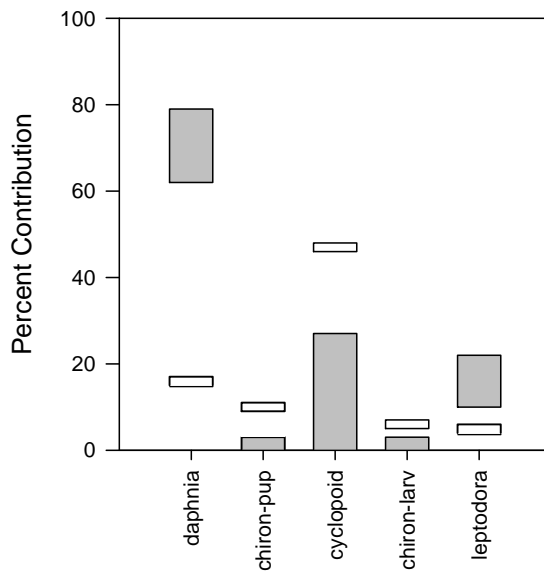
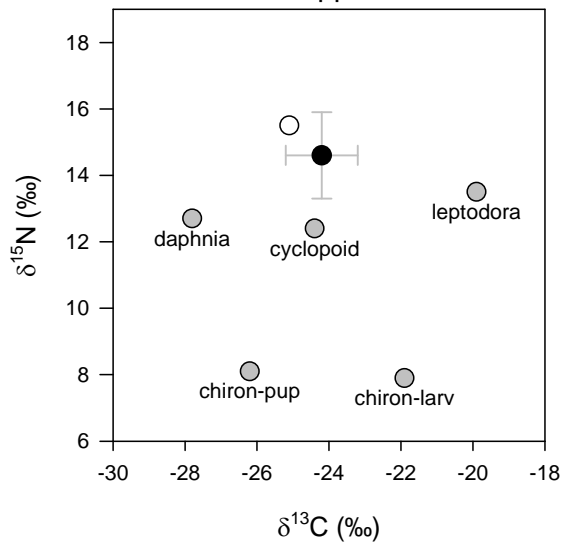
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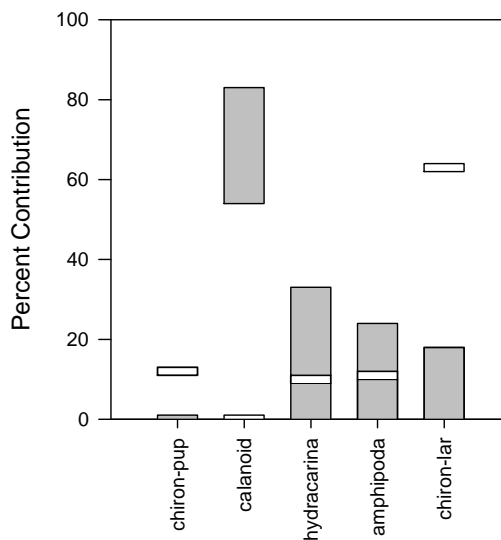
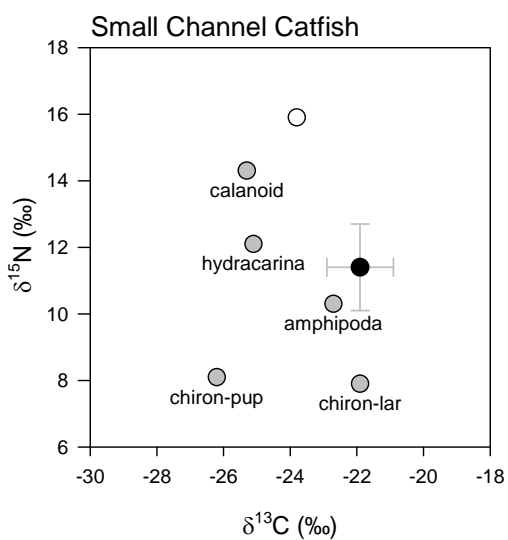
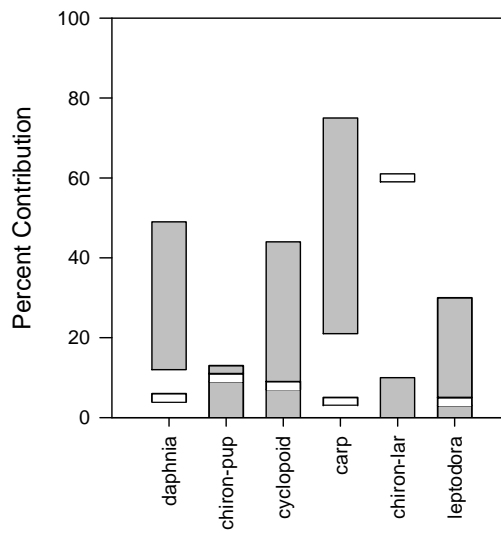
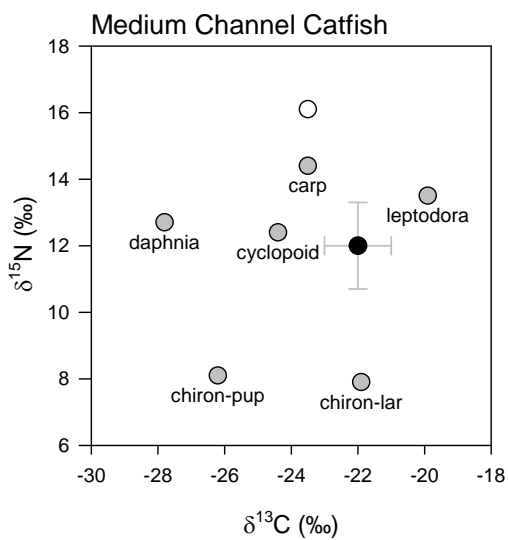
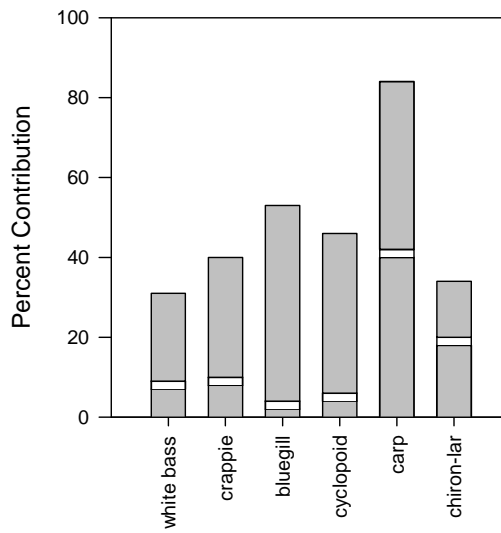
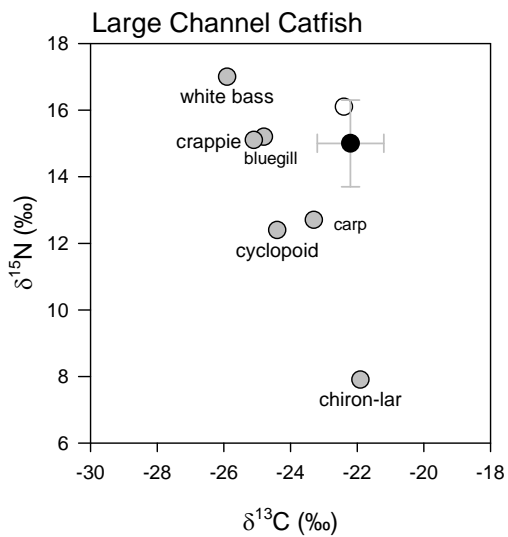


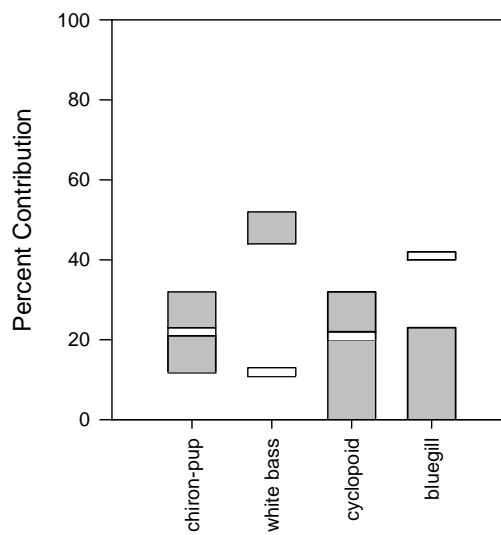
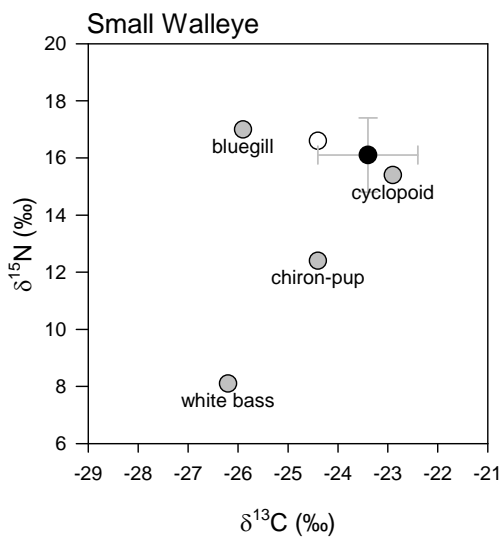
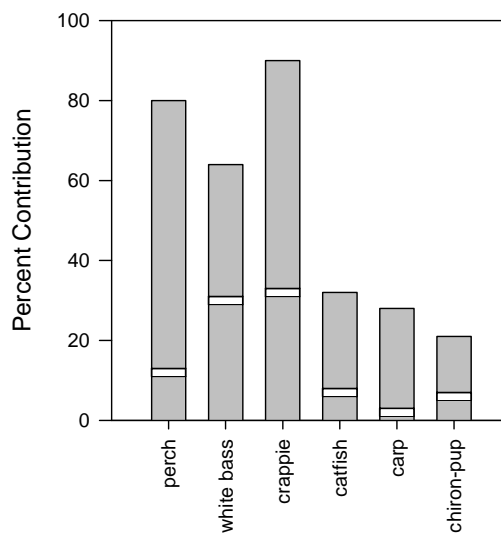
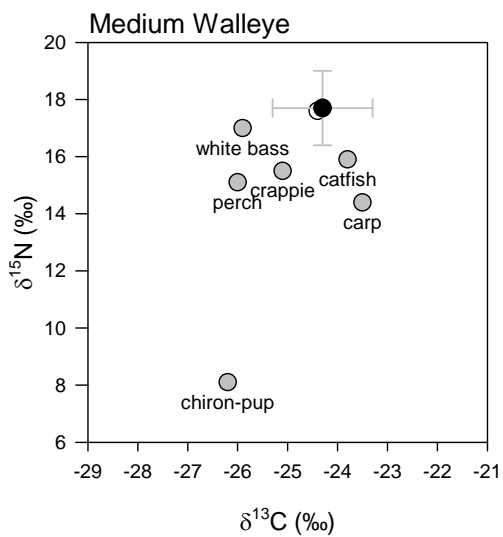
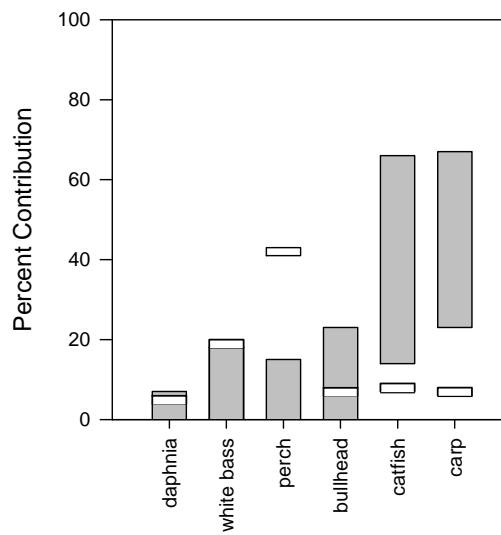
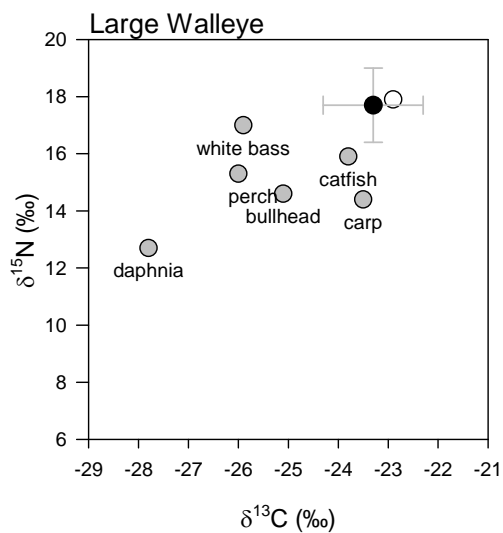
Large Black Crappie

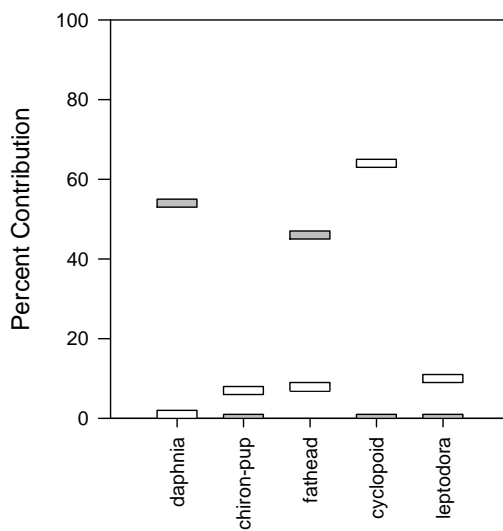
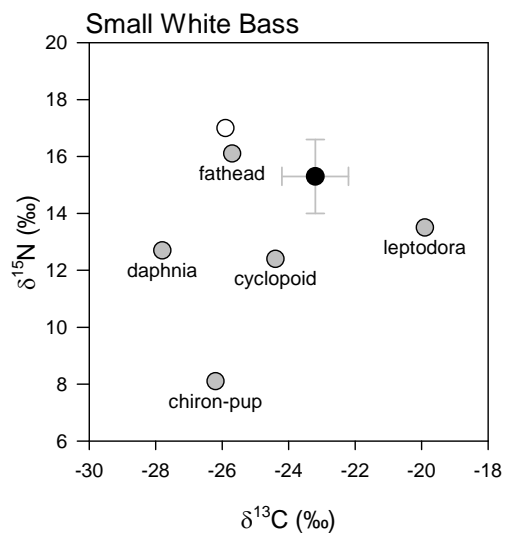
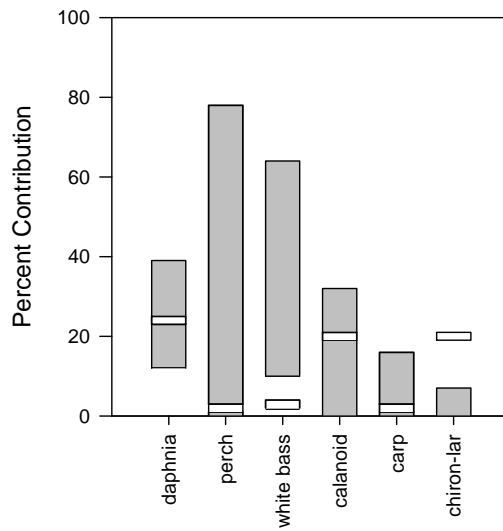
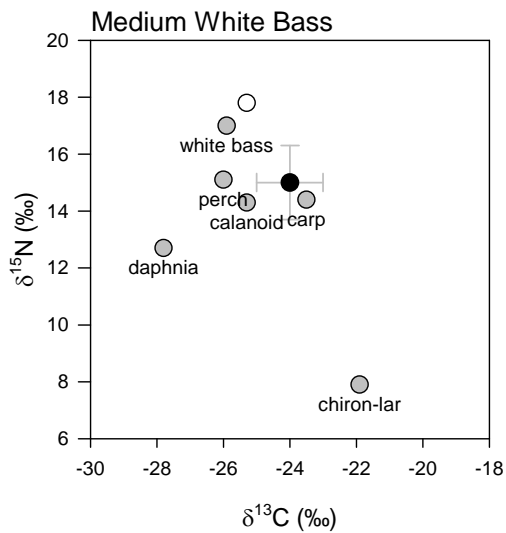
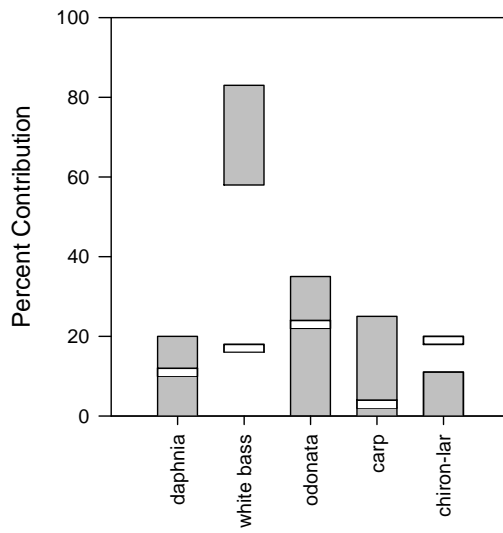
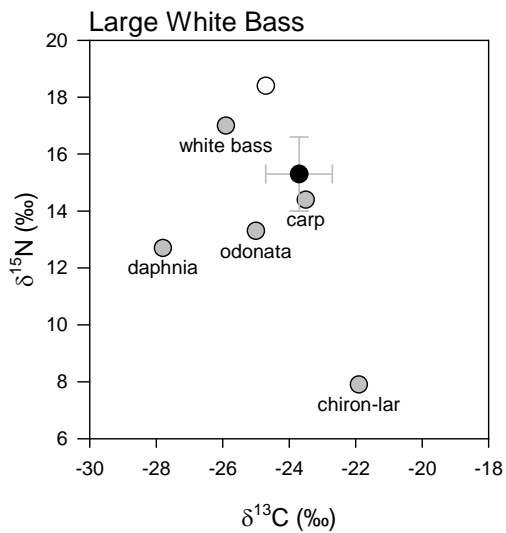


Small Black Crappie









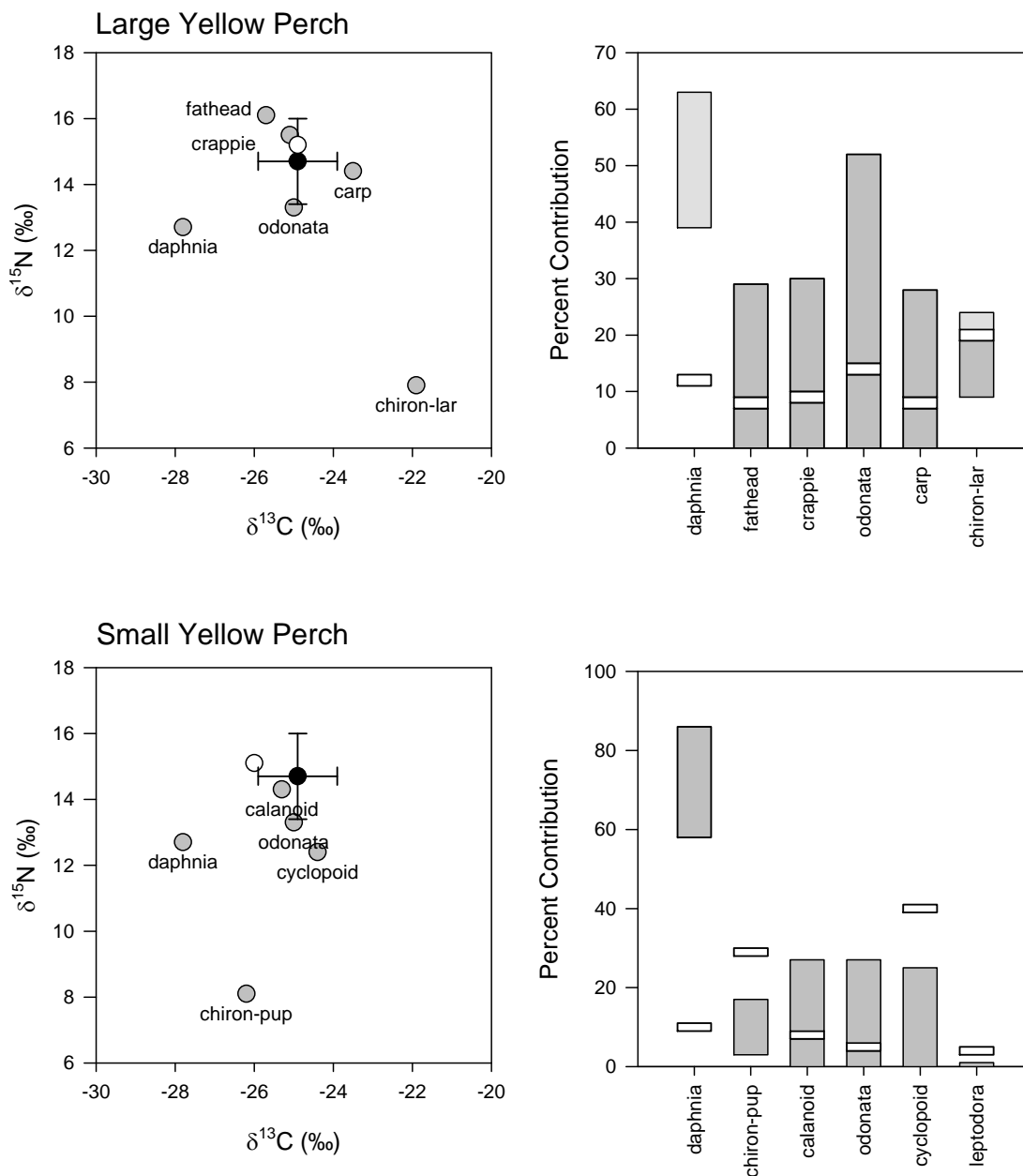


Figure 8. Comparison of observed and predicted stable isotope values, quantified diet and stable isotope mixing model results for all piscivore size-classes and species. (Left panels) Mean $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) values observed in sport fish muscle tissue (white circle) and the primary prey species (grey circles), compared with the predicted predator values (black circle) based on the mean contribution of each prey species to the total diet biomass. Error bars depict the possible errors associated with applying a mean discrimination factor ($\pm\text{SD}$ estimated from controlled fish diet studies). (Right panels) Isosource range of feasible solutions (grey bars) for the percent contribution of each prey species isotope composition to the piscivores isotope composition, and the mean percent biomass of each prey species estimated from quantified diet (white bars).

APPENDIX D

Table 6. Gape to total length relationships for Utah Lake piscivores. CW=cleithrum width, GH=gape height, GW=gape width.

Species	Size range	Gape method	Gape size	n	r ²
Black bullhead	144-344	CW	$0.0528x^{1.2202}$	94	0.91
		GH	$0.1521x^{1.0023}$	99	0.86
		GW	$12.261e^{0.0049x}$	99	0.86
Black crappie	90 - 332	CW	$5.117e^{0.0055x}$	119	0.70
		GH	$25.863\ln(x)-104.93$	139	0.88
		GW	$28.073\ln(x)-114.21$	139	0.87
Brown trout	168-379	CW	$0.1561x^{0.8948}$	13	0.89
		GH	$0.2101x^{0.9177}$	13	0.87
		GW	$0.1986x^{0.9148}$	13	0.92
Channel catfish	145-710	CW	$0.0313x^{1.248}$	83	0.98
		GH	$0.095x^{0.9958}$	90	0.97
		GW	$11.386e^{0.0033x}$	91	0.95
Green sunfish	77-161	CW	$0.0055x^{1.61}$	16	0.76
		GH	$0.3431x^{0.8308}$	16	0.86
		GW	$0.2628x^{0.9006}$	16	0.91
Walleye	77 - 721	CW	$0.0151x^{1.301}$	116	0.95
		GH	$0.3308x^{0.8314}$	128	0.93
		GW	$0.2502x^{0.8981}$	128	0.94
White bass	52 - 412	CW	$0.0355x^{1.1571}$	179	0.87
		GH	$0.3145x^{0.8259}$	180	0.95
		GW	$0.2402x^{0.8966}$	180	0.97
Yellow perch	109 - 251	CW	$0.0459x^{1.1114}$	48	0.53
		GH	$0.1151x^{1.0073}$	48	0.82
		GW	$0.1412x-1.7698$	48	0.75

Table 7. Body depth to total length relationships for Utah Lake fishes.

Species	Size range	Body depth	n	r ²
Black crappie	30 - 291	$0.2686x^{1.0511}$	205	0.98
Bluegill	18 - 220	$0.1528x^{1.1989}$	120	0.99
Black bullhead	37 - 344	$0.1702x^{1.034}$	102	0.90
Brown trout	168-379	$0.3558x^{0.8742}$	13	0.92
Channel catfish	21 - 696	$0.1561x^{1.0177}$	64	0.99
Common carp	20 - 603	$-0.0003x^2+0.3732x-4.9708$	99	0.98
Fathead minnow	21 - 72	$0.2623x-3.4309$	76	0.90
Green sunfish	77-161	$0.3971x^{0.9629}$	13	0.91
Utah chub	175-297	$0.035x^{1.3347}$	6	0.98
White bass	33 - 370	$0.1909x^{1.0589}$	366	0.99
Walleye	77 - 620	$0.1168x^{1.0612}$	82	0.97
Yellow perch	38 - 251	$0.1335x^{1.1105}$	69	0.99

Table 8. Length conversions for Utah Lake fishes. Relationships are for conversions from standard length to total length, and fork length to total length. Regressions equations are in the form $a+b(x)$, where (x) =either standard or fork length. Black bullheads effectively lack a forked tail, therefore, only a standard to total length conversion was obtained.

Species	Size range	Standard length	n	r ²	Fork length	n	r ²
Black bullhead	86-335	4.3349+1.1542	157	0.99	.	.	.
Black crappie	112-293	5.6388+1.2431	216	0.98	2.6908+1.0334	248	0.99
Bluegill	83-185	-0.1185+1.2464	17	0.99	2.0237+1.0355	24	0.99
Brown trout	180-412	11.137+1.122	10	0.99	1.0743+1.0483	16	0.99
Channel catfish	100-682	8.843+1.1986	127	0.99	7.9503+1.0903	137	0.99
Common carp	125-734	-0.3081+1.2643	357	0.99	1.3903+1.1139	383	0.99
Fathead minnow	30-72	0.7976+1.2407	54	0.98	1.4246+1.0648	40	0.98
Green sunfish	66-162	3.4709+1.1696	5	0.99	8.959+0.9665	8	0.96
June sucker	299-574	33.187+1.1167	140	0.98	13.168+1.034	185	0.90
Largemouth bass	171-473	3.2307+1.197	5	0.99	2.3988+1.0241	6	0.99
Rainbow trout	258-425	13.836+1.1171	6	0.99	-3.8961+1.0534	5	0.99
Utah chub	159-285	4.9726+1.2066	7	0.99	-4.6617+1.1118	7	0.99
Utah sucker	327-555	12.049+1.1592	12	0.99	-4.7542+1.0717	12	0.99
Walleye	178-705	9.1734+1.1691	38	0.99	2.3789+1.0548	53	0.99
White bass	121-370	-9.8998+1.3513	300	0.99	-6.6822+1.1182	363	0.99
Yellow perch	122-300	3.4802+1.1801	8	0.99	-0.4995+1.0456	8	0.99