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Ecomorphological and Genetic Investigations into the Utah Lake, UT Sucker Complex with Comparisons to the Jackson Lake, WY Sucker Complex

David Cole

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ECOMORPHOLOGICAL AND GENETIC INVESTIGATIONS INTO THE UTAH LAKE, UT SUCKER COMPLEX WITH COMPARISONS TO THE JACKSON LAKE, WY SUCKER COMPLEX

by

David D. Cole

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

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

Todd Crowl Major Professor	Karen Mock Committee Member
Phaedra Budy Committee Member	Chris Luecke Committee Member
Mike Pfrender Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Ecomorphological and Genetic Investigations into the Utah Lake, UT Sucker Complex with Comparisons to the Jackson Lake, WY Sucker Complex

by

David D. Cole, Doctor of Philosophy

Utah State University, 2014

Major Professor: Dr. Todd A. Crowl
Department: Watershed Sciences

Ecomorphological specialization within Catostomidae in several large western North American lakes has produced populations including typical benthic suckers (*Catostomus*) and lakesuckers (*Chasmistes*), mid-water planktivores, with a continuum of morphologies existing between them. All extant lakesuckers are endangered, and population declines have been attributed in part to hybridization with sympatric *Catostomus* spp.

Chapter 2 describes assessment for concordance of morphological and genetic variation in suckers in Utah Lake, Utah (June sucker, *Chasmistes liorus*; Utah sucker, *Catostomus ardens*; and suckers of intermediate morphology) by comparing a morphological analysis with amplified fragment length polymorphism and microsatellite analyses. Suckers were differentiated using characters associated with presumed feeding strategies: zooplanktivory (June sucker) and benthivory (Utah sucker). No molecular evidence was found for deep genetic divergence between morphs or for hybridization among ancient lineages. Slight population structuring accompanied substantial morphological variation.

Chapter 3 describes the investigation of distribution and movement, spawning behavior, and diet of suckers in Utah Lake and their growth at different densities in a laboratory experiment. Acoustic / radio telemetry revealed little difference in movement and distribution of June sucker and Utah sucker or in timing of spawning runs. Stable isotopes analysis revealed that Utah sucker were enriched in ^{13}C relative to June sucker as presumed diets would predict. Intermediate morphs were intermediate for $\delta^{13}C$ and $\delta^{15}N$. Neither species nor density was a significant predictor of growth rate of June sucker or Utah sucker reared at different conspecific densities.

Chapter 4 examines morphology, genetics, and diet of the sucker population in Jackson Lake, Wyoming, once home of the extinct Snake River sucker, *Chasmistes muriei*, a lakesucker known from a single specimen. Currently, suckers in Jackson Lake are identified as Utah sucker; however, recently sampled individuals resemble lakesucker. No molecular evidence was found for deep genetic divergence between lakesucker and benthic morphs or for hybridization among ancient lineages. The benthic morph was significantly enriched in ^{13}C relative to the lakesucker morph, consistent with presumed diets. Morphologically, the lone Snake River sucker holotype specimen grouped strongly with extant lakesucker morphs, suggesting that the status of the Snake River sucker be updated accordingly.

(262 pages)

PUBLIC ABSTRACT

Ecomorphological and Genetic Investigations into the Utah Lake, UT Sucker Complex with Comparisons to the Jackson Lake, WY Sucker Complex

David D. Cole

Natural selection within the sucker family of fishes has produced populations including typical benthic (bottom-feeding) suckers (*Catostomus*) and lakesuckers (*Chasmistes*), mid-water plankton eaters, in several large western North American lakes. Suckers of intermediate morphology (shape) exist in a continuum of head, mouth, and body characteristics between these two extremes. All current lakesuckers are listed Endangered, and population declines have been attributed in part to hybridization with their *Catostomus* neighbors.

Chapter 2 describes the investigation of the relationship between morphology and genetics of June sucker, a lakesucker, and Utah sucker, a benthic sucker, in Utah Lake, Utah. Despite the substantial morphological differences, June sucker and Utah sucker were indistinguishable genetically. Although many suckers were of intermediate morphology, there was no evidence of hybridization between ancient June sucker and Utah sucker lineages, suggesting perhaps the Utah Lake population is diverging into two populations rather than converging into one.

Chapter 3 describes the ecology of Utah Lake suckers. Telemetry studies using surgically implanted transmitters revealed little difference in movement and

distribution of June sucker and Utah sucker or in the timing of their spawning runs. An investigation into diet confirmed that June sucker were predominantly planktivorous (plankton eaters) whereas Utah sucker were benthivorous (bottom feeders), with intermediates in between.

Chapter 4 examines morphology, genetics, and diet of the sucker population in Jackson Lake, Wyoming, once home of the extinct Snake River sucker, *Chasmistes muriei*, a lakesucker known from a *single* specimen. Currently, suckers in Jackson Lake are identified as Utah sucker, however, recently sampled individuals resemble lakesuckers (Snake River sucker?). Similar to the Utah Lake suckers, no genetic evidence was found for deep divergence between lakesucker and Utah (benthic) sucker in Jackson Lake or for hybridization among two ancient lineages. Also as in Utah Lake suckers, an investigation into diet showed that lakesuckers were predominantly planktivorous (plankton eaters) whereas Utah sucker were benthivorous (bottom feeders), with intermediates exploiting both food sources. Morphologically, the *lone* Snake River sucker specimen was extremely similar to current lakesuckers in Jackson Lake, suggesting that the Snake River sucker is not extinct and in need of a status update.

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CHAPTER 1

INTRODUCTION

Schluter (1996) defined ecological speciation as the evolution of reproductive isolation, directly or indirectly, via divergent selection on traits between populations (or subpopulations) in contrasting environments or exploiting different resources; i.e., the process by which barriers to gene flow between populations evolve because of divergent ecological adaptation. The divergence of benthic and limnetic morphs exploiting different trophic resources has occurred multiple times in fish populations in freshwater lakes (Lu & Bernatchez 1999; Schluter 1996, 2001; Lu *et al*. 2001; Barluenga & Meyer 2004). Several large western North American lakes support recent populations of lakesucker (*Chasmistes* spp.) in addition to benthic feeding sucker (*Catostomus* spp.) populations (Miller & Smith 1981; Scoppettone and Vinyard 1991). Lakesuckers are long-lived, mid-water, adfluvial planktivores that inhabit large lakes or sluggish rivers and typically spawn in tributary streams in spring and early summer. Extant *Chasmistes* spp. are sympatric over all or part of their range with one or more species of benthic-feeding sucker (*Catostomus* spp.), and suckers of intermediate morphologies, presumably the result of hybridization, are common. Four recent species of *Chasmistes* are recognized: *Ch. brevirostris*, the shortnose sucker; *Ch. cujus*, the cui-ui sucker; *Ch. liorus*, the June sucker; and the presumably extinct Snake River sucker, *Ch. muriei*. All extant *Chasmistes* spp. are federally listed as Endangered, with their declines attributed to anthropogenic changes in aquatic habitat, historic overexploitation, competition with and predation by nonnative fish species, and hybridization with the sympatric *Catostomus* spp. (Carter 1969; Fuhriman et al. 1981; Scoppettone and Vinyard 1991). The subsequent three chapters describe the morphological variation, genetic variation, and ecology of two sucker populations: Utah Lake, habitat of June sucker and Utah sucker (*Ca. ardens*); and Jackson Lake, habitat of the presumably extinct Snake River sucker and Utah sucker.

Chapter 2 quantitatively describes and assesses the concordance of the morphological and genetic variation in the Utah Lake sucker complex, with June sucker at one extreme of the morphological continuum and the sympatric benthivore, Utah sucker, at the other. This was achieved by comparing a morphological analysis with amplified fragment length polymorphism and microsatellite analyses.

Chapter 3 describes the investigation of distribution and movement, spawning behavior, and diet of adult suckers in Utah Lake and their growth at different densities in a laboratory experiment. The first objective of this chapter was to compare the spatial distribution and movement patterns, including spawning migrations and seasonal movements, of adult June sucker and Utah sucker in Utah Lake via radio and acoustic telemetry. The second objective was to investigate diet for concordance with morphology via comparison of stable isotopic signatures for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of adult June sucker, Utah sucker, and suckers of intermediate morphology. The third objective was to explore if the component Allee effect reported in larval June sucker (Gonzalez 2004) also occurred in juvenile June sucker and / or juvenile Utah sucker, through a laboratory experiment assessing growth rate, as a measure of fitness, at different rearing densities.

Chapter 4 examines the morphology, genetics, and diet of the sucker population in Jackson Lake, Wyoming, once home of the extinct Snake River sucker, *Chasmistes muriei*. Currently, suckers in Jackson Lake are identified as Utah sucker, however, recently sampled individuals resemble lakesuckers. The objective if this Chapter was to assess concordance of morphological variation with molecular variation (microsatellites) and with variation in diet as measured by stable isotope analysis.

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CHAPTER 2

MORPHOLOGICAL AND GENETIC STRUCTURING IN THE UTAH LAKE SUCKER COMPLEX

ABSTRACT

Population decline in the federally endangered June sucker (Chasmistes liorus), a lakesucker unique to Utah Lake, Utah, has been attributed in part to hybridization with the more widespread Utah sucker (Catostomus ardens). As a group, suckers in Utah Lake exhibit considerable external morphological variation. Meristic and morphological ambiguities, presumably the result of hybridization, create a continuum of intermediate forms between Chasmistes and Catostomus extremes and prevent definitive identification to species. Here we describe and evaluate the morphological and genetic variation in suckers in Utah Lake by comparing a morphological analysis with amplified fragment length polymorphism (AFLP) and microsatellite analyses. Suckers were morphologically differentiated using mouth characters associated with different feeding strategies: planktivory (June sucker) and benthivory (Utah sucker). Although we found no genetic evidence for a deep divergence between June and Utah morphs, slight, but significant population structuring accompanied the substantial morphological variation. Bayesian model-based genetic clustering analyses detected two sucker populations in Utah Lake, however, these clusters were not strongly concordant with morphological groupings or between marker systems. The suckers in Utah Lake present an interesting dilemma regarding conservation: should one

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conserve (breed and stock) a subset of the morphotypic variation in the Utah Lake sucker complex, focusing on the endangered June sucker morphotype, or should one conserve both June sucker and Utah sucker morphotypes in this complex, possibly maximizing evolutionary potential? We explore this question in the context of current genetic and morphological variation in the Utah Lake sucker complex as well as historical information on this complex and other lakesuckers.

INTRODUCTION

A recurring motif in many fish populations in freshwater lakes is the divergence of benthic and limnetic morphs exploiting different trophic resources, benthic/littoral macroinvertebrates and zooplankton, respectively (Schluter 1996, 2001; Pigeon *et al.* 1997; Lu & Bernatchez 1999; Taylor 1999; Lu *et al*. 2001; Barluenga & Meyer 2004); whether the morphs are recognized as distinct species varies. This divergence sometimes occurs via sympatric ecological speciation following a single invasion of a recently formed crater, fault, or postglacial lake (tilapia, *Tilapia deckerti*, Schliewen *et al.* 2001; cisco, *Coregonus* spp., Turgeon & Bernatchez 2003; pumpkinseed sunfish, *Lepomis gibbosus*, Jastrebski & Robinson 2004; Midas cichlid, *Amphilophus citrinellus* and *A. zaliosus*, Barluenga *et al*. 2006; Arctic charr, *Salvelinus alpinus*, Knudsen *et al*. 2006; European whitefish, *Coregonus lavaretus*, Østbye *et al*. 2006; barb, *Barbus tanapelagious* and *B. humilis*, De Graaf *et al*. 2007; sailfin silverside, *Telmatherina* spp., Roy *et al*. 2007). Ecologically driven speciation into benthic and limnetic morphs has occurred multiple times within several fish lineages, and populations from different lakes exhibit varying degrees of gene flow between the morphs (threespine stickleback, Taylor & McPhail 1999; lake whitefish, Lu & Bernatchez 1999; cisco, Turgeon *et al.*1999). In other cases, allopatric speciation followed by secondary invasion, the double invasion hypothesis, has led to sympatric limnetic and benthic morphs (threespine stickleback, *Gasterosteus aculeatus*, McPhail 1992, Schluter & McPhail 1992, Kassen *et al.* 1996; lake cisco, *Coregonus artedi*, Turgeon & Bernatchez 2001). Some species (lake whitefish, *Coregonus clupeaformis*, Pigeon *et al*. 1997, Lu *et al*. 2001; Derome *et al*. 2006; Landry *et al*. 2007) appear to have evolved benthic and limnetic morphs via single invasion in some lakes and by double invasion in other lakes.

Several large western North American lakes support populations of planktivorous lakesucker (*Chasmistes* spp.) in addition to benthic feeding sucker (*Catostomus* spp.) populations (Miller & Smith 1981; Scoppettone & Vinyard 1991). *Chasmistes* spp. and *Catostomus* spp. fossils are known from late Miocene to Pleistocene deposits in six western states and are nearly always found together, occasionally with intermediate forms (Cope 1872; Miller & Smith 1981; Smith 1981; Smith *et al.* 2002). Lakesuckers have terminal oblique mouths, thin lips with reduced papillation and wide gaps between the lower lip lobes, and highly branched or dendritic gill rakers (Miller & Smith 1981; Sigler & Sigler 1987; Smith 1992). They are long-lived, mid-water planktivores that inhabit large lakes or sluggish rivers and typically spawn in spring and early summer in tributary streams. Four recent species of lakesuckers are recognized in four different hydrologic basins: June sucker (*Chasmistes liorus mictus*) in the Bonneville basin; cui-ui sucker (*Chasmistes cujus*) in the Truckee River drainage; shortnose sucker (*Chasmistes brevirostris*) in the Klamath River watershed; and the presumably extinct Snake River sucker (*Chasmistes muriei*) in the upper Snake River basin (Miller & Smith 1981). Extant *Chasmistes* spp. are sympatric over all or part of their range with at least one species of benthic-feeding sucker (*Catostomus* spp.). *Catostomus* spp. have subterminal to ventral mouths; large, heavily papillated lips with a narrow gap between the lower lobes; and non-branching, filamentous gill rakers (Eddy & Underhill 1978; Sigler & Sigler 1987). Members of *Catostomus* inhabit a wider geographical and ecological range than any other North American fish genus (Uyeno & Smith 1972).

The June sucker, a lakesucker unique to Utah Lake, Utah, has an evolutionary and taxonomic history that is complicated by its putative hybridization with the Utah sucker (*Catostomus ardens*) (Jordan 1891; Tanner 1936; Miller & Smith 1981; Evans 1997; Cook 2001). The Utah sucker is native to a wide variety of habitats ranging from large, deep, cold lakes to relatively warm streams and shallow lakes within the ancient Lake Bonneville drainage and the Snake River drainage above Shoshone Falls (Sigler & Sigler 1987). Historically, Utah sucker in Utah Lake spawned earlier in the spring than June sucker, named for the month of their peak spawning period (Miller & Smith 1981), perhaps associated with the ascending and descending hydrographs, respectively. June sucker were once believed extinct in Utah Lake following a severe drought in the 1930s (Tanner 1936). Those currently persisting are thought to be morphologically distinct from specimens collected in the 1880s due to hybridization with the sympatric Utah sucker during those drought years; hence, post-drought specimens are designated *Ch. liorus mictus* whereas pre-drought specimens are *Ch. liorus liorus* (Miller & Smith 1981; Smith 1983). The impact of the 1930s drought years is, however, ambiguous. Jordan (1878) concluded a century earlier that suckers with intermediate morphologies in Utah Lake arose from hybridization between June sucker and Utah sucker, but Li (1999) was unable to find a genetic distinction between preserved pre-1930 specimens of *Ch. liorus liorus* and current specimens of *Ch. liorus mictus*.

Lakesucker populations have been subjected to varying degrees of commercial, recreational, and subsistence exploitation by humans (Carter 1969; Sigler & Sigler 1987; Cooke *et al*. 2005), and all extant *Chasmistes* spp. are federally listed as endangered (USFWS 1967, 1986, 1988). Their declines have been attributed to historic over-exploitation, changes in aquatic habitat (degraded water quality, flow alterations, channelization, and loss of littoral zones), competition with and predation by nonnative fish species, and hybridization with *Catostomus* spp. (Carter 1969; Fuhriman *et al*. 1981; Scoppettone & Vinyard 1991). In 1986, the June sucker was listed because of its localized distribution, the population’s failure to recruit new adult fish, and continued threats to its survival. By the late 1990s, the estimate for the wild adult spawning population was about 300 individuals (Keleher *et al*. 1998). Hybridization among catostomids has been documented as common, confounding taxonomy and conservation issues (Hubbs & Hubbs 1947; Hubbs & Miller 1953; Hubbs 1955; Miller *et al*. 1989; Markle *et al*. 2005; Tranah & May 2006). Where sympatry of *Chasmistes* spp. and *Catostomus* spp. occurs, suckers of intermediate morphology exist, and this has been attributed to hybridization (Miller & Smith 1981; Scoppettone & Vinyard 1991; Tranah & May 2006). Extant *Chasmistes* spp. appear to be phylogenetically closer to sympatric *Catostomus* spp. than to allopatric *Chasmistes* spp. (Li 1999; Mock *et al*. 2006; Tranah & May 2006), and no phylogenetic analysis that utilizes genetic data has recovered either genus as monophyletic (Li 1999; Harris & Mayden 2001; Mock *et al*. 2006; Tranah & May 2006; Sun et al. 2007). Although suckers in Utah Lake exhibit considerable external morphological variation, a recent genetic analysis found no molecular evidence for a history of hybridization between deeply divergent lineages in Utah Lake, and suggested that Utah Lake suckers may be a single interbreeding group; of 43 sampled individuals that included both June sucker and Utah sucker morphotypes, 37 shared a single haplotype that was unique to Utah Lake, 1 contained a closely related mitotype, and 5 contained mitotypes indicative of the northern clade of Utah Suckers (Mock *et al*. 2006). The conclusions of this study were limited, however, because morphological data were not included and genetic differentiation between morphs was not directly tested. Building on Mock *et al*. (2006), we hypothesize that within Utah Lake, genetic structuring will be found that correlates with morphological variation in a concordant, though not necessarily explanatory way, allowing for the discrimination and description of two (or three) morphologically and genetically distinct groups. The morphological variation exhibited by Utah Lake suckers and uncertainty about their taxonomic status and evolutionary history present a difficult situation for the effective conservation and management of Utah Lake suckers. Recovery efforts targeting the federally endangered June sucker currently rely on highly subjective interpretation of external characters (Table 2-1) to distinguish June sucker from other morphs in the collection of eggs and sperm for the conservation breeding and stocking program. Unfortunately, gill rakers, the best character for differentiation, cannot be examined on live fish. Externally observable characters - mouth structure and lip papillation and size - have an ecological basis related to feeding strategies, benthivory (*Catostomus*) and planktivory (*Chasmistes*) (Cole 2008), and are presumably shaped by natural selection. The objective of this study was to quantitatively describe the morphological and genetic variation in the Utah Lake sucker complex, with June sucker, an endangered planktivore, at one extreme of the morphological continuum and the sympatric benthivore, Utah sucker, at the other, and assess their congruence.

MATERIALS AND METHODS

Study Site

Utah Lake is a large (38 km x 21 km; approximately 392 km^2), shallow, highly eutrophic lake located in Utah County, Utah, approximately 65 km south of the Great Salt Lake (Fig. 2-1). It is one of the largest freshwater lakes west of the Mississippi River in the contiguous United States and has existed for 8000-10,000 years. For over 30,000 years prior to that, Lake Bonneville covered most of the intermontane basins of the Wasatch Front, undergoing dramatic fluctuations in depth and salinity. Utah Lake, the largest freshwater remnant of Lake Bonneville, has an average depth of 2.8 m and a maximum depth of 4.2 m (Fuhriman *et al*. 1981). Major tributaries include the Provo, Spanish Fork, and American Fork Rivers; the outlet, the Jordan River flows north to the Great Salt Lake. Frequently, conductivity is above 2000 µS, temperatures at shallow depths in summer exceed 30ºC, and turbidity is greater than 120 Ntus (Cole 2008). The anthropogenic impacts of urbanization, agriculture, flow regulation, and exotic introductions on Utah Lake and its tributaries are manifest as declines in both water quality and quantity, especially during drought years. June sucker and Utah sucker are effectively the only native fish persisting in Utah Lake; 12 other native species have become extinct or have been essentially extirpated from the lake, whereas many non-native species thrive, including predators and competitors of native suckers (SWCA 2002). What was once a lake with clear water and extensive beds of littoral macrophytes (Heckmann *et al*. 1981) is now carp infested, populated with numerous introduced predatory fish species, turbid, and practically void of aquatic vegetation (Miller & Crowl 2006). Utah Lake's water level fluctuates dramatically, seasonally and annually, limiting the re-establishment of submerged macrophytes and fringes of emergent vegetation may or may not be inundated for years at a time. Even moderate winds can prevent stratification of the lake because of the large fetch, shallow depth, and lack of vegetation.

Morphological Analysis

During the 2001 and 2002 spawning runs, 75 live, wild sucker were captured by Utah Department of Wildlife Resources personnel, who also provided measurements of total length, from the Provo River (n = 72, captured by dip netting spotlighted fish) and the Spanish Fork River (n = 3, captured by electrofishing) and photographed individually in a shaded Plexi-glas® live well (l×w×h: 60cm × 15cm × 45cm). Other investigators have pinned out anaesthetized fish into precise poses in the collection of images for analysis (Douglas *et al*. 1989, 1998, 2001; Douglas 1993; McElroy & Douglas 1995; McElroy *et al*. 1997). Instead, we used a shaded live well and minimized handling to reduce stress on suckers sampled during the already traumatic spawning period. June sucker were subjectively identified by external characters using a *Ch. liorus mictus* model (Miller & Smith 1981) (Table 2-1). Utah sucker were similarly identified using a less stringent definition than that of Sigler and Sigler (1987), allowing for slight reductions in lip size and papillation (*e.g.*, a *C. ardens “mictus”* model for Utah sucker) (Table 2-1). Intermediates were those not identified as June sucker or Utah sucker. The external characters used for this initial identification are also the ones generally used by managers in the field during spawning and monitoring activities (Keleher pers. comm.). Sex was initially determined by presence or absence of breeding tubercles and anal fin shape, but corroborated during propagation activities: June sucker - 13 females, 14 males; intermediates - 13 females, 15 males; and Utah sucker - 9 females, 11 males. Despite length being a poor predictor of age in long-lived suckers, all fish were roughly aged from their total length (TL) via a standard curve derived from the only published length/age data (Belk 1998) for suckers from Utah Lake to roughly estimate when the last successful natural spawn occurred. The mean standard deviation of length at age for the standard curve used in age estimation was 54.3 mm. Digital photographic images from two perspectives, full body profile and ventral head shot, were obtained using a Nikon 990 digital camera, and fin clips from the same fish were collected for genetic analysis. Images were digitized via the program tpsDIG (©Rohlf, 2001), meristic counts and angle measurements were performed, and morphometric landmarks were identified and the distances (in mm) between them calculated. Descriptions of the morphometric (17) and meristic (2) characters used in this study appear in Table 2-2 and Fig. 2-2.

The relationship of total length to sucker morph and sex was examined via two factor analysis of variance (ANOVA). Linear regression was used to explore the relationship between TL and the individual morphological variables and to generate residuals for use in subsequent size-adjusted ANOVA. We used principal component analysis (PCA) based on the correlation matrix among variables to illustrate morphological variation in Utah Lake suckers and to generate phenotypic variables (principal components, PCs) for comparison with genetic data. Congruence between morphological variation, defined both subjectively (identification) and objectively (phenotypic PCs), and genetic variation was subsequently assessed. All morphological analyses were performed using the program SAS (2002).

Genetic Analysis

Fin (pelvic) clips were collected from 78 suckers during photography and preserved in 95% ethanol. Samples represent the 75 individuals included in the morphometric dataset plus three individuals not included in the morphometric analysis because of spinal deformations or incomplete photographic data, neither of which prevented subjective assignment of these suckers to morphological group. DNA was extracted using a salt/chloroform protocol (Mullenbach *et al*. 1989). DNA quantity and quality was assessed on 0.7% agarose gels stained with ethidium bromide.

Amplified fragment length polymorphism (AFLP) and microsatellite analyses were used to characterize nuclear divergence and diversity among the 78 individuals subjectively identified morphologically. Our AFLP data were derived by identical methods and represent a subset of the individuals characterized genetically by Mock *et al*. (2006) using 113 polymorphic AFLP loci from nine primer combinations, selected on the basis of overall amplification quality and bimodality (distinct presence/absence). Additionally, five microsatellite loci were amplified in these individuals following protocols and using equipment described by Cardall *et al*. (2007).

For AFLP profiles within morphologically defined groups, the percentage of polymorphic loci (95% criterion) and Nei's (1978) average unbiased heterozygosity were estimated using the program Tools for Population Genetic Analysis (TFPGA; Miller 1997) assuming Hardy–Weinberg equilibrium (HWE), as AFLP analysis yields dominant markers; allele frequencies of the recessive genotype were estimated via the Taylor expansion method (Lynch & Milligan 1994). We also used the program TFPGA to estimate unbiased heterozygosity based on microsatellite genotypes. Allelic richness was calculated for microsatellite data using the program FSTAT2.9.3.2 (Goudet 2001). The program Arlequin 3.1 (Excoffier *et al.* 2005) was used to evaluate deviations from Hardy-Weinberg equilibrium (Bonferroni-adjusted $\alpha = 0.01$) in microsatellite profiles via an analog of Fisher's exact test (Guo & Thompson 1992) and to assess linkage disequilibrium among microsatellite loci (Bonferroni-adjusted $\alpha = 0.005$). The program GenePop was used to evaluate instances of HW disequilibrium (Raymond & Rousset 1995). We evaluated the microsatellite profile for null alleles via the program Micro-Checker (van Oosterhout *et al*. 2004). We used the program GenAlEx (Peakall & Smouse 2006) to calculate the numbers and frequencies of private alleles by group, adjusted for group size, for the microsatellite data. The program TFPGA was used to calculate F_{ST} via the estimator θ_{ST} (Weir & Cockerham 1984) for AFLP and microsatellite data and to calculate *F*IS for microsatellite data among the subjectively identified morphs; 95% confidence intervals for θ_{ST} and *F*IS were estimated by bootstrapping 1000 times over loci. Using the AFLP data, a pairwise matrix of Jaccard distances between individuals was constructed without *a priori* population assignment and summarized via principal coordinate analysis (PCoA) using the program R.2.2.1 (R Development Core Team 2005) to illustrate genetic variation within and among morphs.

For the microsatellite data we used the program Arlequin to perform a genotype (population) assignment test that requires *a priori* knowledge of population identity. Mantel tests (Mantel 1967) were conducted to examine the congruence of subjective morphological grouping with the AFLP and microsatellite datasets and the congruence between the genetic marker systems via the program GenAlEx. Congruence between genetic and phenotypic variation was further examined using the program ALLELES IN SPACE (Miller 2005), inputting pairs of PC scores from the morphometric PCA for each individual sucker rather than geographic coordinates to generate morphological, rather than geographic, distance matrices for subsequent comparison with AFLP and microsatellite dissimilarity matrices via Mantel tests.

Finally, we used a Bayesian clustering program, STRUCTURE 2.2 (Pritchard *et al*. 2000), that requires no *a priori* assignment of individuals to morphs to search the AFLP and microsatellite data for population structure. We ran the model with correlated allele frequencies (Falush *et al*. 2003) and with (microsatellite profile) and without (AFLP profile) admixture (Pritchard *et al*. 2000). Five runs of the model were made at each presumed number (1-4) of genetic clusters (K). For each Markov chain Monte Carlo run, estimates of the probability of K were taken after 1 000 000 iterations that were preceded by a burn-in of 30 000 iterations. Variation in assignment probabilities across replicates was examined using the program CLUMPP 1.1.1 (Jakobsson & Rosenberg 2007). Contingency tests were conducted to examine the association of genetic and morphological groupings.

RESULTS

Morphological Analysis

Two-factor ANOVA (Type III sums of squares) revealed that while female suckers (TL = 548.0 ± 18.3 mm; mean ± 95%CI) were significantly longer than males (mean TL = 516.3 ± 12.5 mm) regardless of morph, $F_{1,69} = 7.92$ and $P = 0.0064$, there were no significant differences in mean TL among morphs, $F_{2,69} = 1.20$ and $P = 0.3060$, and no significant effect due to the interaction of sex and morph, $F_{2,69} = 1.43$ and $P = 0.2468$. Calculation of age from TL revealed that the sampled suckers had an average estimated age of approximately 24.8 years (y) with a range of 8 y to 54 y; the mean estimated age of males was 21.1 y (range: 8 y to 32 y) and that of females was 29.0 (range: 10 y to 54 y). The upper age values are likely underestimates given the extremely slow growth larger suckers exhibit, particularly males (Scoppettone, personal communication; Belk 1998).

Total length was significantly correlated, at Bonferroni-adjusted $\alpha = 0.0026$, with all morphological variables except EN, GP, JW, UP, and LP (see Table 2-2); *P* values for these five variables were 0.0032, 0.2960, 0.4655, 0.0893, and 0.4360, respectively, whereas all other variables' TL regressions had *P* values of less than 0.0001. After adjusting (via linear regression) the morphological variables significantly correlated with TL, ANOVA revealed that only the residual for LO differed significantly among morphs ($F_{2,72} = 26.09$, $P < 0.0001$). All of the variables not significantly correlated with TL except EN differed significantly among morphs; for GP, UP, and LP, $P < 0.0001$ whereas for JW, $P = 0.0003$. June sucker morphs had narrower lower lip lobes, wider lower lip gaps, steeper jaw angles, and fewer rows of upper and lower papillae than Utah sucker morphs and intermediates (Table 2-3).

The first four PCs generated by PCA explained 87.3% of the variation in the 19 morphological characters; overall body size was correlated with PC1, as were all variables except GP, JW, UP, and LP (the variables not correlated with TL) were highly correlated with PC1 (Table 2-4). Several mouth character variables (LO, GP, JW, UP, and LP) were highly correlated with PC2, and PP was less highly correlated with PC2. A mix of head and body characters were correlated with PC3 and PC4 (Table 2-4). Linear regression revealed that TL was highly significantly correlated (at Bonferroni adjusted $\alpha = 0.0167$) with PC1 ($r^2 = 0.717$, $P < 0.0001$) and uncorrelated with PC2 ($r^2 = 0.0157$, $P = 0.2837$) and PC3 ($r^2 = 0.0636$, $P = 0.0291$). Morphs were differentiated along the oral character correlated PC2 (Fig. 2-3), and the signs (+/−) of their correlations relative to one another are in accordance with June morphs having narrower lower lip lobes, wider lower lip gaps, steeper jaw angles, and fewer rows of upper and lower papillae than Utah morphs and intermediates. PC1, PC3, and PC4 did not distinguish among morphs, and for PC 3 and PC4, signs of the correlations did not follow the observed morphological differences (*e.g.*, JW, UP and LP are all positively correlated with PC4; compare their correlations with PC2). Perhaps other morphometric analyses more sensitive to shape (*e.g.*, geometric morphometrics, thin plate spline analysis, relative warp analysis) would have detected differences in head and body shape among the sucker groups, however, we chose our methods to emphasize ecologically important mouth characters.

Genetic Analysis

Population-specific measures of AFLP diversity were very similar among morphs (Table 2-5). All microsatellite loci were polymorphic, with US4, US6, Dlu45, Dlu409, and Dlu4283 exhibiting 18, 27, 19, 19, and 28 alleles, respectively. Using microsatellites, June sucker morphs exhibited slightly higher levels of unbiased heterozygosity and higher levels of total allelic richness over all loci than Utah sucker morphs or intermediates (Table 2-5). The number of private alleles, adjusted for group size, was 6.0 for June sucker morphs, 1.0 for intermediates, and 0.8 for Utah sucker morphs, although all private alleles had frequencies less than 0.103.

When all morphs were combined, only two (US4 and US6) of five microsatellite loci were in HWE (Table 2-6); all instances of HW disequilibrium were due to heterozygote deficiencies. We detected two locus pairs (US4 and Dlu45, $P = 0.00219$; US4 and Dlu4283, $P = 0.00019$) showing linkage disequilibrium at the Bonferroni-adjusted $\alpha = 0.005$ when all suckers were considered as a single group. These pairs involved two of the three loci not in HWE and US4, which exhibited near significance in the HWE test at the Bonferroni-adjusted $\alpha = 0.01$ (Table 2-6). When morphological groups were assessed separately, both HW and linkage disequilibria were reduced. Within the June sucker morph, all loci were in HWE, whereas three and four loci were in HWE in the Utah morph and intermediates, respectively (Table 2-6). No linkage disequilibrium was detected in June sucker or intermediate microsatellite profiles, whereas two locus pairs exhibited linkage disequilibrium within the Utah sucker profile: US4 and US6, $P = 0.00150$ and US4 and Dlu4283, $P < 0.00001$. Micro-Checker detected the likely presence of null alleles at three (US4, Dlu45, and Dlu4283) of the five microsatellite loci when morphological groups were combined (Table 2-6). Testing within the groups reduced the number of loci with the likely presence of null alleles: within the June sucker morph, null alleles were likely present at two loci (Dlu 45 and Dlu4283); null alleles were likely present at two loci (US4 and Dlu4283) in the Utah sucker morph; and within intermediates, null alleles were likely present at one locus (Dlu45).

As measured by θ_{ST}, both AFLP and microsatellite datasets displayed significant, but weak population structure among subjectively defined morphological groups (Table 2-7); structure was more pronounced with the AFLP data than microsatellite data. Mean F_{IS} over all loci was 0.1102 (95% confidence intervals: 0.0496 – 0.1710). PCO ordination of the AFLP data showed this slight structuring and reflected the morphological PCA ordinations (Fig. 2-4). Together, the first three eigenvectors (principal coordinates - PCos) explained 19.4% of the total variation in the AFLP data.

Over all morphs, the genotype assignment test, which utilizes *a priori* morphological classification, of the microsatellite data revealed a mis-assignment rate of 5.1%. June morphs and intermediates were mis-assigned at a rate of 3.4 %. A single June sucker was classified as an intermediate, and one intermediate was identified as a Utah sucker. Utah morphs were mis-assigned at a rate of 10.0%; two Utah suckers were assigned as intermediates. A three dimensional log-log likelihood plot of genotypes demonstrates the difficulty differentiating Utah morphs from intermediates (Fig. 2-5).

Although Pearson’s correlation coefficients between distance matrices generated from morphological grouping and genetic data were low, Mantel tests for group structure were significant in both AFLP and microsatellite datasets (Table 2-7). Distance matrices generated from the AFLP and microsatellite data were significantly correlated with one another (r = 0.103, P = 0.005). Mantel tests of congruence between phenotype and genotype, conducted by creating morphological rather than geographical distance matrices in the program

ALLELES IN SPACE, revealed that PC2 (correlated with mouth characters), which morphologically differentiated the groups, also differentiated the morphs genetically (Table 2-7, see Fig. 2-3). Morphological distance matrices derived from individual scores for PC2, which was not significantly correlated with TL and thus not correlated with age, and PC3, which was correlated with head and body characters and also not significantly correlated with TL, were most highly correlated with both microsatellite and AFLP profiles ($r = 0.1925$ and $r = 0.1212$, respectively). Distance matrices produced from individual scores for PC1, which was highly significantly correlated with TL and thus age, and PC2 resulted in lower correlations of morphology with the microsatellite and AFLP data ($r = 0.0828$ and $r = 0.0773$, respectively). Distance matrices generated from individual scores for PC1 and PC3 showed little correlation with the genetic distances (Table 2-7).

For both AFLP and microsatellite data, Bayesian clustering via the program STRUCTURE determined that the most likely number of sucker populations of in Utah Lake was two (Table 2-8, Fig. 2-6), and the program CLUMPP detected minimal variation in assignment probabilities across replicate runs for $K = 2$. Other values of K, the proposed number of genetically defined populations, resulted in lower likelihoods, and larger values of K resulted in individuals being equally likely to be assigned to one cluster or another. Although the genetically defined clusters were somewhat incongruent with morphological groupings and between genetic marker systems, contingency tests revealed highly significant association of genetic and morphological groupings for both microsatellite (*P* < 0.001) and AFLP (*P* < 0.001) datasets. For the microsatellite data, one cluster (*n* = 44) included 28 morphologically identified June sucker, 10 intermediates, and 6 Utah sucker, whereas the other cluster (*n* = 34) was comprised of 14 morphologically identified Utah sucker, 19 intermediates, and 1 June sucker. For the AFLP data, one cluster (*n* = 29) was composed of 19 morphologically identified June sucker, 3 intermediates, and 7 Utah sucker, while the other cluster (*n* = 49) included 13 morphologically identified Utah sucker, 26 intermediates, and 10 June sucker. The STRUCTURE cluster assignments were concordant for 45 individuals (58%) between the AFLP and microsatellite datasets.

DISCUSSION

Morphological and Genetic Congruence

June suckers and Utah suckers in Utah Lake are currently classified as members of distinct genera (*Chasmistes* and *Catostomus*, respectively) based on morphological features. This taxonomy, however, belies the complex evolutionary history of suckers in Utah Lake and perhaps elsewhere in western North America. The taxonomy of Utah Lake suckers and other sympatric *Chasmistes*/*Catostomus* pairs has long been problematic (Jordan 1891; Tanner 1936; Miller & Smith 1981; Cook 2001; Markle *et al*. 2005; Tranah & May 2006), and hybridization has typically been invoked to explain the presence of morphologically intermediate forms and genetic ambiguity (Miller & Smith 1981;

Evans 1997; Li 1999; Markle *et al*. 2005; Tranah & May 2006). This view has led managers to view current hybridization as a threat to the persistence of an ancient endangered lineage. However, we suggest that another possibility exists, at least in the Utah Lake suckers: this complex may have a long, reticulated history of genetically shallow but morphologically pronounced divergence and convergence, following fluctuating environmental conditions. Under this scenario, gene flow between morphologically dissimilar subpopulations may be an asset to the long term persistence of the complex (Arnold 1997; Dowling & Secor 1997), ironically including both ends of the morphological spectrum. This situation presents an interesting management dilemma: should management of the federally endangered June sucker include maintenance of the entire sucker complex in Utah Lake?

Mock *et al*. (2006) found that Utah Lake suckers as a group contained no highly divergent mitotypes and were not unusually diverse or divergent with respect to mitochondrial or nuclear diversity compared to other populations of Utah sucker within the southwestern clade. This southwestern clade of Utah suckers, however, including Utah Lake and its tributaries as well as the Sevier River basin was highly divergent (4.5% mitochondrial sequence divergence) from the northeastern clade of Utah suckers. Utah Lake suckers are nearly fixed for a unique mitotype relative to Utah suckers in the Sevier River basin where no lakesucker morph exists, but this mitotype is different by only 0.75% to 1.75% sequence divergence. Unless there has been a history of severe bottlenecks and asymmetric hybridization in Utah Lake, these findings suggest that Utah Lake suckers may not be the product of recent collapse of two ancient and highly divergent lineages, as is commonly supposed. The inferences of Mock *et al*. (2006), however, were limited with respect to Utah Lake suckers because Utah and June suckers were not morphologically defined and directly compared. In this study, we were able to objectively quantify specific morphological features and multivariate principal components separating June and Utah suckers in Utah Lake (as currently recognized and managed) for comparison with the genetic variation of Utah Lake suckers. Additionally, we subjectively classified individuals into morphological groups and assessed the genetic differentiation among these groups. The pronounced, ecologically relevant differences in morphology between June sucker and Utah sucker were reflected by a significant, but small degree of genetic structuring between these groups, as assessed using multiple molecular markers and statistical approaches. The lack of a stronger signal between neutral molecular markers and quantitative traits is not unexpected (Lynch *et al*. 1999; Pfrender *et al*. 2000) and suggests some degree of historical assortative mating and selection that may be acting to maintain trait variation, perhaps via variance in a low number of loci, despite gene flow between the morphs.

A history of shallow, reticulating divergence in the Utah Lake sucker complex would be consistent with the hydrologic history of Utah Lake. Lake Bonneville (existing from about 34 000 to 10 000 years before present - BP) was the last in a series of ancient, intermittent freshwater lakes that have formed in the endorheic Bonneville basin since volcanism diverted the flow of the Bear River into the basin from the Snake River watershed approximately 160 000 BP (Currey & Oviatt 1985; Link *et al*. 1999; Oviatt *et al*. 1992, 1999). Utah Lake has continued to fluctuate dramatically in depth and area, seasonally and annually, since its formation when Lake Bonneville receded approximately 10 000 BP. Lake bed core samples from Utah Lake provide evidence of drastically reduced lake levels and perhaps complete drying during three prolonged droughts occurring 6000, 4000, and 600 BP, with the drought of 6000 BP persisting for 700 years (Antevs 1948; Montillo 1968); many minor droughts (e.g., 1930s) have also occurred since its formation. Thus, during their evolutionary history, the suckers in Utah Lake have survived the decline of Lake Bonneville (surface area of 50 000 km^2 and hundreds of meters deep) to Utah Lake (392 km^2 surface area and maximum depth of 4.2 m) and the subsequent droughts that have at times severely desiccated Utah Lake. These dynamics may be similar to those in the three African Great Lakes, where lake level fluctuations have played a major role in gene flow among populations and cichlid diversification (Danley *et al.* 2000; Sturmbauer *et al.* 2001). It is possible that this reduction in depth has enhanced the persistence of intermediates by decreasing the distance between the limnetic and benthic habitats, enabling them to more efficiently exploit both niches and thus reduce selection against them. Gene flow among suckers (*Chasmistes* and *Catostomus*) in Utah Lake is not a recent phenomenon (Jordan 1878), and the paleontological record includes specimens that fall between the two morphological extremes with some sites yielding *Chasmistes* fossils exhibiting considerable variation (Miller & Smith 1981; Smith 1981). These transitional specimens are described as more primitive *Chasmistes*, but perhaps they represent intermediates in diverging or converging populations.

Divergence in response to ecological selection for benthic vs. limnetic forms, a common dichotomy in lake-dwelling fish species, would be reinforced by the evolution of distinct spawning times for different morphs, and opposed by ecological conditions that promote common spawning times. Although both morphs spawn in the same tributary locations, Utah morphs historically spawned earlier than June morphs (U.S. FWS 1999). It is possible that this temporal difference in spawning period evolved because of temporal differences in the types of prey available for consumption by larval and juvenile suckers in Utah Lake; perhaps zooplankton become available later than benthic macroinvertebrates. In the Klamath River basin, larval Klamath largescale sucker remain in spawning tributaries whereas larval shortnose sucker migrate downstream to nearshore and wetland habitats in Upper Klamath Lake (Markle & Clauson 2006; Burdick *et al*. 2008; Crandall *et al*. 2008). Anthropogenic flow alterations of the Provo River, which began shortly after Europeans settled Utah Valley, have likely interfered with natural spawning cues in an already extremely stochastic environment and increasingly compressed suitable spawning periods, potentially increasing gene flow among morphs. Our rough age estimates indicate the last successful natural spawn of wild suckers occurred around the early 1990's, and the smallest (youngest) suckers we sampled include all morphs. Recent telemetry studies failed to detect the historically described timing of June sucker spawning runs (Buelow 2006) or the temporal separation of spawning periods of June sucker and Utah sucker (Cole 2008).

The nature of the morphological variation in Utah Lake suckers is consistent with the concept of benthic (benthivorous) vs. limnetic (planktivorous) fitness peaks. The limnetic niche would be expected to favor the June sucker morph's terminal mouth position and reduction in lower lip size, whereas the benthic niche would be expected to favor the large, heavily papillated lips and ventral mouth orientation of the Utah sucker morph. In a pilot study, lip size and lower lip gap size were shown to be heritable (Mark Belk, unpublished data). Recently, Utah Lake suckers of intermediate morphology (as defined in the present study) have been shown to have stable isotopic signatures for ^{13}C and ^{15}N that are intermediate to those of June and Utah morphs (Cole 2008), further indicating that these morphologies have an ecological basis.

Three of the five microsatellite loci used in our study exhibited HW and linkage disequilibria. These disequilibria, resulting from heterozygote deficiencies, could be explained by population substructure, inbreeding, linkage to genes under selection, null alleles, Wahlund effects, or any combination of these factors. The strong likelihood of null alleles at three of the five loci warrants caution in interpreting results of the microsatellite analyses as the presence of null alleles can lead to over-estimation of population structure (Chapuis and Estoup 2007) and also because the program STRUCTURE operates by examining data for deviations from HWE and linkage equilibrium. That said, however, the results of the microsatellite analyses do mirror those of the AFLP analyses, and except for θ_{ST}, microsatellite analyses detected more structuring than AFLP analyses, as expected given the rapid rate of mutation in microsatellites. Additionally, when morphologically defined groups were assessed separately, HW and linkage disequilibria and the number of loci with the likely of the presence of null alleles were reduced. The higher degrees of HW and linkage disequilibrium in Utah morphs relative to June morphs (Table 2-6) are interesting findings that warrant further investigation. The presence of family grouping within the Utah morph is one potential explanation; this might lead to overestimation of population structure and could explain differences in diversity indices among morphs. Clearly, however, there is not a signal of deep genetic divergence between the June sucker and Utah sucker morphs in Utah Lake.

Our results continue to raise questions about the evolution of *Chasmistes* and *Catostomus*, especially in light of the several studies, some including a broader range of species in these genera, presenting evidence that *Chasmistes* and *Catostomus* may not be monophyletic groups (Harris & Mayden 2001; Mock *et al*. 2006; Tranah & May 2006; Sun *et al*. 2007). In the Klamath drainage in the northwestern US, researchers detail a pattern similar to the one described here for Utah Lake suckers: sympatric populations of morphologically defined shortnose sucker and Klamath largescale sucker (*Catostomus snyderi*) were found to exhibit minimal genetic structuring despite pronounced morphological variation (Tranah & May 2006). We recommend a broader study of *Catostomus/Chasmistes* species pairs in western US lakes to characterize their evolutionary history.

Conservation Implications

Identifying distinct population segments (DPSs; *e.g.*, evolutionarily significant units, stocks, management units) is a complex and much debated subject (Avise 1989; Moritz 1994, 2002; Bowen 1999; Dimmick *et al*. 1999; Paetkau 1999; Crandall *et al.* 2000; Fraser and Bernatchez 2001; Green 2005; Palsbøll *et al*. 2006), and much of the discourse involves the relative weight given to adaptive variation (*e.g.*, morphology, ecology, life history - Waples 1991; Bowen 1999; Crandall *et al.* 2000; Waples *et al.* 2001) and variation of neutral genetic markers (Avise 1989; Moritz 1994, 2002; Dimmick *et al.* 1999; Palsbøll *et al*. 2006) . Currently, among Pacific northwest salmonids, to be considered an ESU, a population (or group of populations) must be substantially reproductively isolated from other conspecific populations and represent a significant component in the species' evolutionary legacy, and in populations with multiple life histories (*e.g.*, resident and anadromous forms), management policies extend to all forms (National Marine Fisheries Service 1991). Both the National Marine Fisheries Service and the U.S. Fish and Wildlife Service accept this policy as consistent with ESA policy in designating DPSs. The legal defining criteria are:

discreteness of the population segment in relation to the remainder of the species to which it belongs; significance of the population segment to the species to which it belongs; and the population segment's conservation status in relation to the Act's standards for listing (U.S. FWS 1996).

Despite the suckers in Utah Lake exhibiting extreme morphological variability without excessive genetic variation, two populations of suckers can be differentiated genetically in Utah Lake, although incongruence between morphological and genetic identities exists. In the Klamath drainage, four species catostomids occur sympatrically: Klamath smallscale sucker (*Catostomus rimiculus*), Klamath largescale sucker, the endangered shortnose sucker, and the endangered Lost River sucker (*Deltistes luxatus*). The authors of a recent genetic investigation of Klamath basin suckers recommend management focusing on the preservation of the genetic diversity of all four species, and they emphasize the linked evolutionary legacies of shortnose sucker and Klamath largescale sucker (Tranah & May 2006). Regardless of whether the sucker population in Utah Lake is a product of incipient speciation, hybridization, perhaps in a syngameon-like evolutionary trajectory, or a reticulating process of divergence and convergence, maintenance of the unique morpho- and genotypes in the future may well depend on the maintenance of overall genetic diversity, with divergent forms emerging as environmental conditions fluctuate (Crandall *et al.* 2000; Allendorf *et al.* 2001, 2004, 2005; Moritz 2002; Tranah & May 2006).

The suckers in Utah Lake present a vexing dilemma for managers. The federally endangered June sucker is a unique morph found only in Utah Lake, and is ecologically distinct in terms of feeding ecology from the Utah sucker morph found there and elsewhere. Federal protection requires a recovery program to implement management actions promoting the persistence of the June sucker, and both recovery and program success are defined by the near term abundance of this morph. Thus, the current hatchery program focuses exclusively on breeding and stocking the June sucker morph, despite the potential loss of genetic diversity and the possibility of hatchery-induced morphological variation (Belk *et al*. 2008) and reduced genetic fitness (Lynch & O'Hely 2001). Our findings, along with those of Li (1999) and Mock *et al*. (2006), indicate that the June sucker morph, although genetically differentiable from the Utah sucker morph, is a portion of the larger, yet still genetically unique, interbreeding complex of suckers in Utah Lake. The June sucker morph is distinctive and worthy of special protection, but given the evolutionary and ecological history of this complex, long term persistence of this morph may well depend on the persistence of the entire genetic complex. Selecting one end of the morphological continuum for protection without monitoring the status of the remainder of the complex may ultimately lead to reduced overall genetic diversity, limiting future behavioral and ecological adaptation essential in such a dynamic lake system. Because we cannot know the future direction of change in physical habitat, food resources, or other potential bottlenecks or forcing functions, we also cannot know what the required genetic variation will be to preserve the unique morphs or the overall unique genome that currently resides in Utah Lake. Thus, it would seem prudent to prevent loss of genetic diversity in the complex as a whole, with particular attention to the unique June morph, to ensure the survival of the distinctiveness of the Utah Lake sucker fauna.

Management actions with these goals in mind would represent a novel and progressive approach to endangered species management. However, effective management of the sucker complex will require a clearer understanding of several aspects of Utah Lake sucker biology, including the genetic architecture and fitness consequences of trait variation and the natural and anthropogenic drivers of morphological diversification. These are not trivial tasks. The situation described here is not unique, especially for aquatic species with migratory spawning patterns. In the case of the endangered June sucker, we suggest that conservation of the broader gene pool would be a conservative alternative to focusing only on one end of the morphological spectrum. Such an approach would be consistent with our understanding of the evolutionary history of this complex, and until additional information becomes available, it could minimize loss of evolutionary potential in this complex.

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Table 2-1 Characteristics used to differentiate June Sucker and Utah sucker

CHARACTERISTIC	June sucker (*Chasmistes liorus*)	Utah sucker (*Catostomus ardens*)
Mouth	lobes of lower lip separated by a wide median notch	lower lip with deep medial cleft but lobes usually adjacent
	thin, protrusive upper lip may be concealed by overhanging snout	thick, wide, pendant upper lip
	narrow lips almost nonpapillose; lower lip with broken plicae	both lips papillose
	large, somewhat oblique, subterminal to terminal mouth;	small, inferior mouth
	large mandibles	small mandibles
Head	head flat or depressed (concave)	head convex and subconical or cuneate
	interorbital span broad and nearly flat	interorbital span convex
	eye positioned at mid-head	eye positioned at anterior margin at mid-head
	eye diameter/isthmus width ratio large	eye diameter/isthmus width ratio small
Color	profusely stippled/mottled olive to brown to blackish dorsum	darker dorsum crimson to dark green, or bronze to gray
	flat white venter	whitish venter
	spawning males have a red lateral stripe	spawning males have a rosy lateral band
Scales	lateral line scales 55-65	lateral line scales 60-72
Gills	nodules of gill rakers strongly branched or knobbed	nodules of gill rakers slightly to unbranched
Fins	caudal fin deeply forked; lower lobe is longer	caudal fin short and broad; lobes even
	dorsal fin anterior ray = 2x height of posterior ray	dorsal fin anterior ray = 1.5 x height of posterior ray
	dorsal fin's dorsal edge nearly straight	dorsal fin's dorsal edge curved
	small ventral fins	short, broad pectorals; squat pelvics; deep, long anals
Body Shape	predorsal length/standard length < 1/2	predorsal length/standard length > 1/2
	broad back and shoulders	narrow back and shoulders

(from Eddy and Underhill 1978; Miller and Smith 1981; Sigler and Sigler 1987; Evans 1997; Cook 2001)

Table 2-2 Morphometric and *meristic (italics)* variables measured or counted from digital photographs (abbreviations in parentheses). Total length (TL) was provided by the Utah Division of Wildlife Resources.

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snout to nostril distance (NS)
snout to eye distance (EY)
head length (HD)
eye to nostril distance (EN)
eye diameter (DI)
head depth at position of eye (HE)
head depth at posterior of occiput (HO)
snout to dorsal fin distance (DO)
snout to pectoral fin distance (PT)
snout to pelvic fin distance (PL)
snout to anal fin distance (AN)
dorsal fin to pelvic fin distance (DP)
pectoral fin to pelvic fin distance (PP)
mouth width (MO)
lower lip lobe length (LO)
lower lip gap width (GP)
jaw angle (JW)
number of rows of upper lip papillae (UP)
number of rows of lower lip papillae (LP)

Table 2-3 Means and standard deviations (*s*) for morphological variables exhibiting significant differences (Bonferroni-adjusted α = 0.0026) among morphs (* because LO was significantly correlated with length, TL residuals were compared among morphs; here, lobe lengths are reported)

Morphological variable	June morph (n = 27)		Intermediates (n = 28)		Utah morph (n = 20)	
	Mean	± *s*	Mean	± *s*	Mean	± *s*
LO*	8.09	± 1.39 mm	10.69	± 1.41 mm	11.42	± 2.78 mm
GP	3.70	± 1.36 mm	1.94	± 0.78 mm	1.23	± 0.38 mm
JW	52.33	± 5.69 °	48.29	± 4.65 °	46.50	± 4.07 °
UP	0.52	± 0.80 mm	2.64	± 1.03 mm	3.75	± 0.91 mm
LP	1.19	± 1.47 mm	4.21	± 1.34 mm	6.00	± 0.92 mm

Table 2-4 Variation (%) explained by and important loadings of variables on the first four principal components (PCs) from PCA of morphological characters of suckers (*n* = 75) from Utah Lake.
(* |loading| < 0.15)

	PC1	PC2	PC3	PC4
Variation explained (%)	58.6	18.1	7.1	3.5
Variable	Loadings			
NS	0.276901	*	-0.18263	*
EY	0.264101	*	-0.29546	*
HD	0.278634	*	*	*
EN	0.178446	*	-0.54724	*
DI	0.255863	*	*	*
HE	0.281681	*	*	0.186177
HO	0.276971	*	*	0.185244
DO	0.285199	*	*	*
PT	0.278773	*	*	*
PL	0.288770	*	0.158282	*
AN	0.270537	*	0.215875	*
DP	0.239894	*	0.202830	*
PP	0.213952	0.156065	0.440357	-0.17428
MO	0.252618	*	*	-0.27474
LO	0.186659	0.333250	*	-0.20651
GP	*	-0.44077	0.202415	-0.20549
JW	*	-0.32966	0.394030	0.691899
UP	*	0.485329	*	0.272604
LP	*	0.490636	*	0.352835

Table 2-5 Diversity indices for AFLP and microsatellite profiles of Utah Lake suckers: unbiased heterozygosity (H), percent polymorphic loci - 95% criterion (%P), and allelic richness (AR – sums for all five loci). * Total sample sizes reported for AFLP diversity indices; mean sample sizes reported for microsatellite heterozygosity (due to missing data for one locus); and minimum sample size upon which richness is based reported for allelic richness.

Genetic	Diversity	June morphs		Intermediates		Utah morphs	
marker	index	*n**	Index	*n**	Index	*n**	Index
AFLP	H	29	0.324	29	0.329	20	0.313
	%P	29	86.73	29	83.19	20	84.07
Microsatellite	H	29	0.920	28.8	0.885	20	0.902
	AR	20	79.86	20	62.81	20	61.00

Table 2-6 *P* values from tests for HWE on microsatellite profile for Utah Lake suckers (*n* = 78); one individual was missing data regarding Dlu4283 (***bold italics***: significant at Bonferroni-adjusted α = 0.01) and estimated null allele frequencies over all fish (**bold**: null allele{s} likely present)

	June morph		Intermediate		Utah morph		All fish combined		Null Allele
Locus	*n*	*P* value	*n*	*P* value	*n*	*P* value	*n*	*P* value	frequency
US4	29	0.17538	29	0.16381	20	***0.00247***	76	0.01212	**0.0600**
US6	29	0.38153	29	0.40303	20	0.34568	76	0.24582	0.0296
Dlu45	29	0.01181	29	***0.00545***	20	0.27115	76	***0.00092***	**0.0968**
Dlu409	29	0.64358	29	0.37296	20	0.04284	76	***0.00996***	0.0098
Dlu4283	29	0.01323	28	0.01238	20	***0.00023***	75	***0.00021***	**0.0967**

Table 2-7 F-statistic estimator, θ_{ST} (with 95% confidence intervals), for Utah Lake suckers (J, I, and U morphs) determined from AFLP and microsatellite profiles; and microsatellite and AFLP Mantel test correlation coefficients and probabilities for group structure and for congruence of morphological and genetic profiles. Group structure analysis performed via the program GenAlEx. Mantel tests for concordance of phenotype and genotype were conducted using the program Alleles In Space; pairwise scores of PCs 1 - 3 from the PCA of morphological variables were entered for each sucker instead of geographic coordinates to generate morphological (phenotypic) dissimilarity matrices for comparison with microsatellite and AFLP dissimilarity matrices. (Bold: significant at α = 0.05; ***Bold italic***: significant at Bonferroni-adjusted α = 0.0167)

		Microsatellite		AFLP	
θ_{ST} (95% CI) *n* = 78		**0.0199 (0.0123 - 0.0279)**		**0.0448 (0.0315 -0.0595)**	
Mantel tests		Correlation coefficient *r*	Probability *P*	Correlation coefficient *r*	Probability *P*
Group structure *n* = 78	(3 morphs)	**0.1127**	**0.0001**	**0.0998**	**0.0001**
Congruence of	PCs				
phenotype and	1 and 2	***0.0828***	***0.0060***	0.0773	0.0370
genotype	1 and 3	0.0128	0.3237	0.0085	0.4376
n = 75	2 and 3	***0.1925***	***0.0010***	***0.1212***	***0.0020***

Table 2-8 Means and ranges of likelihoods [P(D)] from five runs of STRUCTURE fitting different assumed numbers of subpopulations (*K*) for microsatellite and AFLP profiles of Utah Lake suckers (*n* = 78) (**bold**: highest posterior probability)

	Microsatellite		AFLP	
K	Mean lnP(D)	Range ln P(D)	Mean lnP(D)	Range ln P(D)
1	–2149	–2150 to –2149	–4331	–4332 to –4331
2	**–2127**	**–2129 to –2126**	**–4305**	**–4309 to –4303**
3	–2434	–2496 to –2395	–4415	–4450 to –4367
4	–2366	–2486 to –2246	–4507	–4550 to –4439

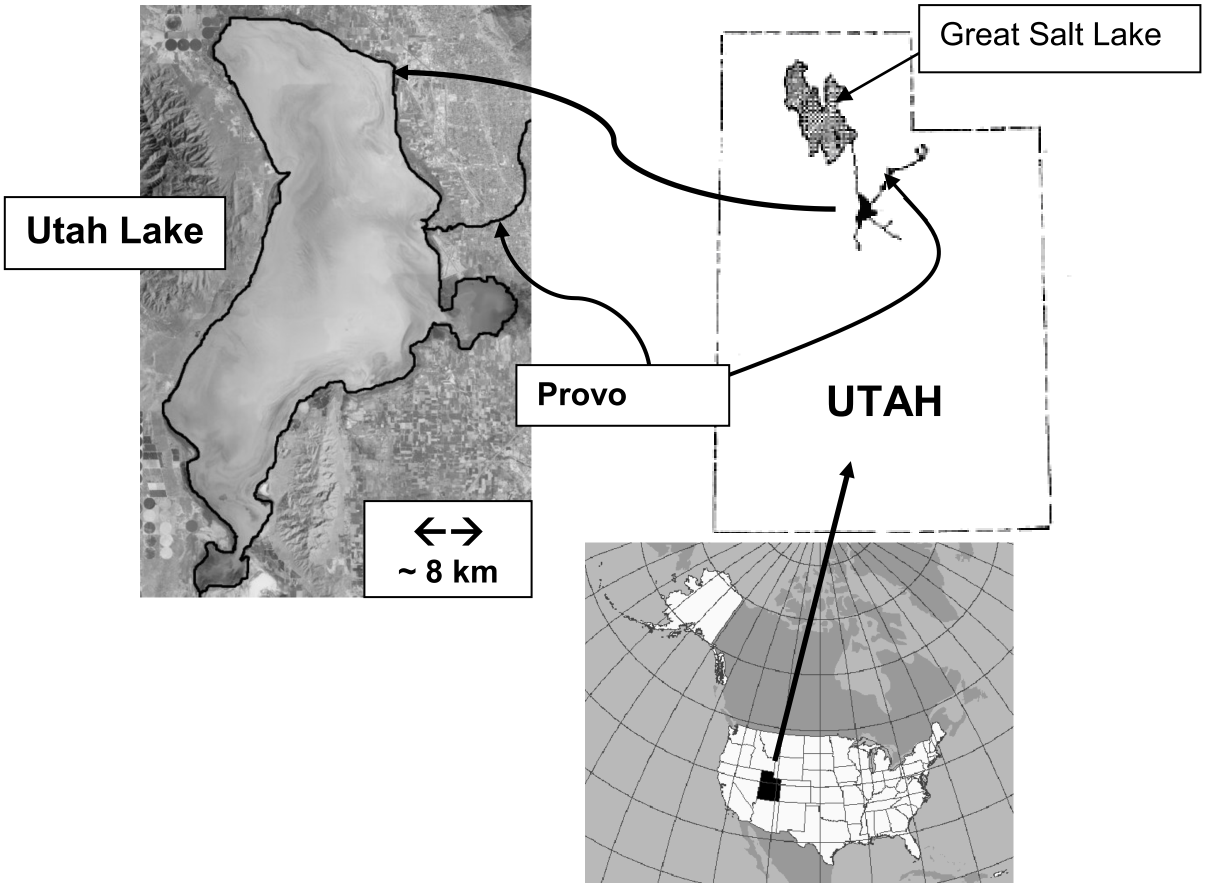

Fig. 2-1 Geographical setting of Utah Lake, Utah, USA, home of the endangered June sucker.

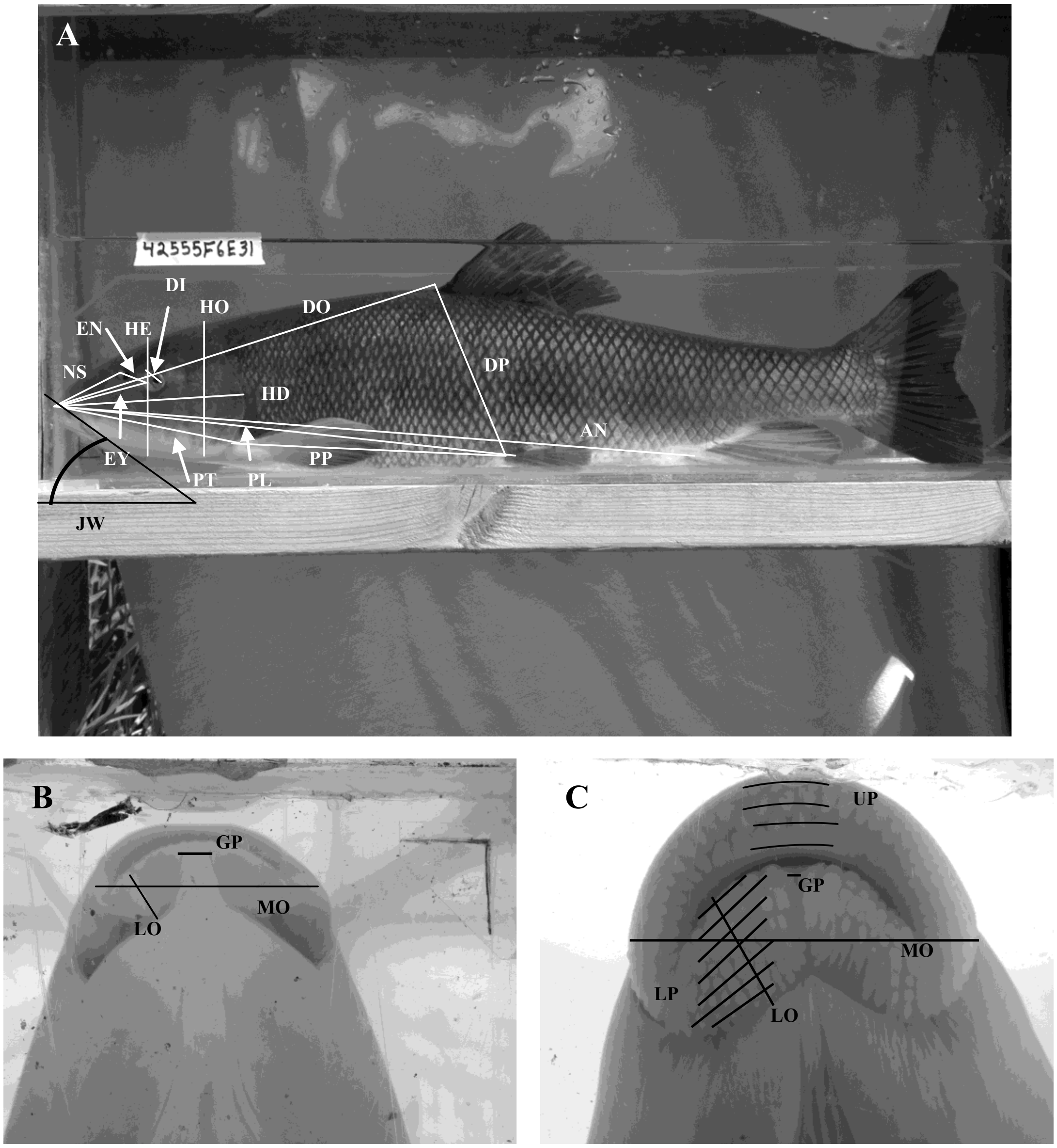

Fig. 2-2 Variables used in morphological analysis (See Table 2 for descriptions): A) NS, EY, HD, EN, DI, HE, HO, DO, PC, PL, AN, DP, PP, and JW overlaid on Utah sucker profile; B) MO, LO, and GP overlaid on June sucker ventral image; and C) MO, LO, GP, UP, and LP overlaid on Utah sucker ventral image. Total length (not shown) provided by Utah Division of Wildlife Resources.

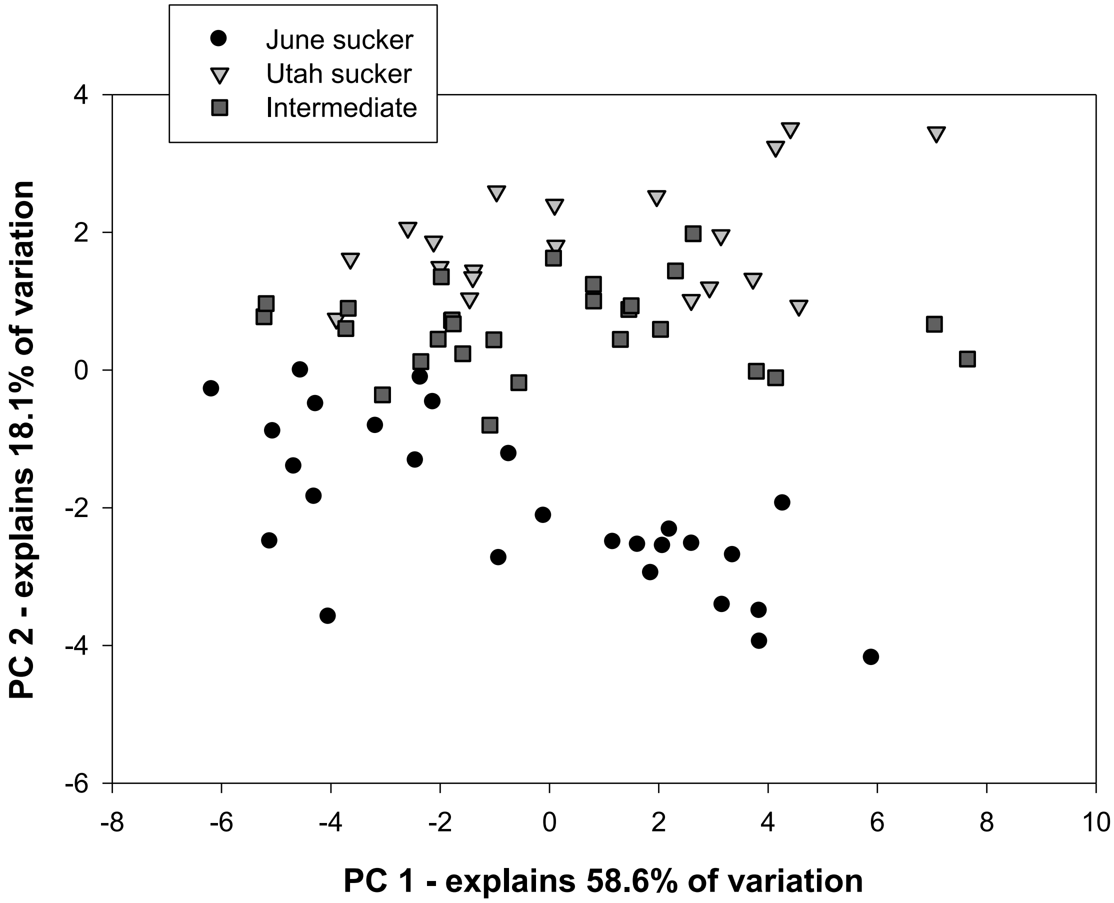

Fig. 2-3 PCA ordination of individuals' scores for the first two PCs for sucker (*n* = 75) identified subjectively using a *Ch. liorus mictus* model for June sucker and a more lenient definition of Utah sucker than Sigler and Sigler (1987) that allowed classification of Utah morphs having slightly reduced lip size and papillation (*e.g.*, a *C. ardens "mictus"* model for Utah sucker). PC1 is correlated with overall size (size increases as PC1 increases) and explains 58.6% of the morphological variation, and PC2 is correlated with mouth character variables and explains 18.1% of the variation. (Circles - June sucker; triangles - Utah sucker; and squares - intermediates)

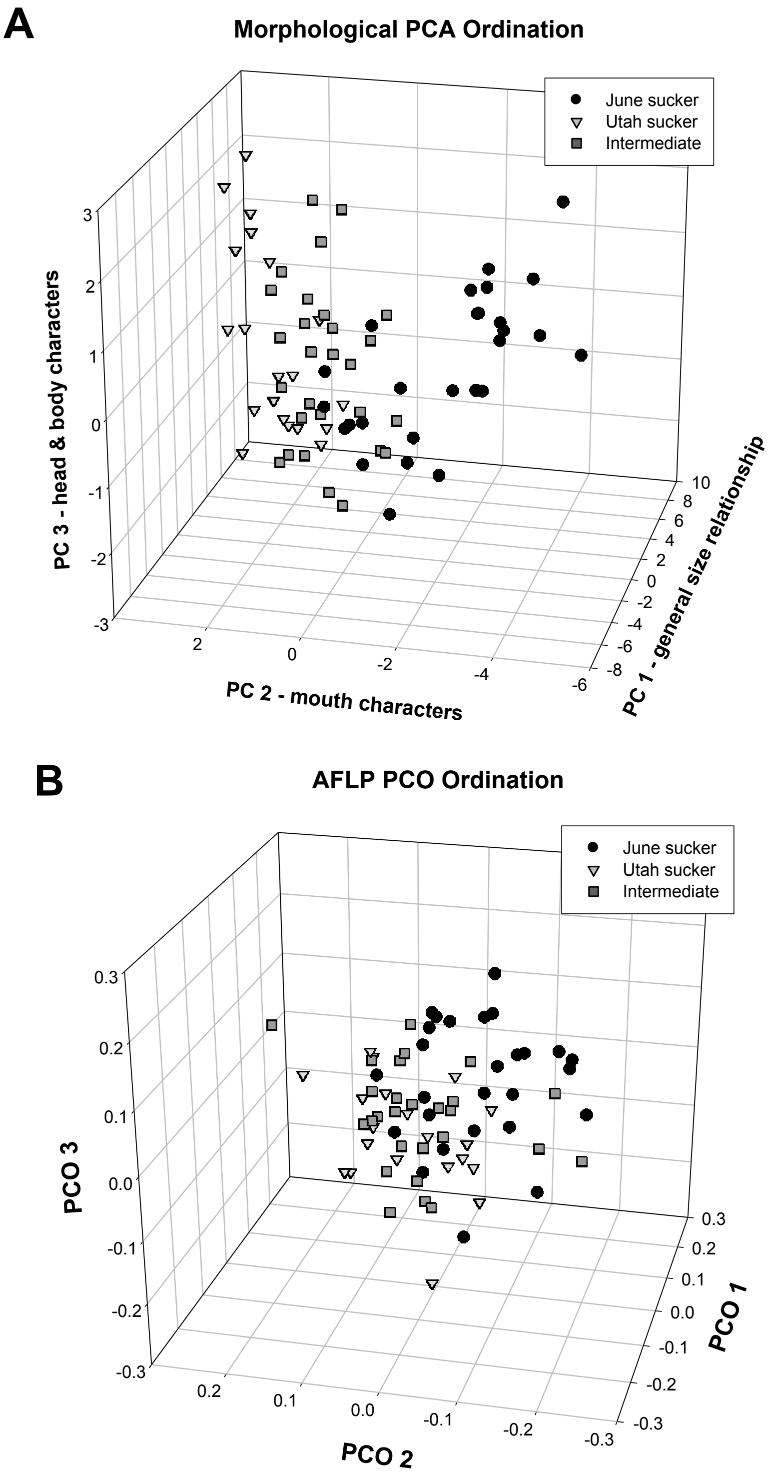

Fig. 2-4 Three dimensional ordinations of (A) the first three PCs of the morphological PCA and (B) the first three principal coordinates of the genetic (AFLP) PCoA of suckers (*n* = 75) from Utah Lake (circles - June sucker; squares - intermediates; and triangles - Utah sucker).

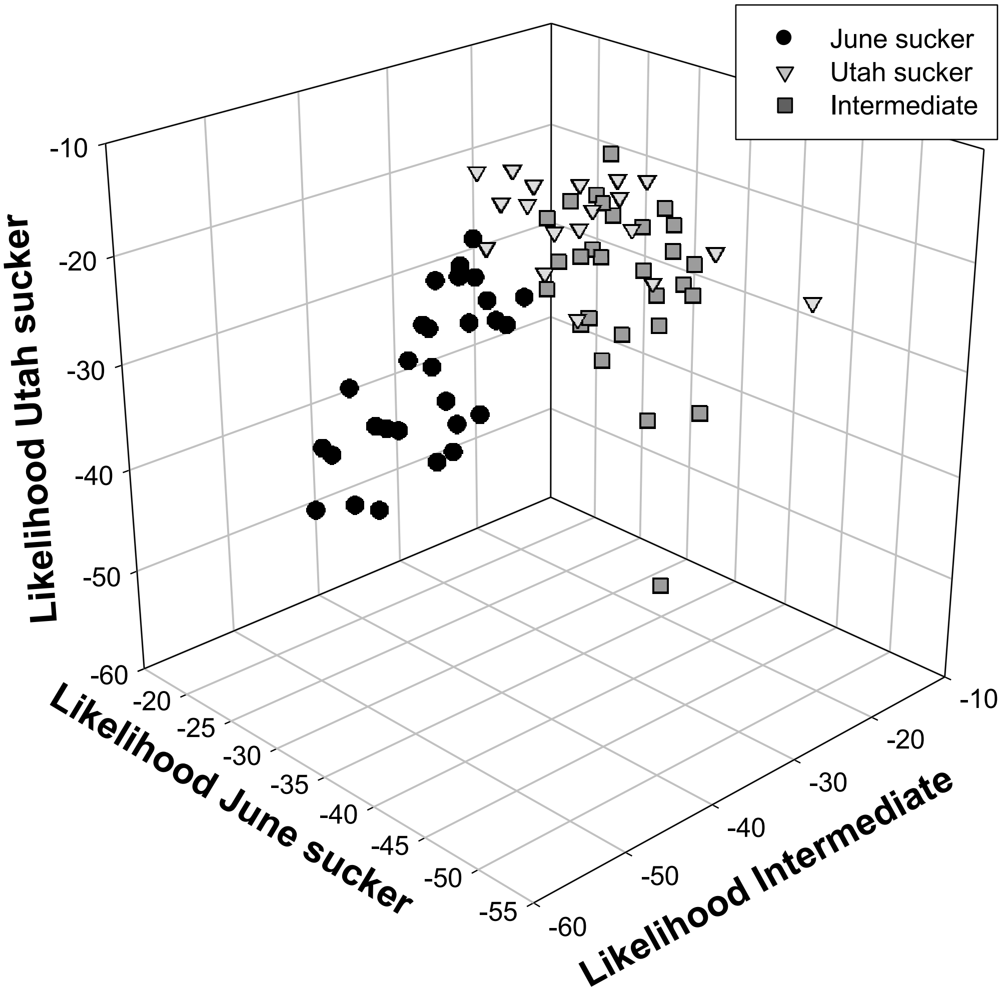

Fig. 2-5. Log-log likelihood plot of genotypes from population assignment test (that requires *a priori* identification) of suckers (*n* = 78) from Utah Lake (circles - June sucker; squares - intermediates; and triangles - Utah sucker).

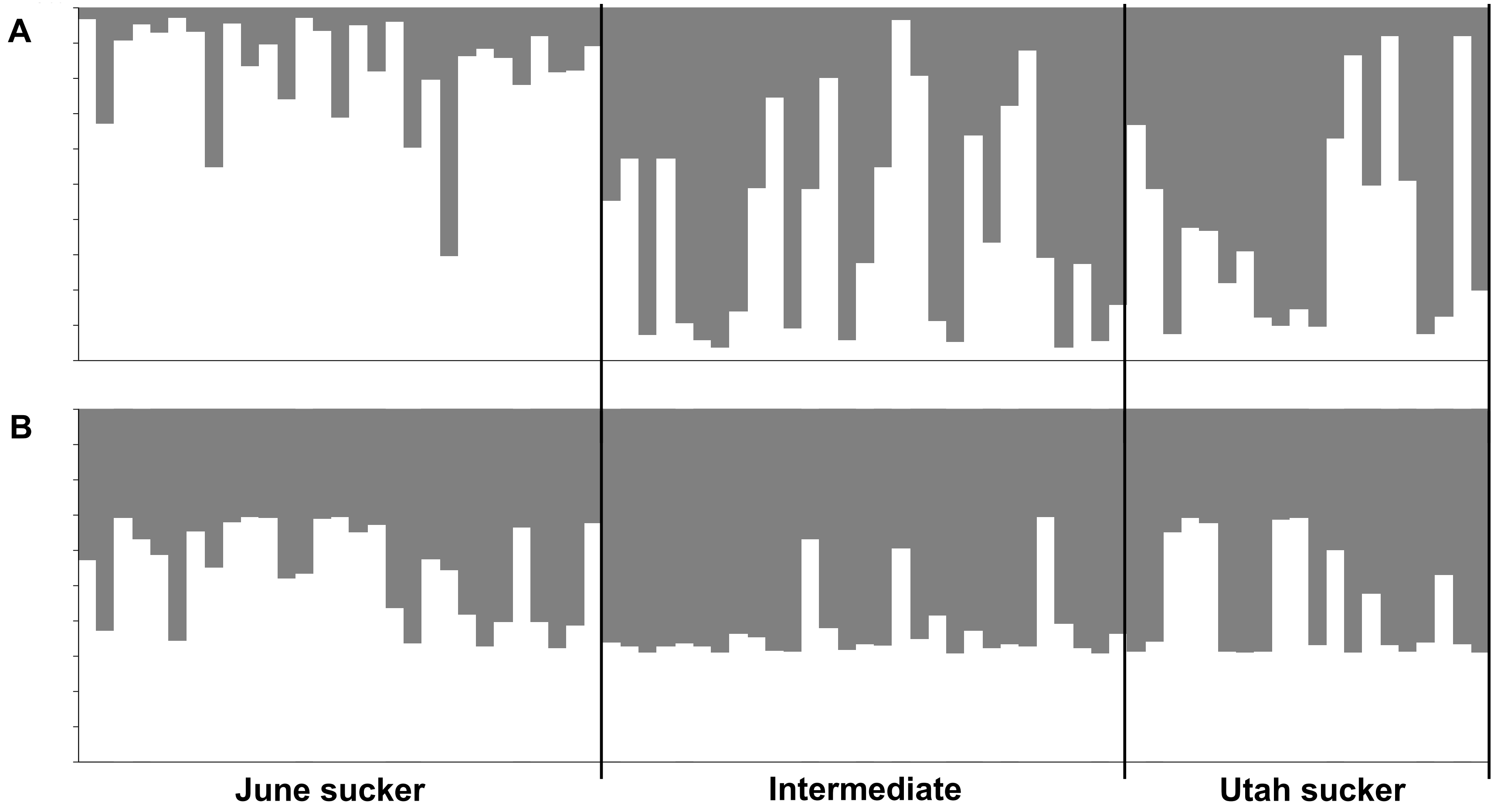

Fig. 2-6. STRUCTURE output displaying probable ancestry (mean of posterior probabilities of five Bayesian clustering runs without *a priori* classification) of individual Utah Lake suckers (*n* = 78) by morphological grouping determined from: A) Microsatellite profiles; B) AFLP profiles. (each column represents an individual; white - probability of Cluster 1 ancestry, grey - probability of Cluster 2 ancestry).

CHAPTER 3

DISTRIBUTION AND MOVEMENT, SPAWNING RUN BEHAVIOR, AND STABLE ISOTOPIC SIGNATURES (δ^{13} C AND δ^{15} N) IN THE UTAH LAKE SUCKER COMPLEX

ABSTRACT

Ecomorphological specialization within the Catostomidae in several large western North American lakes has produced populations including both typical benthic suckers (*Catostomus*) and lakesuckers (*Chasmistes*), mid-water planktivores. The June sucker, a lakesucker endemic to Utah Lake, is sympatric over its entire range with the more widely distributed Utah sucker, *Catostomus ardens*. A continuum of morphologies exists in Utah Lake from benthic to limnetic extreme with a large proportion of suckers intermediate in morphology. There is no molecular evidence for a deep divergence between June sucker and Utah sucker, and only very slight population structuring accompanies the substantial morphological variation.

The morphological differences in Utah Lake suckers are presumably the result of ecological selection, although little is known of the ecology of adult suckers. Here, the distribution and movement, spawning behavior, and diet of Utah Lake suckers in Utah Lake and their growth at different conspecific densities in a laboratory experiment are reported. Combination acoustic and radio transmitter telemetry revealed essentially no differences in the movement and distribution behavior of June sucker and Utah sucker. No differences were detected in the timing of spawning runs between the species, although spring runoff differed by an order of magnitude between study years (drought year to wet year), perhaps influencing behavior. Random forests analysis revealed that water temperature played a major role in sucker distribution and movement around the lake. Suckers of both species were detected more often along the eastern versus western shoreline and in limnetic versus littoral zones. Stable isotopes analysis revealed that Utah sucker were significantly enriched in ^{13}C relative to June sucker as would be predicted given their presumed diets based on morphology. June sucker, Utah sucker, and intermediates were all tertiary consumers (trophic level = ~ 4.0), and fish eggs or larvae were likely an important component in their diets. Intermediate morphs were intermediate to the extremes for both δ^{13}C and δ^{15}N. Neither species nor density was a significant predictor of growth rate of June sucker and Utah sucker reared at different conspecific densities, although the effect of density approached statistical significance, perhaps indicative of a small Allee effect.

INTRODUCTION

The idea of ecological speciation dates to the time of the development of the biological species concept (Dobzhansky 1937; Mayr 1942). Schluter (1996) defined ecological speciation as the evolution of reproductive isolation, directly or indirectly, via divergent selection on traits between populations (or subpopulations) in contrasting environments or exploiting different resources; i.e., the process by which barriers to gene flow between populations evolve because of divergent ecological adaptation. Ecological competition drives divergence, and a species is defined as “a number of related populations the members of which compete more with their own kind than with members of other species" (Colinvaux 1986). The greater the similarity between two organisms, the greater the probability their needs overlap and they will compete, hence the greater the probability they are the same species.

Ecological speciation has been described in a variety of fauna, with natural selection typically shaping mouth and head characters related to food acquisition / ingestion (Grant and Grant 1996; Rice et al. 2009; Monteiro and Nogueira 2011) or limb and body characters associated with foraging strategies or inhabiting a particular environment (Losos 1990; Dhuyvetter et al. 2007; De Busschere et al. 2010). Among fishes, ecological speciation has played a key role in major adaptive radiations in a variety of taxa (Meyer 1993; Schluter 1996; Hunt et al. 1997; Turgeon and Bernatchez 2003; Barluenga et al. 2006; Feulner et al. 2007; Adams et al. 2008; Bernatchez et al. 2010).

In freshwater lakes, the evolution of limnetic and benthic morphs has been a recurring event in many fish lineages with populations exhibiting differences in phenotypic plasticity among lakes and within lakes between morphs (Skúlason et al. 1999) and varying levels of gene flow between morphs within lakes (Taylor and McPhail 1999; Turgeon et al. 1999, Skúlason et al. 1999). Common garden experiments have demonstrated that the relative contributions of genetic variation and epigenetic variation (i.e., plasticity) to phenotype vary among species and within species among populations: threespine stickleback, *Gasterosteus* sp. (Day et al. 1994; McCairns and Bernatchez 2012); pumpkinseed sunfish, *Lepomis gibbosus* (Robinson and Wilson 1996; Mittelbach et al. 1999); Arctic charr, *Salvelinus alpinus*, (Skúlason et al. 1999, Alexander and Adams 2004); brook charr, *Salvelinus fontinalis*, (Proulx and Magnan 2004); cichlids, Cichlidae (Stauffer and van Snik Gray 2004); and Eurasian perch, *Perca fluviatilis* (Svanbäck and Eklöv 2006). Recent models of speciation suggest that inherited differences in phenotype are not crucial precursors of evolutionary divergence within a single population, and they reveal how environmentally induced phenotypic plasticity at the level of the individual can result in divergence prior to any genetic differentiation.

In the first stage of a four-stage species divergence model (Skúlason et al. 1999) based on phenotypic plasticity, individuals within a single gene pool express alternative adaptive traits. Initially, epigenetic evolutionary mechanisms are most likely to act on variation in behavior (West-Eberhard 1989), and foraging-related behavioral phenotypes are likely candidates for subsequent divergence because of the possibility of alternative strategies for foraging success and its potential effects on fitness (Wimberger 1994; Smith & Skúlason 1996; Skúlason et al.1999). In the second stage, phenotypic plasticity in anatomical traits may manifest as morphological modifications driven by behavioral specialization, and these environmentally regulated, discrete, stable morphological traits precede but then promote genetic divergence (Wimberger

1994; Skúlason et al. 1993, 1999). Once this phase of evolution has occurred, differential habitat use or sexual selection among different phenotypic variants (morphs) may then result in reproductive isolation in the third stage of divergence (Seehausen et al. 1997; Wood and Foote 1996). In stage four, different morphs are exposed to varying selective pressures, and genetic fixing of morphological characters can occur (West-Eberhard 1989; McPhail 1994; Skúlason et al. 1999).

Ecologically driven trophic polymorphism within the Catostomidae (sucker family) has produced populations of typical benthivorous suckers (*Catostomus* spp. – *Ca.*) and lakesuckers (*Chasmistes* spp. – *Ch.*), mid-water planktivores, in several large western North American lakes. *Ch.*spp. have many closely spaced branched or dendritic gill rakers, terminal, oblique mouths, and thin, sparsely papillated lips with wide gaps between the lower lobes (Miller and Smith 1981; Sigler and Sigler 1987). *Ca.*spp. have fewer and more widely spaced non-branching, filamentous gill rakers, subterminal to ventral mouths, and large, heavily papillated lips with narrow gaps between the lower lobes (Sigler and Sigler 1987). Four recent species of *Chasmistes* are recognized: *Ch. brevirostris*, the shortnose sucker; *Ch. cujus*, the cui-ui sucker; the presumably extinct Snake River sucker, *Ch. muriei* (see Chapter 4); and *Ch. liorus*, the June sucker. All extant *Ch.* spp. are federally listed as endangered (USFWS 1967, 1986, 1988), and their declines have been attributed to anthropogenic changes in aquatic habitat (flow alterations, degraded water quality, channelization, and loss of littoral zones), historic overexploitation, competition with and predation by nonnative fish species, and hybridization with the sympatric *Ca.* spp. (Carter 1969; Fuhriman et al. 1981; Scoppettone and Vinyard 1991).

The June sucker, a lakesucker endemic to Utah Lake, Utah, is sympatric over its entire range with the more widely distributed Utah sucker, *Ca. ardens*. The Utah sucker is native to a wide variety of habitats ranging from relatively warm streams and shallow lakes to large, deep, cold lakes within the ancient Lake Bonneville basin and the Snake River drainage above Shoshone Falls (Sigler and Sigler 1987, although see Mock et al. 2006). A continuum of morphologies exists in Utah Lake from benthivore to planktivore (Figure 3-1), and suckers intermediate in morphology outnumber those at either end of the morphological spectrum. Putative hybridization between June sucker and Utah sucker may have obscured their evolutionary and taxonomic history (Jordan 1878, 1891; Miller and Smith 1981; Smith 1983; Cook 2001). Miller and Smith (1981) established the new subspecies *Ch. liorus mictus* to replace *Ch. liorus liorus*, which they presumed became extinct (via introgression from *Catostomus ardens*) following a severe drought in the 1930s. However, decades prior to the drought of the 1930s, Jordan (1891) observed and described Utah Lake suckers of intermediate morphology. Moreover, a genetic investigation by Li (1999) failed to find a genetic distinction between preserved pre-1930 specimens of *Ch. liorus liorus* and current specimens of *Ch. liorus mictus*.

In light of recent phylogenetic studies of lakesuckers and other western North American catostomids it appears the already convoluted history of the taxonomy and nomenclature of the June sucker will soon add another chapter. Chen and Mayden (2012) synonymized *Chasmistes* (and *Deltistes* and *Xyrauchen*) into *Catostomus*, and Smith et al. (2013) classified *Pantosteus* into *Catostomus* and recommended that all western North American catostomids be included in the single genus, *Catostomus*.

In 1986, the June sucker was declared endangered because of its localized distribution, the population’s failure to recruit new adult fish, and continued threats to its survival; the lower 7.8 km of the main channel of the Provo River, the only known spawning location at the time of wild June sucker, was designated as critical habitat (USFWS 1986). By the late 1990s, the estimate for the wild adult spawning population was less than 300 individuals (Keleher et al. 1998). The June sucker population decline has resulted from changes in aquatic habitat (flow alteration, degraded water quality), competition with and predation by nonnative fish species, commercial fishing, and the killing of adults during spawning runs (Carter 1969; Fuhriman et al.1981; USFWS 1986). The Utah sucker population in Utah Lake has suffered similar declines (K. Wilson, UDWR, personal communication). In recent years, nearly all June sucker captured in Utah Lake and its tributaries have been stocked fish. The size distribution of Utah sucker and wild June sucker collected for a genetic and morphological analysis (Cole et al. 2008) and monitoring data (K. Wilson, UDWR, personal communication) suggests the last successful natural recruitment occurred in the early 1990s for both morphs. Failure to recruit, likely the result of predation by nonnative fishes coupled with altered habitats and discharge regimes (USFWS 1999), has resulted in a sucker population in Utah Lake dominated by adults.

June sucker, like other lakesuckers, are slow growing and long lived; specimens have been aged to over 40 years (Scoppettone 1988; Belk 1998). They are late maturing (age five to ten years) with males maturing earlier than females (Belk 1998) and highly fecund with females producing tens to hundreds of thousands of eggs depending on age and size (Scoppettone and Vinyard 1991). The combination of longevity and high fecundity are adaptations for their highly stochastic desert lake environment where prolonged droughts or extensive flooding may preclude annual spawning. Lakesuckers spawn predominantly in tributaries although some within lake spawning in areas near groundwater input has been documented in cui-ui sucker (Scoppettone et al. 2000) and shortnose sucker (National Research Council 2004). Billman (2005) described successful spawning by a refuge population of June sucker in a lake environment (Red Butte Reservoir) at rocky shoreline sites. It is unknown if June sucker use spawning sites within Utah Lake, which contains a number of springs and several locations with rocky shores. Historically, June sucker are described as spawning in all tributaries of Utah Lake (USFWS 1999) with peak activity occurring in June (hence the common name) following pre-spawning staging at tributary mouths in April and May (Shirley 1983; Radant and Hickman 1984; Modde and Muirhead 1994). Utah sucker in Utah Lake are described as historically spawning in tributaries in March and April (Sigler and Miller 1963; USFWS 1999); whether any historical spatial isolation (*e.g*., use of different tributaries or different reaches within a tributary) of June sucker and Utah sucker occurred during spawning is unknown. Recently, the available spawning habitat for both morphs of Utah Lake suckers has been anthropogenically reduced from many kilometers of several tributaries to less than eight kilometers of a single, highly regulated, structurally altered tributary that exhibits unnatural spring runoff discharge and temperature characteristics.

Outside of the spawning season, very little is known of the distribution and movement of adult suckers in Utah Lake. Captures of June sucker in offshore mid-water gill nets were common in the 1950s, however, most captures since the 1960s have occurred in Provo Bay and Utah Lake shoreline areas (USFWS 1999). A post-spawning aggregation of June sucker in the mouth of Provo Bay in July and August was described by Radant and Shirley (1987); the sucker were presumably exploiting the high zooplankton productivity in the bay (USFWS 1999). In the 1990s, June sucker capture rates in Utah Lake during monitoring and sampling efforts were so low (in some years no sucker were captured) that meaningful interpretation of distribution or habitat use was impossible (USFWS 1999). The first of two earlier telemetric studies of June sucker had limited success and ended prematurely, likely because of reduced signal strength (due to Utah Lake’s shallowness and high specific conductance and turbidity) and a general lack of information regarding June sucker behavior; this led to an underestimation of the effort that would be required to actively search a very large lake. A more recent telemetric study of June sucker was conducted, but made no comparisons with Utah sucker (Buelow 2006).

June sucker and Utah sucker are differentiated using externally observable oral characters including mouth position, lip size and degree of papillation, lower lip gap width, and jaw angle that are presumably shaped by ecological selection; suckers with intermediate morphologies confound identification. Like many other catostomids, Utah Lake suckers are opportunistic feeders, but morphology suggests that June sucker are primarily zooplanktivores whereas Utah sucker are primarily benthivores. A gut content analysis of June sucker in the Red Butte Reservoir refuge population suggested adults fed almost exclusively on cladocerans and copepods in this oligotrophic habitat whereas a stable isotope analysis that included some of the same fish suggested a more varied diet (Billman 2005). Furthermore, Billman (2008) observed schools of refugial June sucker presumably feeding on zooplankton in Red Butte Reservoir, UT; such grouping behavior may reduce predation risk (or the stress associated with it) and likely enhances fitness. Gonzalez (2004) has described a component Alee effect (Allee et al. 1949) in June sucker, with growth and survival of larvae increasing with density. At low population densities, an increase in individual fitness can result from increasing density via cooperative defense, cooperative feeding, environmental conditioning, and overcoming mate limitation (Kramer et al. 2009).

The purpose of this study was to examine the ecology of the Utah Lake sucker complex, and specifically, to determine if there are any ecological characteristics that distinguish or characterize the morphologies. This group exhibits a continuum of morphological variation between benthivorous Utah sucker and planktivorous June sucker accompanied by slight genetic population structuring that is not concordant with the morphological variation (Cole et al. 2008). The first objective of this investigation was to compare the spatial distribution and movement patterns, including spawning migrations and seasonal movements, of adult June sucker and Utah sucker in Utah Lake using radio and acoustic telemetry. A second objective was to examine diet for concordance with morphology via comparison of stable isotopic signatures for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of adult June sucker, Utah sucker, and suckers of intermediate morphology. The third objective was to explore if the component Allee effect reported in larval June sucker also occurred in juvenile June sucker, with comparison to juvenile Utah sucker, through a laboratory experiment assessing growth rate, as a measure of fitness, at different rearing densities.

MATERIALS AND METHODS

Study Site

Geological and climatic changes during the Cenozoic Era that shaped the North American landscape profoundly influenced the evolution of many taxa (Riddle 1995; Klicka and Zink 1997; Soltis et al. 1997; Hershler and Sada 2002;

Liu and Hershler 2007; Kohn and Fremd 2008). In western North American fishes, long periods of population isolation have been interrupted by sporadic events such as stream captures or floods, at times coincident with major climatic episodes, enabling dispersion among hydrological basins (Smith 1981; Minckley et al. 1986; Smith et al. 2002; Spencer et al. 2008). Phylogenetic evidence indicates that since the Miocene epoch, the Bonneville Basin has shared connections at various times with the upper Snake River drainage, the Lower Colorado River via the Virgin River drainage, the Upper Colorado River, and the Lahontan Basin (Johnson 2002; Smith et al. 2002; Johnson et al. 2004; Mock et al. 2006; Spencer et al. 2008; Houston et al. 2010).

During the Pleistocene epoch in western basins, large pluvial lakes formed and receded with glacial advances and retreats, respectively, with sub-basins experiencing repeating periods of isolation and connectivity, and Lake Bonneville, in existence from about 40,000 – 14,500 years before present, was the most recent to fill the Bonneville Basin. The boundary between the Bonneville Basin and the Snake River Basin's southeastern edge is seismically active (Smith and Sbar 1974; Smith 1978), and throughout the Pleistocene (and possibly earlier), the Bear River's course has been altered between the two drainages multiple times by volcanism and tectonic activity (McCoy 1987; Currey 1990; Oviatt et al. 1992; Bouchard et al. 1998). The most recent connection between the Snake River drainage and the Bonneville Basin occurred about 14,500 YBP when Lake Bonneville overflowed the drainage divide at Redrock

Pass, cut a huge gap, and flooded catastrophically into the Snake River drainage (Currey et al. 1984; Bright and Ore 1987; Jarrett and Malde 1987; Currey 1990). As the climate warmed and dried and glaciers retreated, water levels in the once again endorheic Bonneville Basin receded, isolating Great Salt Lake, Utah Lake, and Sevier Lake in sub-basins.

Utah Lake (Figure 3-2) is one of the largest (38 km x 21 km; approximately 392 km^2) freshwater lakes west in western North America and has existed for 8,000 – 10,000 years. For over 30,000 years prior to that, Lake Bonneville covered most of the intermontane basins of the Wasatch Front, undergoing dramatic fluctuations in depth and surface area. Utah Lake, the largest freshwater remnant of Lake Bonneville, is located in Utah County, UT about 65 km south of Great Salt Lake, the largest remnant of the historic lake. Utah Lake is highly eutrophic and shallow, with an average depth of 2.8 m and a maximum depth of 4.2 m at compromise elevation (Fuhriman et al. 1981). Major tributaries include the Provo, Spanish Fork, and American Fork Rivers and Hobble Creek. The outlet, the Jordan River flows north to the Great Salt Lake. Frequently, Utah Lake’s temperature at shallow depths in summer exceeds 30ºC, conductivity surpasses 2000 µS, and turbidity is greater than 120 Ntus (T. Crowl, Utah State University, unpublished data). Anthropogenic impacts (e.g., urbanization, agriculture, flow regulation, exotic introductions) on Utah Lake and its tributaries include declines in both water quality and quantity, especially during drought years. June sucker and Utah sucker are the only native fishes persevering in

Utah Lake as 12 other native species have become extinct or have been essentially extirpated from the lake, whereas many non-native species thrive including predators and competitors of native suckers (Peterson 1996; Thomas 1998; SWCA 2002; Miller and Crowl 2006). Though it once had clear water and extensive beds of littoral macrophytes of several species (Heckmann et al. 1981), today, it has an enormous common carp (*Cyprinus carpio*) population (SWCA 2002) and is turbid and void of submergent vegetation except for widely scattered beds of *Potamogeton pectinatus* (Miller and Crowl 2006). The most abundant summer phytoplankter is *Aphanizomenon flos-aquae*, dense blooms of which occur annually in late summer and early fall (Rushforth et al. 1981). Utah Lake's surface elevation fluctuates dramatically (seasonally and annually) limiting the re-establishment of submergent macrophytes, and fringes of emergent vegetation (*Typha latifolia*, *Scirpus validus*, *Phragmites australis*) may or may not be inundated for years at a time. Even moderate winds can prevent stratification of the lake because of the large fetch, shallow depth, and lack of vegetation.

Radio / Acoustic Telemetry

Telemetry Tagging Procedures.—During the spring spawning seasons of 2003 and 2004, adult June sucker (14 males, 14 females) and Utah sucker (16 males, 8 females) were captured in the Provo River or near its mouth and surgically implanted with digitally encoded combination radio and acoustic transmitters (CARTs) manufactured by Lotek Wireless (Appendix: Table 3-A-1). Suckers were subjectively identified to morph as defined by Cole et al. (2008), and suckers of intermediate morphology were excluded from tagging. The goal of tagging equal numbers of June sucker and Utah sucker as well as males and females failed as insufficient numbers of female Utah sucker were captured. Digitally encoded transmitters permitted multiple fish to transmit on a single frequency while still allowing individual identification. Between 22 May and 5 June 2003, all fish were captured at night by the UDWR via spotlighting and dip-netting spawning suckers in the Provo River. Between 23 April and 2 June 2004, suckers were captured by trammel net in Utah Lake near the mouth of the Provo River and by the UDWR using the 2003 protocol. All Utah sucker implanted with transmitters were wild fish whereas 11 implanted June sucker were wild and 17 were naturalized fish stocked into Utah Lake from the UDWR Fisheries Experimental Station hatchery (n = 4) in Logan, UT and from two refuge populations, Red Butte Reservoir, UT (n = 12) and Camp Creek Reservoir, UT (n = 1) (Appendix: Table 3-A-1); naturalized June sucker were identified from individual Passive Integrated Transponder (PIT) tags implanted prior to stocking. The battery life of the CART tags was 2 years, and their dimensions were approximately 16 mm x 60 mm with a weight of 25.3 g. Attempts were made to limit transmitter weight to less than 2% of fish weight (Winter 1996), but this limit was slightly exceeded (2.1%) in two cases when fish of sufficient size were unavailable. Transmitters implanted in 2003 were programmed to turn off from late October 2003 through February 2004) to conserve battery life. The contrasts between Utah Lake and its tributaries led to the use of CART tags: acoustic transmission was effective in shallow Utah Lake with its high specific conductance and turbidity, and radio transmission was effective in manual and stationary tracking of tributaries with their limited access points, low specific conductance, and turbulent flows.

After capture and prior to surgical implantation, suckers were held in net-pens for approximately 12 h to assess their condition (Winter 1996). Suckers were anesthetized in a 100 – 120 mg/L solution of tricaine methanesulfonate (MS-222) before surgery, and fish gills were continually irrigated with the anesthetic solution throughout the surgical procedure. Transmitters were implanted via the modification of Ross and Kleiner’s (1982) shielded needle technique described in Isaak and Bjornn (1996). A dose of oxytetracycline (50 mg/kg body weight) accompanied transmitter insertion into the peritoneal cavity to minimize infection risk (Summerfelt and Smith 1990). Incisions were closed with two – three sutures and covered with a cyanoacrylate tissue adhesive. The surgical procedures were performed during early daylight hours in shade to minimize heat stress, and required from 4 – 8 min to complete. Following recovery from anesthesia in a freshwater holding tank, suckers were transferred to a net-pen and held for 1 – 3 h to monitor their condition. Fish were released near their site of capture, and all actively swam away. Several mortalities and / or tag expulsions occurred, and in three instances, recovered tags from implantations performed in 2003 were placed into different fish in 2004 (Appendix: Table 3-A-1). One Utah sucker that expelled a tag in 2003 was recaptured during the 2004 spawning run in apparent excellent condition with a fully healed scar; it was implanted with a new transmitter.

Random Tracking Telemetry Procedures and Data Analysis— To investigate the distribution and movement of suckers in Utah Lake, the lake was divided into eight sectors: four strata north to south, each with an east and west side (Figure 3-2). Provo Bay was not included in the random tracking study. Sampling was conducted during six “seasonal” time periods (Appendix: Table 3-A-2): summer (2004); late summer (2004 and 2005); autumn (2004 and 2005); and winter (2005). During each approximately four week seasonal period, two wireless hydrophones were placed in both the eastern and western sectors of a randomly selected stratum (range 6 to 10 days; weather and lake conditions prevented adhering to a strictly 7-day schedule) after which time they were relocated to the next stratum until all four strata were monitored for that season (Figure 3-2). Within a sector (e.g., 2W), a six-element Yagi antenna and the receiver / data-logger (programmed to scan all frequencies in use; gain = 75) were placed on shore, and one hydrophone was randomly located (mounted on an iron fence post) in the littoral zone in water approximately 1 m in depth. The second hydrophone was placed (suspended from an anchored buoy) in the limnetic zone in water greater than 1.5 m (when possible) within approximately 2 km of shore to ensure sufficient signal strength at the receiver and in parallel with the littoral hydrophone and the antenna (see Buelow 2006 for a more detailed description of random hydrophone placement). Each hydrophone had a temperature data logger (HOBO H8) attached to it collecting water temperature data hourly. The substrate (mud, sand, or rock) at the location of each hydrophone was also determined during all 2004 sampling and most 2005 sampling. After the equipment in a sector was in place, a test CART tag was used to determine the maximum detection range for the hydrophones: littoral – 350 m (mean; range 250 – 450 m) and limnetic – 373 m (mean; range 250 – 450 m).

Designing and conducting a lake wide telemetric investigation of distribution and movement of fish in a large, shallow, turbid, slightly saline lake with a long fetch can present many technical obstacles. Not only is radio transmission reduced by water quality, but weather (wind, lightening) on large, shallow Utah Lake can create sampling hazards and/or situations that can damage, displace, or remove equipment preventing data collection. Where data gaps occurred, the most complete dataset available that included all variables in question was analyzed (Appendix: Table 3-A-2). At the onset of the random tracking survey (6 July 2004), there were 24 tagged June sucker (11 females – 3 wild, 8 stocked; 13 males – 8 wild, 5 stocked) and 22 tagged Utah sucker (8females; 14 males) surviving. No mortalities were known to occur during the study (through 27 October 2005), however, seven June sucker and six Utah sucker were undetected during the last sampling period, Autumn 2005. For analysis, a single “detection” (or presence) was defined as one or more “hits” at a hydrophone by an individual sucker during a 12 hr period (high light period: 0600 hours to 1800 hours; low light period: 1800 hours to 0600 hours).

Initially, the data was explored by analyzing hits and detections without considering the effort (e.g., hydrophone set hours) required obtaining them. Two factor analysis of variation (ANOVA) was used to analyze the effects of morph and sex on individual Utah Lake suckers' numbers of hits and detections (dependent variables) and to analyze the effects of sex and origin (wild versus stocked) on individual June sucker's numbers of hits or detections (dependent variables). Pearson's correlation coefficient (*r*) for hits with interference signals by year, season, stratum, and shore was calculated. Three factor ANOVA was used to analyze the effects of the predictor variables, season, morph, and sex, on the dependent variable, proportion of sectors visited seasonally by individual Utah Lake suckers during random telemetric tracking in Utah Lake, and to analyze the effects of the predictor variables, season, sex, and origin, on the proportion of sectors (dependent variable) visited seasonally by individual June suckers. Proportions were arcsine-square root transformed prior to analysis.

Detections per unit effort (DPUE) were calculated for each hydrophone deployed during each approximately one week sampling episode, factoring the number of male and female June sucker and Utah sucker tagged and the time period each hydrophone was set. I modeled the relationship between DPUE, the dependent variable, and predictor variables with randomforests (RF) analysis

(Breiman 2001) via the randomForest package (Liaw and Wiener 2002) in the program R (R Development Core Team 2013). Predictor variables included:

morph	June sucker, Utah sucker
gender	female, male
season	summer, late summer, autumn, winter
stratum	north, north-central, south-central, south
shore	east, west
zone	limnetic, littoral
light	day, night (high light, low light)
substrate	mud, rock, sand
temperature	mean in °C during sampling period
oDPUE	detections per unit effort of the *other* morph at the same location (hydrophone / receiver) during the same sampling period; thus when DPUE for June sucker was the dependent variable, the predictor, oDPUE, was detections per unit effort for Utah sucker, and vice versa.

Among the advantages RF analysis has over other analytical methods are its ability to handle nonlinear relationships, its resistance to overfitting, and its capacity to cope with interactions among independent variables (Breiman and Cutler 2005; Cutler et al. 2007). Random forests analysis constructs many classification and regression trees (the “forest” – 5000 trees per model in this study) by randomly extracting subsets of independent variables (out-of-bag observations) that are used to calculate a running unbiased estimate of the classification error as trees are added to the forest and to estimate variable importance. Each predictor variable's importance is determined from the average percent increase in mean square error (MSE) in prediction across all trees when that variable's value is randomized; the greater the increase in MSE, the more important the variable. Pearson's correlation coefficient for DPUE with oDPUE was determined. Relationships between DPUE and predictors were further examined via partial dependency plots, which provide a graphical depiction of the marginal effect of a predictor variable on the class probability (classification) or response (regression); *e.g.*, they illustrate a given variable's effect after accounting for the joint effect of the remaining predictor variables. Conservative estimates of the minimum distances traveled by individual suckers during the random tracking study were calculated by summing the Euclidean distances between chronologically ordered hydrophone detections and then analyzed via ANOVA.

Targeted Telemetry Procedures and Data Analysis— To investigate pre-spawning and spawning behavior of June sucker and Utah sucker, the Provo River (2004 and 2005) and the Spanish Fork River (2005) were each monitored via two wireless hydrophones with attached temperature data loggers (HOBO H8s; collecting data hourly) and a receiver / data-logger located near their confluences with Utah Lake (Appendix: Figure 3-A-1). One post-mounted hydrophone (mouth) was placed near the mouth of the tributary whereas the second hydrophone (lake) was suspended from an anchored buoy and placed offshore in deeper water approximately 500 m from the first. The receiver / data logger (river) at the Provo River was placed on a foot bridge upstream of the mouth and was capable of detecting tagged fish in the lower 300 m of the river; water temperature was recorded via a temperature data logger hourly. The receiver / data logger at the Spanish Fork River was located adjacent to the mouth and was incapable of detecting tagged suckers in the lower river. The Provo River was telemetrically monitored from 1 April 2004 through 22 June 2004 for sucker detections. A 92 h gap in data collection caused by technical problems occurred from 5 – 9 May 2004. From 12 April 2004 through 15 June 2004, two wireless hydrophones and a receiver / data logger were used to monitor the mouth of Provo Bay (approximately 6.5 km from Provo River mouth) where post-spawn aggregations of June sucker have been reported (Radant and Shirley 1987). Technical difficulties resulted in two brief gaps in data collection: 15 – 16 May 2004 for 20 h and 23 – 26 May 2004 for 68 h.

The following year, the Provo River was monitored (telemetrically) from 16 February 2005 through 20 July 2005; littoral (at river mouth) and river temperature monitoring began on 25 February 2005 and 4 April 2005, respectively, and continued throughout the spawning run sampling period. The Spanish Fork River was monitored (telemetrically) from 25 February through 20 July, as was temperature (lake, littoral, and river). Active manual tracking surveys (via foot or truck) began on 15 April and continued approximately semiweekly until 9 June using a radio receiver (Lotek SRX 400) and a four element Yagi antenna on the lower 5 km of the Provo River during the 2004 spawning season, and UTM coordinates of sucker positions were recorded. Similar surveys were performed approximately weekly in 2005 on the lower 7.8 km of the Provo River (the entire critical habitat reach; USFWS 1986) from 4 March to 12 July and on the lower 3.2 km of the Spanish Fork River from 3 March to 28 June. Also in 2005, Battle Creek was surveyed three times and the American Fork River was surveyed twice in similar fashion during the spawning season. Only June sucker (N = 9) and Utah sucker (N = 4) CART-tagged in 2003 were included in 2004 spawning season data and analyses. Discharge data for the Provo and Spanish Fork Rivers were obtained from the USGS Instantaneous Data Archive (http://ida.water.usgs.gov/ida/). The relationships between discharge, temperature, and the daily proportions of tagged June sucker and Utah sucker detected at a given hydrophone or receiver during the 2005 Provo and Spanish Fork Rivers' spawning runs were examined via linear regression; proportions were arcsine-square root transformed prior to analysis. The effects of morph and sex, and for June sucker morphs only, origin (wild versus stocked) on median date of first detection were investigated via exact tests. These same variables' effects on minimum distance (sum of the Euclidean distances between chronologically ordered hydrophone detections) traveled by individual suckers during the 2005 spawning season sampling period were examined via ANOVA.

Stable Isotopes Analysis

Fin (left pelvic) clip samples were collected during the spring and summer in 2001, 2002, and from 2004 through 2006 for stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) from wild adult suckers spanning the morphological continuum present in Utah Lake (11 June sucker, 26 Utah sucker, and 12 intermediate morphs). Suckers were captured by a variety of methods: dip-netting spawning fish by spot-light at night in the Provo River, and trammel, trap, and trawl netting in Utah Lake. On 30 August and 13 September 2006, samples of potential sucker diet items, including zooplankton, benthic/littoral macroinvertebrates, and phytoplankton (seston), were collected from several locations and habitats for stable isotope analysis. All isotope samples were stored in 90 % ethanol prior to processing and analysis. Samples were oven dried at 60 °C for ~24 h to constant mass and then homogenized with a mortar and pestle. Samples were analyzed at the University of California – Davis Stable Isotope Lab via a PDZ Europa 20–20 isotope ratio mass spectrometer for dual carbon and nitrogen using Pee Dee belemnite limestone and atmospheric nitrogen as the carbon and nitrogen standards, respectively. All $\delta^{13}C$ values for fishes included in analyses were lipid-normalized (Kiljunen et al. 2006). Isotopic signatures were compared among sucker morphs via ANOVA. Niche width (NW) was estimated for each sucker morph by calculating the convex hull area encompassed by the smallest polygon containing all individuals of a given morph within the two dimensional $\delta^{13}C$ – $\delta^{15}N$ bi-plot space (isotopic niche space), and niche overlap among morphs was estimated as the overlapping area of polygons (Layman et al. 2007). Area estimates were generated using the program ArcGIS 10 (ESRI 2010). The total ranges (Layman et al. 2007) of δ^{13}C and δ^{15}N and trophic position (Vander Zanden and Rasmussen 1999; Vander Zanden et al. 2003) were calculated for each morph:

$$\text{range } \delta^{13}\text{C} = \max(\delta^{13}\text{C}) - \min(\delta^{13}\text{C}) \qquad \text{range } \delta^{15}\text{N} = \max(\delta^{15}\text{N}) - \min(\delta^{15}\text{N})$$

$$\text{Trophic Position}_{\text{consumer}}=((\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4) + 2$$

To determine trophic position, baseline δ^{15}N was estimated via a δ^{13}C – δ^{15}N relationship:

$$\delta^{15}\text{N}_{\text{baseline}} = -0.0096\ (\delta^{13}\text{C}_{\text{consumer}})^2 - 1.1605\ (\delta^{13}\text{C}_{\text{consumer}}) - 11.185$$

calculated using a primary consumer δ^{13}C – δ^{15}N bi-plot (Vander Zanden and Rasmussen 1999; Vander Zanden et al. 2003). *Amphipoda* spp., *Ceriodaphnia* spp., *Daphnia* spp., and *Diaphanosoma* spp. were the primary consumers. Additional isoptope data from analysis of *frozen* samples were used in bi-plot construction following corrections for preservation differences: isotopic signatures for *Amphipoda* spp. and *Daphnia* spp.samples (frozen) from a Utah Lake food web study (Landom 2010), and data for Amphipoda spp. samples collected concurrently with the current study's ethanol-preserved samples. For macroinvertebrates, the corrections (frozen to ethanol) were -0.04 ‰ for δ^{13}C and 0.21 ‰ for δ^{15}N (Sarakinos et al. 2002), and for zooplankton, 0.8 ‰ for δ^{13}C and 0.2 ‰ for δ^{15}N (Feuchtmayr and Grey 2003).

Mixing polygons (Phillips and Gregg 2003) were generated within the δ^{13}C – δ^{15}N bi-plot space, plotting the mean coordinates for each morph; mean coordinates for potential diet items were plotted assuming trophic fractionation of 0.4 ‰ for δ^{13}C and 3.4 ‰ for δ^{15}N (Post 2002). Isotopic signatures from analysis (Landom 2010) of frozen samples of common carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*), and white bass (*Morone chrysops*) were corrected for the different isotopic sample preservation method (90 % ethanol) used in this study prior to the addition of the assumed trophic level increases. For freshwater fish samples preserved in ethanol, Sarakinos et al. (2002) observed 0.21 ‰ δ^{13}C and 0.37 ‰ δ^{15}N enrichment for Sacromento sucker (*Catostomus occidentalis*) relative to frozen controls whereas Kelly et al. (2006) described 0.78 ‰ δ^{13}C and 0.35 ‰ δ^{15}N enrichment for Arctic charr (*Salvelinus alpinus*) relative to controls that were frozen, then dried. The means of their reported values (0.495 ‰ for δ^{13}C and 0.36 ‰ for δ^{15}N) were used as preservation correction factors for isotope signatures calculated from these frozen samples of fishes. In the mixing polygons, these mean values for adults were also used to represent larval fish (i.e., potential prey for suckers).

Density / Growth Lab Experiment

To investigate the reported Allee effect in June sucker (Gonzalez 2004) with comparisons to Utah sucker, I maintained juvenile (age 2 and 3) June sucker and Utah sucker at densities (conspecific) of 1, 5, and 10 fish in 75 l aquaria filled to a volume of approximately 60 l from 31 January to 2 April 2007 at Utah State University's Millville Endangered Species and Aquatic Research Facility. Fish in different aquaria could not see one another. The re-circulated water of the flow through system was maintained at approximately 20°C. Fish were fed a surplus of ground Razorback 400 fish feed (Silver Cup Fish Feed) starting at the rate of 2 % of the initial total fish weight per aquarium and increased proportionally assuming a daily increase in total weight per aquarium of 2 % to ensure that food availability did not limit growth. Suckers were weighed to the nearest 0.1 g at the start and finish of the 61 d experiment and at days 20 and 40 to adjust the dietary allotments. There were three replicate blocks (i.e., three rows) of six aquaria with June sucker and Utah sucker randomly assigned at conspecific densities of 1, 5, and 10 fish per aquarium (total of 3 blocks, 18 aquaria, and 96 suckers). Suckers of both morphs were obtained in 2004 and 2005 as larvae from Utah Division of Wildlife's Fisheries Experiment Station located in Logan, Utah and maintained at the Millville facility prior to use in this experiment. Growth rate (g/g/d) was used as a measure of fitness, and the effects of morph, density, and block on it were analyzed via ANOVA (mixed model with block as random factor). All ANOVA, linear regression analyses, correlation analyses and exact tests reported here were conducted via the program, SAS (SAS Institute Inc. 2002).

RESULTS

Radio / Acoustic Telemetry

Random Tracking Telemetry — During the random monitoring investigation, 14,033 sucker hits, which converted to 1015 individual detections, were recorded from Utah Lake in 2004 and 2005 (Appendix: Table 3-A-3). Over 60 % of the hits (8754) and 11% of the detections (112) occurred at the south-central, eastern sector in the vicinity of Long Bar (see Figure 3-2) during the Summer 2004 sampling period. Two-factor ANOVA revealed no statistically significant differences ($P > 0.05$) when using individual June suckers' and Utah suckers' numbers of hits or detections as the dependent variable and species, gender, and their interaction as predictor variables, nor were there differences in individual June suckers' numbers of hits or detections gender, origin (wild versus stocked), and their interaction as predictor variables for (Appendix: Table 3-A-4). More than 28,000 interference signals were recorded during the random monitoring study (Appendix: Table 3-A-3), and their occurrences were significantly correlated ($r = 0.4165$; $P = 0.0049$) with hit detections by year, season, stratum, and shore (i.e., correlated with hits at a single receiver / datalogger).

Substantial variation existed among individual suckers in the proportion of sectors visited seasonally during random telemetric monitoring of Utah Lake (Appendix: Figure 3-A-2). Using the predictors season, morph, gender, and their interactions, three factor ANOVA revealed the proportion (arcsine square root transformed data) of sectors visited by individual adult Utah Lake suckers declined significantly($F_{3,260}$ = 2.66; P = 0.0486) from Summer to Winter (Figure 3-3; Appendix: Table 3-A-5;). Regarding June sucker specifically, three factor ANOVA revealed no statistically significant differences ($P > 0.05$) in the proportion of sectors visited dependent on season, gender, origin, and their interactions, although the effect of season approached significance (Appendix: Table 3-A-5).

Regardless of the dataset modeled with RF analysis or the accompanying predictor variables, morph (species) was an extremely poor predictor of DPUE, consistently performing worst or near to it among variables, and its inclusion in models as a predictor variable *increased* the model's MSE (Figure 3-4; Appendix: Table 3-A-6). Light (i.e., day versus night) and gender performed nearly as poorly as species as predictor variables (Figure 3-4; Appendix: Table 3-A-6). No models identified any of the three as important independent variables, and in all RF models not containing temperature or oDPUE as predictors, inclusion of species, gender, and light led to decreases in variation explained (Appendix: Table 3-A-6). Including the only predictor variables that were biological characteristics of Utah Lake suckers, morph and gender, in RF models reduced explanatory power. Substrate was also a poor predictor variable for DPUE by RF analysis, and although several models identified it as marginally important, its inclusion among important variables decreased the percentage of variation explained (Appendix: Table 3-A-6).

All RF analyses identified zone, shore, season, and stratum in some order as among the important predictor variables regardless of the dataset analyzed; when models excluded temperature and oDPUE, these four predictors explained about half the variance in DPUE (Appendix: Tables 3-A-6, 3-A-7 and Figure 3-A-3). Partial dependency plots (Figure 3-5), which illustrate the marginal effects of predictor variables, revealed: DPUE for limnetic zone hydrophones was more than twice that for littoral zone hydrophones; eastern shore hydrophone DPUE was approximately 25 % greater than for western shore hydrophones; hydrophones deployed in summer and late summer had greater DPUE than those deployed in fall and winter; and southern stratum hydrophone DPUE was much less than those for the more northern strata.

Temperature, which ranged from 2.8° - 26.0°C during the study, was an important predictor of DPUE for Utah Lake suckers, and its inclusion in RF models not including oDPUE among predictors increased the variance explained to about 70 % (Figure 3-4; Appendix: Tables 3-A-6, 3-A-7 and Figure 3-A-3). The partial dependency plot for temperature (Model 8i) demonstrated that the greatest DPUE occurred between temperatures of 13° - 19°C (peak at 16°C), and below this range, DPUE was fairly constant (DPUE = ~ 0.0009) down to 2.8°C, whereas above this range, DPUE was again constant to 26.0°C, but at a reduced level (DPUE = ~ 0.0006) (Figure 3-6).

Interpretation of RF modeling of datasets including temperature as a predictor was hindered by gaps in those datasets (Appendix: Table 3-A-2), and more specifically, ecological interpretation of the partial dependency plot for temperature (Figure 3-6) was confounded by the lack of information regarding other predictor variables. Evidence, however, of the importance of temperature includes the high correlation (r = 0.98) between the mean seasonal proportion of sectors visited by individual Utah Lake suckers and mean seasonal temperature (Figure 3-3). Additional evidence of the importance of temperature in sucker distribution and movement can be found by plotting daily detections of individual suckers and daily mean temperature by shore and zone for the for late summer (August – September) and autumnal (October – November) telemetric sampling periods in 2004 for the three northernmost strata of Utah Lake (Figure 3-7). During the late summer period, similar numbers of detections were recorded in eastern littoral and limnetic and western limnetic sites when temperatures of the two shores were similar. Very few detections in the western, littoral zones of these strata were recorded during the entire late summer and autumnal sampling periods in 2004. As water temperatures declined during the autumnal sampling period, the temperature at the western limnetic hydrophone warmed relative to the other three hydrophones, and many more suckers were detected there (Figure 3-7). In winter, the suckers returned to the eastern shore (3.44 ± 0.07 °C), where winter mean water temperatures were greater than along the western shore (3.19 ± 0.10 °C) (see Figure 3-8; 2005 Winter).

Whenever oDPUE (DPUE for the other morph) was used as a predictor variable in a RF model, regardless of the other independent variables included, it was the most important of the predictors (Figure 3-4; Appendix: Table 3-A-6 and Figure 3-A-4). The partial dependency plot for oDPUE depicted its close relationship with DPUE (Figure 3-6), and correlation analysis confirmed this (*r* = 0.90); the graph's plateau resulted from DPUE being calculated separately for the sexes whereas oDPUE calculation included both sexes. When oDPUE was used as a predictor in RF models also including temperature as a predictor, its removal resulted in greater loss in variation explained than removal of temperature from the model (Appendix: Table 3-A-6). Random forests analysis of June sucker and Utah sucker separately further demonstrates the importance of DPUE of the other species as a predictor (Appendix: Figure 3-A-4). However, good models can be developed without oDPUE if temperature data is included; given the similarity in the variable importance plots and partial dependency plots for temperature of the two species, it is not surprising oDPUE was a good predictor (Appendix: Figure 3-A-5).

There was considerable variation in the minimum distances traveled by individual Utah Lake suckers during random telemetric monitoring in 2004 and 2005 (Appendix: Table 3-A-8). Two factor (morph and sex) ANOVA of the distances traveled during random monitoring by individual Utah Lake suckers revealed no statistically significant differences based on sex, morph or their interaction (Appendix: Table 3-A-9, Random distance). Two-factor (sex and origin) ANOVA of the distances traveled during random monitoring by individual

June sucker revealed no statistically significant differences based on sex, origin, or their interaction (Appendix: Table 3-A-9, Random distance).

Targeted Telemetry (passive and active)— During the 2004 spawning run, all of the Utah Lake suckers (nine June sucker; four Utah sucker) that were tagged in 2003 were detected at least once at one or more of the four Provo River monitoring locations (Appendix: Table 3-A-10 and Figure 3-A-6). Six June sucker and three Utah sucker were detected at least once at the mouth of Provo Bay (approximately 6.5 km from river confluence) with one June sucker and one Utah sucker making 18 trips between Provo Bay and the Provo River during the monitoring period. Single factor (morph) ANOVA (model df = 3, 42) revealed no significant difference in the mean number of trips by individuals between the two locations (June sucker mean = 3.44; Utah sucker mean = 6.50; F value = 0.625; P = 0.446).

During early April 2004, all Utah sucker and all but two of the June sucker were detected at least once at the Provo River lake hydrophone, but only a single Utah sucker was detected after this period in the lake in mid June (Figure 3-9; Appendix: Figure 3-A-6). Suckers of both species were detected at the mouth of the Provo River throughout most of the monitoring period with a peak in detections in late May (Figure 3-9; Appendix: Figure 3-A-6). The radio receiver at the lower river location detected four June sucker at the beginning of April 2004, but only one after that, and two Utah sucker in May (Figure 3-9; Appendix: Figure 3-A-6). Active tracking of the upper Provo River, which began on 15 April 2004 and continued approximately semiweekly until 9 June 2004, detected three of the four tagged Utah sucker and three of the nine tagged June sucker (Figure 3-9; Appendix: Tables 3-A-10, 3-A-11 and Figure 3-A-6).

The first June sucker was detected on 12 May 2004 when mean daily water temperature was 10.8 °C and mean daily discharge was 1.90 m^3/s, and the first Utah sucker were first detected in the upper Provo River on 15 April 2004 (the first active tracking survey) when mean daily water temperature was 9.9 °C and mean daily discharge was 1.58 m^3/s (Figure 3-9; Appendix: Tables 3-A-10, 2-A-11 and Figure 3-A-6). Peak mean daily discharge in the Provo River of 4.18 m^3/s occurred on 4 May 2004 (Figure 3-9). Two Utah sucker (codes 2 and 178) and one June sucker (code 203) were detected in the upper river prior to or without detection in the lower river though all three suckers were previously detected at either the mouth or lake hydrophone (Appendix: Table 3-A-10 and Figure 3-A-6). In 2004, all suckers detected in the upper river were in low velocity habitats (pools, runs, or eddies). Median exact tests (when conducted) revealed no significant differences ($P > 0.05$) in median date of first detection between the morphs at any of the Provo River monitoring locations in the 2004 spawning run (Appendix: Table 3-A-10).

During the 2005 spawning run, 13 June sucker (of the 24 tagged; Appendix: Table 3-A-10 and Figure 3-A-7) and 15 Utah sucker (of the 22 tagged; Appendix: Table 3-A-10 and Figure 3-A-8) were detected at least once at one or more of the four Provo River monitoring locations, and 22 June sucker and 21

Utah sucker (Appendix: Table 3-A-10 and Figure 3-A-9) were detected at least once at one or more of the three Spanish Fork River monitoring locations. There was considerable variation in the number of trips (and distances traveled) by individual suckers between the Spanish Fork and Provo Rivers during 2005 spawning season monitoring (Appendix: Table 3-A-8). Between June sucker and Utah sucker that were detected at least once at either river, two-factor (species and gender) ANOVA revealed no statistically significant differences ($P > 0.05$) in distances traveled during the spawning season (Appendix: Table 3-A-9, Spawning distance). Two factor (species and gender) ANOVA also revealed no significant differences in total distances (sum of random and spawning distances) traveled, although the effect of gender approached significance ($P =0.0585$; Appendix: Table 3-A-9, Total distance). Among the June sucker that were detected at least once at either river, two factor (gender and origin) ANOVA revealed no statistically significant differences ($P > 0.05$) in distances traveled during the spawning season (Appendix: Table 3-A-9, Spawning distance). Two-factor (gender and origin) ANOVA also revealed no significant differences ($P > 0.05$) in total distances traveled (Appendix: Table 3-A-9, Total distance).

Five June sucker were detected at the Provo River lake hydrophone between 28 February and 28 May 2005 with no further June sucker detections occurring there during the spawning run sampling period (Figure 3-10; Appendix: Table 3-A-10 and Figure 3-A-7). Nine Utah sucker were detected at the lake hydrophone between 28 May and 20 July 2005 with the majority of detections occurring in April and a minor peak in detections occurring in late June – July, a period when no June sucker were detected (Figure 3-10; Appendix: Figure 3-A-8). Five June sucker and seven Utah sucker were detected at the Provo River mouth hydrophone in February prior to any of either species being detected at the lake hydrophone (Figure 3-10; Appendix: Figures 3-A-7 and 3-A-8). Detections of both species greatly decreased in March before increasing in April – early May at the mouth of the Provo River, with four June sucker and 11 Utah sucker detected (Figure 3-10; Appendix: Figures 3-A-7 and 3-A-8). During June and July, eight June sucker were infrequently detected whereas nine Utah sucker were detected during this period, with a secondary peak in Utah sucker occurring in July at the mouth hydrophone (Appendix: Figures 3-A-7 and 3-A-8). Just four June sucker were detected infrequently in the lower Provo River during the 2005 spawning run monitoring, a period when nine Utah sucker were detected, several frequently, with the majority of detections occurring in April (Appendix: Figures 3-A-7 and 3-A-8).

A lone June sucker (code 144; a wild female) was detected in the upper Provo River in 2005 via active tracking; she was first detected on 18 May 2005 (and during seven of eight subsequent surveys through 23 June) in the upper Provo River when mean daily discharge was 33.1 m^3/s and mean daily temperatures for the littoral and river sites were 13.8 °C and 9.0 °C, respectively (Figure 3-10; Appendix: Table 3-A-11 and Figure 3-A-7). The lower river receiver detected this sucker prior to its upper river detections on 14 May 2005 and then next on 25 June 2005 after its last upper river detection (Appendix: Figure 3-A-7). The first of seven Utah sucker detected in the upper Provo River via active tracking was encountered during the first active survey on 4 March 2005, when mean daily discharge was 2.5 m^3/s and mean daily temperature for the littoral site was 7.8 °C (river temperature unavailable) (Figure 3-10; Appendix: Table 3-A-11 and Figure 3-A-8). Peak mean daily discharge of 45.59 m^3/s occurred on 24 May 2005 when the Provo River temperature was 11.4 °C (Figure 3-10).

Linear regression modeling of proportions (arcsine square root transformed) of June sucker or Utah sucker detected at Provo River hydrophones / receivers during the ascending and descending hydrographs revealed ten significant models with 20 significant predictor variables or interactions (Table 3-2). In the significant models, the proportion of suckers detected was always positively related to temperature (lake, mouth, or river) and / or discharge, regardless of species or hydrograph status, and negatively related to the interaction of temperature and discharge (Table 3-2). Median exact tests (when conducted) revealed no differences ($P > 0.05$) in median date of first detection between June sucker and Utah sucker at any of the Provo River monitoring locations in the 2005 spawning run (Appendix: Table 3-A-10). Utah sucker were detected in greater numbers than June sucker throughout the spawning season at all four monitoring sites in 2005; this was especially evident at both river sites and at the lake and mouth sites in July (Figure 3-10; Appendix: Figures 3-A-7 and 3-A-8). One Utah sucker (code 101; a male) was detected in the upper Provo River during all but three active tracking surveys (Appendix: Figure 3-A-8). The mouth hydrophone detected this sucker on two days during this period (in June) indicating at least two trips out of and back into the river, however, the lower river receiver did not detect it at all during the 2005 spawning run (Appendix: Figure 3-A-8).

Seventeen June sucker were detected at the Spanish Fork lake hydrophone prior to April during spawning run telemetry in 2005, and by the end of the monitoring period, 22 of the 24 tagged June sucker had been detected (Appendix: Table 3-A-10 and Figures 3-A-9 and 3-A-10). Utah sucker showed a similar detection pattern with 17 individuals detected in March 2005 at the lake hydrophone, followed by few detections in the first weeks of April and by many detections from late April to early July; by the monitoring period’s end, 21 of the 22 tagged Utah sucker had been detected (Appendix: Table 3-A-10 and Figures 3-A-9 and 3-A-10). The Spanish Fork mouth hydrophone detected 10 June sucker and 12 Utah sucker during the 2005 spawning run monitoring with June sucker detections peaking in late June, and Utah sucker detections peaking in early April and again in late June (Appendix: Table 3-A-10 and Figures 3-A-9 and 3-A-10). Only a single significant model and variable were generated by linear regression modeling of proportions (arcsine square root transformed) of June sucker or Utah sucker detected at Spanish Fork River hydrophones during the ascending and descending hydrographs (Table 3-2). The proportion (transformed) of June sucker detected at the mouth hydrophone during the ascending hydrograph was positively related to river temperature. Median exact tests revealed no significant differences (*P* > 0.05) in median date of first detection between the species at either the lake or mouth hydrophone in the 2005 Spanish Fork River spawning run (Appendix: Table 3-A-10).

A single June sucker (code 154; a stocked female originally from Red Butte Reservoir) was detected via active tracking in the Spanish Fork River approximately 2 km upstream from the mouth on 20 April 2005 when mean daily river temperature was 7.7 °C, mean daily lake temperature was 8.9 °C, and mean daily discharge was 9.2 m^3/s (Appendix: Table 3-A-11). One Utah sucker (20 April 2005) and one June sucker (19 May 2005) were detected by active tracking at the mouth of the Spanish Fork River (Appendix: Table 3-A-11); both were also detected by the mouth hydrophone. Active tracking detected no Utah sucker in the upper Spanish Fork River in 2005.

Active tracking in Battle Creek on three dates in late April and early May 2005 detected no suckers of either species (Appendix: Table 3-A-11). No suckers were detected via active tracking in the American Fork River on two dates in May and June 2005 (Appendix: Table 3-A-11).

Stable Isotopes Analysis

Single-factor (morph) ANOVA revealed that mean $\delta^{15}N$ for June sucker (mean ± 95 % confidence interval; 17.73 ‰ ± 0.55 ‰) was significantly greater ($F_{2,48} = 12.10$, $P = 5.55 \times 10^{-5}$) than that of Utah sucker (16.33 ‰ ± 0.27 ‰) whereas the Utah sucker mean $\delta^{13}C$ (– 22.62 ‰ ± 0.26 ‰) was significantly enriched ($F_{2,48}$ = 15.44, P = 6.64 x 10^{-6}) relative to that for June sucker (– 24.57 ‰ ± 0.66 ‰) (Figure 3-11). Mean δ^{15}N (16.81‰ ± 0.48 ‰) and mean δ^{13}C (–23.51 ‰ ± 0.76 ‰) for intermediate suckers followed morphology and both were intermediate to, but not significantly different from, the respective isotopic signatures of June sucker and Utah sucker (Figure 3-11).

Niche width for June sucker (5.09) was narrower than for Utah sucker (6.78) and intermediates (6.67), thus polygon overlap area with other morphs comprised a greater proportion of niche width for June sucker than of the other morphs (Table 3-3; Figure 3-11). The 36 % niche overlap between June sucker and intermediates comprised 61 % of the niche width of June sucker and 46 % of that of intermediates; niche widths of June sucker and Utah sucker displayed 11 % overlap, which represented 23 % and 17 % of their respective niche widths. Only a small proportion of the niche width of intermediates did not overlap with those of June sucker or Utah sucker (Figure 3-11). June sucker and Utah sucker displayed substantially smaller δ^{13}C ranges, 3.59 ‰ and 2.76 ‰, respectively, than intermediates, 4.52 ‰, whereas their respective δ^{15}N ranges, 2.99 ‰ and 3.19 ‰, were slightly greater than that for intermediates, 2.81 ‰.

Despite their morphological and isotopic signature differences, June sucker, Utah sucker, and intermediates were at essentially the same trophic level (~ 4.0), tertiary consumer (Table 3-4). The mixing polygon (Figure 3-12) generated for June sucker revealed that fish eggs (or larvae) likely contributed to their diet, and this was supported by the June sucker trophic level of 3.99. When fish eggs (or larvae) were excluded from potential prey items, June sucker isotopic bi-plot coordinates fell outside the convex polygon bounded by planktonic food sources whereas inclusion of fish eggs (or larvae) with planktonic prey items generated a polygon which bounded June sucker coordinates (Figure 3-12, June sucker – dashed line excludes fish sources). Similarly, the diet of intermediates likely included fish eggs (or larvae) as their exclusion as potential diet sources created a mixing polygon (benthic and planktonic sources) that excluded intermediate sucker $\delta^{13}C$ and $\delta^{15}N$ coordinates (Figure 3-12, Intermediate – dashed line excludes fish sources); here too, the trophic level of 3.93 supported this. The mixing polygon created using benthic / littoral diet sources bounded Utah sucker $\delta^{13}C$ and $\delta^{15}N$ coordinates, suggesting contributions from fish eggs (or larvae) to Utah sucker diet were unnecessary (Figure 3-12, Utah sucker), however, the trophic level of 3.97 indicates otherwise.

Plotting the mean isotopic signatures of the three morphs of Utah Lake suckers on Landom's (2010) Utah Lake biota $\delta^{13}C$ – $\delta^{15}N$ bi-plot (i.e., Utah Lake food web), corrected for different preservation methods, revealed that June sucker diet exploited the pelagic sub-web predominantly and Utah sucker diet exploited primarily the benthic / littoral sub-web. The diet of suckers of intermediate morphology exploited both pelagic and benthic / littoral sub-webs (Figure 3-13).

Density / Growth Lab Experiment

Mixed model (block as random factor) ANOVA of the growth rates of June sucker and Utah sucker reared at different conspecific densities revealed no differences due to sucker morph ($F_{1,84} = 1.24$, $P = 0.268$), fish density ($F_{2,84} = 2.79$, $P = 0.067$), or their interaction ($F_{2,84} = 0.71$, $P = 0.496$) (Table 3-5; Figure 3-14). The effect of density approached statistical significance, perhaps indicating biological significance in the slight trend for increased growth rate with increasing density.

DISCUSSION

Keleher et al. (1998) estimated fewer than 300 wild adult June sucker remained in Utah Lake by the mid to late 1990s, with a similar estimate for Utah sucker (K. Wilson, UDWR, personal communication). With essentially no recruitment of suckers of any morph since the early 1990s (K. Wilson, UDWR, personal communication), the number of surviving wild Utah Lake suckers likely declined further because of mortalities in the years prior to this study. Thus, despite the small sample sizes, the 11 wild June sucker used in the telemetry study, the 11 different wild June sucker used in the stable isotopes analysis, the 22 Utah sucker used in the telemetry study, the 29 Utah sucker (which included some of the CART tagged fish) used in the stable isotopes study, and the 12 sucker of intermediate morphology used in the stable isotopes analysis represented substantial proportions of the surviving wild sucker morphs in Utah Lake.

Radio / Acoustic Telemetry

Interference signals during acoustic / radio telemetry undoubtedly reduced sucker hits and detections, although June sucker and Utah sucker acoustic and radio transmissions were assumed equally affected. The decision prior to RF analysis to equate a single hit to a detection was influenced by the number of interference signals (twice the number of hits) recorded, and because interference signals and single hits were frequently associated. Interference signals were typically observed to occur concurrently with the detection of at least one CART tagged sucker and one or more of the following events (Cole, personal observation): motorized watercraft in the vicinity of a hydrophone or receiver antenna; sonar depth detector operating in vicinity of a hydrophone; or an aircraft flying near receiver antenna or hydrophone. Such events were common, as Utah Lake is a popular destination for anglers and users of motorized watercraft and a busy municipal airport, with its main flight path directly over the Provo River radio receiver / data-logger and antenna, is located on the southeastern shore between the Provo River confluence and Provo Bay. Additionally, radio transmissions associated with mining, gravel, and transportation industries on the western shore of Utah Lake likely contributed to interference signals.

Another factor confounding telemetric analysis and interpretation was the difference between the 2004 and 2005 water years. During 2004, the last year of a five year drought, the maximum water level in Utah Lake was about 1.3 m below the compromise elevation of 1368.261 m, and by the end of summer, the minimum lake level was 2 m below compromise elevation. Provo Bay was greatly reduced by the drought. The southernmost region of Goshen Bay was inaccessible to telemetric monitoring and perhaps to suckers. This may have contributed to the relatively low DPUE associated with the southern stratum. Along much of Utah Lake's shoreline, the water level failed to inundate vast beds of emergent vegetation in 2004, perhaps contributing to the greater detection rates at limnetic compared to littoral hydrophones. In 2005, the maximum lake level was 0.3 m below compromise elevation (1.0 m greater than the maximum in 2004) and the minimum level was about 0.7 m below compromise elevation (1.3 m greater than the minimum in 2004). Large stands of littoral emergents (e.g., *Typha latifolia*, *Scirpus validus*, *Phragmites australis*) were re-inundated, and Utah Lake was fringed with vegetation; the surface area of Utah Lake in late summer of 2004 was approximately 83 % of that in spring of 2005 (interpolated from Fuhriman et al. 1981). The Provo River's peak mean daily discharge during spring runoff was an order of magnitude greater and occurred three weeks later at cooler water temperature in 2005 (45.6 m^3/s; 24 May; 11.4 °C) than in 2004 (4.18 m^3/s; 4 May; 12.0 °C), and thus spawning cues for Utah Lake suckers varied considerably between the two years.

June sucker and Utah sucker used all sectors of Utah Lake monitored in this study, and although there was considerable variation among individuals in distance traveled, individuals of both morphs traveled great distances (approaching 1000 km) during the course of monitoring. Random forests analysis revealed that variation in the distribution and movement of June sucker and Utah sucker in Utah Lake was better explained by environmental factors (oDPUE, temperature, zone) rather than biological characters (morph or sex) of individual suckers. By far the best predictor of detection of June sucker at a hydrophone / receiver during a sampling period was the detection of Utah sucker during the same sampling period and vice versa. Perhaps in Utah Lake, suckers of all morphologies school together similar to feeding June sucker (Billman 2008) in the Red Butte Reservoir refugium The Red Butte Reservoir population also displayed a morphological continuum from benthivorous to planktivorous although the morphological differences were not as pronounced as in the Utah Lake population (Cole, personal observation; unpublished data). For most of 2004, Utah Lake had essentially no littoral zone (or at least no emergent and very few submergent macrophytes) and its maximum depth was about 2 m. A school of Utah Lake suckers of diverse morphologies could move together, exploiting planktonic and / or benthic resources separated by only 2 m.

Temperature was also an important predictor, and its inclusion in models excluding oDPUE increased the proportion of variation in DPUE explained even when temperature was not the most important predictor. Evidence suggests that Utah Lake suckers selected habitats based on temperature differences among locations rather than simply being more active at higher or more optimal temperatures. Such temperature related changes in activity likely did influence seasonal differences in DPUE.

A much more extensive telemetric investigation of shortnose sucker and Lost River sucker in Upper Klamath Lake, OR documented use of a refugium containing groundwater springs when water quality in other regions of the lake was degraded (high temperature, supersaturated or very low dissolved oxygen levels, high pH) by extensive blooms followed by decomposition of the cyanobacter, *Aphanizomenon flos-aquae* (Banish et al. 2009). Although *A. flos-aquae* is the most common phytoplankter in Utah Lake with blooms occurring annually in late summer and autumn (Rushforth et al. 1981) and nutrient levels classify Utah Lake as hypereutrophic (Fuhriman et al. 1981), monthly limnological monitoring (Crowl, unpublished data) detected no anoxic periods in Utah Lake during this study. Given the water temperatures at the hydrophone locations in the autumn of 2004, the shift in sucker detections from the eastern to the western shore of Utah Lake is likely temperature related rather than an oxygen issue. Groundwater springs (Fuhriman et al. 1981) likely contributed to the temperature differences between the western limnetic sites and the littoral and eastern sites. Utah Lake suckers exhibited a similar seasonal shift from eastern to western shore in 2005, however temperature data for the western shore was absent. In the late summer and autumn of 2004, common carp and walleye (*Sander vitreus*) also showed a similar shift from eastern to western shore (Landom et al. 2006).

Suckers’ nearly twofold detection rate at limnetic compared to littoral hydrophones may be indicative of the importance of the open water habitat in Utah Lake although other factorsmay have contributed to the DPUE difference between zones. The mean detection range of limnetic hydrophones (373 m) was slightly greater than that for littoral hydrophones (350 m), thus limnetic hydrophones monitored about 14 % more area than littoral hydrophones. Littoral hydrophones were occasionally placed within their detection distance of shoreline when the bottom dropped off more steeply, decreasing the area of potential habitat surveyed. In 2004, the effects of drought may have led to fewer sucker visits to near shore habitats as littoral emergents were absent because of low lake level failing to inundate these stands thus eliminating a shallow, productive habitat that provided potential cover from aquatic and avian predators. In average and wet years, these marsh habitats provide cover for suckers, other fishes, and invertebrates and dampen wind and wave action. In late summer and autumn of 2004, some littoral hydrophones were placed several hundred meters offshore at water depths of about one meter where a mud / silt bottom with no vegetation very gradually sloped up to the shoreline, which was still several hundred meters away across a mud flat from where emergents thrived in wetter years. Suckers occupying this habitat would have been especially susceptible to avian predators, and although no sucker mortalities could be documented over the course of random telemetric monitoring, some fish eventually ‘disappeared’ from detection. It is possible that some tagged suckers fell prey to pelicans or other avian predators (see Scoppettone et al. 1986).

The greater detection rate of eastern shore relative to western shore hydrophones may be related to all major tributaries entering on the eastern side of Utah Lake. Productive Provo Bay is also on the eastern side. This study documented suckers of both morphs visiting Provo Bay just prior to and during the spawning season, and post-spawning aggregations of June sucker have been described there in July and August (Radant and Shirley 1987). Suckers likely visited Provo Bay during the course of random telemetric monitoring, and such fish would have been more susceptible to detection by eastern as opposed to western hydrophones. Finally, Long Bar, located on the eastern side of Utah Lake between the mouth of Provo Bay and the confluence of the Provo River and essentially the only structure in the main lake besides Bird Island, appears to be important habitat for Utah Lake suckers of both species. More hits occurred at the two hydrophones there during a single sampling period than at all other hydrophones for the duration of the study combined. In addition toJune sucker and Utah sucker, other fish species (e.g., common carp, walleye, white bass) also congregate near Long Bar (Landom et al. 2006; B. Loy, fourth generation Utah Lake commercial fisherman, personal communication). Because of its structure and location near the mouth of Provo Bay, Long Bar may concentrate food sources (especially planktonic) as wind driven currents push water into or out of productive Provo Bay.

Although no differences between June sucker and Utah sucker were revealed in timing of pre-spawning staging near the mouths of the Provo and Spanish Fork Rivers or of the spawning run, the magnitude order difference in Provo River peak discharge between 2004 and 2005 and the small sample sizes (especially of suckers detected in the upper rivers) confounded interpretation of the results. Spawning cues available to Utah Lake suckers varied considerably between the two years, considering the differences in spring runoff magnitude and duration. Linear regression analysis of 2005 Provo and Spanish Fork Rivers spawning run data revealed significant relationships of the proportion of suckers of either morph detected with water temperature, discharge, and their interaction. Hines (2011), in a subsequent study examining June sucker spawning cues at several Utah Lake tributaries, found total dissolved solids at the lake side of the lake / river interface to be the best predictor of June sucker pre-spawn staging, stream discharge to be the best predictor of June sucker spawning (i.e., upriver migration), and water temperature to be relative unimportant in predicting either staging or spawning. This discrepancy regarding the importance of water temperature might be related to the many additional predictor variables Hines (2011) examined; also, all of the June sucker monitored in that study were stocked fish (most from the smaller, cooler Red Butte Reservoir refugium), whereas of the June sucker used in the current investigation, 11 were wild and 13 were stocked. Comparison of wild versus stocked June sucker behavior warrants further investigation, but must be undertaken quickly before wild June sucker disappear. Continued monitoring of Utah Lake tributaries will provide important information regarding spawning behavior and larval sucker emergence and drift as the JSRIP improves stream habitat and breeds and stocks increasing numbers of June sucker. It is unknown if June sucker (or Utah sucker) have a natal homing instinct, and such knowledge would surely be valuable in the quest for sucker recruitment.

One shortcoming of the telemetric investigation was the lack of CART tagged intermediate suckers, which comprised a larger proportion of the Utah Lake sucker population than June sucker of Utah sucker. That said, two (codes 130 and 169) of the CART tagged Utah sucker (identified as such by a technician) were included in the stable isotope analysis as intermediates (identified morphologically as established in Cole 2008); their isotopic signatures grouped with the Utah sucker rather than the June sucker. Given the lack of differences in distribution, movement, and spawning behavior between June sucker and Utah sucker, there is little reason to expect otherwise regarding intermediate morphs.

Stable Isotopes Analysis

Because of exposure to less water turbulence, periphyton in lakes are enriched in ^{13}C relative to phytoplankton; thus benthic / littoral food webs are ^{13}C enriched relative to planktonic (pelagic) food webs, and this uncoupling of carbon flows between benthic and planktonic food webs may be a global feature of lakes (France 1995). For Utah Lake suckers, $\delta^{13}C$ was a function of morphology: Utah sucker, as predicted, with their large, papillose lips and ventral mouth were enriched in^{13}C relative to June sucker with their small, smooth lips and terminal oblique mouth, and suckers of intermediate morphology had intermediate values of δ ^{13}C. A stable isotope-derived food web developed for Utah Lake described slight decoupling in energy flow between planktonic and benthic-littoral subwebs (Landom 2010). The degree of decoupling is related to the number of transzonal migrants that integrate both ^{13}C bases. Plotting of Utah Lake suckers' mean δ^{13}C and δ^{15}N coordinates (after conversion for different preservation method) on the δ^{13}C – δ^{15}N bi-plot space of Landom (2010) depicting the Utah Lake food web reveals suckers' morphologies predicted their positions in the food web: June sucker were indeed components of the planktonic subweb, Utah sucker were components of the benthic / littoral subweb, and intermediate suckers fell almost directly on the line dividing the two subwebs and exploited both ^{13}C bases (Figure 3-13).

Several lines of evidence indicate that the diets of Utah Lake suckers included fish eggs, or perhaps larvae, and foremost were the trophic positions of all three morphs as tertiary consumers (TP = ~ 4.0). Although predatory copepods can be enriched in ^{15}N relative to herbivorous zooplankton (Ventura and Catalan 2008) and might account for some ^{15}N enrichment in June sucker and intermediates, they are unlikely to be a major component of Utah sucker diet. Presumed zooplanktivores, rainbow smelt (*Osmerus mordax*), have been documented (Crowder 1980; Hrabik et al. 1998) to prey on pelagic larval fishes, which may display elevated $\delta^{15}N$ (Vander Zanden et al. 1998; Murchie and Power 2004). Similar predation might explain some ^{15}N enrichment in June sucker or intermediates, but again, not in benthivorous Utah sucker; also, larvae of the most common fishes in Utah Lake are not pelagic. When mean $\delta^{13}C$ and $\delta^{15}N$ coordinates for June sucker, Utah sucker, and intermediates are plotted on Landom's (2010) Utah Lake food web $\delta^{13}C$ – $\delta^{15}N$ bi-plot, the suckers group with fishes with large piscivorous components in their diets: walleye, white bass, channel catfish (*Ictalurus punctatus*), and black bullhead (*Ameiurus melas*). Also, only the mean $\delta^{13}C$ and $\delta^{15}N$ coordinates for Utah sucker fell within the mixing polygon created by presumed diet sources (benthic / littoral macroinvertebrates); coordinates fell outside of the polygon of presumed prey items for June sucker (seston and zooplankton) and for intermediates (seston, zooplankton, and benthic / littoral macroinvertebrates). Given the large populations of common carp, fathead minnows, white bass, and other nonnative fishes in hypereutrophic Utah Lake, fish eggs represent the most probable source of this ^{15}N enrichment in suckers. In eggs, $\delta^{15}N$ is typically similar to or greater than $\delta^{15}N$ of adult fish (Bilby et al. 1996; Murchie and Power 2004). Inclusion of the isotopic signatures of three common Utah Lake fish species (as surrogates for fish eggs) as potential prey items in mixing polygons resulted in coordinates for June sucker and intermediates falling within their respective mixing polygons. Gut content analyses (K. Landom, USU, personal observation) of Utah Lake fishes have revealed that fish eggs are consumed by many species, including walleye and channel catfish, which exhibit isotopic signatures similar to Utah Lake suckers.

June sucker had the narrowest niche width and $\delta^{13}C$ range of Utah Lake suckers. Suckers of intermediate morphology had a wider $\delta^{13}C$ range (by over 1 ‰) than either of the extreme morphs, indicative of their exploitation of both food sub-webs whereas the narrower $\delta^{13}C$ ranges of the extreme morphs are indicative of more restrictive diets within a single sub-web predominantly (June sucker – planktonic sub-web; Utah sucker – benthic sub-web). Despite the considerable niche width overlap intermediates share with the two extreme morphs, intermediates appeared in good condition (Cole, personal observation), a testament to Utah Lake's productivity.

Density / Growth Experiment

Although neither morph, rearing density, nor their interaction had significant effects on juvenile sucker growth rate, the effect of density approached significance: as sucker density increased, there was a trend among both morphs for growth rate to increase (Figure 3-18). This supports the described Allee effect among June sucker (age 0) raised in cages on natural prey in Provo Bay (Gonzalez 2004), although it does raise questions regarding the mechanism involved. Likely, the increased growth rate at higher densities has a physiological basis related to predation risk and safety in numbers. Sucker, when in larger aggregations, (i.e., schools) may simply secrete less stress hormones (e.g., cortisol, epinephrine, and / or norepinephrine) known to inhibit growth, because they perceive less threat from potential predators.

Conclusions and Management Implications

Despite the morphological and correlated dietary (as determined via $\delta^{13}C$ and $\delta^{15}N$) differences among Utah Lake suckers, morphology (and gender) explained little variation regarding distribution and movement, pre-spawning staging, or spawning timing. However, the extreme contrast between 2004 and 2005 in spring runoff and lake levels may have introduced variation masking effects of morphology or gender. Utah Lake suckers reach large size (> 600 mm) and are long-lived (> 40 years), late-maturing, and highly fecund, life-history adaptations to a stochastic desert lake ecosystem where highly variable environmental conditions are not conducive for successful spawning and recruitment annually, or even regularly. In 2004, the last year of a 5-year drought, peak discharge of the Provo River during spring snowmelt was an order of magnitude less than in spring 2005, when an extensive snowpack produced an extended runoff with very high discharge raising the lake level nearly 2 m from the previous autumn. The telemetric sampling included two spawning seasons with environmental conditions at opposite ends of the precipitation / runoff spectrum (e.g., drought year versus wet year), both of which are conditions that historically may have reduced suckers’ spawning numbers. The tributaries in which Utah Lake suckers spawn have been drastically anthropogenically modified since the mid-1800s. Habitat degradation, channelization, and flow alteration have confounded cues that perhaps in the past resulted in temporal segregation of morphs during spawning, although suckers of intermediate morphology have been reported since the earliest ichthyological explorations of Utah Lake (Jordan 1878). Management of spring runoff in tributaries to more closely mimic historic discharges and temperatures would likely enhance the detection of spawning cues by Utah Lake suckers and perhaps promote temporal segregation of June sucker and Utah sucker spawning.

As the JSRIP continues improving multiple tributaries' spawning and rearing habitats and maintains the breeding and stocking program using hatchery bred and hatchery and refugium reared June sucker, continued monitoring (via PIT tag telemetry) of the increasing number of stocked sucker will provide information (e.g., temporal or spatial patterns in spawning) that can be used to further enhance recovery and make decisions in light of predicted changes in precipitation patterns in a warming environment. Hatchery and refugium June sucker stocks, which are genetically differentiated from wild June sucker (Mock et al. 2004), should be supplemented when possible with sperm and / or eggs from *wild suckers of any morphology* spawning in the Provo River (or other tributaries). This is especially important given how few wild suckers persist. Also, as the JSRIP's common carp removal program progresses, continued stable isotopic monitoring of suckers and other components of the Utah Lake food web could be used to track changes in energy flow that accompany the removal of millions of kilograms of common carp from Utah Lake. Determining whether June sucker (and Utah sucker) benefit from fewer common carp and the predicted accompanying changes, an increase in submerged aquatic macrophytes and lower turbidity, or if the energy freed up by common carp (adult) removal benefits juvenile common carp or some other nonnative competitor(s) with or predator(s) on June sucker (and Utah sucker) is important.

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Table 3-1. Seasonal periods during which Utah Lake was surveyed in the random tracking telemetric investigation of sucker distribution and movement.

Seasonal period	Duration
Summer 2004	6 July 2004 - 10 August 2004
Late summer 2004	11 August 2004 - 22 September 2004
Autumn 2004	10 October 2004 - 4 November 2004
Winter 2005	20 January 2005 - 15 February 2005
Late summer 2005	2 August 2005 - 2 September 2005
Autumn 2005	30 September 2005 - 27 October 2005

Table 3-2. Significant predictor variables from significant linear regression models ($P < 0.05$) examining the relationship between the dependent variables, proportions (arcsine square root transformed) of June sucker or Utah sucker detected at Provo and Spanish Fork River hydrophones / receivers, and the independent variables, temperature (lake, mouth, or river), discharge, and their interaction during the 2005 spawning season split by ascending and descending hydrograph.

				Model statistics			Predictor statistics			
River	Hydrograph	Hydrophone / Receiver	Model	*F* (*df*)	*P*	adj R^2	Significant variable	Relationship	*t* value	*P*
Provo	Ascending	Lake	1 June sucker ~ lake temperature * discharge	11.7 (3, 94)	1.40E-06	0.249	Lake temperature	Positive	5.610	2.0E-07
							Interaction	Negative	-2.043	0.04390
			2 Utah sucker ~ lake temperature * discharge	10.42 (3, 94)	5.56E-06	0.226	Lake temperature	Positive	5.207	1.1E-06
		Mouth	3 June sucker ~ mouth temperature * discharge	15.0 (3, 85)	6.41E-08	0.323	Mouth temperature	Positive	6.655	2.6E-09
							Interaction	Negative	-2.985	0.00370
			4 Utah sucker ~ mouth temperature * discharge	15.04 (3,85)	6.15E-08	0.324	Mouth temperature	Positive	6.585	3.6E-09
							Discharge	Positive	2.370	0.02006
							Interaction	Negative	-3.493	0.00076
	Descending	Mouth	5 June sucker ~ mouth temperature * discharge	23.53 (3, 53)	8.13E-10	0.547	Mouth temperature	Positive	5.243	2.8E-06
							Discharge	Positive	4.961	7.6E-06
							Interaction	Negative	-5.384	1.7E-06
			6 June sucker ~ river temperature * discharge	19.32 (3, 53)	1.36E-08	0.495	River temperature	Positive	4.966	7.5E-06
			7 Utah sucker ~ mouth temperature * discharge	22.18 (3, 53)	1.94E-09	0.532	Mouth temperature	Positive	3.463	0.00107
							Discharge	Positive	3.129	0.00285
							Interaction	Negative	-3.905	0.00027
			8 Utah sucker ~ river temperature * discharge	18.35 (3, 53)	2.72E-08	0.482	River temperature	Positive	3.155	0.00264
		Downstream	9 Utah sucker ~ mouth temperature * discharge	5.6 (3, 53)	0.00207	0.198	Mouth temperature	Positive	3.899	0.00027
							Discharge	Positive	3.026	0.00382
							Interaction	Negative	-2.575	0.01284
			10 Utah sucker ~ river temperature * discharge	4.064 (3, 53)	0.01133	0.141	River temperature	Positive	2.835	0.00648
Spanish Fork	Ascending	Mouth	11 June sucker ~ river temperature * discharge	10.35 (3, 83)	7.38E-06	0.246	River temperature	Positive	2.015	0.04710

Table 3-3. Niche width and percent niche overlap {and percent overlap width / morph niche width} between pairs of Utah Lake sucker morphs. Percent niche overlap equaled overlap area / total area x 100 for a pair of morphs; percent overlap / morph niche width was the percentage of a morph's niche width the overlap area with another morph comprised (JS – June sucker, IS – Intermediate, US – Utah sucker).

Morph	Niche width	Niche overlap (%) {overlap / morph niche width [%]}		
		JS	IS	US
June sucker	5.10		35 {60}	11 {23}
Intermediate	6.67	35 {46}		47 {65}
Utah sucker	6.40	11 {18}	47 {62}	

Table 3-4. Isotopic signature for ^{15}N ($\delta^{15}N$), $\delta^{15}N_{baseline}$, and trophic level determined for June sucker, Utah sucker, and suckers of intermediate morphology.

Morph	$\delta^{15}N$ (‰)	$\delta^{15}N_{baseline}$ (‰)	Trophic level
June sucker	17.73	10.97	3.99
Intermediate	16.81	10.25	3.93
Utah sucker	16.36	9.67	3.97

Table 3-5. Mean growth rate and standard deviation (g/g/d) for juvenile June sucker and Utah sucker reared at three different densities (conspecific) with excess food availability.

Morph	Density (fish/tank)	Mean growth rate (g/g/d)	Standard deviation (g/g/d)
June sucker	1	0.0113	0.0016
	5	0.0121	0.0026
	10	0.0130	0.0022
Utah sucker	1	0.0087	0.0031
	5	0.0125	0.0039
	10	0.0124	0.0027

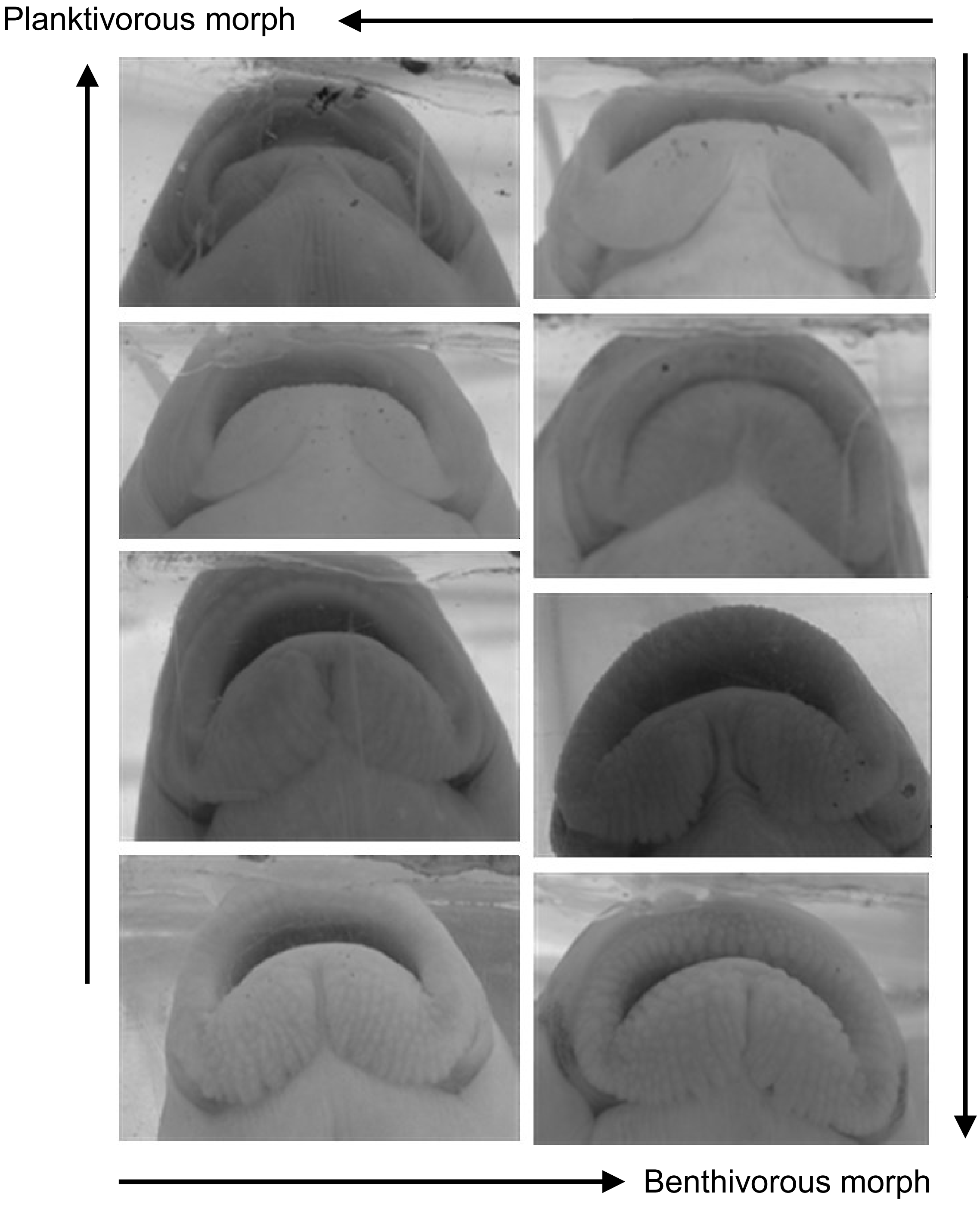
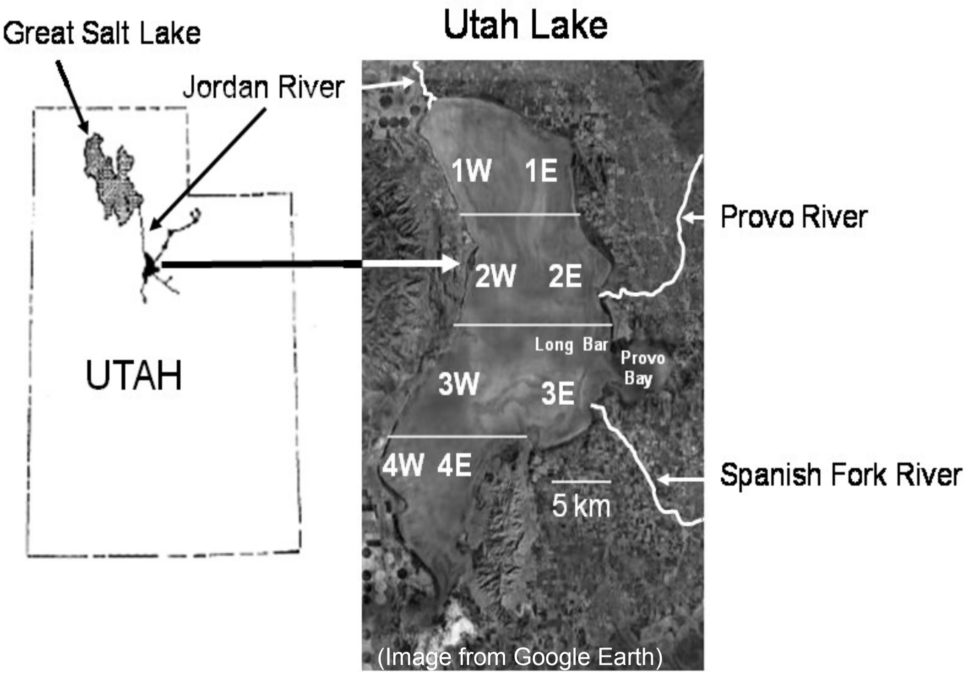


Figure 3-1. Digital images (among those analyzed in Cole et al. 2008) demonstrating the continuum of variation in mouth morphology (ventral view) exhibited by suckers in Utah Lake, UT. Planktivorous morphologies appear towards upper left (June sucker: minimal lip papillation; wide lower lip gap; and reduced lower lip lobes) whereas benthivorous morphologies appear towards lower right (Utah sucker: extensive lip papillation; narrow lower lip gap; and pronounced lower lip lobes). Variation in maxillary angle and head shape also contributes to intermediate morphologies.



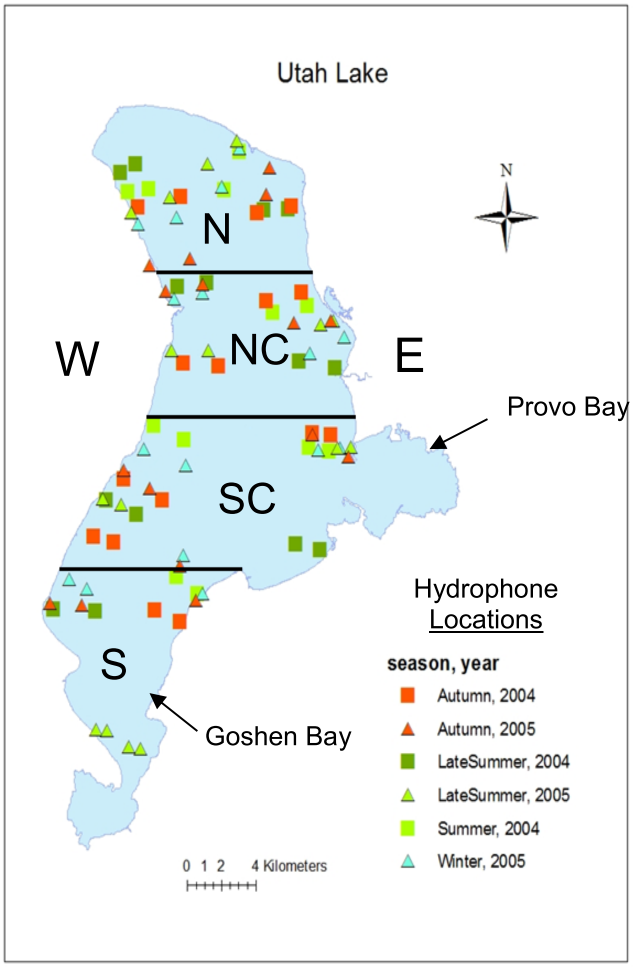


Figure 3-2. Maps showing geographical setting of Utah Lake, UT and locations of hydrophones with set dates during lake wide random survey via radio / acoustic telemetry. The Provo and Spanish Fork Rivers are Utah Lake's largest tributaries, and the Jordan River is its outlet. Long Bar, a large sandbar between the mouths of the Provo River and Provo Bay, is one of the few prominent bathymetric structures in Utah Lake.

N – north;
NC – north central;
SC – south central;
S – south;
E – east;
W – west

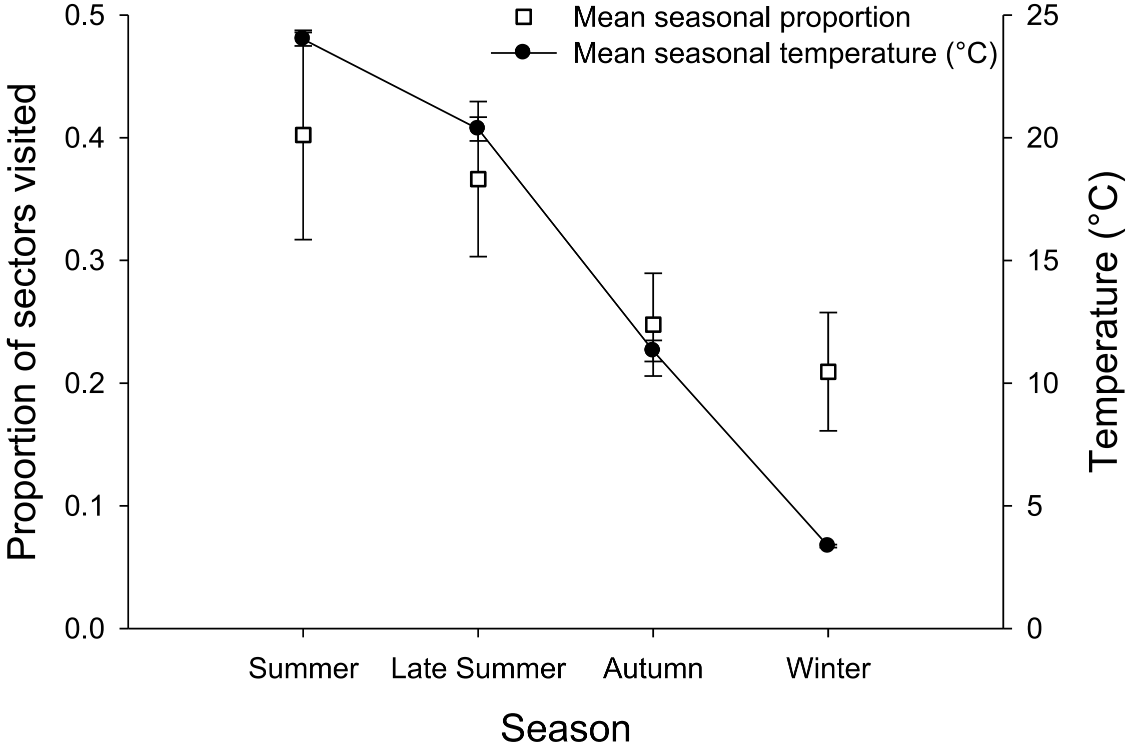


Figure 3-3. Means (±95 % confidence intervals) of the proportion of sectors in which individual Utah Lake suckers were detected during random telemetric monitoring in Utah Lake plotted by season with mean (±95 % confidence interval) seasonal temperature (°C).

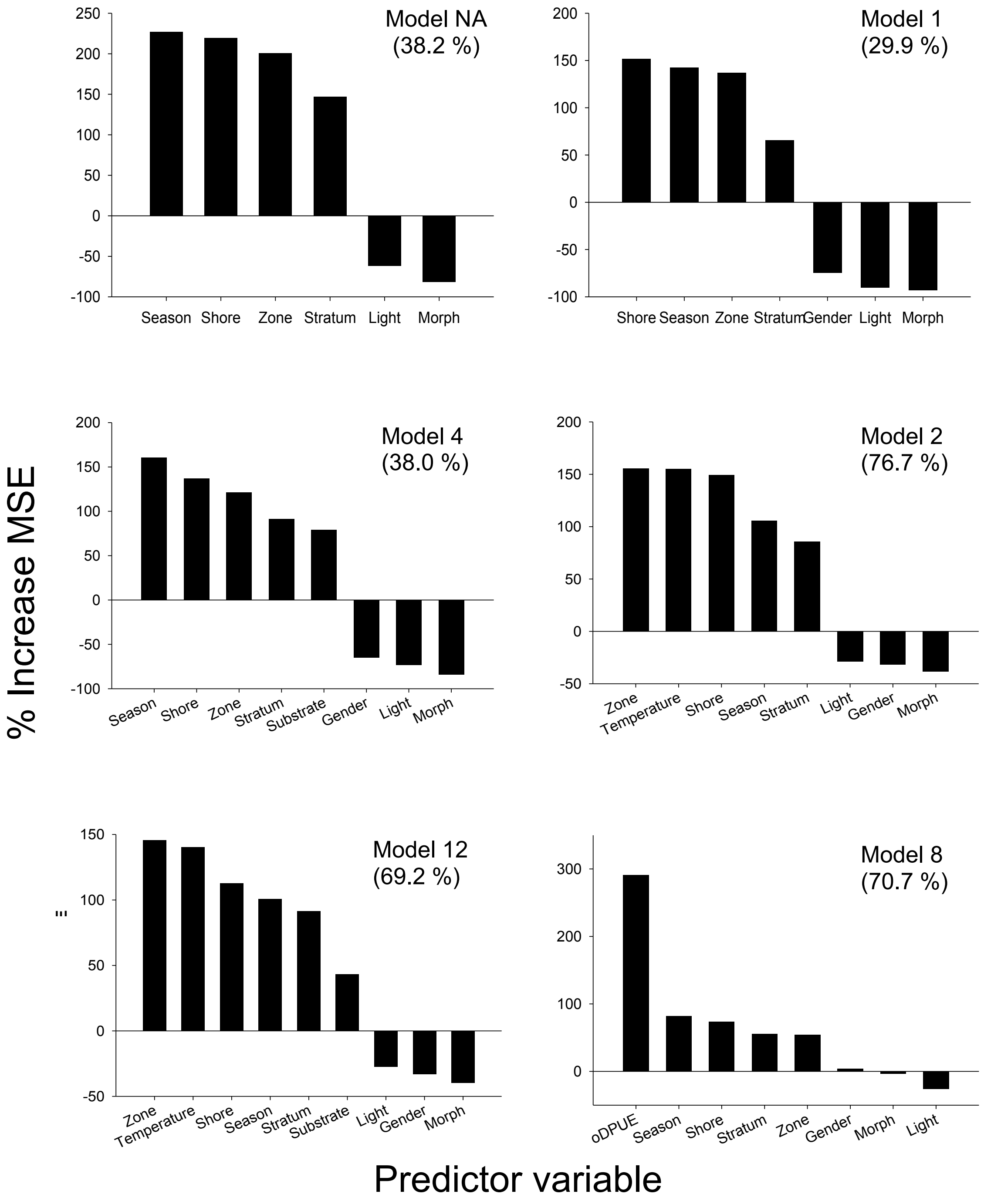


Figure 3-4. Variable importance plots (with percentage variance explained) from RF analysis of DPUE regressed with a variety of predictor variables. Models NA, 1, and 2 examined the most temporally and spatially complete telemetric dataset; Model 4 examined the most complete dataset including substrate data; Model 8 examined the most complete dataset including temperature data; and Model 12 examined the most complete dataset including substrate and temperature data. (See Appendix: Table 3-A-6)

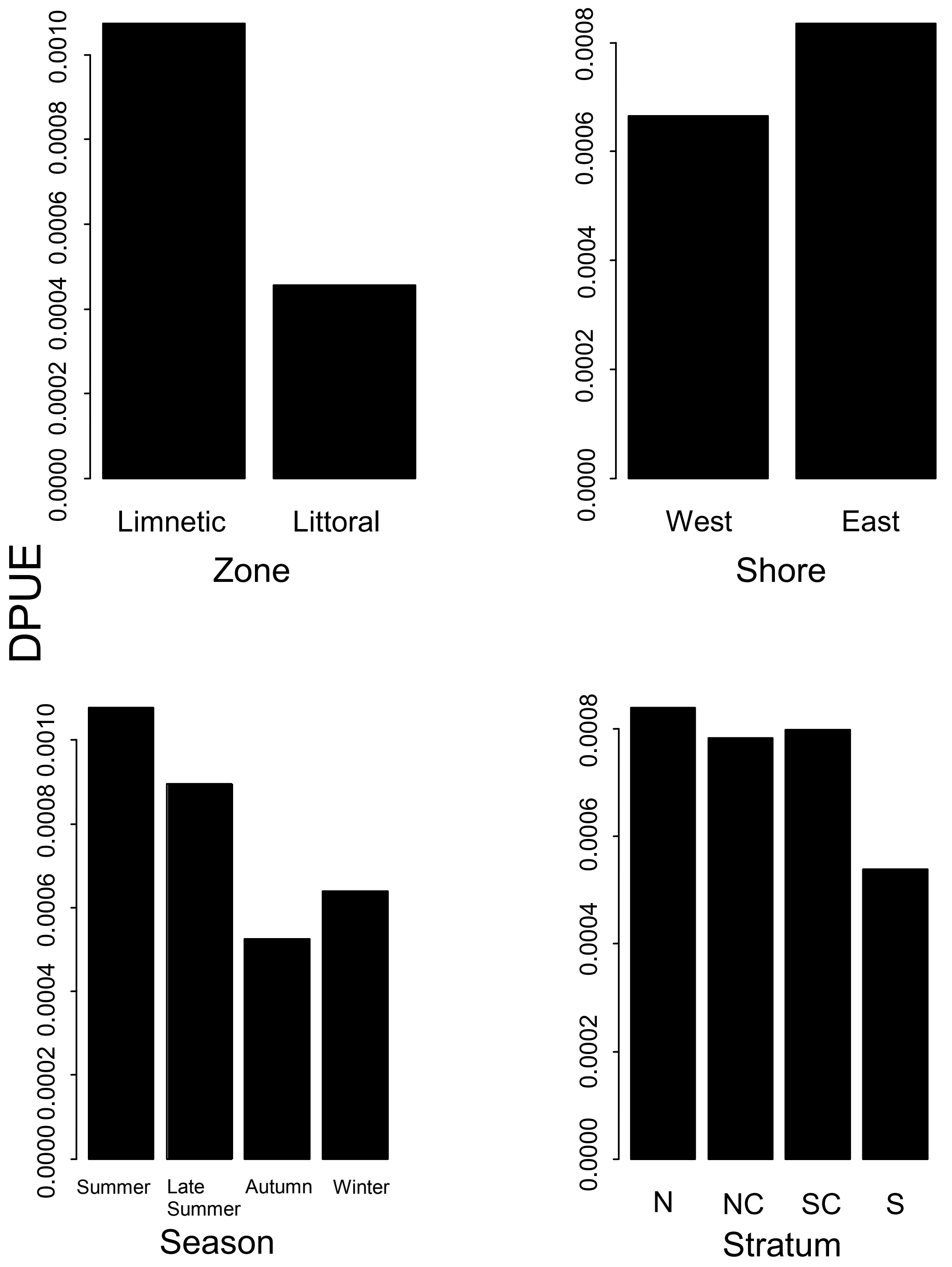


Figure 3-5. Partial dependency plots for zone, shore, season, and stratum generated by RF analysis of important variables of the most temporally and spatially complete telemetric dataset using DPUE as the dependent variable and not including oDPUE among predictors (See Appendix: Table 3-A-6, Model 1i).

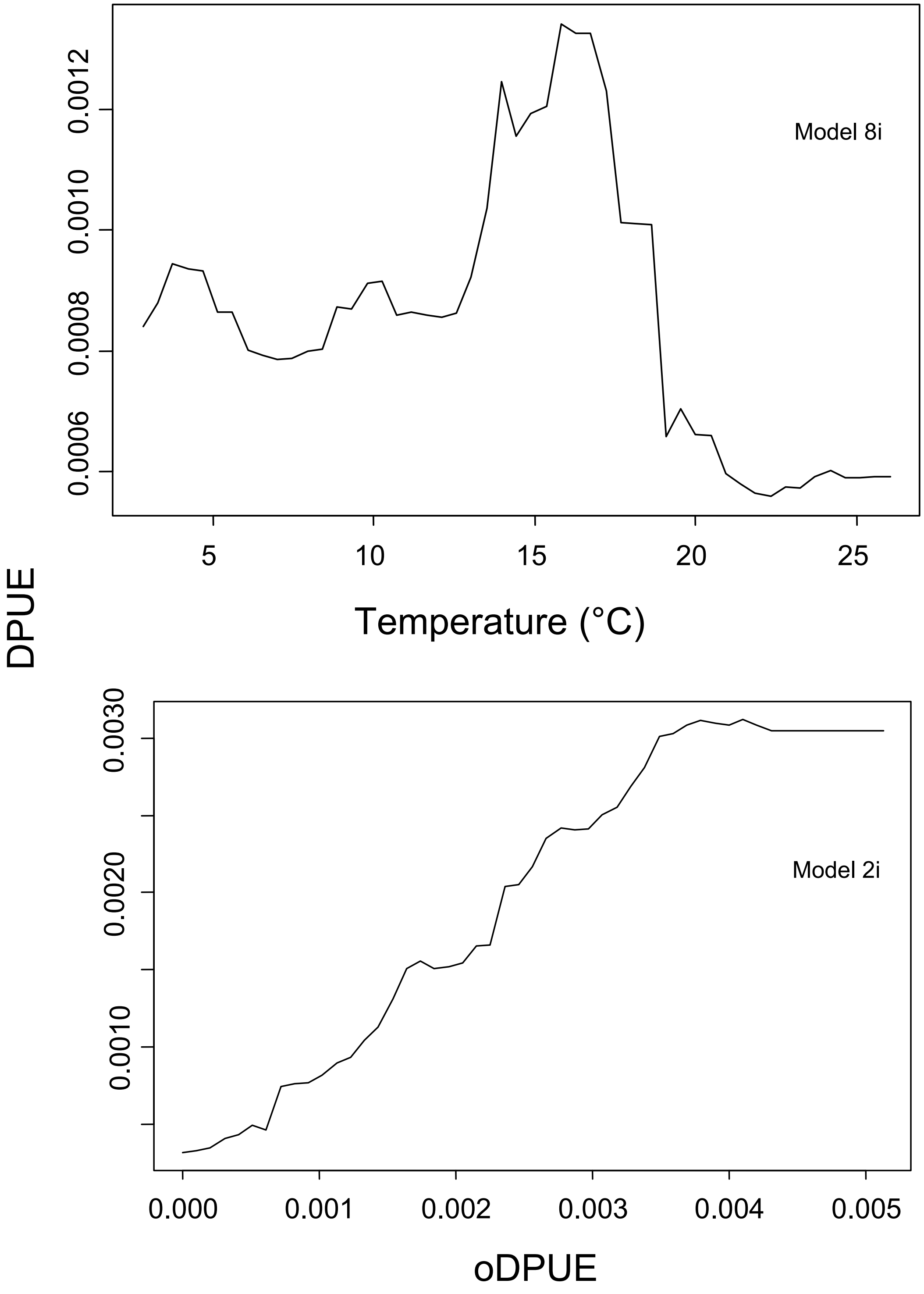


Figure 3-6. Partial dependency plots for temperature and oDPUE for Models 8i and 2i, respectively (see See Appendix: Table 3-A-6 for model descriptions).

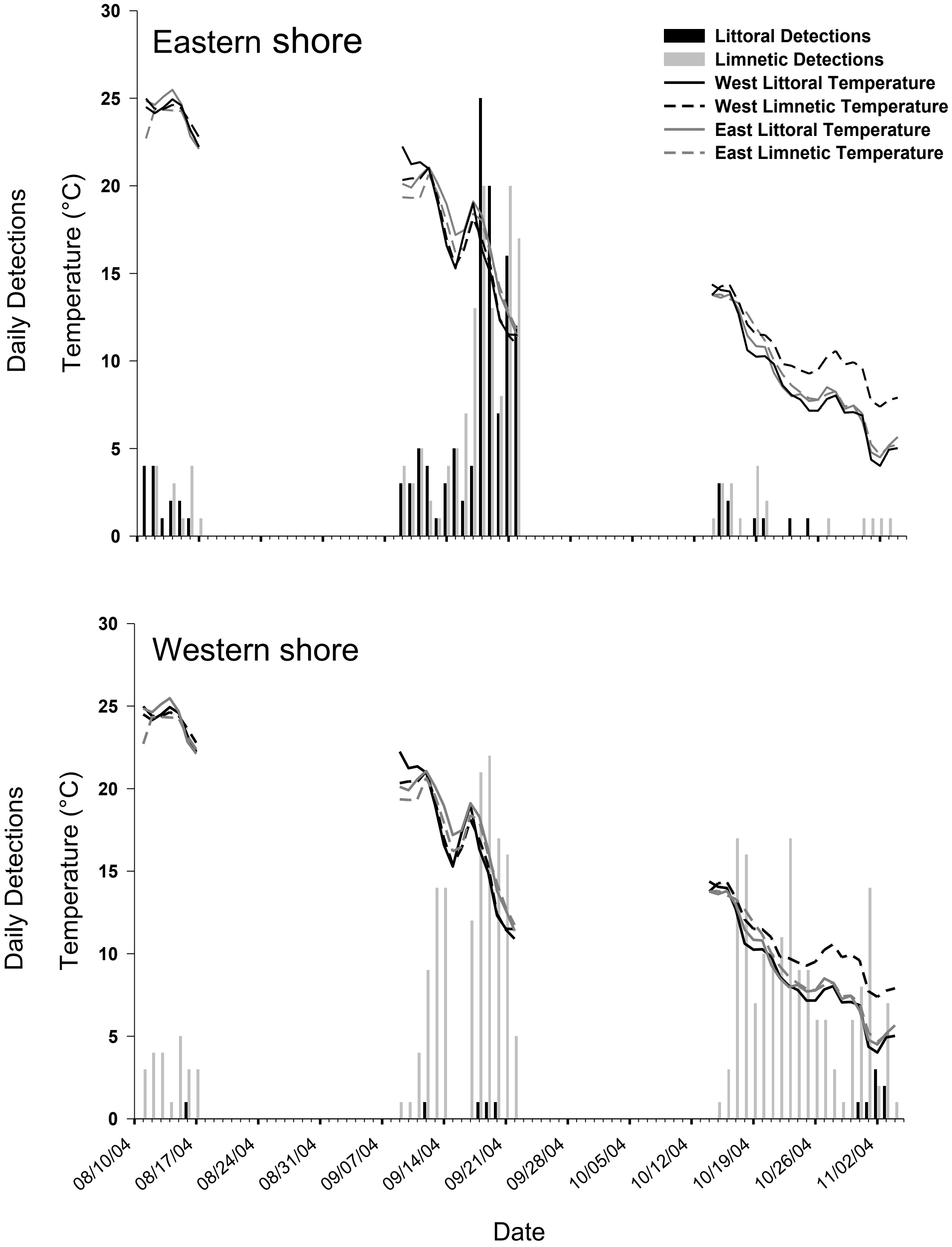


Figure 3-7. Plots show the summed daily detections of individual suckers and daily mean temperature for the late summer (August – September) and autumn (October – November) telemetric sampling periods in 2004 for the eastern and western shores of the three northernmost strata of Utah Lake.

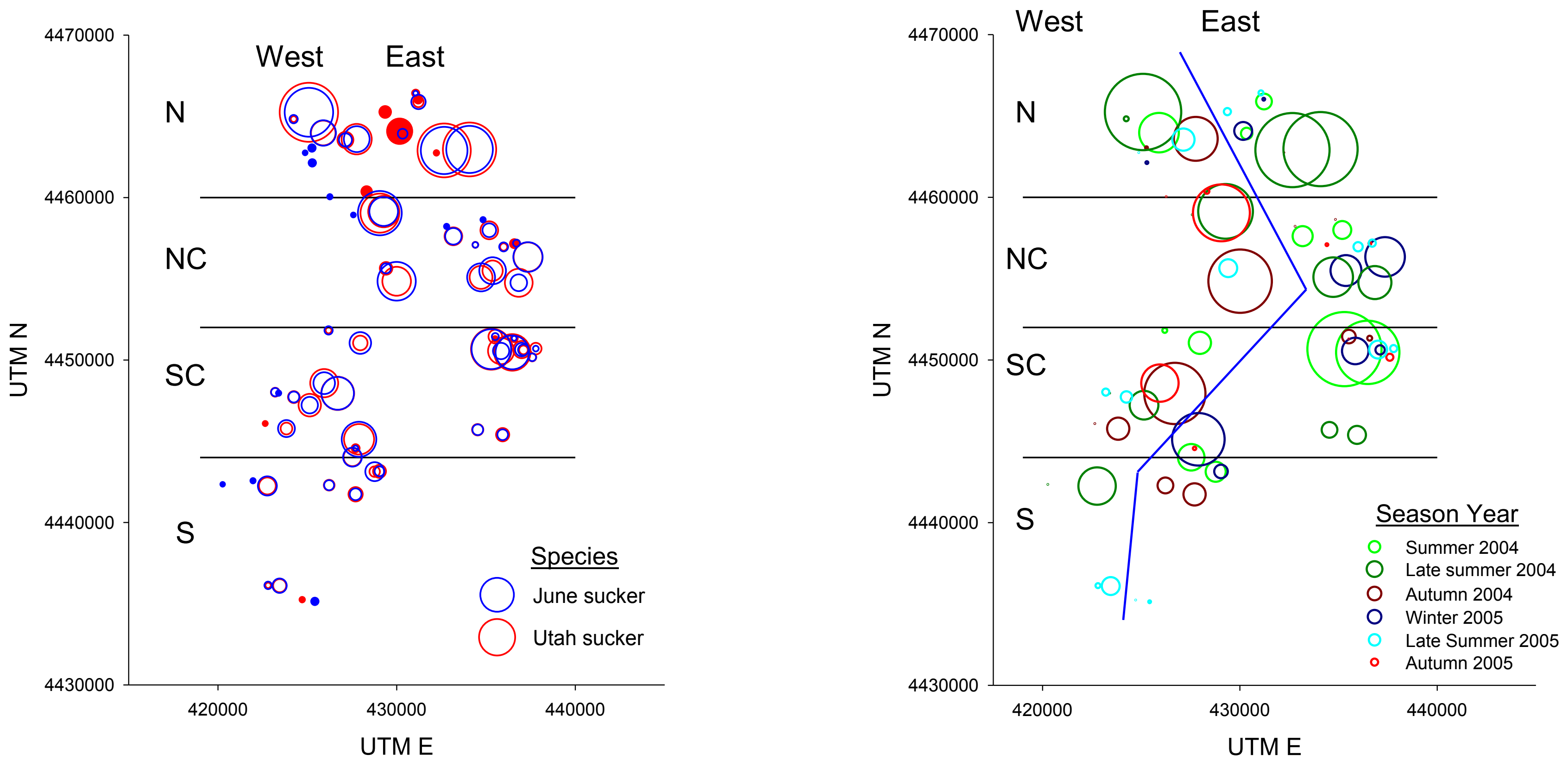


Figure 3-8. Hydrophone UTM coordinates of Utah Lake sucker detections displayed using bubble plots (diameters proportional to DPUE; scales differ between plots) to depict the influence of species, season (by year), stratum, and shore on June sucker and Utah sucker distribution and movement in 2004 – 2005 random survey. Each point represents the presence of at least one sucker; absences (DPUE = 0) were not plotted. Regarding species, out of 90 hydrophone sets, there were: 52 sets (58 %) with detection of both morphs (open circles; often overlap with several obscured); 11 sets (12 %) with only June sucker detected (solid blue circles); 9 sets (10 %) with only Utah sucker detected (solid red circles); and 18 sets (20 % of sets) with no suckers detected (not plotted).

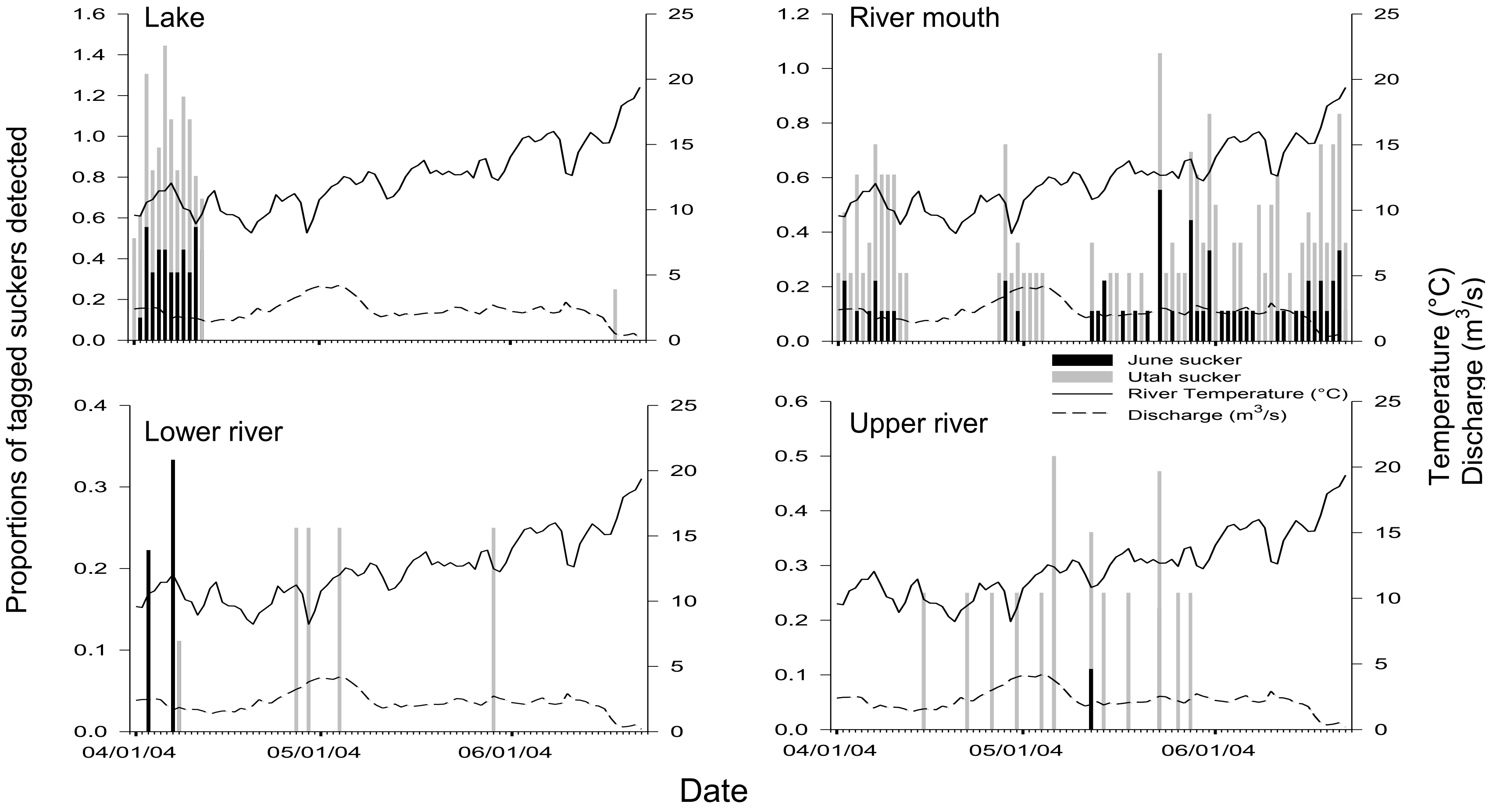


Figure 3-9. Plots depicting proportions (by species) of tagged Utah Lake suckers detected daily in 2004 via continuous telemetric monitoring of the lake, river mouth, and lower river sites (stationary hydrophones and receiver) and via intermittent monitoring (mobile tracking by foot or vehicle) of the upper river during the Provo River spawning run plotted with Provo River temperature and discharge.

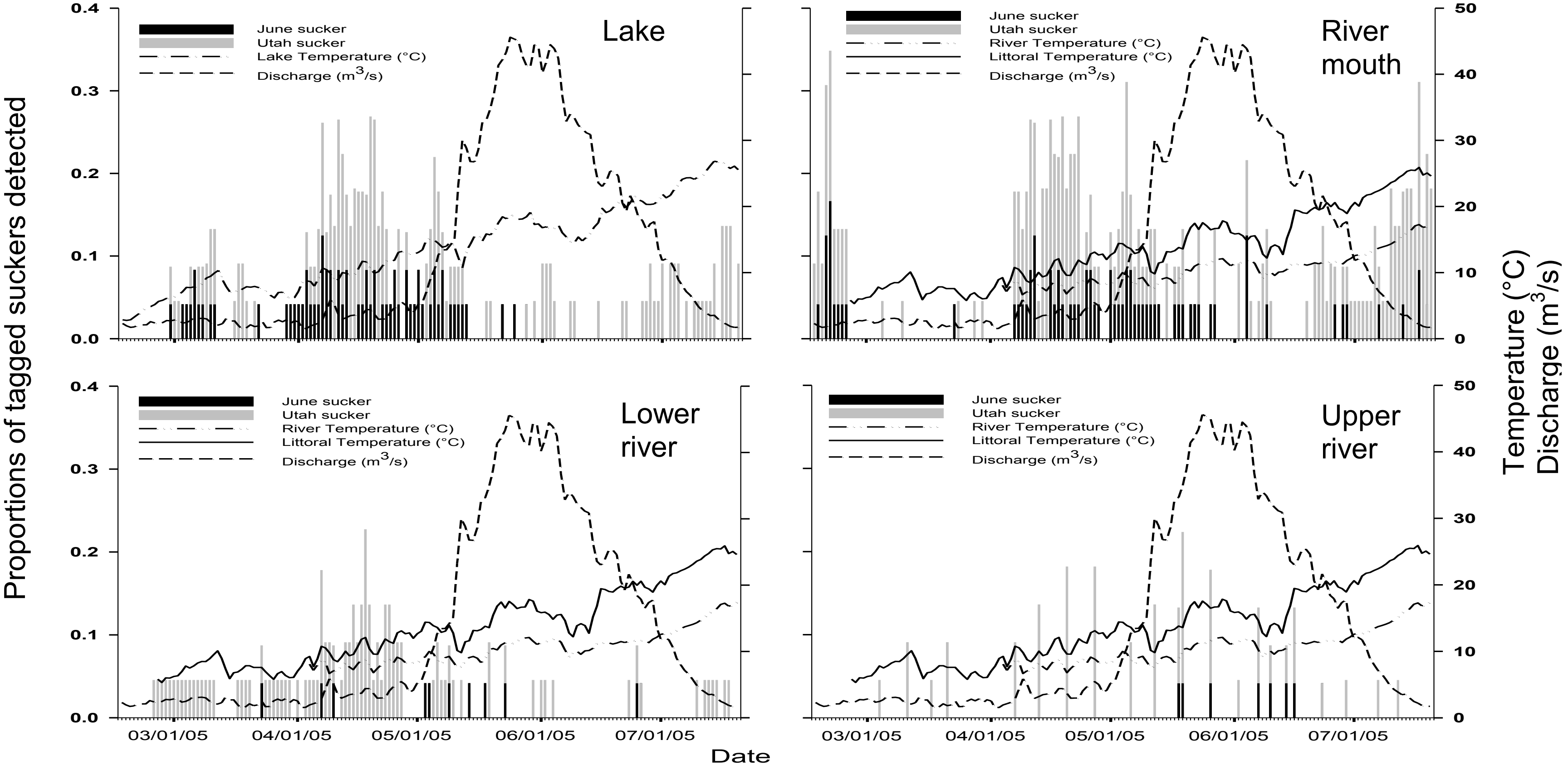


Figure 3-10. Proportions (by species) of tagged Utah Lake suckers detected daily in 2005 via continuous telemetric monitoring of the lake, river mouth, and lower river sites (stationary hydrophones and receiver) and via intermittent monitoring (mobile tracking by foot or vehicle) of the upper river during the Provo River spawning run plotted with Provo River temperature and discharge, littoral (river mouth) temperature, and lake temperature.

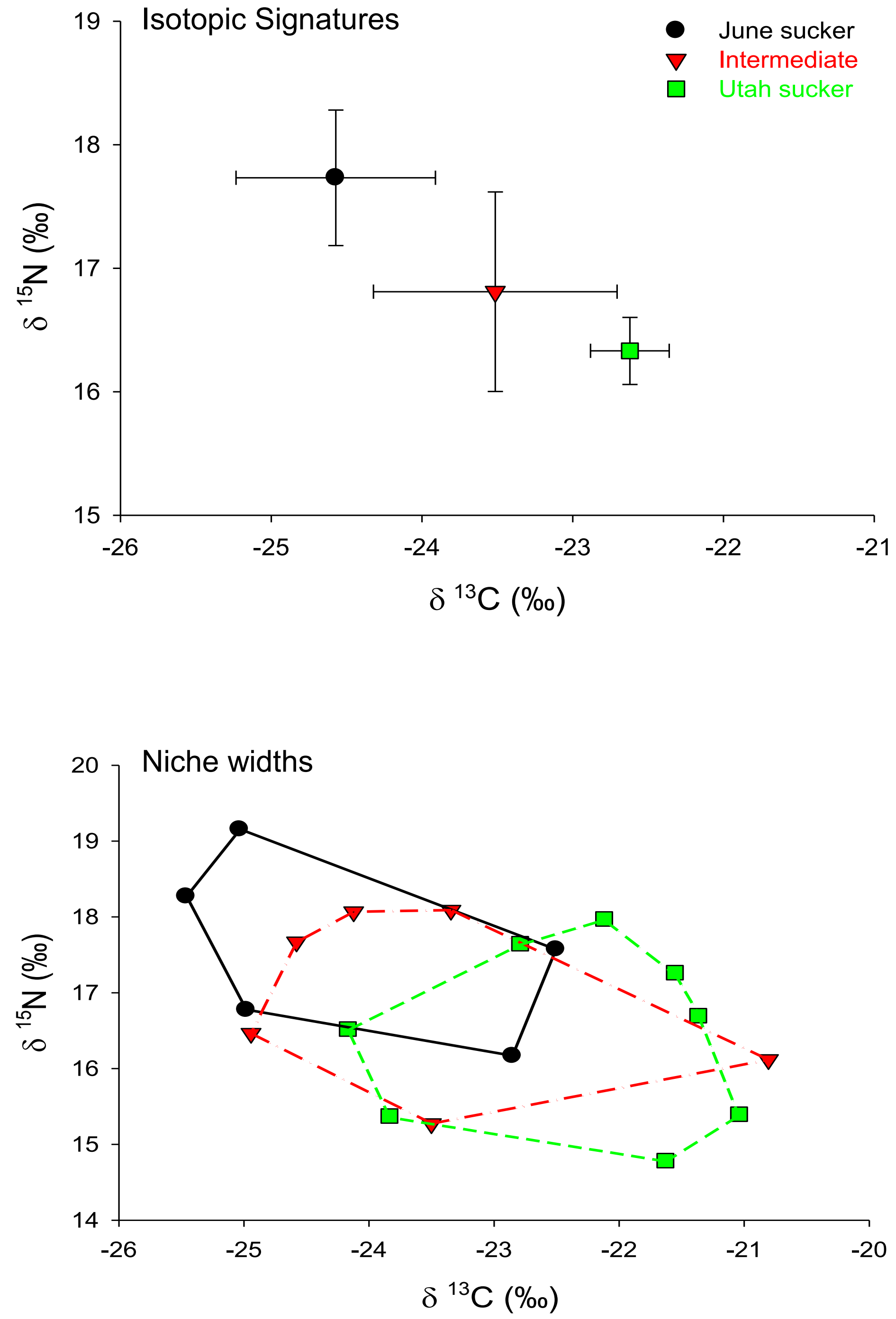


Figure 3-11. Isotopic signatures (δ^{13}C and δ^{15}N; means ± 95 % confidence intervals) and niche widths for Utah Lake suckers plotted by morph within the two dimensional δ^{13}C – δ^{15}N bi-plot space.

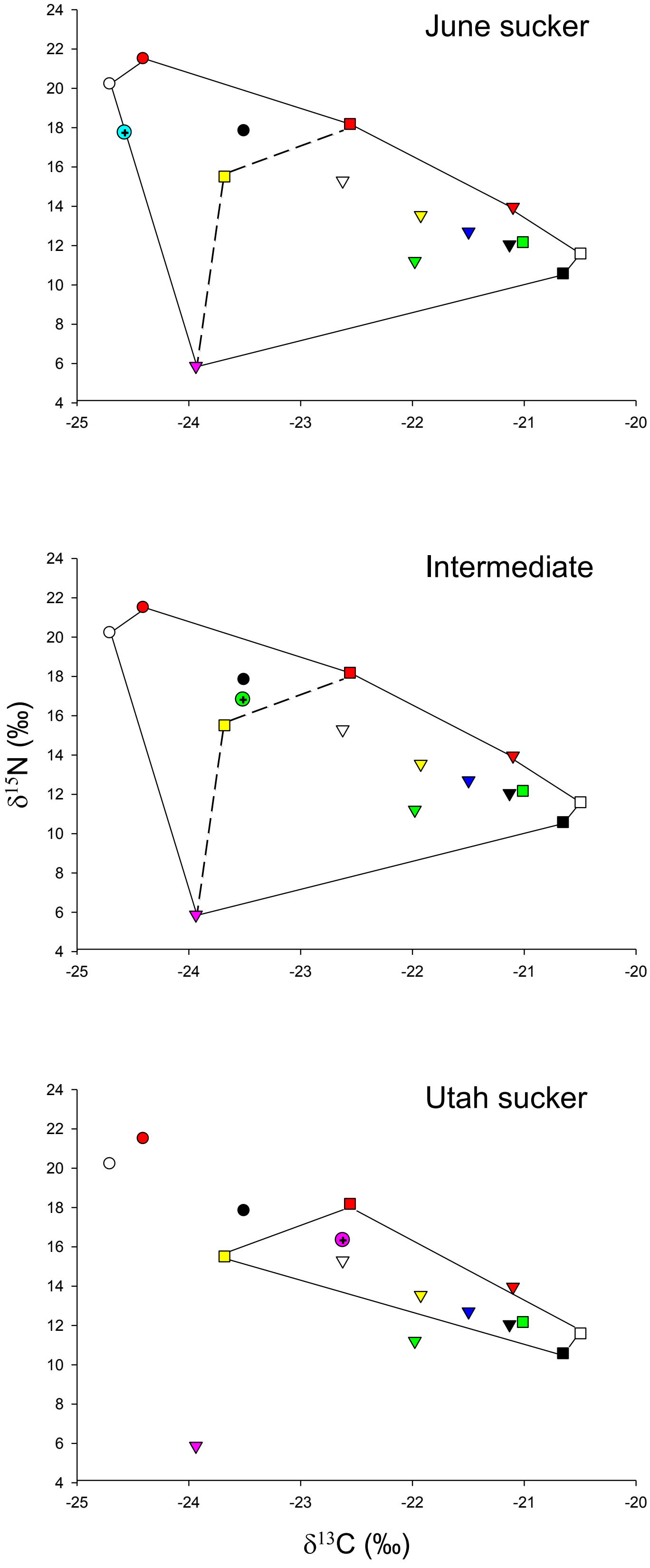


Figure 3-12. Mixing polygons generated within the δ^{13}C–δ^{15}N bi-plot space plotting the mean coordinates for each morph and for potential diet items assuming per trophic level increases of 0.4 ‰ for δ^{13}C and 3.4 ‰ for δ^{15}N (Post 2002). Triangular symbols = zooplankton / seston; square symbols = benthic / littoral macroinvertebrates; and circular symbols = fish. June sucker mixing polygon included zooplankton / seston and fish; intermediate sucker mixing polygon included all potential prey groups; and Utah sucker mixing polygon included benthic / littoral organisms. (Dashed lines on June sucker and intermediate plots exclude common carp, white bass, and fathead minnow as diet sources.)

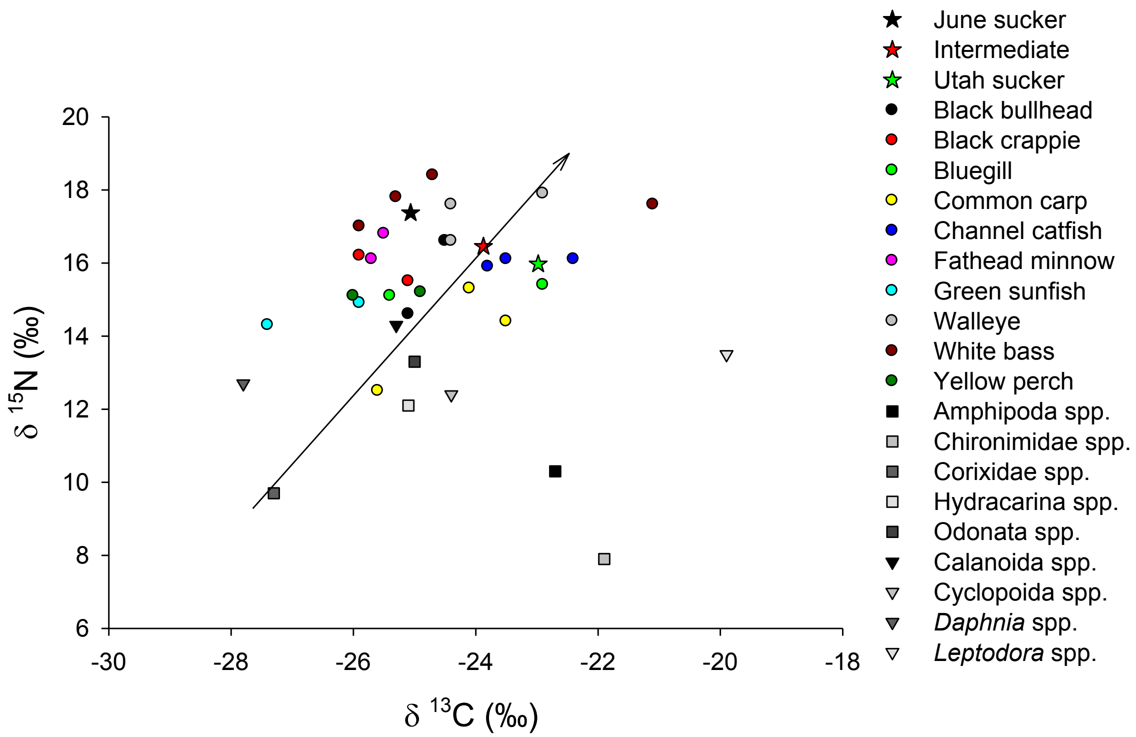


Figure 3-13. Utah Lake food web (Utah Lake biota $\delta^{13}C$ – $\delta^{15}N$ bi-plot) modified from Landom (2010) and including the mean isotopic signatures of June sucker, Utah sucker, and intermediates. Arrow indicates the slight de-coupling in energy flow between the pelagic and benthic / littoral sub-webs. (Symbols: stars – suckers; circles – other fishes; squares – macroinvertebrates; triangles – zooplankton)

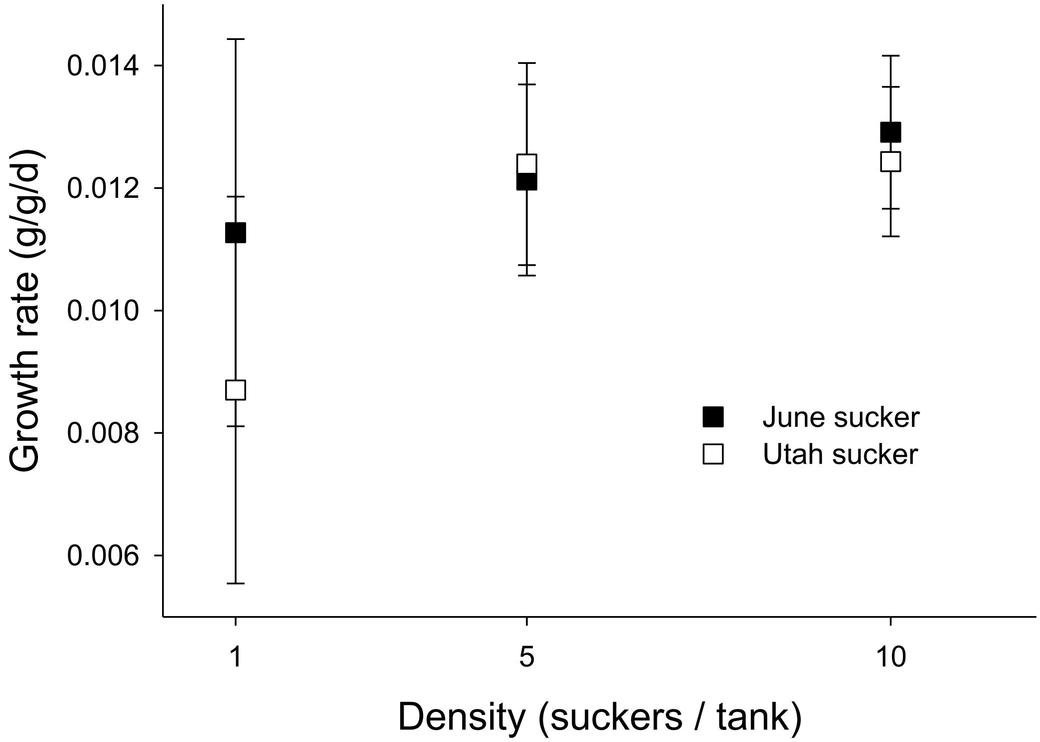


Figure 3-14. Mean growth rate (g/g/d) and 95 % confidence intervals for juvenile June sucker and Utah sucker reared at three different densities with excess food availability.

APPENDIX

Table 3-A-1. Transmitter code identifier, sucker origin, implantation date, sex, standard length, and weight of June and Utah suckers surgically implanted with CART tags in Provo River and Utah Lake in 2003 and 2004.

Morph	Code	Origin	Tag date	Sex	Length (mm)	Weight (g)
June sucker	1	Red Butte	06/05/03	f	380	1400
	18	Red Butte	05/22/03	m	385	1100
	29	Wild	05/22/03	m	413	1840
	34	Red Butte	05/28/03	f	419	1450
	44[a]	Red Butte	06/05/03	f	420	1700
	100	Hatchery	06/05/03	f	500	2900
	109[a→b]	Hatchery	05/22/03	f	418	1200
	121[a]	Hatchery	05/22/03	m	404	1420
	129	Red Butte	05/28/03	m	375	1150
	143	Red Butte	05/22/03	m	380	1204
	183	Wild	05/22/03	m	405	1250
	203	Red Butte	05/22/03	f	413	1400
	3	Wild	05/14/04	m	442	1900
	5[a]	Red Butte	05/27/04	f	394	1300
	8	Hatchery	05/11/04	m	399	1500
	10	Red Butte	05/28/04	f	438	1200
	12	Wild	04/30/04	f	411	1380
	14	Wild	05/28/04	m	448	2000
	115	Red Butte	04/25/04	f	392	1300
	116	Camp Creek	04/25/04	m	362	1200
	133	Wild	04/25/04	m	395	1200
	144	Wild	06/02/04	f	493	2720
	154	Red Butte	05/27/04	f	405	1450
	159	Wild	05/12/04	m	415	1800
	170	Wild	05/27/04	m	414	1600
	177	Wild	06/02/04	m	415	1480
	204	Red Butte	04/30/04	f	395	1500
	205	Wild	05/14/04	f	412	1840
Utah sucker	2	Wild	05/22/03	f	505	3780
	138[c]	Wild	05/22/03	m	425	2070
	152	Wild	05/22/03	m	424	1050
	156	Wild	05/22/03	m	442	1240
	169[a→d]	Wild	05/22/03	m	484	1920
	178	Wild	05/22/03	m	483	1850
	193[a→e]	Wild	05/22/03	m	520	2700
	4	Wild	05/14/04	f	394	1420
	6	Wild	05/12/04	f	521	3200
	7[c]	Wild	05/12/04	m	438	2140
	9	Wild	05/11/04	f	505	3140
	11	Wild	05/28/04	m	421	1300
	13	Wild	05/06/04	f	433	1800
	15	Wild	04/29/04	m	445	2040
	16	Wild	05/11/04	f	478	2780
	22	Wild	04/29/04	m	454	1980
	30	Wild	04/23/04	f	421	2200
	40	Wild	04/24/04	f	420	1650
	45	Wild	04/29/04	m	482	2340
	101	Wild	04/29/04	m	477	2620
	109[b]	Wild	05/11/04	m	454	2280
	130	Wild	04/29/04	m	485	2340
	157	Wild	05/27/04	m	413	1800
	169[d]	Wild	04/29/04	m	475	2140
	193[e]	Wild	04/23/04	m	404	1300

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[a] Mortality

[b] Transmitter recovered from 2003 mortality (a) and implanted into another sucker (b) in 2004

[c] Sucker expelled 2003 transmitter (138) and was implanted with another (7) in 2004

[d] Transmitter recovered from 2003 mortality (a) and implanted into another sucker (d) in 2004

[e] Transmitter recovered from 2003 mortality (a) and implanted into another sucker (e) in 2004

Table 3-A-2. Data collection periods for telemetry, substrate, and temperature data during the random tracking study.

		Sector															
		1W		1E		2W		2E		3W		3E		4W		4E	
Time period	Data	littoral	limnetic	littoral	limnetic	littoral	limnetic	littoral	limnetic	littoral	limnetic	littoral	limnetic	littoral	limnetic	littoral	limnetic
Summer 2004	Telemetry	X	X	X	X			X	X	X[a]	X[a]	X[a]	X[a]			X	X
	Substrate	X	X	X	X			X	X	X	X	X	X			X	X
	Temperature	X	X	X				X		X	X					X	
Late summer 2004	Telemetry	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
	Substrate	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
	Temperature	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
Autumn 2004	Telemetry	X	X	X	X	X	X	X	X	X[b]	X[b]	X	X			X	X
	Substrate	X	X	X	X	X	X	X	X	X[b]	X[b]	X	X			X	X
	Temperature	X	X	X	X	X	X	X	X	X[b]	X[b]	X	X			X	X
Winter 2005	Telemetry	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Substrate	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Temperature	X		X	X	X		X	X	X		X	X	X		X	X
Late summer 2005	Telemetry	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Substrate		X		X			X	X	X	X	X	X	X	X	X	X
	Temperature			X	X			X	X			X	X			X	X
Autumn 2005	Telemetry	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Substrate																
	Temperature			X	X			X	X			X	X			X	X

[a] Consecutive rather than concurrent telemetric sampling periods for east and west sectors of stratum.

[b] Telemetrically sampled for two consecutive approximately 1 wk periods; concurrent sampling of the east sector occurred during the latter period.

Table 3-A-3. Hits, detections, and interference signals recorded during random telemetric monitoring of Utah Lake in 2004 and 2005 by year, season, stratum, and shore.

Year	Season	Stratum	Shore	Hits	Detections	Interference
2004	Summer	SC	e	8754	112	1677
		SC	w	28	18	795
		NC	e	39	22	487
		N	e	16	15	607
		N	w	41	22	675
		S	e	343	36	1268
Late	Summer	SC	e	100	22	1466
		SC	w	28	19	686
		S	w	125	26	872
		NC	e	85	41	1656
		NC	w	82	38	708
		N	e	408	106	1511
		N	w	299	61	841
	Autumn	S	e	36	23	1046
		SC	e	604	16	615
		SC	w	145	44	796
		SC	w	18	14	619
		NC	e	68	3	784
		NC	w	762	40	790
		N	e	36	1	86
		N	w	227	37	1098
2005	Winter	SC	e	599	22	1102
		SC	w	0	0	13
		S	e	279	45	782
		S	w	0	0	81
		NC	e	141	49	879
		NC	w	0	0	205
		N	e	38	16	746
		N	w	13	2	Na
Late	Summer	S	e	3	3	240
		S	w	14	14	512
		NC	e	9	9	381
		NC	w	14	11	563

	SC	e	24	14	777
	SC	w	15	12	493
	N	e	7	7	152
	N	w	27	15	517
Autumn	NC	e	20	4	93
	NC	w	109	38	603
	SC	e	425	7	495
	SC	w	44	23	369
	N	e	0	0	61
	N	w	4	4	111
	S	e	3	3	79
	S	w	1	1	34
		Total	14033	1015	28371

Table 3-A-4. Two factor ANOVA F values and probabilities (*P*): from analysis of individual Utah Lake suckers' (model df = 3,42) numbers of hits or detections during random telemetric monitoring in Utah Lake (2004 – 2005) as dependent variable and morph, gender, and their interaction as predictor variables; and from individual June suckers' (model df = 3,20) numbers of hits or detections as dependent variables and gender, origin, and their interaction as predictor variables.

			Hits		Detections	
Sucker group	Predictor	df	F value	*P*	F value	*P*
Utah Lake suckers	Morph	1	0.65	0.424	0.67	0.418
	Gender	1	3.10	0.085	2.92	0.095
	Morph and gender	1	0.09	0.764	0.76	0.388
June sucker	Gender	1	1.61	0.219	0.01	0.925
	Origin	1	0.35	0.558	1.54	0.229
	Gender and origin	1	0.89	0.356	0.04	0.834

Table 3-A-5. Three factor ANOVA F values and probabilities (*P*) from analyzing the proportion of sectors visited by individual Utah Lake suckers (model df = 15, 260) during random telemetric monitoring in Utah Lake (2004 – 2005) as the dependent variable and season, morph, gender, and their interactions as predictor variables; and the proportion of sectors visited by individual June sucker (model df = 15, 128) as the dependent variable and season, gender, origin, and their interactions as predictor variables (**Bold** – significant at α = 0.05). (arcsine square root transformed data)

Sucker group	Predictor variables	DF	F value	*P*
Utah Lake suckers	Season	3	2.66	**0.049**
	Morph	1	1.15	0.285
	Season, morph	3	0.20	0.900
	Gender	1	0.01	0.914
	Season, gender	3	0.18	0.908
	Morph, gender	1	0.83	0.363
	Season, morph, gender	3	0.02	0.995
June sucker	Season	3	4.01	0.053
	Gender	1	0.22	0.724
	Season, gender	3	0.19	0.803
	Origin	1	5.58	0.219
	Season, origin	3	0.78	0.746
	Gender, origin	1	0.05	0.839
	Season, gender, origin	3	0.18	0.915

Table 3-A-6. Datasets and models examined in RF analysis of random telemetric monitoring of adult suckers in Utah Lake and percentages of variance explained. (**Bold text**, ***bold italic text*** – same predictor variables applied to different datasets; i – important predictor variables; ii – substrate included among important predictor variables)

Dataset	Model	Predictor variables (→in decreasing order of importance→)	Variance (%)
Telemetry	**1**	**Shore Season Zone Stratum Gender Light Species**	**29.9**
	1i	**Zone Shore Season Stratum**	**43.4**
	2	***oDPUE Season Shore Stratum Zone Gender Species Light***	***76.7***
	2i	***oDPUE Season Shore Stratum Zone***	***74.9***
Telemetry Substrate	**3**	**Shore Season Zone Stratum Gender Light Species**	**35.6**
	3i	**Shore Season Zone Stratum**	**54.3**
	4	Season Zone Shore Stratum Substrate Gender Light Species	38.0
	4i	Season Zone Shore Stratum Substrate	53.3
	5	***oDPUE Season Shore Stratum Zone Gender Species Light***	***76.1***
	5i	***oDPUE Shore Season Stratum Zone***	***74.3***
	6	oDPUE Season Shore Stratum Zone Substrate Gender Species Light	75.8
	6i	oDPUE Season Shore Stratum Zone Substrate	73.6
Telemetry Temperature	**7**	**Zone Shore Season Stratum Gender Light Species**	**36.2**
	7i	**Zone Shore Season Stratum**	**47.5**
	8	Zone Temperature Shore Season Stratum Light Gender Species	70.7
	8i	Zone Shore Temperature Season Stratum	70.0
	9	***oDPUE Season Zone Shore Stratum Species Gender Light***	***75.0***

	9i	***oDPUE Season Stratum Zone Shore***	***74.2***
	10	oDPUE Zone Temperature Shore Stratum Season Gender Light Species	76.1
	10i	oDPUE Zone Stratum Shore Temperature Season	74.7
Telemetry	**11**	**Zone Shore Season Stratum Gender Light Species**	**44.5**
Substrate	**11i**	**Zone Shore Season Stratum**	**53.3**
Temperature	12	Zone Temperature Shore Season Stratum Substrate Light Gender Species	69.2
	12i	Zone Temperature Shore Season Stratum	69.8
	12ii	Zone Temperature Shore Season Stratum Substrate	67.5
	13	Zone Shore Season Stratum Substrate Gender Light Species	44.1
	14	Zone Temperature Shore Season Stratum Light Gender Species	70.3
	15	***oDPUE Zone Season Shore Stratum Species Gender Light***	***74.4***
	15i	***oDPUE Zone Season Stratum Shore***	***73.7***
	16	oDPUE Zone Shore Temperature Stratum Season Substrate Light Gender Species	75.2
	16i	oDPUE Zone Shore Temperature Stratum Season	74.3
	16ii	oDPUE Zone Temperature Shore Stratum Season Substrate	74.1
	17	oDPUE Zone Season Stratum Shore Substrate Species Gender Light	73.9
	18	oDPUE Zone Temperature Shore Stratum Season Gender Light Species	75.4

Table 3-A-7. Datasets and models examined in RF analysis of random telemetric monitoring of adult June sucker and Utah sucker in Utah Lake and percentages of variance explained. (i – important predictor variables).

Dataset	Species	Model number	Predictor variables [→in decreasing order of importance→]	Variance (%)
Telemetry	JS	J1	Season Shore Zone Stratum Light Gender	23.7
	JS	J1i	Season Shore Stratum Zone	45.0
	US	U1	Shore Zone Season Stratum Gender Light	21.8
	US	U1i	Shore Season Zone Stratum	39.9
Telemetry + Temperature	JS	J2	Shore Zone Season Stratum Light Gender	28.1
	JS	J2i	Shore Zone Season Stratum	48.5
	JS	J3	Temperature Zone Shore Season Stratum Light Gender	73.7
	JS	J3i	Temperature Zone Shore Season Stratum	76.0
	US	U2	Zone Shore Season Stratum Gender Light	29.8
	US	U2i	Shore Zone Season Stratum	41.1
	US	U3	Zone Temperature Shore Season Stratum Gender Light	62.0
	US	U3i	Temperature Zone Shore Season Stratum	61.5

Table 3-A-8. Minimum distances traveled by Utah Lake suckers during random (2004-2005) and spawning season (2005) telemetric monitoring, and the number of trips between the Provo and Spanish Fork Rivers (Trips) that individual suckers undertook during the 2005 spawning season.

					Distance (km)		
Code	Species	Gender	Origin	Trips	Spawn	Random	Total
1	JS	f	stocked	15	110.7	971.2	1081.9
3	JS	m	wild	4	29.3	351.4	380.7
8	JS	m	stocked	2	15.3	212.0	227.3
10	JS	f	stocked	0	0.0	259.8	259.8
12	JS	f	wild	0	0.0	169.4	169.4
14	JS	m	wild	0	0.0	286.8	286.8
18	JS	m	stocked	1	7.4	525.2	532.6
29	JS	m	wild	4	29.9	348.4	378.3
34	JS	f	stocked	4	30.1	318.5	348.6
100	JS	f	stocked	0	0.0	154.3	154.3
115	JS	f	stocked	1	7.4	172.4	179.8
116	JS	m	stocked	28	211.6	665.4	877.0
129	JS	m	stocked	0	0.0	77.3	77.3
133	JS	m	wild	0	0.0	80.1	80.1
143	JS	m	stocked	0	0.0	41.0	41.0
144	JS	f	wild	5	37.6	281.8	319.4
154	JS	f	stocked	12	88.9	375.8	464.7
159	JS	m	wild	2	14.8	134.8	149.6
170	JS	m	wild	0	0.0	34.0	34.0
177	JS	m	wild	0	0.0	312.5	312.5
183	JS	m	wild	0	0.0	38.2	38.2
203	JS	f	stocked	0	0.0	35.7	35.7
204	JS	f	stocked	1	7.4	347.3	354.7
205	JS	f	wild	0	0.0	61.3	61.3
2	US	f	wild	36	268.9	927.9	1196.8
4	US	f	wild	13	99.4	274.1	373.5
6	US	f	wild	30	226.0	620.1	846.1
7	US	m	wild	2	15.2	365.4	380.6
9	US	f	wild	2	15.4	62.3	77.7
11	US	m	wild	0	0.0	200.6	200.6

13	US	f	wild	0	0.0	282.2	282.2
15	US	m	wild	15	111.9	516.4	628.3
16	US	f	wild	0	0.0	521.4	521.4
22	US	m	wild	3	22.3	244.0	266.3
30	US	f	wild	9	66.8	630.6	697.4
40	US	f	wild	0	0.0	190.7	190.7
45	US	m	wild	3	22.2	148.8	171.0
101	US	m	wild	3	22.2	198.0	220.2
109	US	m	wild	1	7.5	77.9	85.4
130	US	m	wild	0	0.0	216.3	216.3
152	US	m	wild	0	0.0	82.7	82.7
156	US	m	wild	8	61.0	413.6	474.6
157	US	m	wild	3	22.2	148.7	170.9
169	US	m	wild	0	0.0	49.3	49.3
178	US	m	wild	6	46.4	236.3	282.7
193	US	m	wild	2	15.2	458.9	474.1

Table 3-A-9. Results (F values and probabilities, *P*) of two factor ANOVA of minimum mean distances traveled during random and targeted (2005 spawning season) telemetric monitoring by individual suckers for all Utah Lake suckers (factors: species and gender; model df = 3, 42) and for June sucker (factors: gender and origin; model df = 3, 20).

All suckers	Class variables		N	Mean distance (km)	Standard deviation (km)	Factor(s)	F value	*P*
Spawn distance	JS		24	24.6	48.9			
	US		22	46.5	72.8	Species	2.79	0.1020
	female		19	50.5	78.9			
	male		27	24.2	44.7	Gender	2.97	0.0922
	JS	female	11	25.6	39.2			
	JS	male	13	23.7	57.5			
	US	female	8	84.6	107.4			
	US	male	14	24.7	30.8	Species*gender	2.61	0.1137
Random distance	JS		24	260.6	222.0			
	US		22	312.1	223.6	Species	1.38	0.2473
	female		19	350.4	270.7			
	male		27	239.4	170.8	Gender	3.54	0.0667
	JS	female	11	286.1	253.0			
	JS	male	13	239.0	200.1			
	US	female	8	438.7	285.5			
	US	male	14	239.8	146.3	Species*gender	1.35	0.2521
Total distance	JS		24	285.2	259.8			
	US		22	358.6	283.7	Species	1.82	0.1850

	female		19	400.8	334.1			
	male		27	263.7	204.3	Gender	3.78	0.0585
	JS	female	11	311.8	287.0			
	JS	male	13	262.7	243.9			
	US	female	8	523.2	373.8			
	US	male	14	264.5	169.1	Species*gender	1.76	0.1923
June sucker								
Spawn distance	female		11	25.6	39.2			
	male		13	23.7	57.5	Gender	0.09	0.7718
	stocked		13	36.8	63.6			
	wild		11	10.1	15.0	origin	1.58	0.2232
	female	stocked	8	30.6	44.2			
	female	wild	3	12.5	21.7			
	male	stocked	5	46.9	92.3			
	male	wild	8	9.3	13.6	Gender*origin	0.20	0.6629
Random distance	female		11	286.1	253.0			
	male		13	239.0	200.1	Gender	0.00	0.9910
	stocked		13	319.7	269.5			
	wild		11	190.8	127.8	Origin	1.73	0.2031
	female	stocked	8	329.4	283.1			
	female	wild	3	170.8	110.2			
	male	stocked	5	304.2	277.7			
	male	wild	8	198.3	140.1	Gender*origin	0.07	0.7960
Total distance	female		11	311.8	287.0			
	male		13	262.7	243.9	Gender	0.00	0.9487
	stocked		13	356.5	318.6			

wild		11	200.9	137.7	Origin	1.86	0.1878
female	stocked	8	359.9	321.2			
female	wild	3	183.3	129.6			
male	stocked	5	351.0	352.1			
male	wild	8	207.5	148.7	Gender*origin	0.02	0.8894

Table 3-A-10. Date of first detection of individual Utah Lake suckers and probabilities (*P*) resulting from median exact tests (if conducted) comparing median first day of detection between species at Provo River locations during the 2004 and 2005 spawning seasons and at Spanish Fork River locations during the 2005 spawning season. (JS – June sucker; US – Utah sucker)

	2004 Provo River				2005 Provo River				2005 Spanish Fork River		
Code	Lake	Mouth	Lower River	Upper River	Lake	Mouth	Lower River	Upper River	Lake	Mouth	Upper River
JS											
1	04/02	04/02/04	04/03/04		03/06/05	02/17/05			02/26/05	03/29/05	
3					05/25/05	02/19/05			03/04/05	05/07/05	
8							04/10/05		03/25/05		
10									03/13/05		
12									03/12/05	04/02/05	
14									04/28/05		
18	04/02/04	04/30/04	04/07/04	05/23/04		02/20/05			03/04/05	05/31/05	
29	04/08/04	05/14/04	04/07/04	05/12/04		02/19/05			03/04/05	05/14/05	
34	04/03/04	04/02/04				06/04/05	03/23/05		03/10/05	06/18/05	
100	04/09/04	05/23/04				06/04/05					
115						07/19/05[#]			03/13/05	03/29/05	
116					04/03/05	04/11/05	04/07/05		03/02/05	04/06/05	
129	04/03/04	04/10/04							03/13/05		
133											
143	04/03/04	05/21/04	04/03/04						03/04/05		
144					04/07/05	04/07/05	05/03/05	05/18/05	04/22/05	04/22/05	
154					02/28/05	04/12/05			03/09/05	02/26/05	04/20/05
159						06/09/05			03/23/05		
170									03/17/05		
177									05/16/05		
183		04/06/04							06/25/05		
203		04/07/04		05/23/04					03/25/05		
204						02/20/05			06/25/05		

205									03/16/05		
US											
2	04/01/04	04/04/04		05/23/04	03/05/05	02/16/05	05/06/05		02/26/05	03/07/05	
4					04/19/05	04/19/05	02/24/05	03/11/05	03/04/05		
6					04/07/05	02/17/05	04/07/05	04/20/05	03/04/05	04/02/05	
7						04/08/05			03/22/05	04/02/05	
9							04/07/05		04/20/05	03/29/05	
11									03/12/05		
13									03/13/05		
15					06/26/05	02/20/05	04/09/05		03/08/05	05/05/05	
16									03/17/05		
22						03/05/05			03/05/05	04/27/05	
30					02/28/05	04/19/05			03/03/05	03/03/05	
40									03/17/05	05/05/05	
45						02/20/05			03/14/05	07/16/05[#]	
101						06/09/05		03/04/05	03/23/05		
109						02/16/05			04/20/05	04/02/05	
130									03/25/05		
152	04/03/04	06/21/04							03/13/05		
156	04/01/04	04/01/04	05/04/04	05/06/04	03/17/05	02/19/05	04/18/05	04/27/05	03/16/05	03/16/05	
157					04/10/05	04/10/05	04/18/05	04/27/05	03/10/05	04/08/05	
169											
178	04/06/04	04/27/04	04/27/04	04/15/04	04/14/05	04/14/05	04/15/05	04/20/05	04/08/05	04/08/05	
193					03/09/05	02/20/05	04/13/05	04/13/05	06/04/05		
P (median exact test)	0.7242	1.0000	*	*	1.0000	0.6951	0.5594	*	0.7635	0.6699	*

[#] date after 1 July – not included in median exact test

*no median exact test conducted

Table 3-A-11. Numbers of Utah Lake suckers, by Species, detected during active telemetric tracking of Utah Lake tributaries during the 2004 (Provo River) and 2005 (Provo, Spanish Fork, and American Fork Rivers and Battle Creek) spawning seasons.

Site Year	Date	June sucker	Utah sucker	Site Year	Date	June sucker	Utah sucker	Site Year	Date	June sucker	Utah sucker
Provo	04/15/04	0	1	Provo	03/04/05	0	1	Spanish	03/03/05	0	0
River	04/22/04	0	1	River	03/11/05	0	2	Fork River	03/10/05	0	0
2004	04/26/04	0	1	2005	03/17/05	0	1	2005	03/17/05	0	0
	04/30/04	0	1		03/21/05	0	2		03/21/05	0	0
	05/04/04	0	1		04/07/05	0	2		03/31/05	0	0
	05/06/04	0	2		04/13/05	0	3		04/13/05	0	0
	05/12/04	1	1		04/20/05	0	4		04/20/05	1	1*
	05/14/04	0	1		04/27/05	0	4		04/26/05	0	0
	05/18/04	0	1		05/06/05	0	2		05/05/05	0	0
	05/23/04	2	1		05/12/05	0	3		05/11/05	0	0
	05/26/04	0	1		05/18/05	1	2		05/19/05	1*	0
	05/28/04	0	1		05/19/05	1	4		05/25/05	0	0
	06/01/04	0	0		05/26/05	1	3		06/01/05	0	0
	06/09/04	0	0		06/02/05	0	1		06/23/05	0	0
					06/07/05	1	2		06/28/05	0	0
					06/10/05	1	1				
Battle	04/20/05	0	0		06/14/05	1	1				
Creek	04/26/05	0	0		06/16/05	1	2	American	05/11/05	0	0
2005	05/11/05	0	0		06/23/05	1	0	Fork River	06/28/05	0	0

06/29/05	0	1	2005
07/07/05	0	1	
07/12/05	0	1	

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* indicates sucker was detected at the tributary / lake confluence

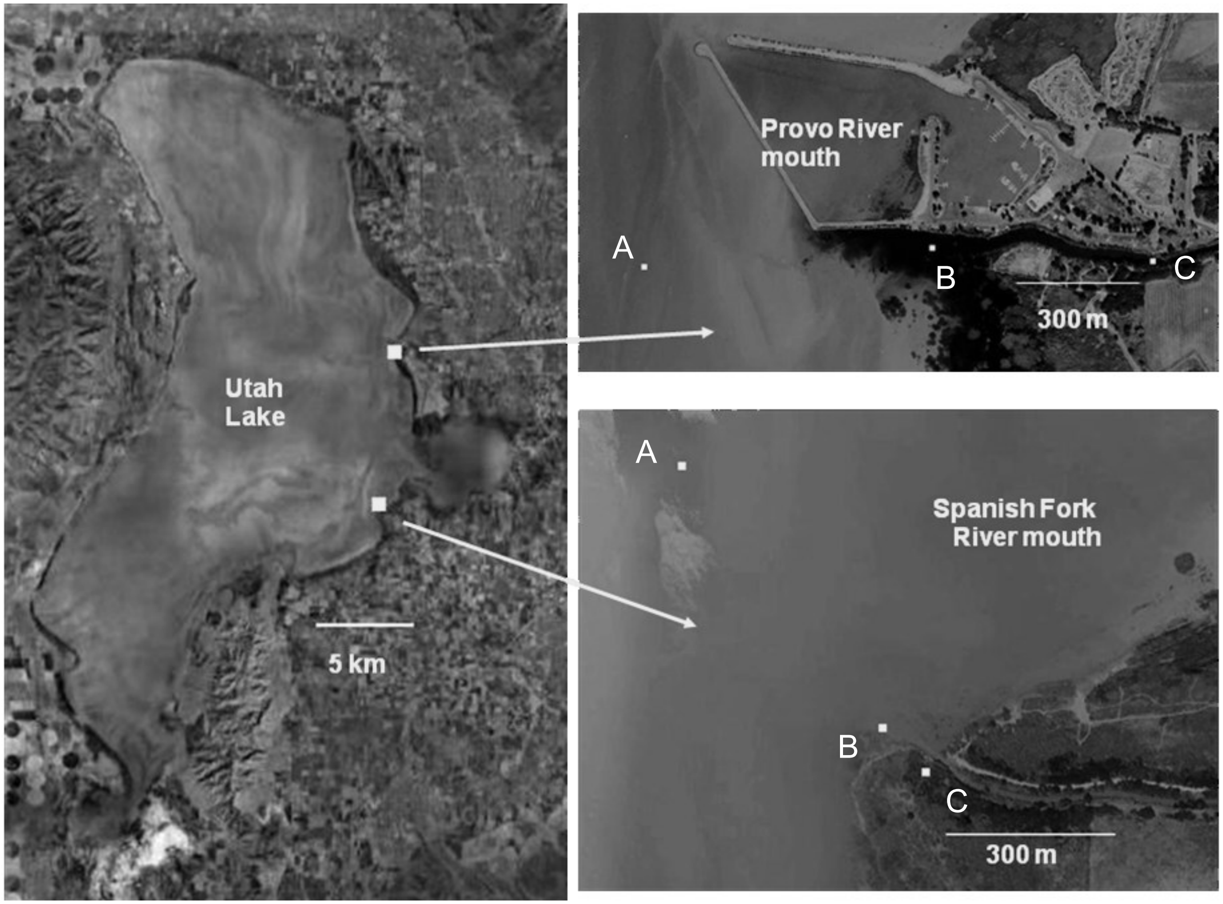

Figure 3-A-1. Locations of hydrophones (A – lake; B – river mouth) and radio receiver / data-loggers (C) at the mouths of the Provo River in 2004 and 2005 and the Spanish Fork River in 2005 during the spring spawning seasons. The receiver at the Provo River was located on a footbridge and able to detect radio transmissions from tagged suckers in the lower river whereas that at the Spanish Fork River was located approximately 30 m from the river channel and unable to detect tagged suckers in the lower river.

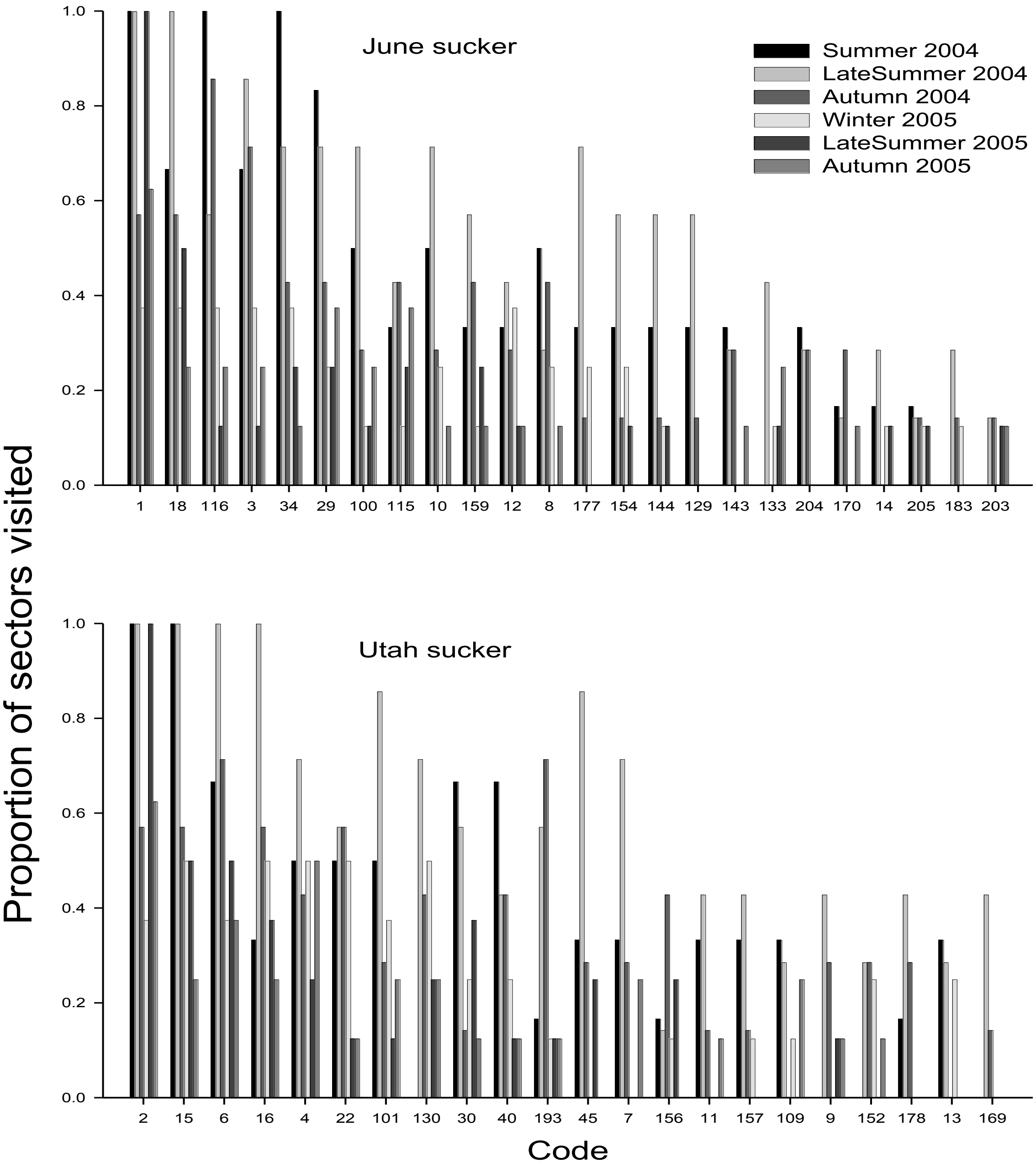

Figure 3-A-2. Proportion of sectors visited by individual suckers (identified by code) during the six seasonal sampling periods of the 2004-2005 random telemetric monitoring of Utah Lake.

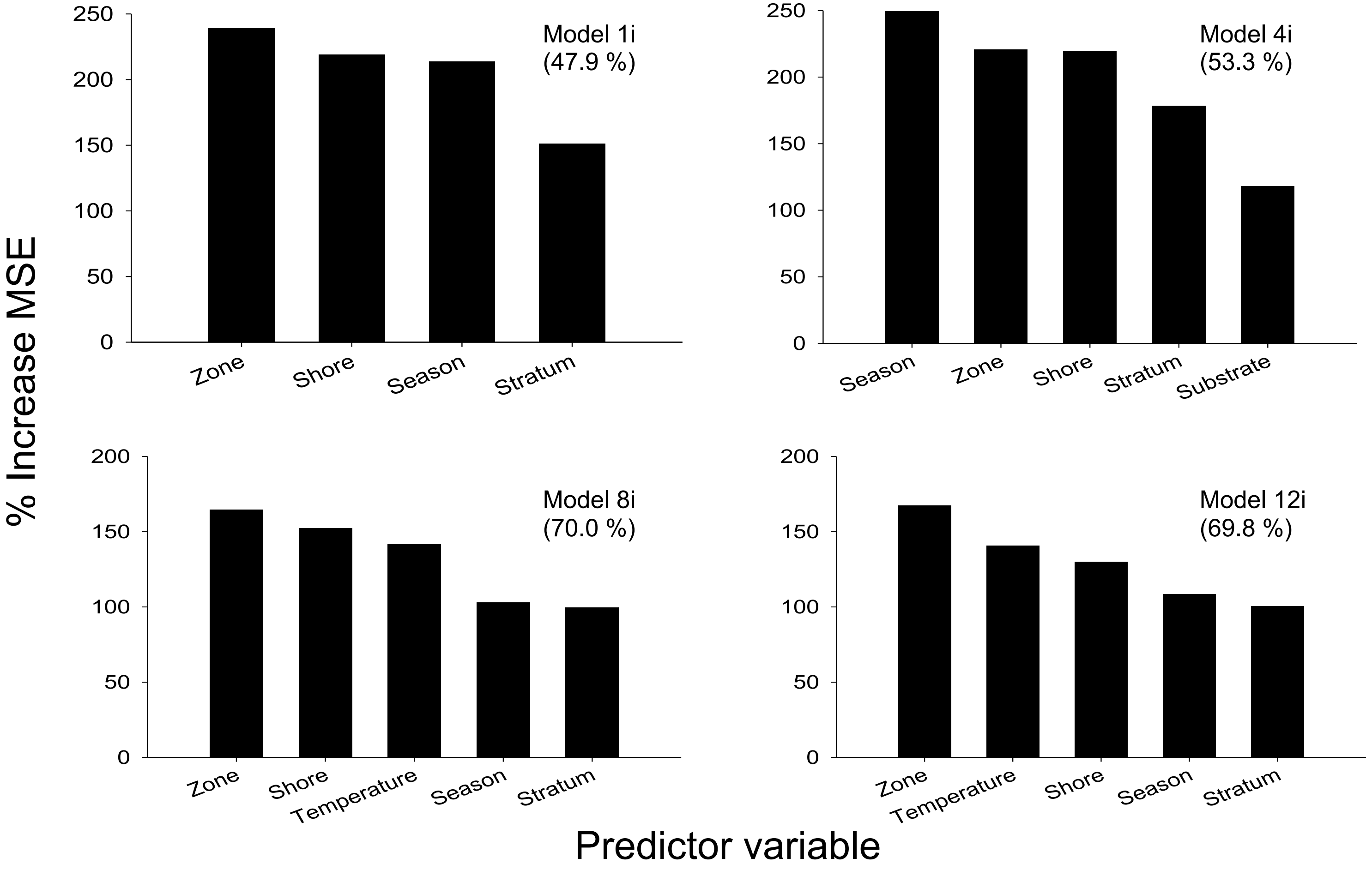

Figure 3-A-3. Variable importance plots for important predictors produced from RF analysis of the most temporally and spatially complete telemetric dataset (DPUE = dependent variable; excluded oDPUE as a predictor). (Percent variance explained in parentheses.) (See Appendix: Table 3-A-6 for models; Figure 5)

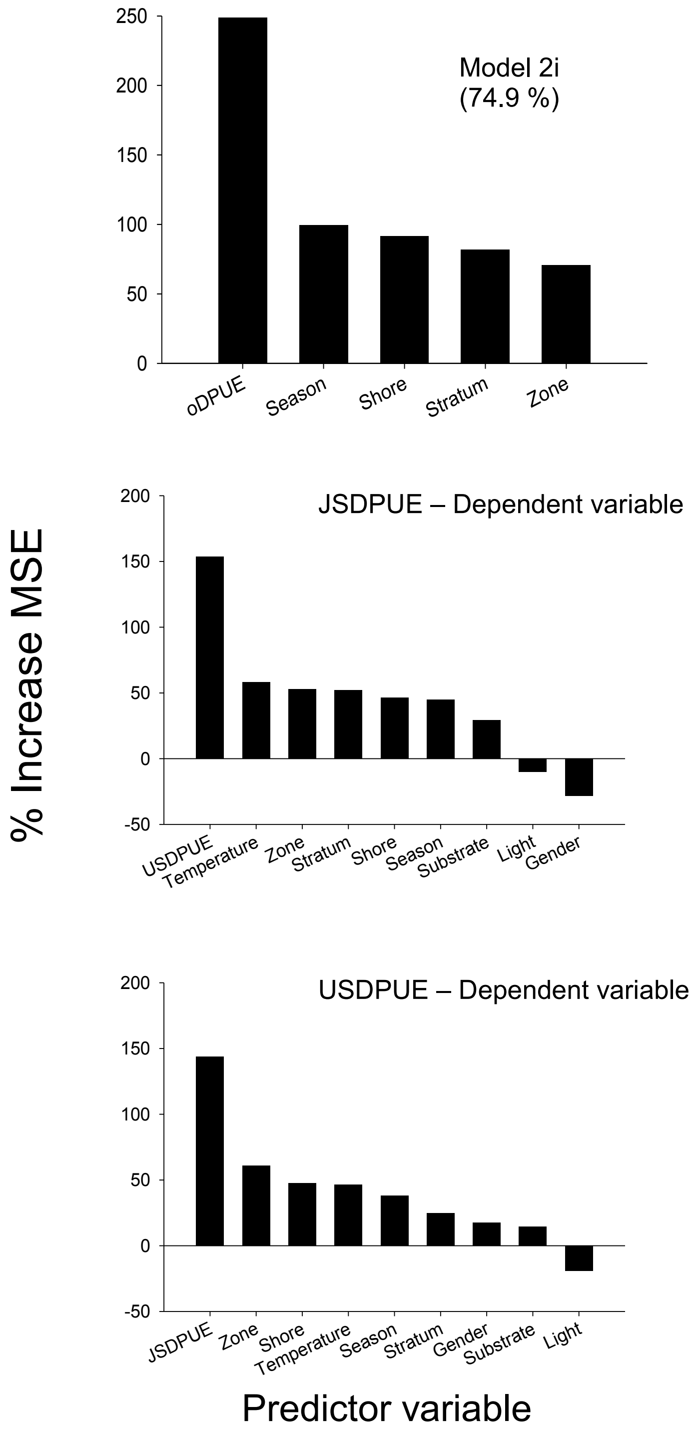

Figure 3-A-4. Variable importance plots: important predictors resulting from RF analysis (Appendix: Table 3-A-6, Model 2i) of the most temporally and spatially complete dataset with DPUE as the response variable and oDPUE among predictors; and all predictors, by species, from analysis included substrate and temperature data. (JSDPUE – June sucker DPUE; USDPUE – Utah sucker DPUE).

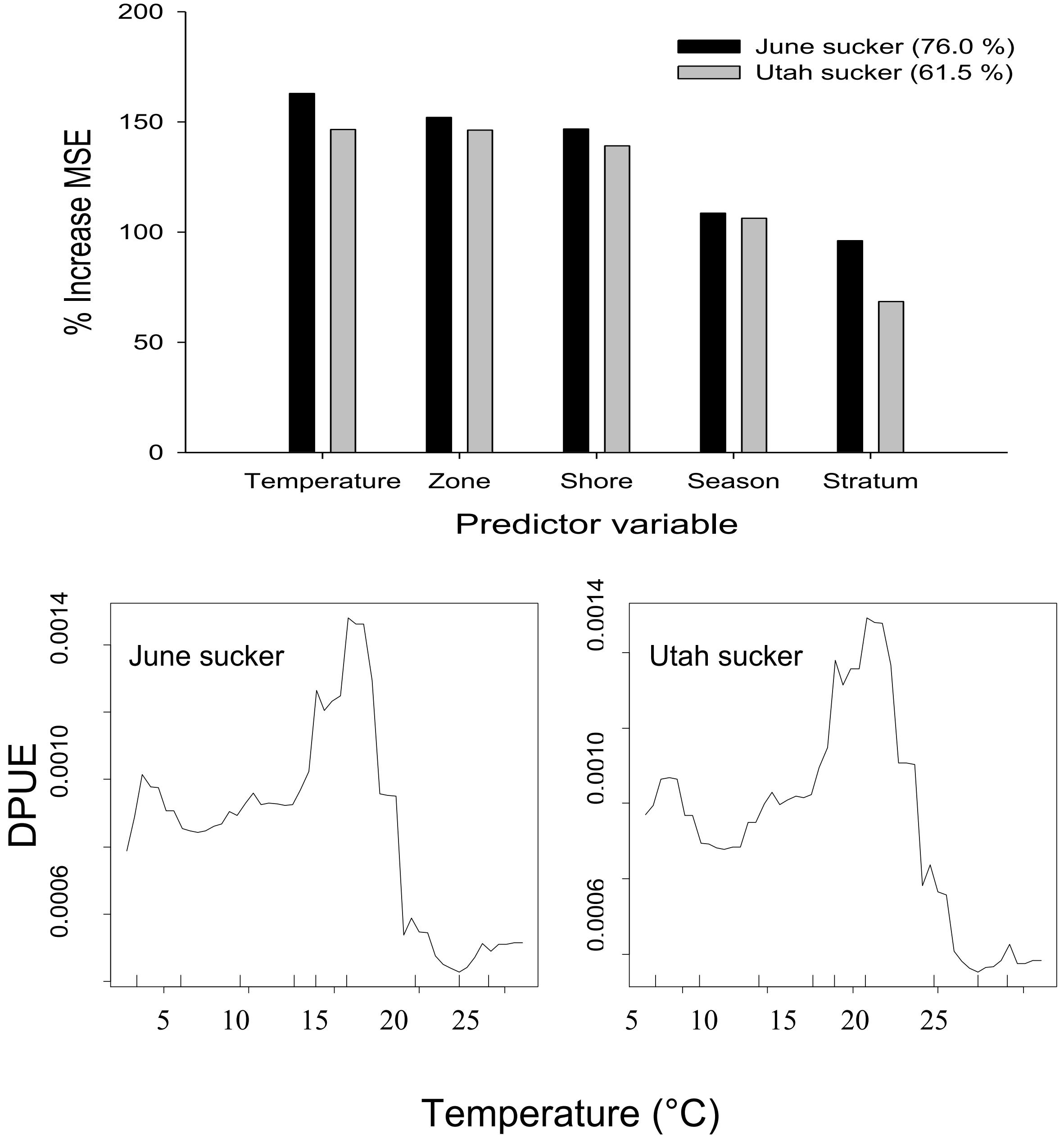

Figure 3-A-5. Variable importance plot showing important predictors by species (with percent variance explained by model) from RF analysis of the most temporally and spatially complete telemetric dataset that included temperature data; and partial dependency plots for temperature by species. The dependent variable was DPUE, and the predictor variables excluded oDPUE. (Appendix: Table 3-A-7, Models J3i and U3i)

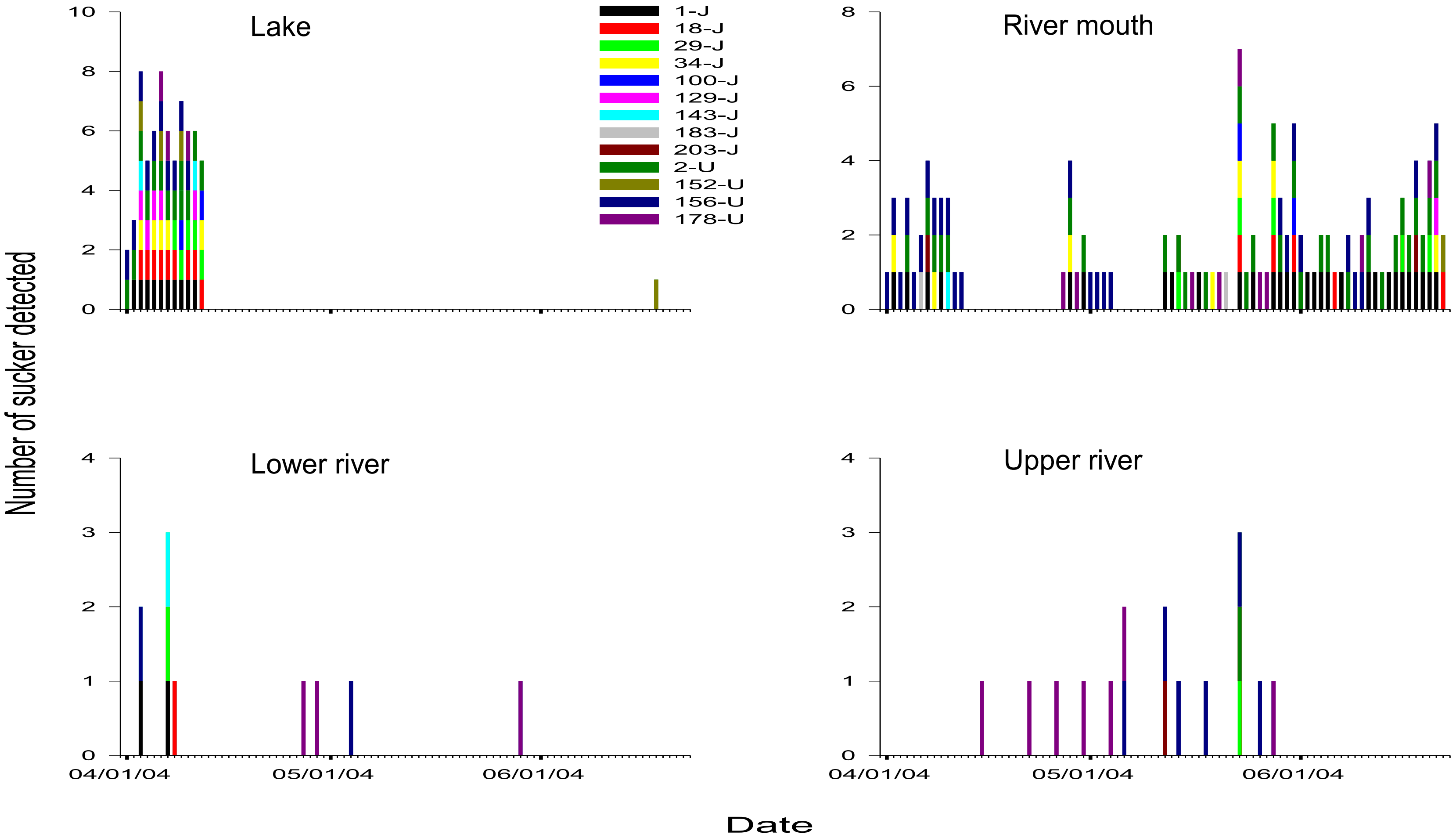

Figure 3-A-6. Numbers of individual tagged June sucker and Utah sucker detected daily via continuous monitoring during the Provo River spawning run in 2004 of the lake, river mouth, and lower river sites (stationary hydrophones and receiver) and via intermittent monitoring (mobile tracking by foot or vehicle) of the upper river. (Legend: codes for individual June sucker and Utah sucker)

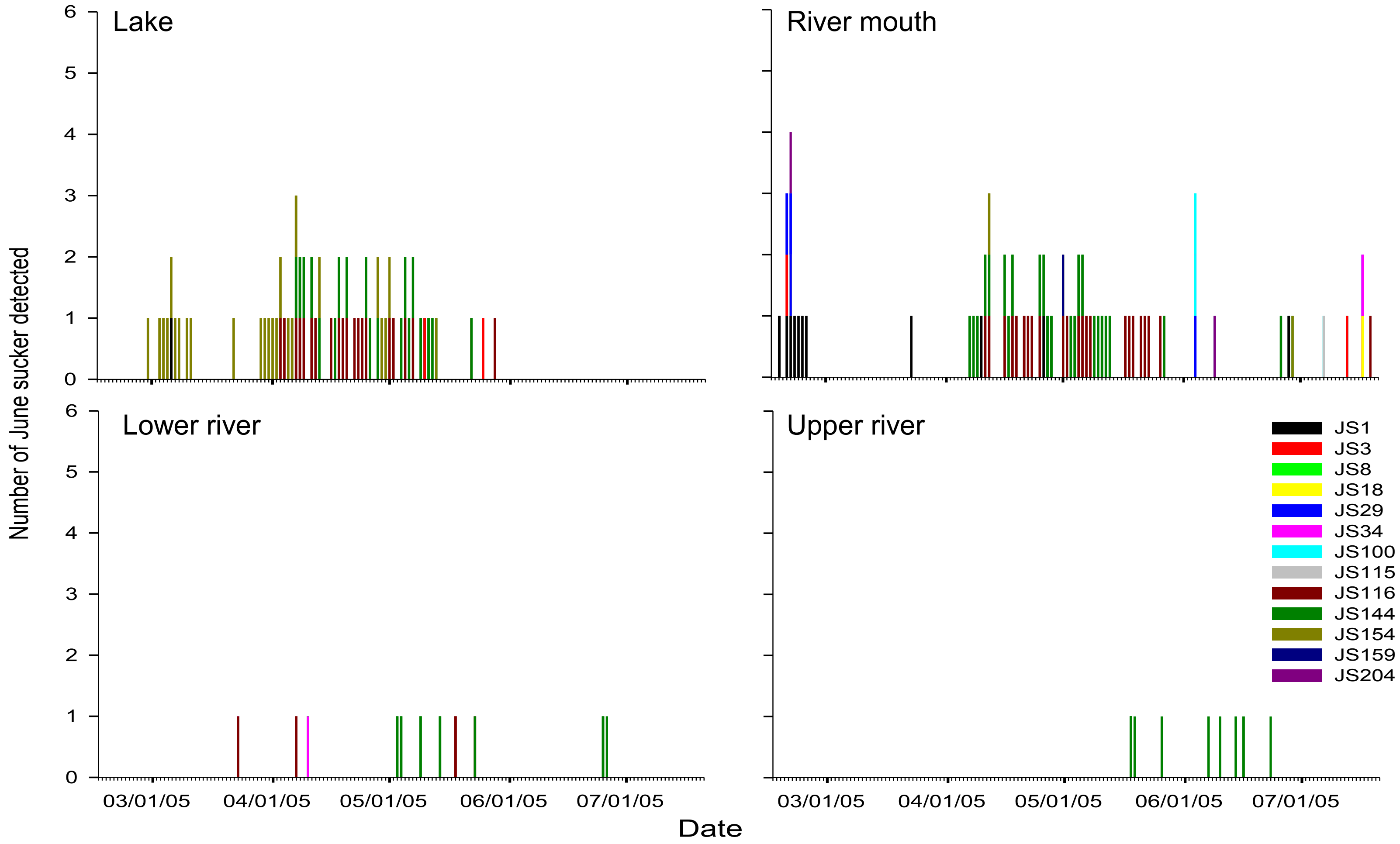

Figure 3-A-7. Numbers of individual tagged June sucker detected daily via continuous monitoring during the Provo River spawning run in 2005 of the lake, river mouth, and lower river sites (stationary hydrophones and receiver) and via intermittent monitoring (mobile tracking by foot or vehicle) of the upper river. (Legend: June sucker codes)

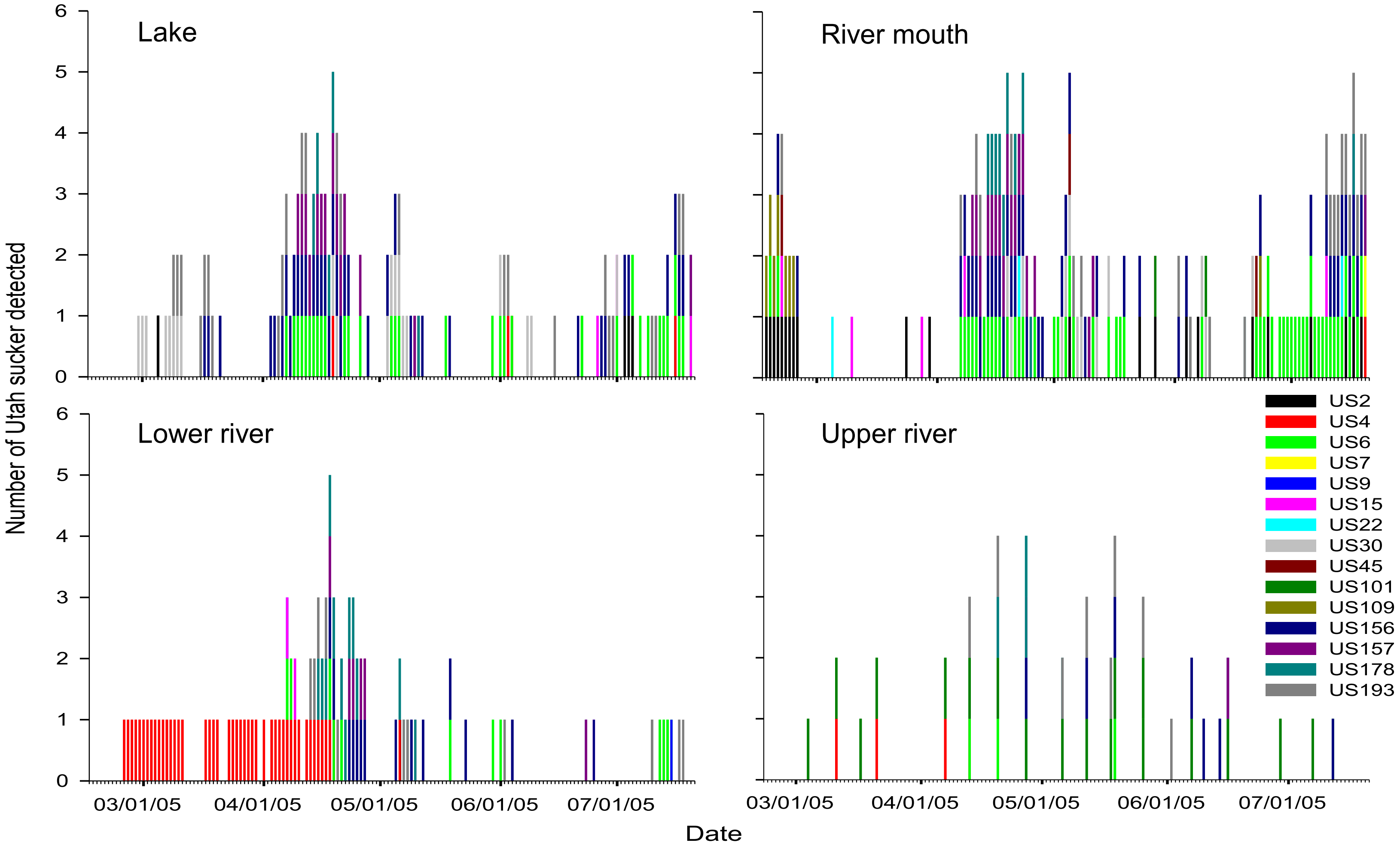

Figure 3-A-8. Numbers of individual tagged Utah suckers detected daily via continuous monitoring during the Provo River spawning run in 2005 of the lake, river mouth, and lower river sites (stationary hydrophones and receiver) and via intermittent monitoring (mobile tracking by foot or vehicle) of the upper river. (Legend: Utah sucker codes)

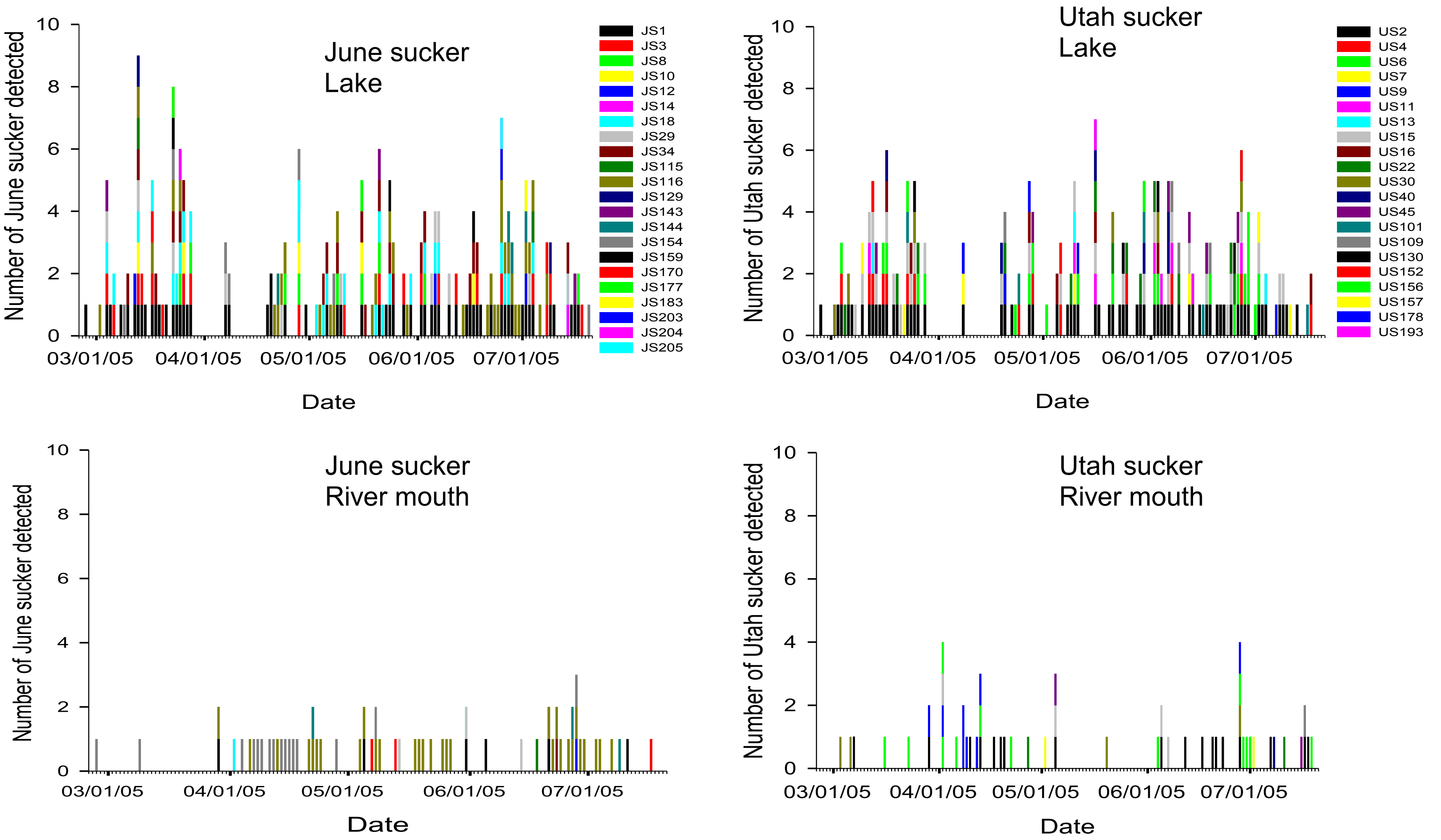

Figure 3-A-9. Numbers of individual tagged June sucker and Utah sucker detected daily via continuous monitoring during the Spanish Fork River spawning run in 2005 of the lake and river mouth (stationary hydrophones and receiver). (Legends: codes for individual Utah sucker and June sucker; fill colors begin repeating at JS 159 and US130)

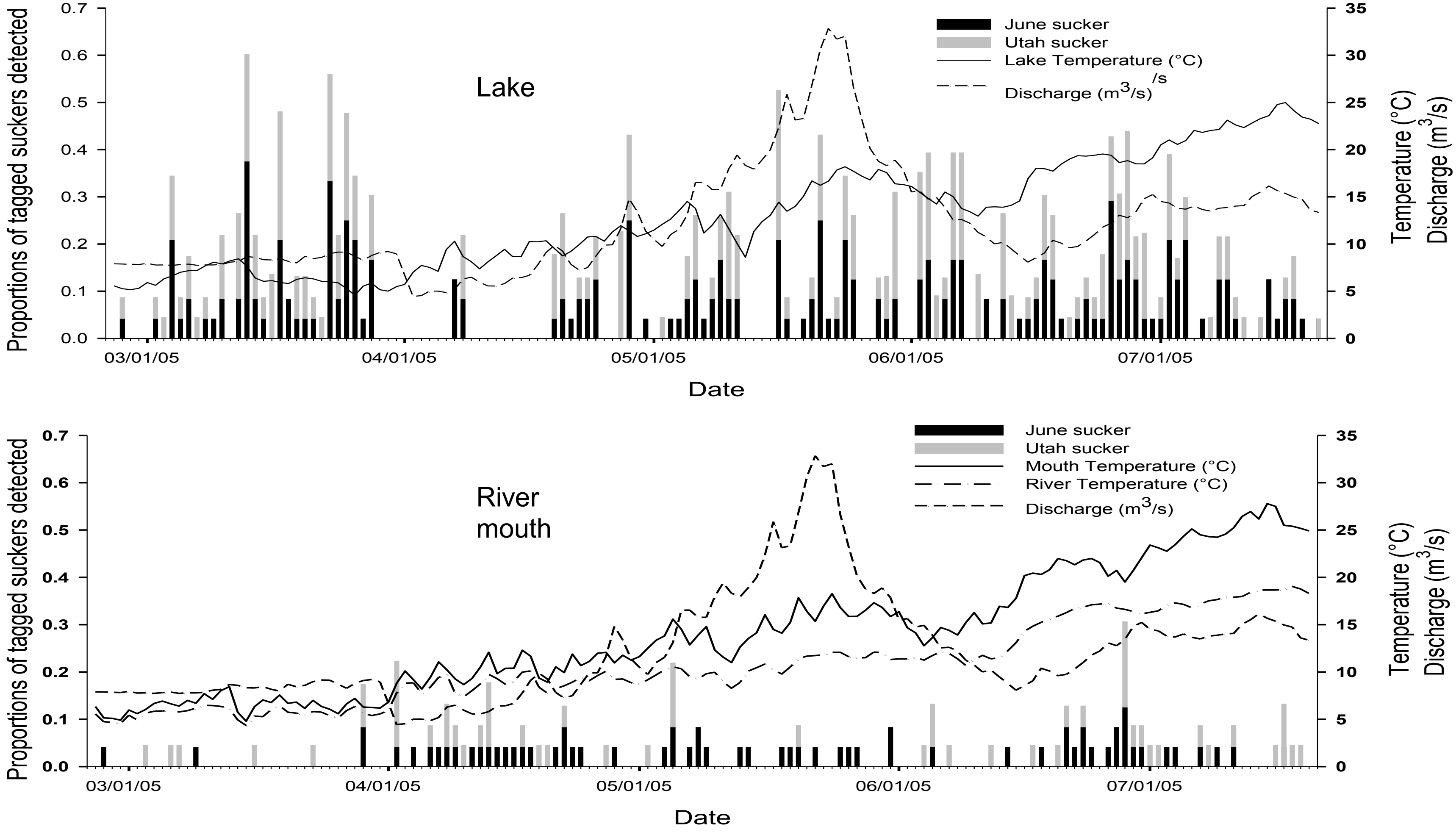

Figure 3-A-10. Proportions (by species) of tagged June sucker and Utah sucker detected daily via continuous telemetric monitoring during the Spanish Fork River spawning run in 2005 of the lake and river mouth sites (stationary hydrophones and receiver) plotted with Spanish Fork River temperature (lake, mouth, and river) and discharge.

CHAPTER 4

EVALUATING CONGRUENCE OF MORPHOLOGY WITH GENETIC STRUCTURE AND STABLE ISOTOPIC SIGNATURES ($\delta^{13}C$ AND $\delta^{15}N$) IN THE JACKSON LAKE SUCKER COMPLEX

ABSTRACT

The Snake River sucker (SRS), *Chasmistes muriei*, a lakesucker believed to inhabit lakes in Jackson Hole, Wyoming prior to its extinction in the early 20th century, is known from a single specimen collected from the Snake River below Jackson Dam in 1927. Currently, suckers in Jackson Lake, its tributaries and outflow, and nearby lakes are identified as Utah sucker, *Catostomus ardens.* Recently sampled individuals from Jackson Lake and the Snake River, however, morphologically resemble limnetic lakesuckers (*Chasmistes*) rather than the benthic Utah sucker. This investigation of the morphologically diverse suckers in Jackson Lake and the upper Snake River assessed concordance of morphological variation with molecular variation and with variation in diet as measured by stable isotope analysis. Suckers were subjectively identified to morph (limnetic, benthic, or intermediate) using mouth characters putatively associated with planktivorous versus benthivorous feeding strategies. Morphologically the lone SRS holotype specimen grouped strongly with the extant limnetic morphs. No molecular evidence was found for deep genetic divergence between morphs or for hybridization among ancient lineages. Stable isotopic analysis revealed that the benthic morph was significantly enriched in

^{13}C relative to the limnetic morph, consistent with their respective presumed diets of benthic/littoral macroinvertebrates and zooplankton. By contrast, $\delta\ ^{15}$N, a metric of trophic level, did not differ significantly among morphs. Here we confirm the persistence of suckers in Jackson Lake and the upper Snake River that are morphologically extremely similar to the lone SRS specimen, and suggest that the status of the SRS be updated accordingly. The presence of lakesuckers in Jackson Lake, along with similar findings in other *Chasmistes*/*Catostomus* species pairs, also raises questions about the validity of the *Chasmistes* genus.

INTRODUCTION

The IUCN Red List (IUCN 2011), a widely accepted standard for quantitatively assessing species' global risks of extinction, classifies almost 20% of extant vertebrate species as Threatened (includes: Critically Endangered, Endangered, and Vulnerable). Recent evidence indicates that aquatic species, especially those inhabiting freshwater, are under greater risk of extinction than terrestrial species (Jenkins 2003). Over 12,000 fish species (approximately one quarter of global vertebrate diversity; Dudgeon et al. 2006) occupy freshwater habitats, although these habitats represent only 0.009% of the Earth's water (Nelson 2006; Helfman 2007; Lévêque et al. 2008). Freshwater fishes (and other fauna) dwell in ecosystems that are among the Earth's most threatened environments, and direct and indirect competition with humans for freshwater has contributed to their rank among the planet's most endangered animals (Leidy and Moyle 1998; Duncan and Lockwood 2001; Dudgeon et al. 2006). The major threats to freshwater biodiversity, all of which interact and have anthropogenic components, include fragmentation, flow alterations, invasion by exotic species, over-exploitation, and pollution (Hilborn et al. 2003; Dudgeon et al. 2006; Helfman 2007). Superimposed upon these threats are global-scale environmental changes including nitrogen deposition, warming, and temporal and spatial shifts in precipitation and runoff patterns (Poff et al. 2002; Galloway et al. 2004).

The Catostomidae (catostomids; sucker family) rank among the most threatened families in North America: 46 catostomid taxa are currently classified as imperiled, representing 6.0% of the total number of imperiled freshwater and diadromous fish taxa in North America, and of the 73 described species of North American catostomids, 36 (49%) are designated as imperiled (Jelks et al. 2008). Catostomids have been historically undervalued, both economically and ecologically, and have been mistakenly assumed to be “weedy” species which are common and tolerant of degraded habitats (Cooke et al. 2005). As a result, catostomids have been understudied relative to more valued families such as salmonids, but increasing concern about the conservation status of many catostomids has led to more interest in their biology and evolutionary history.

Among the most imperiled Catostomidae are the lakesuckers, genus *Chasmistes* (*Ch.*), inhabiting several large western North American lakes and low velocity rivers. Lakesuckers are mid-water zooplanktivores having terminal, oblique mouths, thin lips with reduced papillation, wide gaps between the lower lip lobes, and gill rakers with fimbriate distal ends (Miller and Smith 1981; Sigler and Sigler 1987; Scoppettone and Vinyard 1991). Four recent species of lakesuckers from four different hydrologic basins are recognized: June sucker (*Ch. liorus mictus*; Bonneville Basin), cui-ui sucker (*Ch. cujus*; Truckee River drainage), shortnose sucker (*Ch. brevirostris*; Klamath River watershed), and the purportedly extinct Snake River sucker (SRS; *Ch. muriei*; upper Snake River basin) (Miller and Smith 1981). Some also consider the Lost River sucker (*Deltistes luxatus*; Klamath River drainage) to be a lakesucker, although it has gill rakers with filamentous or cone shaped rather than fimbriate distal ends. All extant *Ch.* spp. (and *D. luxatus*) are federally listed as endangered (U.S. Fish and Wildlife Service 1967, 1986, 1988). Lakesucker declines have been attributed to historical overexploitation (commercial, recreational, and subsistence), changes in aquatic habitat (degraded water quality; flow alterations; stream channelization; and loss of lake littoral zones, especially at tributary confluences), competition with and predation by nonnative fish species, and hybridization with *Catostomus* (*C.*) spp. (Carter 1969; Fuhriman et al. 1981; Scoppettone and Vinyard 1991). Jackson Lake and the upper Snake River basin, native range of the SRS, represent some of the least anthropogenically-impacted lakesucker habitats.

All extant species of *Chasmistes* are sympatric with at least one species of *Catostomus* (benthivorous suckers) over all or part of their range. *Catostomus* spp. have subterminal to ventral mouths with large papillose lips; a narrow cleft between the lower lip lobes; and gill rakers with non-branching, filamentous distal ends (Miller and Smith 1981; Sigler and Sigler 1987). Suckers of intermediate morphology exist where sympatry of *Ch*. spp. and *C*. spp. occurs, and this has been attributed to hybridization, which has been described as common among catostomids, confounding taxonomy and conservation issues (Miller and Smith 1981; Scoppettone and Vinyard 1991; Markle et al. 2005; Tranah and May 2006; Cole et al. 2008; Chen and Mayden 2012; Smith et al. 2013). Molecular studies of lakesuckers, however, have consistently failed to detect evidence of hybridization among ancient lineages, suggesting that lakesuckers are locally evolved ecophenotypes of *Catostomus* rather than a clade (Mock et al. 2006; Tranah and May 2006; Cole et al. 2008). Recently, Chen and Mayden (2012) synonymized *Chasmistes* (and *Deltistes* and *Xyrauchen*) into *Catostomus*, and Smith et al. (2013) classified *Pantosteus* into *Catostomus* and recommended that all western North American catostomids be included in the single genus, *Catostomus*.

Much of the confusion regarding taxonomy and management of lakesuckers (and many other species) arises as attempts are made to overlay presumably neutrally-evolving molecular characters onto existing morphologically-based classification systems (Hendry et al. 2000). Many morphological characters vary continuously and are likely due to the contributions of many loci, environmental, and/or developmental influences. Convergent evolution (Taylor 1999; Rûber and Adams 2001; Barluenga and

Meyer 2010), hybridization (Dowling and DeMarais 1993; Turgeon and Bernatchez 2001; Redenbach and Taylor 2002; Rûber et al. 2002; Sullivan et al. 2004), and epigenetic regulation of plastic morphological characters (Mittelbach et al. 1999; Skúlason et al. 1999; Adams et al. 2003; Proulx and Magnan 2004) can all result in strongly supported but contradictory patterns of morpholocial divergence and genetic group assignment.

Incongruence between morphological and molecular data can manifest as pronounced molecular divergence occurring within a morphologically similar group (e.g., cryptic species: Johnson and Jordan 2000; Colborn et al. 2001; Johnson 2002; Johnson et al. 2004; Santos et al. 2006) or as marked morphological differentiation occurring within a genetically similar group (e.g. McCartney et al. 2003; Tranah and May 2006; Cole et al. 2008). Within the Catostomidae, a major subdivision (4.5% mitochondrial sequence divergence) exists within Utah suckers despite the lack of pronounced morphological variation between southwestern and northeastern clades in the Bonneville Basin and the ancient Snake River drainages, respectively (Mock et al. 2006). Sympatric populations of shortnose sucker and Klamath largescale sucker in the Klamath River drainage (Tranah and May 2006) and June sucker and Utah sucker in the Bonneville Basin (Cole et al. 2008) exhibit marked morphological divergence yet minimal molecular variation.

The SRS is known from a single holotype specimen (UMMZ 81530; Miller and Smith 1981) collected from the Snake River below Jackson Lake Dam in

1927 by the naturalist Olaus Murie and was believed to have become extinct shortly thereafter (Miller and Smith 1981). Snake River sucker were assumed to inhabit lakes in Jackson Hole, WY, occurring sympatrically with Utah sucker (NE clade). Given its reported status of ‘extinct’, the suckers currently existing in Jackson Lake, its tributaries and outflow and nearby lakes are presumed to be Utah sucker. Mountain sucker (*Catostomus platyrhynchus*) and bluehead sucker (*Catostomus discobolus*) are also native to the Snake River basin above Shoshone Falls, but they are easily distinguished from Utah sucker morphologically and their preferred habitat is smaller, higher gradient streams. The Snake River sucker specimen (UMMZ 81530; Miller and Smith 1981) differs from other *Chasmistes* (except those identified as hybrids) in that it has a subterminal mouth and papillated lips, Miller and Smith (1981) concluded that the specimen possessed introgressed characters from Utah sucker (similar to their description of current June sucker, *Ch. liorus mictus*, possessing introgressed Utah sucker characters).

Suckers morphologically resembling lakesuckers have been collected from the Snake River (2004; BC personal observation) and Jackson Lake (2004 and 2005; BC, DC personal observations) during surveys conducted in association with the US Forest Service, WY Game and Fish, and/or the US Geological Survey (Figure 4-1). Consistent with observations of suckers in Utah Lake and Upper Klamath Lake, those in Jackson Lake and the adjacent Snake River (JL) exhibit a continuum between benthic and limnetic morphs (DC personal observation). Mitochondrial DNA analysis (Cardall 2007; NADH dehydrogenase subunit 2 gene: ND2) has revealed that suckers spanning the benthic to limnetic spectrum sampled in the Snake River just upstream of Jackson Lake during the 2004 spawning season were members of the northeastern clade of Utah sucker (Mock et al. 2006), eliminating the possibility that the *Ch.* morphs in JL were transplanted June sucker, which exhibit southwestern clade ND2 haplotypes.

The objectives of this investigation were to test the following hypotheses: 1) the suckers in Jackson Lake are another example of a lakesucker morphological continuum with little or no genetic structuring; 2) the SRS is not an extinct morph but represents one end of the extant morphological continuum, and 3) the distinct morphological ends of the continuum represent a continuum of feeding strategies. To achieve this, (i) recently sampled JL suckers were morphologically analyzed and compared with the holotype of the presumably extinct SRS; (ii) molecular variation and the extent of morphologically-based molecular sub-structuring in JL suckers were examined via five microsatellite loci; (iii) the ^{13}C and ^{15}N isotopic signatures (δ^{13}C and δ^{15}N) and niche widths of JL suckers were determined via stable isotope analysis; and (iv) the variation in the morphological and stable isotopic character sets were compared for concordance.

MATERIALS AND METHODS

Study Site

Jackson Lake (Figure 4-2), located in northwestern Wyoming in Grand Teton National Park, formed when meltwater filled the trough gouged by the Snake River Lobe of the Yellowstone–Absaroka glacier as it retreated about 9,000 years ago at the end of the Pinedale glaciation (Pierce and Good 1992). The boundary between the Snake River Basin's southeastern edge and the Bonneville Basin is seismically active (Smith and Sbar 1974; Smith 1978), and multiple times during the Pleistocene (and likely earlier), the Bear River's course has been shifted between the two drainages by volcanism associated with tectonic activity (Currey 1990; Oviatt et al. 1992; Bouchard et al. 1998). The most recent connection between the Snake River drainage and the Bonneville Basin occurred about 14,500 YBP when the drainage divide at Redrock Pass was topped and failed, and Lake Bonneville flooded catastrophically into the Snake River drainage (Currey 1990; Bright and Ore 1987; Jarrett and Malde 1987).

Jackson Lake is a natural moraine-dammed lake which was enlarged first with the construction of Jackson Lake Dam in 1911 and again in 1916 (Table 4-1). Jackson Lake is classified as oligotrophic based on chlorophyll a concentrations and mesotrophic based on algal assemblages with blooms of nitrogen fixing cyanobacteria (and small coccoid cyanobacteria) occurring in summer after lake stratification (Kilham et al. 1996). The Snake River is Jackson Lake's major tributary. A unique assemblage of native and non-native fishes exists in Jackson Lake, with native species including Utah sucker (northeastern clade), Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*), redside shiner (*Richardsonius balteatus*), Utah chub (*Gila atraria*), speckled dace (*Rhynichthys osculus*), mottled sculpin (*Cottus* bairdii), Paiute sculpin (*Cottus beldingii*), and mountain whitefish (*Prosopium williamsoni*). Nonnative species including lake trout (*Salvelinus namaycush*) and brown trout (*Salmo trutta*).

Sample Collection and Sucker Field Identification

Samples for morphological, genetic, and stable isotopic analyses were collected from suckers captured during the spawning season in the Snake River by raft electrofishing in 2004 (Table 4-2; Figure 4-2 – downstream from location A to the Jackson Lake confluence). Suckers were captured by overnight gill and trammel netting in Jackson Lake in 2004 and 2005 (Table 4-2; Figure 4-2 – locations B – J).

Captured suckers were identified in the field as limnetic, benthic, or intermediate morphs based on visual classification of external characters. These categories follow those used to assess Utah Lake suckers (Cole et al. 2008). ‘Limnetic morphs’ were those with increased lip size and papillation, narrower lower lip lobe gap, and reduced jaw angle (Miller and Smith 1981). ‘Benthic morphs’ were those showing reduced lip size and papillation, wider lower lip lobe gaps, and steeper jaw angles than described by Sigler and Sigler (1987). ‘Intermediate morphs’ were those not identified as limnetic or benthic morphs, but which showed intermediate characters.

Morphological Analysis

Digital photographic images from three perspectives (full body profile, head profile, and ventral head) of 45 (15 of each morph) Jackson Lake suckers in a Plexi-glas live well (l × w × h: 60 × 15 × 45 cm) were obtained using a Nikon 990 digital camera following Cole et al. (2008). Values for twelve morphological variables were determined; nine were ratios of measured distances to standard length, one was a direct measurement, and two were subjective classification variables (Table 4-3; Figure 4-3). Lip morphology of individual suckers was classified subjectively on a scale from one to four: (1) planktivore – lips with no or few papillae and small lower lip lobes (Figure 4-1A); (2) leans planktivore – slightly larger and more papillose lips; (3) leans benthivore – large lips with moderate papillation with papillae not extending the length of the lower lobe; and (4) benthivore – large, fleshy, extensively papillated lips with papillae extending the length of the lower lobe (Figure 4-1B). Three subjective head profile classifications were used: (1) concave (Figure 4-1A); (0) straight; and (-1) convex (Figure 4-1B). Images were digitized via the program tpsDIG (Rohlf 2001), morphological landmarks were identified, and the distances (in mm, determined relative to 12.7 mm scale markers on the live well) between them calculated. To facilitate comparison to the SRS holotype specimen (Miller and Smith 1981), all measured lengths were divided by standard length. Jaw (maxillary) angle was measured from Figure 9a in Miller and Smith (1981). The gap width between lower lip lobes for the SRS holotype specimen was interpolated from values provided in Table 1 and measurements from Figure 9a in Miller and Smith (1981).

Principal component analysis (PCA) based on the correlation matrix among variables was used to ordinate morphological variation in 45 Jackson Lake suckers and the SRS holotype. Morphological data for the SRS used in the PCA (Table 4-3) included values for ratio variables from Miller and Smith (1981); values for the two variables, jaw angle and lower lip gap ratio, derived from Miller and Smith (1981) for this study; and values, lip and head profile classifications, subjectively assigned using images from Miller and Smith (1981). A second morphological PCA was onducted using values for the SRS that adjusted for shrinkage due to preservation (Shields and Carlson 1996; Buchheister and Wilson 2005). Given the comparison made in this study between measurements obtained via calipers on the holotype specimen after preservation in formalin and then ethanol for 50 years and measurements calculated from digital images, accounting for shrinkage seemed reasonable. Because of the skull's bony composition, the shrinkage was presumed to have occurred along the spinal axis because of fluid loss from tissues between vertebrae. The correction for shrinkage (estimated at 4%; Shields and Carlson 1996; Buchheister and Wilson 2005) increased standard length of the holotype specimen from 371 mm to 386 mm. Predorsal, prepelvic, and preanal lengths were adjusted assuming shrinkage was based on their proportion of the spinal length, thus their values increased by 1.0214, 1.0230, and 1.0315 times, respectively. No corrections were made for other variables on the SRS holotype specimen prior to analysis although some shrinkage undoubtedly occurred. Finally, analysis of variance (ANOVA) was used to test for differences among morphs (excluding the SRS specimen from the analysis) in the 10 measured morphological variables.

Gill rakers (1st arch) were removed from morphologically-identified limnetic (n = 2) and benthic (n = 2) gill netting mortalities for examination. Images of these gill rakers were captured using a Nikon 990 digital camera.

Genetic Analysis

Fin (left pelvic) clips were collected from 58 adult suckers captured in the Snake River (via electrofishing in June 2004) and Jackson Lake (via gill netting in June and July 2004) and preserved in 90% ethanol. Among these suckers, 55 were subjectively identified to morph (20 *Ch*. morphs; 20 *Ca*. morphs; and 15 intermediate morphs). Genetic data from three additional suckers that were not photographed (nor identified in the field to morph) were included only in analyses that required no *a priori* identification to morph.

DNA was extracted using a salt/chloroform protocol (Mullenbach et al. 1989). DNA quantity and quality was assessed on 0.7% agarose gels stained with ethidium bromide. Five microsatellite loci (US4, US6, Dlu45, Dlu409, and Dlu4283) were amplified in these individuals following protocols described by Cardall et al. (2007). Microsatellite analyses were used to characterize nuclear divergence and diversity among the Jackson Lake / Snake River suckers.

The program Tools for Population Genetic Analysis (TFPGA; Miller 1997) was used to estimate unbiased heterozygosity based on microsatellite genotypes. Allelic richness was calculated for microsatellite data using the program FSTAT 2.9.3.2 (Goudet 2001). The program Arlequin 3.1 (Excoffier et al. 2005) was used to evaluate deviations from Hardy-Weinberg (HW) equilibrium using an analogue of Fisher's exact test (Guo and Thompson 1992), to assess linkage disequilibrium among microsatellite loci, and to conduct a genotype assignment test. Results of the HW and linkage disequilibrium tests were interpreted using Bonferroni-corrected alpha values. The assignment test used a log-likelihood approach to assess the probability of affiliation of individuals with each of the three morph categories, based on observed allele frequencies within each category (Paetkau et al. 2004; Waser and Strobeck 1998). Instances of HW disequilibrium were evaluated for heterozygote deficiencies using the program GenePop (Raymond and Rousset 1995). The probability of null alleles was assessed using Micro-Checker (van Oosterhout et al. 2004). The program GenAlEx (Peakall and Smouse 2006) was used to calculate the numbers and frequencies of private alleles by morph, to conduct a Mantel test (Mantel 1967) for correlation between genetic distance matrices and morph categories, and to perform principle coordinates analysis (PCoA) using standardized data. The program TFPGA was used to calculate θ_{ST} (an estimator of F_{ST} (Weir and Cockerham 1984) and to calculate F_{IS} among morphs. Ninety-five percent confidence intervals for θ_{ST} and F_{IS} were estimated by bootstrapping 1000 times over loci. Jost's D (Jost 2008) was also calculated using the program SMOGD (Crawford 2010). The Bayesian clustering program STRUCTURE 2.3.1 (Pritchard et al. 2000) was used to search the microsatellite data for population structure; microsatellite profiles of 58 individuals were analyzed, including profiles of three individuals not identified to morph. The model was run with correlated allele frequencies (Falush et al. 2003) and with admixture (Pritchard et al. 2000), and five runs of the model were made at each presumed value (1 – 4) of K, the number of subpopulations. For each Markov chain Monte Carlo run, estimates of the probability of K were taken after 1,000,000 iterations that were preceded by a burn-in of 30,000 iterations. The program, STRUCTURE HARVESTER (Earl and vonHoldt 2012) was used to further examine the output from STRUCTURE in interpreting the probability estimates of K using the method of Evanno et al. (2005).

Stable Isotopes Analysis

Left pelvic fin clip samples were collected from 63 adult suckers captured by gill and trammel netting in Jackson Lake in July 2004 and July and August 2005. These suckers spanned the morphological continuum present in Jackson Lake (16 *Ch.* morphs, 24 *C.* morphs, and 23 intermediate morphs) for stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$). Twenty-nine of these individuals were included in the microsatellite analysis.

Isotope samples were stored in 90% ethanol prior to processing and analysis, oven-dried at 60 °C for ~24 h to constant mass, and homogenized with a mortar and pestle. Samples were analyzed at the University of California – Davis Stable Isotope Lab via a PDZ Europa 20–20 isotope ratio mass spectrometer for dual carbon and nitrogen using Pee Dee belemnite limestone and atmospheric nitrogen as the carbon and nitrogen standards, respectively. Isotopic signatures were compared among sucker morphs via ANOVA. Niche width (NW) was estimated for each sucker morph by calculating the convex hull area encompassed by the smallest polygon containing all individuals of a given morph within the two dimensional $\delta^{13}C$ – $\delta^{15}N$ bi-plot space (isotopic niche space), and niche overlap among morphs was estimated as the overlapping area of polygons (Layman et al. 2007). Area estimates were generated using the program ArcGIS 10 (ESRI 2011). Total ranges of $\delta^{13}C$ [(CR = max($\delta^{13}C$) – min($\delta^{13}C$)] and $\delta^{15}N$ [(NR = max($\delta^{15}N$) – min($\delta^{15}N$)] were calculated (Layman et al. 2007). Regression analysis was used to examine the linear relationship between the first Principle Component (PC1) generated from the morphological PCA and $\delta^{13}C$. Unless stated otherwise, all statistical analyses were conducted using the program R 3.0.1 (R Development Core Team 2013).

RESULTS

Morphological Analysis

The first three PCs explained 75% of the variation in the 12 morphological variables. PC1, which explained 35% of the variation, was heavily loaded by mouth, head, and eye related variables (Table 4-4) and differentiated the morphs

(Figure 4-4). The signs (+/–) of the loadings of these variables on PC1 relative to one another were consistent with limnetic morphs having wider lower lip lobe gaps, steeper jaw angles, smaller and less papillose lips, less concave head profiles, and proportionally larger eyes and heads than *Catostomus* and intermediate morphs (Table 4-4). Neither PC2 nor PC3 differentiated the morphs. About 30% of the variation was explained by PC2, and loadings were based on the magnitudes of length ratios (Table 4-4). The third PC explained about 10% of the variation and was heavily loaded by an assortment of variables, especially peduncle depth to standard length ratio. Using the unadjusted morphological data in PCA, the SRS specimen is a limnetic outlier in the ordination of PC1 and PC2 (Figure 4-4A). Using the adjusted values resulted in the SRS holotype clustering more tightly with limnetic morphs in PCA ordinations (Figure 4-4C). Ordinations (not shown) from PCA of morphological variables excluding data for the SRS holotype specimen exhibited very similar patterns of differentiation among morphs. Because gill netting is a lethal sampling technique, we were able to dissect and examine gill rakers from several suckers at the limnetic and benthic extremes. Suckers morphologically identified as limnetic and presumed to be planktivorous (n = 3) had gill rakers with fimbriate or dendritic distal ends while those identified as benthic and presumed to be benthivorous (n = 3) were more filamentous (Figure 4-1). The distal ends of gill rakers of intermediates (n = 3) were intermediate between dendritic and filamentous (not shown).

ANOVA results showed statistically significant differences among morphs (excluding the SRS holotype specimen), in 4 of the 10 objectively measured morphological variables: jaw angle, preanal ratio, eye diameter ratio, and lower lip gap ratio (Table 4-5). A 3D plot employing these four variables clearly differentiates the morphs, and the SRS holotype specimen groups strongly with the limnetic morph (Figure 4-5).

Genetic Analysis

Although allelic richness varied among morphs and loci, the benthic morph displayed the greatest allelic richness (Table 4-6). The number of private alleles, adjusted for group size, was 10 for limnetic morphs, 11 for intermediates, and 21 for benthic morphs, although all private alleles had frequencies less than 0.140. Levels of unbiased heterozygosity were similar among morphs. When all morphs were analyzed as a single group, two of the five microsatellite loci (Dlu45 and Dlu4283) showed evidence of HW disequilibrium (Table 4-6). Within limnetic morphs, Dlu 4283 displayed HW disequilibrium; within the intermediates, US4 and Dlu4283 showed evidence of HW disequilibrium; and among the benthic morphs, Dlu45 appeared to be in HW disequilibrium (Table 4-6). All instances of HW disequilibrium were due to heterozygote deficiencies. Among all Jackson Lake suckers, null alleles are likely present at low frequencies in four of the five microsatellite loci (US4, Dlu45, Dlu409, and Dlu4283), including the three the exhibited HW disequilibrium (Table 4-6). No locus pairs exhibited linkage disequilibrium when the Jackson Lake suckers were analyzed as a single group.

Population metrics calculated from the microsatellite profiles failed to reveal sub-structuring in the Jackson Lake sucker population; subdivision was substantially less than that present in the minimally structured Utah Lake sucker population (Cole et al. 2008; Table 4-7). Jost's D (0.054) and θ_{ST} (0.0059) suggested high levels of gene flow among morphs in Jackson Lake (Table 4-7). The inbreeding coefficient, F_{IS}, for Jackson Lake suckers was low (0.134) and comparable to that for the Utah Lake sucker population (0.110; Table 4-7). Marginally significant correlation (P = 0.109) was detected between matrices of morph categories and microsatellite distances between Jackson Lake suckers (Table 4-7). No evidence of genetic sub-structuring by morphological classification or by location of capture was revealed by PCoA ordinations (Figure 4-6). The first three coordinates generated via PCoA of the microsatellite data explained 58% of the total variance with PCo1, PCo2, and PCo3 explaining 21%, 20%, and 17%, respectively, however, none of these Principle Coordinates differentiated the morphs. Bayesian model-based genetic clustering analysis determined that K=1 was the most probable number of sucker populations in Jackson Lake (Table 4-8). When the method of Evanno et al. (2005) was used (STRUCTURE HARVESTER), an optimum of K=2 was detected, however, all individuals had essentially equal probabilities of being assigned to either of the two populations, and individual assignments varied among runs.

Assignment testing using allele frequencies from a priori morph groups showed a low mis-assignment rate, 0.0363 overall, due to misclassification of one intermediate morph and one benthic morph as limnetic morphs. These results, illustrated in a log-likelihood plot, indicate that despite the lack of pronounced genetic subdivision, accurate assignment may be possible with prior knowledge of subpopulation allele frequencies (Figure 4-7).

Stable Isotopes Analysis

Single-factor (morph) ANOVA revealed that benthic morphs were significantly enriched in ^{13}C relative to limnetic morphs with intermediates falling between, as would be expected if diet followed morphology (Figure 4-8). Linear regression exposed a statistically significant relationship between PC1, which differentiated the morphs, and δ^{13}C ($r^2 = 0.257$; $P = 0.00826$). Mean δ^{15}N did not differ significantly among morphs (Figure 4-8).

Niche width and range of δ^{15}N for the limnetic morph were much narrower than those for the benthic morph and intermediate morph, whereas the ranges of δ^{13}C among morphs were similar (Figure 4-9). Taken together, these results suggest that the diet of the limnetic morphs encompassed prey from a narrower range of trophic levels than the diets of benthivores or intermediates, but none of the three morphs exclusively exploited a single food sub-web in Jackson Lake (Figure 4-9). The 27% niche overlap between limnetic and intermediate morphs comprised 83% of the niche width of the limnetic morph and only 29% of the niche width of the intermediate morph (Table 4-10; Figure 4-9). The niche widths of limnetic and benthic morphs displayed 22% overlap, which represented 56% and 27% of their respective niche widths, whereas the niche widths of benthic and intermediate morphs displayed 51% overlap, which represented 78% and 59% of their respective niche widths (Table 4-10; Figure 4-9).

DISCUSSION

Historical Context

Deep, cold, oligotrophic Jackson Lake is an interesting contrast to other lakes with lakesucker populations. It formed with the last glacial advance and retreat about 9,000 YPB and is younger than Utah, Upper Klamath, and Pyramid Lakes, which are remnants of ancient pluvial lakes. During the Pleistocene, these older pluvial lakes filled and emptied repeatedly with alternating wetter and dryer climate patterns. As the climate warmed and dried after the last glacial retreat, these large lakes receded, leaving smaller, somewhat saline lakes scattered among sub-basins. Utah Lake (Fuhriman et al. 1981; Crowl, unpublished data) and Upper Klamath Lake (Wood et al. 2006) are warm, shallow (mean depths ~ 2.8 m), and hypereutrophic, with chlorophyll a concentrations more than two orders of magnitude greater than those in Jackson Lake. Both experience annual summer - autumn cyanobacterial blooms (*Aphanizomenon flos-aquae*; *Microcystis aeruginosa*) and have histories of extensive anthropogenic impacts. Pyramid Lake (105 m maximum depth) is the deepest terminal saline lake in the western hemisphere, and although nitrogen-limited and relatively unproductive (Lebo et al. 1992; Reuter et al. 1993), it is more eutrophic than Jackson Lake and also has a history of anthropogenic degradation and experiences summer -

autumn cyanobacterial blooms (*Nodularia spumigena*). Jackson Lake presents an opportunity to study lakesucker evolution and ecology in a more recently formed lake with much less anthropogenic impact. Ancestors of suckers in Utah, Upper Klamath, and Pyramid Lakes inhabited very large, ancient lakes that receded, eventually confining sucker populations to small remnant lakes, whereas the ancestors of the suckers in Jackson Lake invaded a newly formed lake within the last 9,000 years. Heterozygote exact tests for detecting bottlenecks, coupled with negative values for Tajima's D detected in an earlier study at sites near Jackson Lake in the upper Snake River (Cardall 2007), are consistent with an expanding sucker population in the area following late Pleistocene glaciation.

A number of characteristics are common to all described extant species of *Chasmistes*. First, each lakesucker population is sympatric with at least one species of *Catostomus* over all or part of its range (Miller and Smith 1981; Scoppettone and Vinyard 1991) and, where sympatry occurs, a morphological continuum exists from benthivore to planktivore, with a large proportion of individuals exhibiting intermediate morphology (Brussard et al. 1990; Buth et al. 1992; Markle et al. 2005; Tranah and May 2006; Cole et al. 2008). Historical descriptions also describe suckers of intermediate morphology (Jordan 1891). Even the paleontological record includes specimens somewhat intermediate between limnetic and benthic forms, with some sites yielding Miocene fossils described as "primitive" *Chasmistes* (Miller and Smith 1981; Smith 1981).

Chasmistes fossils occur in Miocene to Pleistocene deposits in six western states and are nearly always accompanied by *Catostomus* fossils. Pliocene fossils imply the presence of multiple species at the Glenns Ferry Formation, ID: *Ch. spatulifer*, the most specialized zooplanktivore in the genus, fossil or recent, and an undescribed, less specialized form that varied in a manner not indicative of hybridization with *Catostomus* (Miller and Smith 1981). Pliocene fossils similar to the less specialized *Ch.* spp. of the Chalk Hills and Glenns Ferry Formations have also been recovered from Secret Valley, CA and Honey Lake, CA (Miller and Smith 1981). Second, in two of the three described extant lakesucker populations, suckers of intermediate morphology are indistinguishable from the *Ch.* morph using molecular markers (Brussard et al. 1990; Buth et al. 1992; Tranah and May 2006; Cole et al. 2008). These include Upper Klamath Lake, where *Ch. brevirostris* and *C. snyderii* are sympatric, and Utah Lake, where *Ch. liorus* and *C. ardens* are sympatric (Tranah and May 2006; Cole et al. 2008). By contrast, *Ch. cujus* in Pyramid shows no evidence of gene flow with its sympatric benthivore, *C. tahoensis*, and fish that appeared morphologically to be hybrids were genetically differentiable from *C. tahoensis*, but not from *Ch. cujus* (Brussard et al. 1990; Buth et al. 1992). Third, phylogenetic analyses using molecular data have failed to recovered either *Chasmistes* or *Catostomus* as monophyletic (Mock et al. 2006; Tranah and May 2006; Sun et al. 2007; Cole et al. 2008; Chen and Mayden 2012), and lakesuckers are phylogenetically closer to the sympatric *C*. spp. than to allopatric congeners (Li 1999; Mock et al. 2006;

Tranah and May 2006). Further, no molecular studies have revealed evidence of hybridization between ancient lineages (Mock et al. 2006; Tranah and May 2006; Cole et al. 2008), although demographic events such as bottlenecks or founder effects may have obscured such signals.

Finally, based on morphology, adult lakesuckers are presumed to be primarily mid-water zooplanktivores whereas adults of their sympatric *C*. spp. are presumed to prey predominantly on benthic/littoral macroinvertebrates. Billman (2005) confirmed via gut analysis that zooplankton comprised the vast majority of the diet of adult *Ch. liorus* in a refuge population in Red Butte Reservoir, UT. The stable isotope analysis of adult suckers in Utah Lake described in Chapter 3 (Cole) also confirmed that zooplankton were the major component of the diet of adult *Ch. liorus*, and that benthic/littoral macroinvertebrates were the main prey source for C. *ardens*.

The sucker population in Jackson Lake shares all of the common features described above for lakesucker / benthic sucker populations. Benthic and limnetic forms are apparent, but intermediate forms are common; these forms do not show evidence of molecular differentiation or a history of hybridization, and the limnetic form has a distinct isotopic signature associated with a zooplankton diet. These findings suggest that the similarities between the sucker populations in Jackson, Utah, Pyramid, and Upper Klamath Lakes are likely the result of parallel evolutionary processes. If distinct adaptive optima (benthic vs. limnetic habitats) exist in these lake environments, a population may diverge into benthic and limnetic forms under the influence of natural selection, particularly if divergence is reinforced by reproductive isolation mechanisms (Schluter 1996, 2001; Taylor 1999). Under such a scenario, the degree of genetic divergence would be a function of time, the strength of selection, and the degree of reticulation.

Morphological Analysis

Currently, a continuum of morphologies exists between benthic and limnetic sucker morphs in Jackson Lake. The lone SRS specimen grouped strongly with limnetic morphs (body morphometrics and gill raker structure), particularly when using data adjusted for preservation shrinkage.

Genetic Analysis

Similar to other lakesucker / benthic sucker populations, despite the marked morphological variation found in JL suckers, microsatellite analyses revealed little or no population sub-structuring based on morphological classification. No evidence of hybridization (e.g., private alleles) of ancient lineages was detected. Earlier mitochondrial DNA sequence analysis (Cardall 2007) of samples collected in the Snake River upstream of Jackson Lake from individuals spanning the morphological spectrum confirmed that JL suckers are members of the northeastern clade of Utah sucker. Two caveats must be considered regarding the microsatellite analysis: firstly, this study examined only five microsatellite loci; and secondly, there was a strong likelihood of the presence of null alleles at four (US4, Dlu45, Dlu409, and Dlu4283) of the five loci. The presence of these null alleles likely resulted in the heterozygote deficiencies and HW disequilibrium observed at three of the five loci (US4, Dlu45, and Dlu4283), although other potential contributors include population sub-structuring, inbreeding, linkage to genes under selection, or any combination of these factors. The presence of null alleles can lead to overestimation of population structure in significantly sub-structured populations (Chapuis and Estoup 2007) and to reduction in the proportion of correctly assigned individuals in assignment tests (Carlsson 2008). However, the overall effects of null alleles in this study were likely minimal, given the lack of sub-structuring detected, the excellent performance of the genotype assignment test, and the identification via Bayesian-based cluster analysis of a single sucker population in Jackson Lake.

Stable Isotopes Analysis

Benthic / littoral freshwater food webs are ^{13}C enriched relative to planktonic (pelagic) food webs, and this uncoupling of carbon flows between benthic / littoral and planktonic food webs may be a global feature of lakes (France 1995). Morphological and stable isotopic (e.g., diet) character sets were concordant in Jackson Lake suckers. Benthic morphs, with their ventral mouths and large, papillose lips, were, significantly enriched in ^{13}C (e.g., benthivorous) relative to oblique mouthed, small-lipped limnetic (zooplanktivorous) morphs. Suckers of intermediate morphology exhibited intermediate $\delta^{13}C$ values, suggesting substantial exploitation of both the benthic / littoral and planktonic trophic webs.

The trophic levels of the sucker morphs were very similar in oligotrophic Jackson Lake, with both limnetic and benthic morphs being only slightly enriched in ^{15}N (~ 0.2 ‰) relative to intermediates. However, niche width and range of $\delta^{15}N$ for the limnetic morph were much narrower than for the benthic and intermediate morphs, suggesting that in Jackson Lake, the limnetic morh is more of a trophic specialist and exploits fewer trophic levels than benthic or intermediate morphs. Intermediate morphs exhibited the widest niche width, and showed considerable overlap with both the limnetic and benthic forms. In oligotrophic Jackson Lake, the niche width of intermediates encompassed 83% of the niche width of limnetic morphs and 78% of the niche width of benthic morphs. In hypereutrophic Utah Lake, there was less dietary overlap among morphs, and the niche width of intermediates encompassed 61% of the niche width of June sucker and 63% of the niche width of Utah sucker niche widths (Chapter 3).

The Snake River Sucker (*Casmistes muriei*)

The presence of a lakesucker morph in Jackson Lake suggests that SRS, as originally described, may persist, although whether it represents a genus, or even a species, distinct from *C. ardens* remains nebulous. There are numerous accounts in the literature of the rediscovery of a fish species presumed to be extinct (Miller and Pister 1971; Taylor et al. 1988; Etnier and Starnes 1993;

Jenkins and Burkhead 1994). In Utah Lake, severe drought in the early 1930s led to extremely low water levels, culminating in a devastating winterkill in 1934-35. No spawning June sucker (*Ch. l. liorus*) were observed the following spring, and they were believed extinct (Tanner 1936). Re-discovered extant June suckers were subsequently classified as a different subspecies (*Ch. l. mictus*) from the pre-drought form due to presumed introgression from Utah sucker (Miller and Smith 1981), despite Jordan's (1891) much earlier description of suckers morphologically intermediate between June and Utah suckers. The original description of the *Ch. muriei* holotype also includes reference to introgression from Utah sucker (Miller and Smith 1981).

Implications, Recommendations, and Future Research

Persistence of the purportedly extinct *Chasmistes muriei* in Jackson Lake and the upper Snake River, along with the finding of another benthic-limnetic continuum involving lakesuckers and a *Catostomus* species, raises important questions about lakesucker ecology, evolution, and taxonomy. More immediately, the conservation status and management of this morph should be actively addressed, and lethal capture techniques should be curtailed until these issues are more clearly understood. Further, management programs for the other lakesuckers (all federally endangered) should consider the possibility that these forms may exist as a dynamic continuum with sympatric *Catostomus* species, and that these pairs may share both evolutionary histories and evolutionary futures. In all lakesucker/*Catostomus* pairs, studies using larger numbers of genetic loci to assess divergence, as well as studies on the genetic basis of morphological differences, would be informative.

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Table 4-1. Physical and limnological characteristics of Jackson Lake, WY.

Jackson Lake characteristics	
Age	~ 9,000 y
Surface area	103.4 km^2
Watershed area	2134 km^2
Maximum depth	134 m
Mean depth	37.5 m
Surface elevation	2,064 m
Water temperature	< 16°C
Chlorophyll a	1.42 µg / l *
Nutrient status	Mesotrophic**
Islands	> 15

* Mean of 87 observations collected from 1978 to 1998 from various locations in Jackson Lake (NPS 2001).
** Based on algal assemblages (Kilham et al. 1996); oligotrophic if based on chlorophyll a concentrations.

Table 4-2. Locations and dates of collection of samples for morphological, genetic, and stable isotope analyses of Jackson Lake suckers. Includes samples collected for mitochondrial DNA (ND2 subunit gene) analysis and reported in Cardall 2007.

		Samples collected for analysis			
Location	Sampling dates	Morphological	Genetic (msat)	Genetic (mito)*	Stable Isotope
Snake River (Flagg Ranch)	21 - 22 June 2004	17	20 (3)**	10	0
Jackson Lake	12 - 14 July 2004	21	38	0	30
Jackson Lake	11 - 14 July 2005	6	0	0	20
Jackson Lake	21 -22 August 2005	1	0	0	13
	Totals	45	55 (58)**	10	63

* see Cardall 2007

** Number in parentheses indicates the inclusion of three samples from suckers not identified to morph that were analyzed using the programs STRUCTURE 3.0.1, which requires no a priori classification, and Arlequin when analyzing (HW equilibrium and linkage disequilibrium) the Jackson Lake suckers as a single population.

Table 4-3. Morphological variables analyzed included 10 morphometric measurements (nine are ratios with standard length) and two subjective classifications.

Morphological Variables Analyzed
Predorsal L / Standard L*
Prepelvic L / Standard L*
Preanal L / Standard L*
Head L / Standard L*
Head depth (eye) / Standard L*
Head depth (occiput) / Standard L*
Eye diameter / Standard L*
Peduncle depth / Standard L*
Lower lip gap width / Standard L**
Jaw (maxillary) angle**
Lip classification
Head profile classification

* Miller and Smith (1981)

** for SRS, determined from data and images in Miller and Smith (1981)

Table 4-4. Proportion and cumulative proportion of variance explained by PCs and important variable loadings (> [0.100]) on the first five PCs resulting from PCA of morphological profiles of Jackson Lake suckers. (n = 45, 15 of each morph)

	Principal component				
	1	2	3	4	5
Proportion of Variance explained	0.348	0.297	0.109	0.068	0.053
Cumulative Proportion explained	0.348	0.645	0.753	0.822	0.875
Morphological Variable			Loadings		
Predorsal L / Standard L		-0.395		0.257	-0.643
Prepelvic L / Standard L	-0.109	-0.441	-0.101	0.348	0.107
Preanal L / Standard L	-0.212	-0.371	-0.356	0.155	-0.169
Head L / Standard L	0.237	-0.356	0.356		
Head Depth (Eye) / Standard L	0.156	-0.409	0.304	-0.337	0.162
Head Depth (Occiput) / Standard L		-0.436		-0.131	0.513
Eye Diameter / Standard L	0.381			-0.424	-0.361
Peduncle Depth / Standard L			-0.745	-0.428	
Lip Gap Width / Standard L	0.445				-0.164
Jaw Angle	0.388		-0.257	0.183	0.286
Lip Classification	-0.453			-0.174	
Head Profile Classification	0.395		-0.127	0.474	

Table 4-5. Means (and standard deviations), *F* values, and probabilities (*P*) for morphological variables exhibiting significant differences among morphs (ANOVA with 2, 42 degrees of freedom and α = 0.05).

			Variable means by morph		
Morphological variable	*F* value	*P*	Limnetic	Intermediate	Benthic
Preanal L / Standard L	5.30	0.0089	0.761 (0.015)	0.769 (0.015)	0.779 (0.016)
Eye diameter / Standard L	12.40	5.8×10^{-5}	0.0305 (0.0022)	0.0277 (0.0022)	0.0269 (0.0019)
Lower lip gap width / Standard L	59.09	6.2×10^{-13}	0.0104 (0.0018)	0.00666 (0.0017)	0.00451 (0.00066)
Jaw (maxillary) angle	26.57	3.5×10^{-8}	55.73° (3.75°)	46.33° (5.63°)	44.20° (4.25°)

Table 4-6. Diversity indices for microsatellite profiles of Utah Lake suckers: sample size (*N*); unbiased heterozygosity (H); number of alleles (AN); allelic richness (AR); number of private alleles (PA); and estimated null allele frequency (NA). **Bold** – statistically significant at the Bonferroni-adjusted α = 0.01. ***Bold italics*** – Null allele(s) likely present.

	Index /	Locus					
Morph	Parameter	US4	US6	Dlu45	Dlu409	Dlu4283	All loci
Limnetic	*N*	20	19	19	20	18	19.2
	H (*P*)	0.878 (0.0535)	0.969 (0.0467)	0.865 (0.0189)	0.956 (0.1810)	**0.951 (0.0080)**	0.9240
	AN	10	14	13	15	18	70
	AR	12.34	19.39	9.90	16.19	16.42	74.23
	PA	0	2	3	2	3	10
	NA	0.026	0.023	0.034	0.006	***0.097***	1**
Intermediate	*N*	20	20	20	20	20	20
	H (*P*)	**0.867 (0.0095)**	0.915 (1.0000)	0.887 (0.2039)	0.941 (0.7661)	**0.947 (0.0039)**	0.9120
	AN	13	18	12	18	15	76
	AR	9.17	12.73	11.55	14.07	16.17	63.69
	PA	3	3	1	3	1	11
	NA	***0.126***	-0.041	0.068	-0.008	***0.096***	2**
Benthic	*N*	15	15	15	15	15	15
	H (*P*)	0.922 (0.1384)	0.959 (0.2940)	**0.890 (0.0002)**	0.949 (0.0848)	0.931 (0.0545)	0.9300
	AN	14	22	11	18	18	83
	AR	13.00	18.00	12.00	18.00	15.00	76.00

	PA	7	7	2	2	3	21
	NA	0.032	0.026	***0.188***	***0.070***	0.051	2**
All suckers	*N*	55	54	54	55	53	54.2
	H	0.899	0.945	0.888	0.953	0.951	0.918
	AN	21	29	17	24	26	117
	AR	12.87	16.90	11.33	16.48	16.75	74.32
	PA	10	12	6	7	7	42
	NA	***0.069***	0.016	***0.109***	***0.037***	***0.090***	4**

* N = 58; includes three suckers of unknown morph.

** Number of loci likely to have null alleles present.

Table 4-7. Population structure metrics for Jackson Lake (n = 55) and Utah Lake suckers (n = 78): Jost's D; F_{ST} estimator, θ_{ST} (and 95% CI); inbreeding coefficient, F_{IS} (and 95% CI); and Mantel test generated Pearson's correlation coefficient, *r* (and *P*), between distance matrices derived from morphological identifications and from the microsatellite data.

Population	Location	
parameter	Jackson Lake	Utah Lake*
Jost's D	0.054	0.186
θ_{ST} (95% CI)	0.0059 (0.0004 - 0.0122)	0.0199 (0.0123 - 0.0279)
F_{IS} (95% CI)	0.1338 (0.0773 - 0.1959)	0.1102 (0.0496 - 0.1710)
r (P)	0.028 (0.109)	0.1127 (0.0001)

* Utah Lake sucker population values from Cole et al. 2008 or calculated via their data.

Table 4-8. Means and ranges of likelihoods [P(D)] from five runs of the program STRUCTURE fitting different assumed numbers of subpopulations (K) for microsatellite profiles of Jackson Lake suckers (n = 59) without *a priori* classification of individuals to morph. **Bold**: highest posterior probability.

K	Mean lnP(D)	Range ln P(D)
1	**–1660**	**–1661 to –1660**
2	–1663	–1668 to –1661
3	-1756	–1851 to –1665
4	–2027	–2094 to –1921

Table 4-9. Means and 95% confidence intervals (CI) by morph obtained during ANOVA (2, 60 degrees of freedom) of δ13C ($F = 12.65$; $P = 2.6 \times 10^{-5}$) and δ15N ($F = 0.57$; $P = 0.57$) of Jackson Lake suckers.

Morph	Mean δ13C (±95% CI)	Mean δ15N (±95% CI)
Benthic	-21.79 (±0.80)	7.78 (±0.32)
Limnetic	-25.46 (±1.07)	7.83 (±0.18)
Intermediate	-23.18 (±1.04)	7.61 (±0.31)

Table 4-10. Ranges of $\delta^{13}C$ and $\delta^{15}N$, niche widths, percentage of combined niche widths that overlap area comprises {and percentage of morph niche width that overlap area comprises}.

	Range		Niche width	Niche overlap (%) {overlap / morph niche width (%)}		
Morph (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)		Limnetic	Intermediate	Benthic
Limnetic (16)	7.47	1.20	5.01		30 {96}	24 {65}
Intermediate (23)	8.09	1.55	15.84	30 {30}		52 {60}
Benthic (24)	8.31	2.69	11.75	24 {28}	52 {80}	

Figure 4-1. Digital photographs (full profile, head profile, ventral mouth view, and gill rakers) of (A) limnetic morph and (B) benthic morph (Utah sucker – NE clade) captured in the Snake River or Jackson Lake. Gill rakers from extreme ecomorphotypes were obtained from gill netting mortalities.

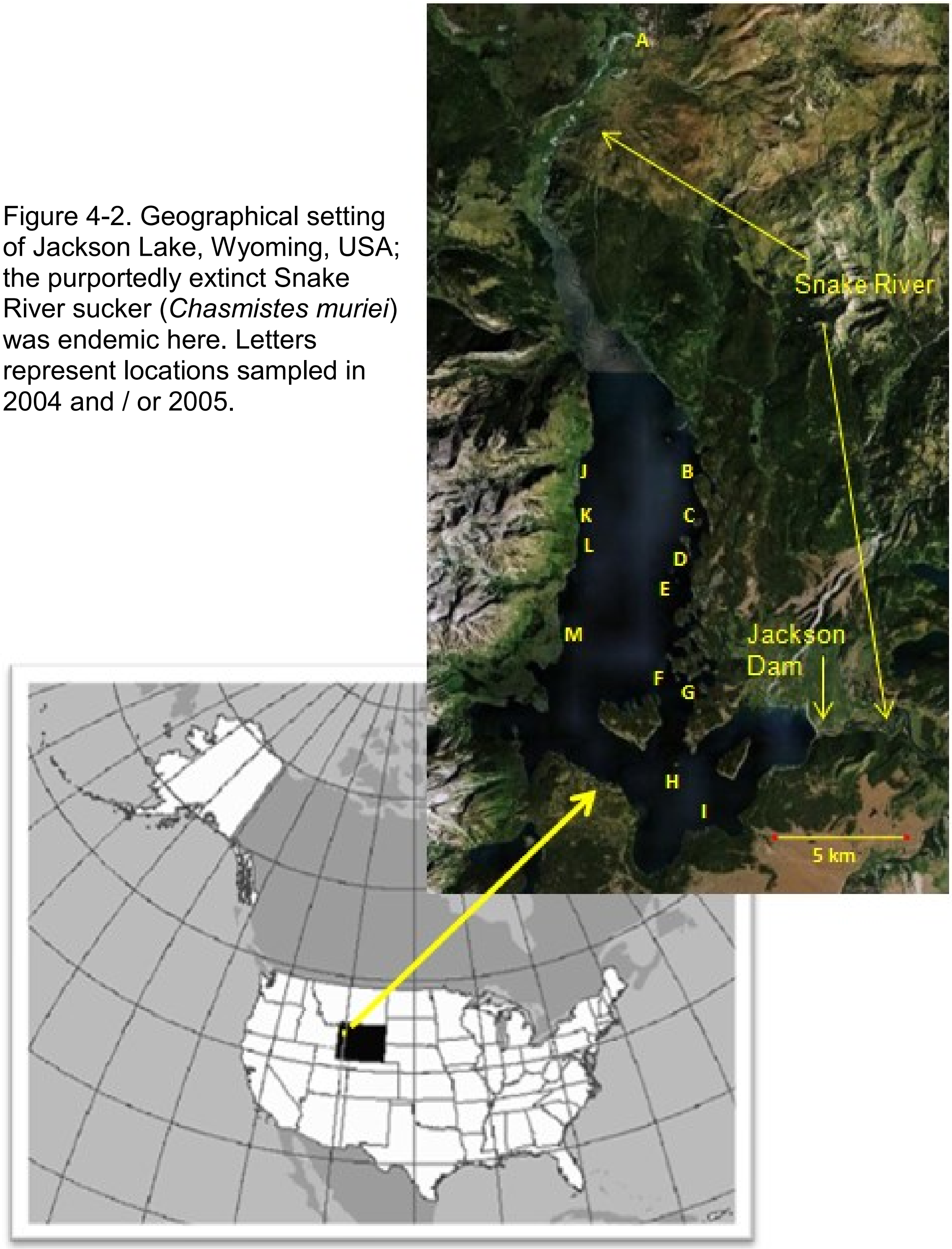

Figure 4-2. Geographical setting of Jackson Lake, Wyoming, USA; the purportedly extinct Snake River sucker (*Chasmistes muriei*) was endemic here. Letters represent locations sampled in 2004 and / or 2005.

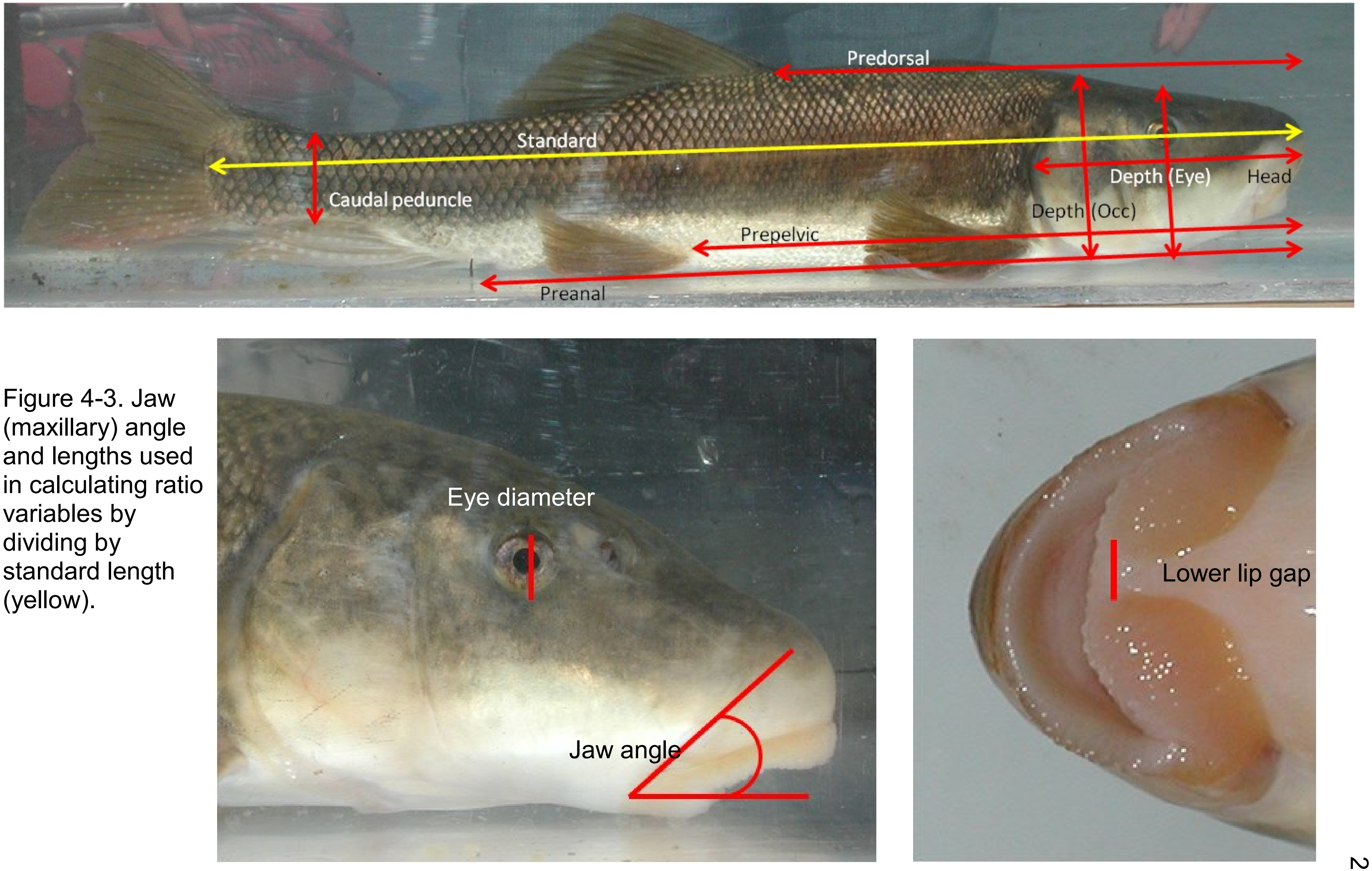

Figure 4-3. Jaw (maxillary) angle and lengths used in calculating ratio variables by dividing by standard length (yellow).

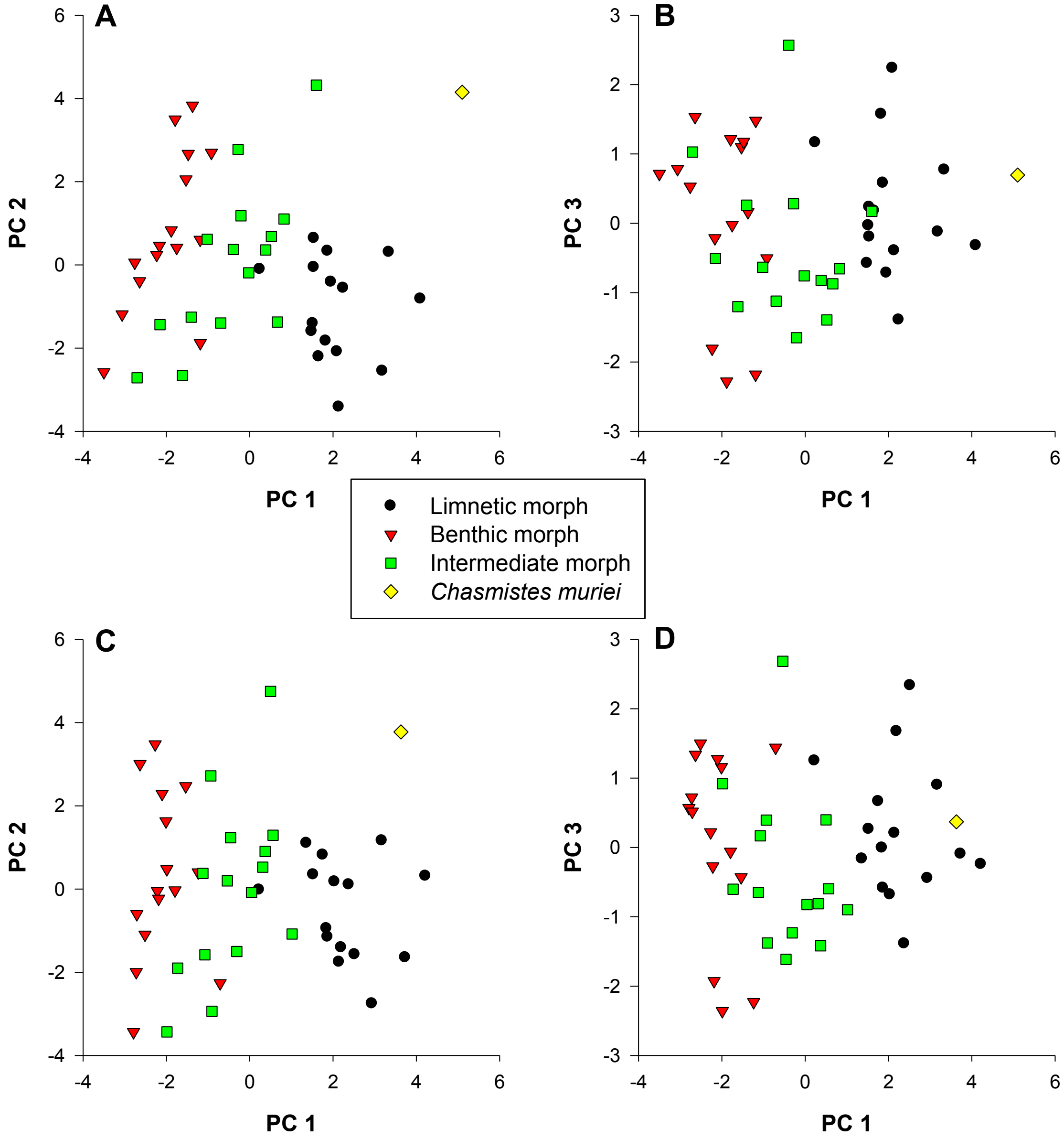

Figure 4-4. Morphological PCA ordinations using scores derived from unadjusted values for *Chasmistes muriei*, (A) and (B), and from adjusted values, (C) and (D), plotting PC1 versus PC2, (A) and (C), and PC1 versus PC3, (B) and (D). (Limnetic morphs, n = 15 – black circles; intermediate morphs, n = 15 – green squares; benthic morphs, n = 15 – red triangles; *Ch. muriei*, n = 1 – yellow diamond).

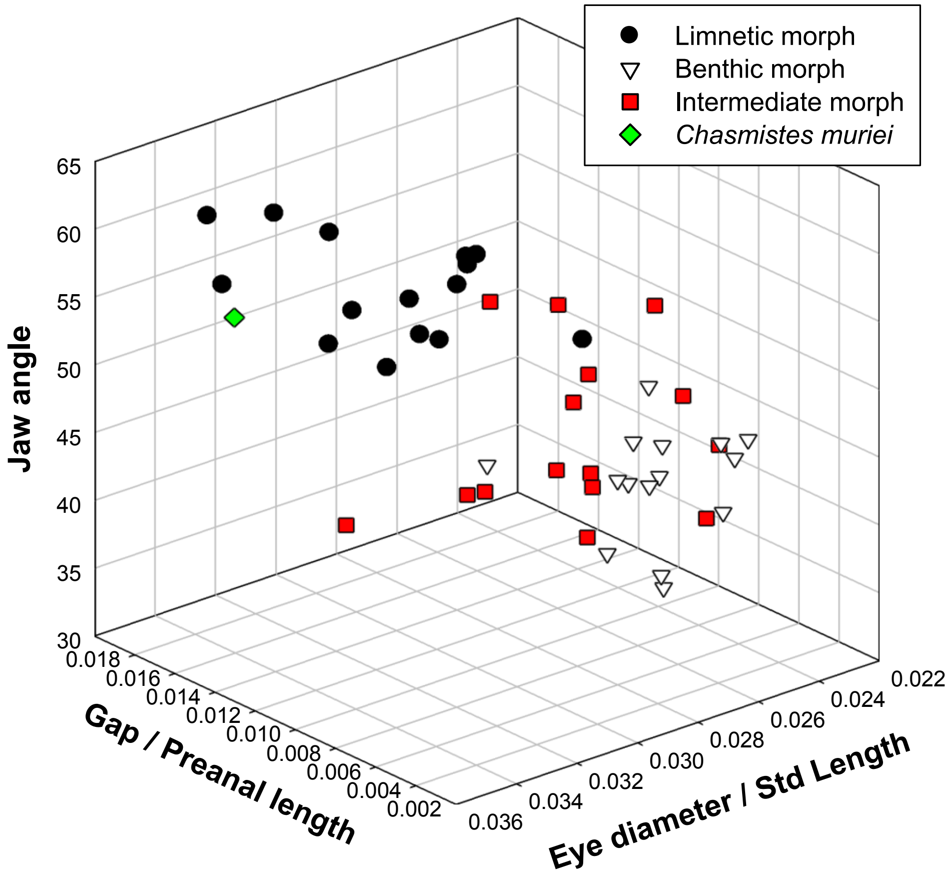

Figure 4-5. Three dimensional plot incorporating the four morphological variables (Table 4-5) that ANOVA revealed to exhibit statistically significant differences among Jackson Lake sucker morphs with shrinkage-adjusted values for the SRS specimen plotted also. (limnetic morphs, n = 15 – black circles; intermediate morphs, n = 15 – red squares; benthic morphs, n = 15 – white triangles; and *Chasmistes muriei*, n = 1 – green diamond).

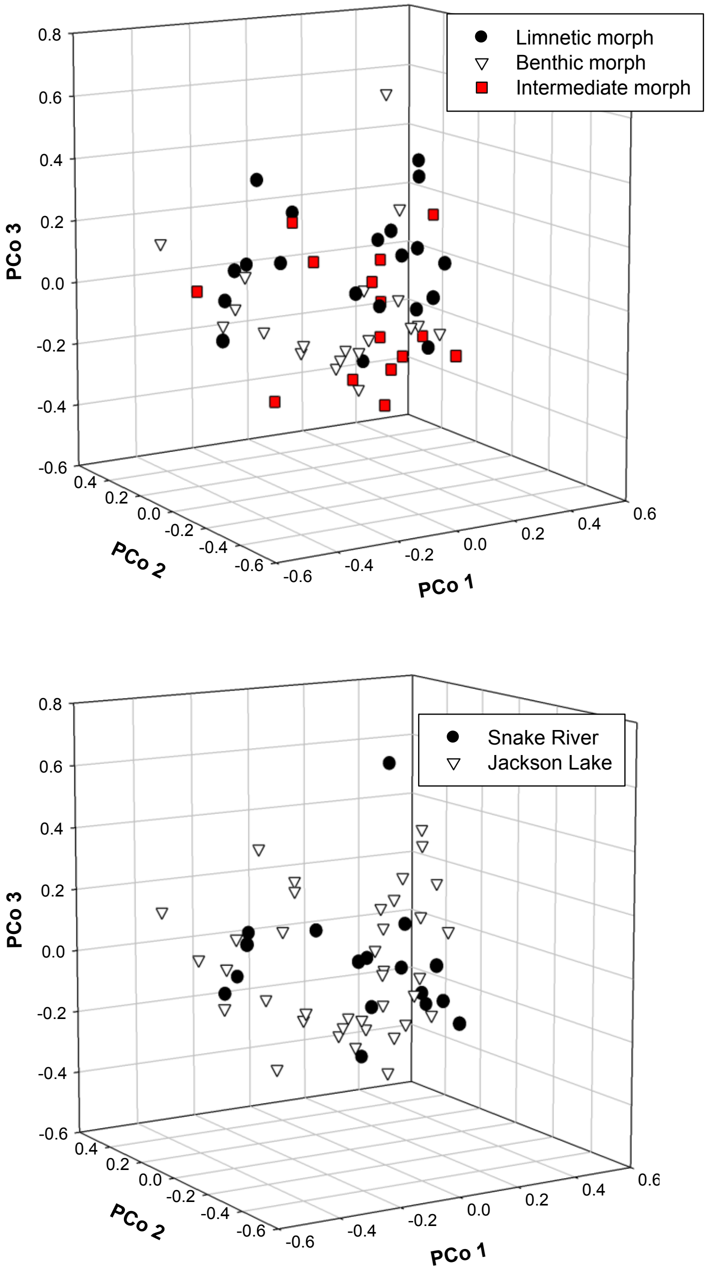

Figure 4-6. Ordinations labeled by morph (A) and by capture site (B) from PCoA of Jackson Lake sucker microsatellite profiles plotting scores of individual suckers for the first three PCos. Together the PCos explained 58% of the variance in the microsatellite profiles. (Limnetic morphs, n = 20 – black circles, intermediate morphs, n = 15 – red squares, and benthic morphs, n = 20 – white triangles).

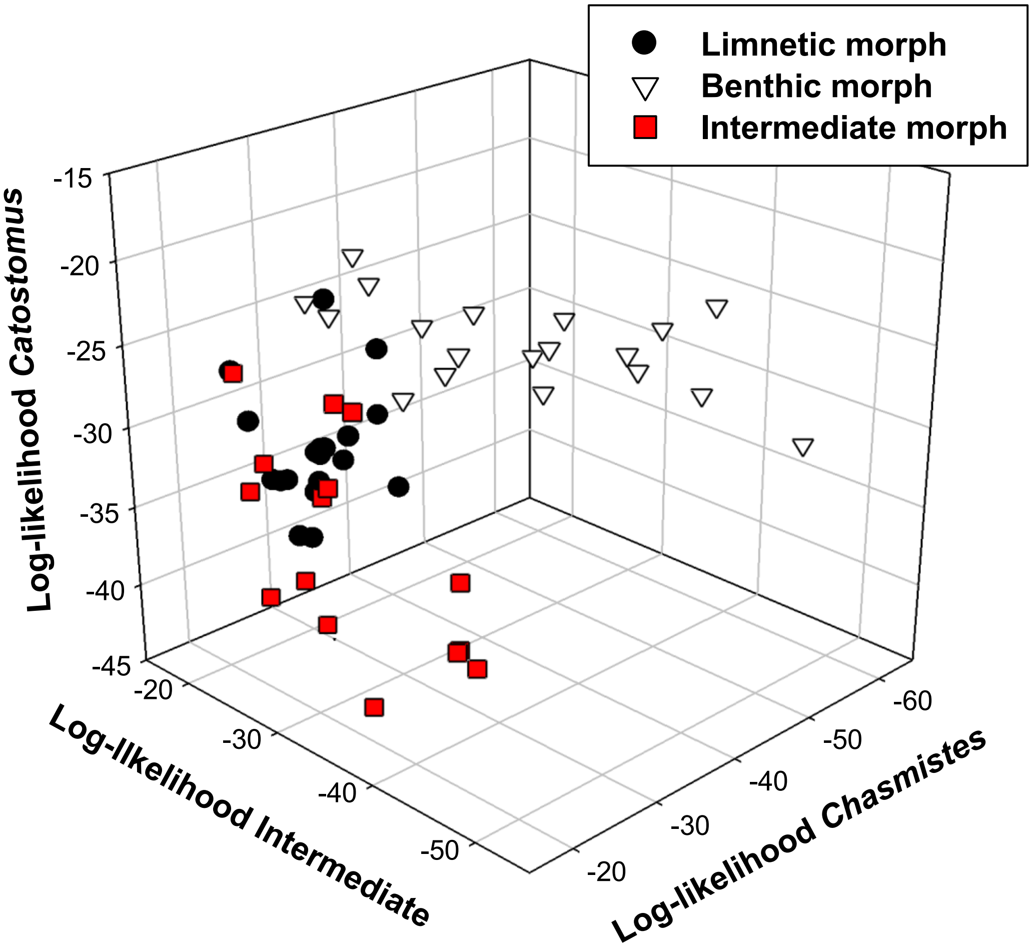

Figure 4-7. Genotype assignment test log-likelihood plot demonstrated that with prior knowledge of group allele frequencies, accurate assignment of individual genotypes is possible (3.6% error rate). (Limnetic morphs, n = 20 – black circles, intermediate morphs, n = 15 – red squares, and benthic morphs, n = 20 – white triangles).

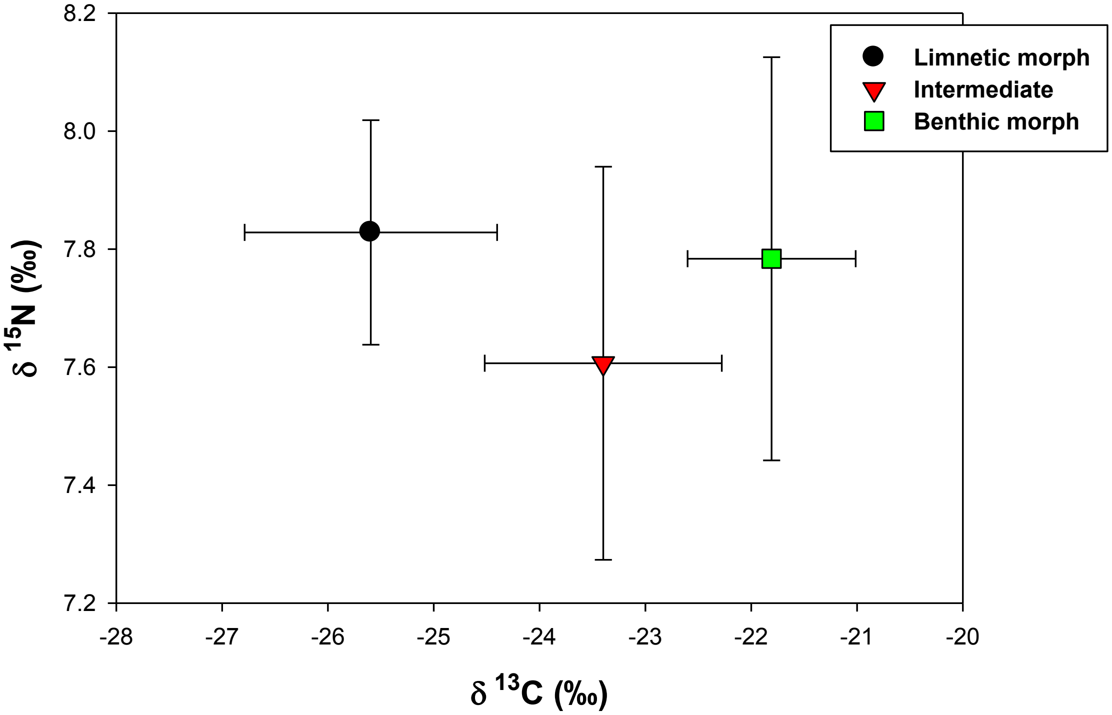

Figure 4-8. Isotopic signatures (means ± 95% confidence intervals) for ^{13}C and ^{15}N for Jackson Lake suckers plotted by morph within the two dimensional δ^{13}C – δ^{15}N bi-plot space. (Limnetic morphs, n = 16 – black circle, intermediate morphs, n = 23 – red triangle, and benthic morphs, n = 24 – green square).

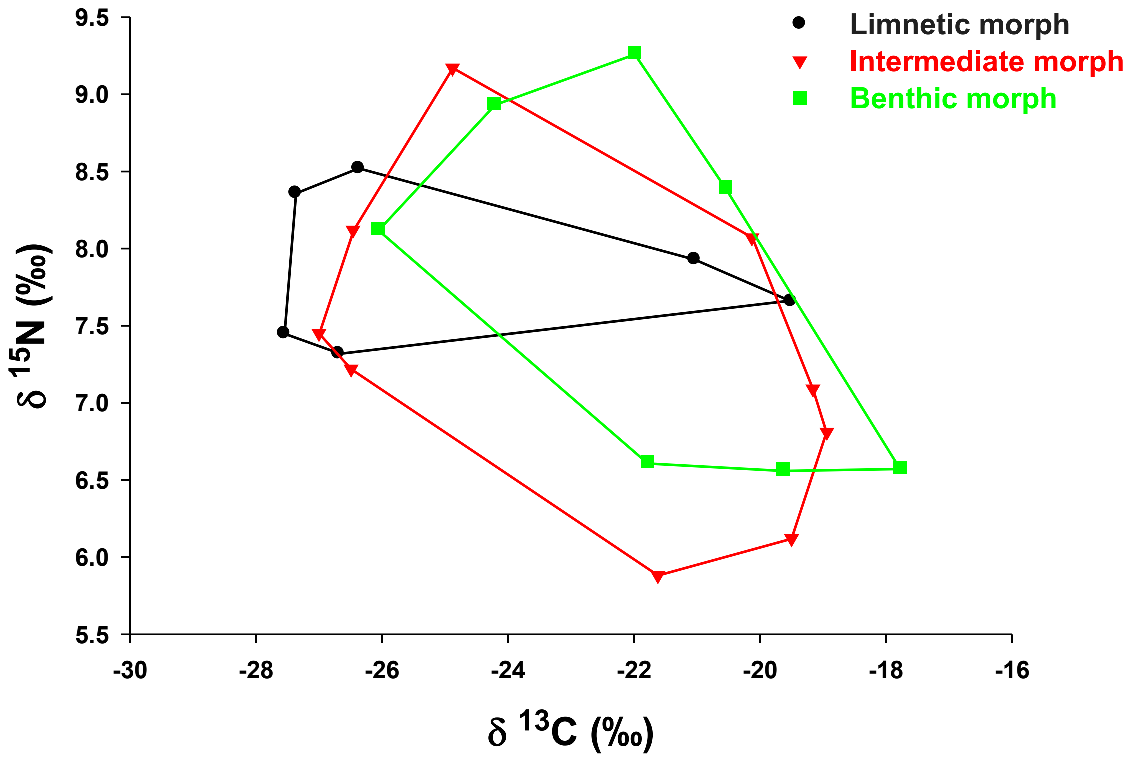

Figure 4-9. Niche width estimation by morph plotted within the two dimensional $\delta^{13}C - \delta^{15}N$ bi-plot space (isotopic niche space) using the convex hull polygon area method. Overlap was estimated as the area of the intersection of polygons for two of the three morphs (limnetic (n = 16), intermediate (n = 23), and benthic (n = 24)).

CHAPTER 5

CONCLUSION

Chapter 2 revealed that no molecular evidence (AFLPs and microsatellites) was found for deep genetic divergence between June sucker and Utah sucker in Utah Lake or for hybridization among ancient lineages. Slight population structuring accompanied substantial morphological variation. Bayesian model-based genetic clustering analyses detected two sucker populations in Utah Lake, however, these clusters were not strongly concordant with morphological groupings or between marker systems.

In Chapter 3, acoustic / radio telemetry in Utah Lake revealed little difference in movement and distribution of June sucker and Utah sucker or in timing of spawning runs. Stable isotopes analysis revealed that Utah sucker were enriched in ^{13}C relative to June sucker as presumed respective diets, benthivory and zooplanktivory, would predict. Intermediate morphs were intermediate for $\delta^{13}C$ and $\delta^{15}N$.

Chapter 4 showed no molecular evidence for deep genetic divergence between lakesucker and benthic morphs in Jackson Lake or for hybridization among ancient lineages. The benthic morph was significantly enriched in ^{13}C relative to the lakesucker morph, consistent with presumed diets. Morphologically, the lone Snake River sucker holotype specimen grouped strongly with extant lakesucker morphs, suggesting that the status of the Snake River sucker be updated accordingly.

The sucker populations in Utah and Jackson Lakes share similarities with other populations of lakesuckers and sympatric benthivores including: a morphological continuum existing from benthivore to planktivore with a large proportion of individuals exhibiting intermediate morphologies, discordant morphological and neutral molecular character sets with minimal molecular divergence accompaning extensive morphological variation, a lack of molecular evidence for hybridization between ancient lineages, planktivores that are phylogenetically closer to sympatric benthivores than to allopatric planktivores; and morphological and stable isotopic character (e.g., diet) sets that are congruent.

Evidence presented here confirms the persistence of suckers in Jackson Lake and the upper Snake River that are morphologically extremely similar to the lone SRS specimen, and suggest that the status of the SRS be updated accordingly. The presence of lakesuckers in Jackson Lake, along with similar findings in other *Chasmistes*/*Catostomus* species pairs, also raises questions about the validity of the *Chasmistes* genus (Chen and Mayden 2012; Smith et al. 2013).

Recent lakesuckers are listed as endangered or extinct, presenting an interesting conservation dilemma. Should one conserve (breed and stock) a subset of the morphotypic variation in lakesucker complexes, focusing on the endangered lakesucker morph, or should one conserve both lakesucker and benthic morphs in these complexes, possibly maximizing evolutionary potential?

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Smith, G. R., J. D. Stewart, and N. E. Carpenter. 2013. Fossil and recent mountain suckers, *Pantosteus*, and significance of introgression in Catostomin fishes of western United States. Occasional Papers of the Museum of Zoology University of Michigan 743:1-59.

APPENDIX

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CURRICULUM VITAE

David D. Cole
388 North 300 East
Logan, Utah 84321
(435)764-4584
daviddcole@gmail.com

Education

Ph.D.	Utah State University, Logan, Utah (Ecology/Fish and Evolutionary)
M.S.	Utah State University, Logan, Utah (Biology/Neurophysiology)
B. A.	Moorhead State University (now Minnesota State University, Moorhead), Moorhead, Minnesota (Biology – *Magna cum laude*)

Additional graduate courses were completed at Idaho State University (Pocatello, ID) from 1983-1984 and at North Dakota State University (Fargo, ND) from 1985-1992. Courses included:

ISU	Freshwater Ecology, Environmental Physiology, Advanced Fish Management, Advanced Studies in Vertebrate (Fish) Physiology, and Ecology of Water Pollution
NDSU	Biochemistry (and Labs), Introduction to Animal Behavior, Comparative Embryology, Introductory Statistics, Regression Analysis, Animal Research Principles, and Isotope Tracer Techniques (and Lab)

PROFESSIONAL EXPERIENCE

June-July 2013 **Ichthyology Instructor. National Science Foundation Summer Science Institute, Jarvis Christian College, Hawkins, Texas.**

I taught a four credit (BIO 4491- Research Techniques in Biology) ichthyology field course directed at high school juniors, seniors, and recent graduates and college freshmen and sophomores with an emphasis on generating interest in environmental science and ecology among minorities. The course covered general ichthyological topics, collection and preservation techniques, fish identification, and basic data analysis and reporting. I also presented lectures in an accompanying lecture course (ENVR 1401 - Introduction to Environmental Science; overall, the NSF course was eight credits). Contact:

Will Godwin (936) 556-2289.

2008-present Senior Fisheries Biologist . Cirrus Ecological Solutions, Logan, Utah.

I currently serve as Cirrus' senior fisheries biologist (a part time position). Past (and on-going) projects include: conducting amphibian field surveys (and boreal owl surveys) on the Cache–Wasatch National Forest to assess effects of changing grazing allotments; a three year contract with PacifiCorp conducting on-call fisheries work (population studies, salvages, FERC related projects, *etc.*) as requested by PacifiCorp related to their dam operations in the West; investigation of the impacts of sediments released during dam repairs on salmonid spawning gravels in the Henry's Fork of the Snake River; conducting fish salvage operations related to dam repairs; and evaluating the fish stranding potential of different ramp down rates at the Grace hydroelectric dam on the Bear River. Duties have included: identification of amphibians and fish; river habitat mapping; identifying stranding potential in river reaches; identifying spawning bars; seining and electrofishing; sediment sample collection (McNeil core sampler); training and supervising technicians; preparing and giving presentations; and writing reports. Contact: Neal Artz (435) 787-1490.

2008-2009 Graduate Research Assistant. Department of Watershed Sciences, Utah State University, Logan Utah.

I conducted field work, supervised technicians, analyzed and interpreted data, attended multi-agency meetings, and wrote reports and gave presentations for several projects related to June sucker conservation on-going in Todd Crowl's Aquatic Ecology Laboratory. Among the projects were: a telemetry study of acoustically tagged June suckers transplanted into a potential refugium, Mona Reservoir, UT; continuing development of a web-accessible June sucker database; and a crayfish removal project at another June sucker refugium, Red Butte Reservoir, UT. Field work has included: acoustic telemetry; limnological and zooplankton sampling of Mona and Red Butte reservoirs and Utah Lake, UT; setting and maintaining drift nets and larval light traps in tributaries of Utah Lake; and installing and maintaining PIT tag antennae in tributaries of Utah Lake. Required skills included: operating and maintaining a variety of watercraft; limnological and fish sampling techniques; statistical analytical abilities (SAS, R); and communication (oral and written) skills. Contact: Todd Crowl (435) 760-1335.

2007-2008 Research Technician. Ecology Center, Utah State University, Logan, Utah.

I conducted field research related to endangered June sucker at Red Butte Reservoir, UT and Mona Reservoir, UT (both reservoirs serve as refugia for June sucker). Duties included: limnological sampling (zooplankton, dissolved oxygen profile, and temperature profile); fish tissue sampling for stable isotopes analysis; collection of fish stomachs for analysis of contents; acoustic telemetry; zooplankton identification; and data entry and analysis. Contact: Todd Crowl (435) 760-1335.

2002-2007 Instructor / Graduate Research Assistant / Graduate Teaching Assistant. Department of Watershed Sciences, Utah State University, Logan Utah.

As an instructor, I taught Graduate Fish Ecology, a 2 credit lecture/readings/discussion course, in Spring, 2006. I was responsible for all aspects of the course (lectures, assignments, grades).

As a research assistant, I conducted field research and analyses (morphometrics, radio/acoustic telemetry, stable isotopes, genetic) related to endangered June suckers and Utah suckers at Utah Lake, UT and Jackson Lake, WY. Required skills included: operating boats and motors; trap, trammel, and gill netting and seining; electrofishing; zooplankton and macroinvertebrate sampling; limnological sampling; and radio/acoustic telemetry (including surgical implantation of transmitters). I also conducted laboratory experiments at USU’s Endangered Species and Aquatic Ecology Research Center, Millville, UT. Among the analyses I performed were a variety of multivariate statistics as well as the development of models (*e.g.*, stable isotope mixing models). Additionally, I supervised numerous technicians in an assortment of field and laboratory settings.

As a teaching assistant, I wrote and graded assignments, quizzes, and exams; answered students’ questions; and presented several lectures in an introductory ecology course for science majors (including pre-professionals). Contact: Todd Crowl (435) 760-1335.

2001-2002 Research Technician. Ecology Center, Utah State University, Logan, Utah.

I conducted field research related to June suckers and Utah suckers at Utah Lake, UT and Mona Reservoir, UT (using techniques similar to those described above). Contact: Todd Crowl (435) 760-1335.

2001 Fisheries Technician (GS 5). US Fish and Wildlife Service, Colorado River Fisheries Project, Vernal, Utah.

I participated in research (population estimation, radio telemetry) regarding endangered species (Colorado pikeminnow, razorback sucker, humpback chub, and bony tail chub) in the Green, Yampa, and White Rivers, UT/CO. Required skills included: operating boats and motors; white water rafting; radio telemetry; electrofishing; and angling. Contact: (435) 789-0351.

1996-2000 Field Technician/Biologist/Writer. Ecosystems Research Institute, Logan, Utah.

I conducted post-alteration monitoring of habitat restoration/improvement projects on the Payette River at Horseshoe Bend, ID and on the Thomas Fork River at Geneva, ID. I conducted research for and wrote portions of the TMDL for the Cub River, ID. I also performed field research (including surveys) regarding a number of endangered species: southwestern willow flycatcher, bald eagle, boreal toad, Colorado pikeminnow, razorback sucker, humpback chub, bony tail chub, Knowlton cactus, Wright fishhook cactus, and Mancos milk-vetch (in the San Juan, Green, Colorado, Animas, and La Plata River drainages, UT/NM/CO) and Little Colorado River spinedace (in the Little Colorado River drainage, AZ). Additionally, I conducted field research and FERC-related monitoring on the Henry's Fork of the Snake River near Island Park, ID. I wrote the wildlife and endangered (terrestrial) species portions of the Animas - La Plata Project Environmental Impact Statement (2000). This position required skills in: boating and rafting; electrofishing and seining; aquatic macroinvertebrate sampling; stream flow measurement; limnological sampling; soil sampling (state certified water and soil sampler - UT); and data analysis and writing. Finally, I supervised field technicians and worked closely with a variety of agencies (federal, state, tribal, and private). Contact: Vince Lamarra (435) 752-2580

1993-1996 Graduate Teaching/Research Assistant. Department of Biology, Utah State University, Logan, Utah.

As a graduate teaching assistant, I taught lower and upper level laboratory courses (including introductory lectures) in invertebrate zoology, vertebrate zoology, human physiology, and animal physiology. I wrote questions for and graded exams, assisted students, and presented several lectures in Brain and Behavior, a non-major elective course.

As a graduate research assistant, I conducted research in neurophysiology; required skills included recording individual neurons, microinjection, and culturing retinal neurons. Contact: USU Biology (435) 797-2485.

1992-1993 Tree Inspector. Department of Parks and Recreation, City of Moorhead, Minnesota.

I identified diseased (Dutch elm disease) elm trees for speedy removal throughout the city (public and private property); supervised wood chipping crews; and answered citizens' questions regarding trees and shrubs. Contact: Moorhead Parks and Recreation (218) 299-5340

1991-1992 Domestic Observer. Arctic Observer, Seattle, Washington.

I identified and estimated catch and by-catch aboard a trawling vessel in the Bering Sea pollock/cod fishery.

1985-1988 Graduate Teaching Assistant. Department of Zoology, North Dakota StateUniversity, Fargo, North Dakota.

I taught laboratory classes in zoology and advanced animal physiology.

1983-1985 Fisheries Technician. Department of Fish and Game, Idaho Falls, Idaho.

I conducted research, performed creel censuses, and assisted in hatchery operations (cutthroat trout and cutthroat/rainbow trout hybrids) at Henrys Lake, ID.

1983-1984 Graduate Teaching Assistant. Department of Biology, Idaho State University, Pocatello, Idaho.

I taught laboratory classes in zoology, cell biology, and botany. I presented introductory lectures and wrote and graded tests and assignments.

1981 Nature Director - Camp Shawondassee. Lake Agassiz Camp Fire Council, Moorhead, Minnesota.

I provided campers (ages 7-17) with an introduction to flora and fauna of the region; developed a self-guided nature trail; and led canoeing/camping trips.

HONORS / AWARDS

Stokes/Leopold Scholar, Utah State University, 2006.

Quinney Fellowship, Utah State University, 2002-2004.

Sigma Xi Research Grant, North Dakota State University, 1987.

Presidential Scholarship, Moorhead State University, 1976.

SPECIAL COURSES / TRAINING

ARC-GIS short course, Utah State University, 2005. (In 2006, I served as a teaching assistant when a similar course was offered at the Bonneville Chapter meeting of the American Fisheries Society.)

US Fish and Wildlife Service Electrofishing Certification, 2001.

Microinjection short course, Woods Hole Marine Biological Laboratory, 1994.

PUBLICATIONS (peer reviewed)

Cole, DD, BL Cardall, K Mock, and TA Crowl. 2008. Morphological and genetic structuring in the Utah Lake sucker complex. *Molecular Ecology* 17:5189–5204.

PUBLICATIONS (non-peer reviewed)

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PRESENTATIONS

Morphology, Genetic Structure, and Stable Isotopic Signatures of the Sucker Complexes in Utah Lake, UT and Jackson Lake, WY. Western Division of the American Fisheries Society Annual Meeting. 2010. Salt Lake City, UT.

Morphological Variation, Genetic Structuring, and Stable Isotopic Signatures in the Sucker Complex in Eutrophic Utah Lake, Utah with Comparisons to the Suckers in Oligotrophic Jackson Lake, Wyoming. Ecological Society of America Annual Meeting. 2009. Albuquerque, NM.

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Ecomorphological Investigations of the Utah Lake Sucker Complex. Ecology Center (Utah State University) Ecolunch. 2007. Logan, UT.

Morphometric Analysis of the Utah Lake Sucker Complex. Bonneville Chapter of the American Fisheries Society Annual Meeting. 2005. Garden City, UT.

REFERENCES

Todd Crowl
The Ecology Center &
Department of Watershed Sciences
Utah State University
Logan, Utah 84322
(435) 760-1335
facrowl@gmail.com

William Godwin
East Texas Natural History Collection
Jarvis Christian College
Hawkins, Texas 75765
(936) 556-2289
WGodwin@jarvis.edu

Phaedra Budy
Department of Watershed Sciences &
Resources & Utah Cooperative Fish &
Wildlife Research Unit
Utah State University
Logan, Utah 84322-5290
(435) 797-7564
Phaedra.Budy@usu.edu

Karen Mock
Department of Wildland
The Ecology Center
Utah State University
Logan, Utah 84322-5230
(435) 797-7870
karen.mock@usu.edu

Neal Artz
Cirrus Ecological Solutions
965 South 100 West, Suite 200
Logan, Utah 84321
(435) 787-1490
nartz@cirruses.com