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Retrospective Food Web Analysis of Gila River Fishes Reveals Hydrologic parameters Influence non-native Species Effects

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RETROSPECTIVE FOOD WEB ANALYSIS OF THE GILA RIVER FISHES REVEALS HYDROLOGIC PARAMETERS INFLUENCE NON-NATIVE SPECIES EFFECTS

by

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B.S., Biology, University of Arkansas, 2012

Thesis

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LOW FLOWS INTENSIFY BIOTIC INTERACTIONS IN THE

GILA RIVER FISH COMMUNITY:
A RETROSPECTIVE STABLE ISOTOPE ANALYSIS

by

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ABSTRACT

The relatively pristine upper Gila River in New Mexico is a stronghold for endemic native fishes despite the presence of non-native fishes. In other, more severely human-impacted tributaries in the Colorado River basin, non-native fishes are a major factor in native species decline and extirpation. I tested whether presumed negative effects of non-natives on natives are compounded during drought using an approach based on Stable Isotope Analysis (SIA) and comparisons of resource use overlap during different flow conditions. Fish specimens were selected from natural history collections to represent a time series that encompassed wet and dry years, as well as varying non-native abundances. I estimated 'isotopic niche space' by plotting $\delta^{13}C$ vs. $\delta^{15}N$ for native and non-native fishes and statistically compared breadth and overlap in niches among species. I hypothesized that during low-flow periods, the availability of resources is constrained, causing isotopic niches of non-natives and natives to overlap more, which increases the potential for competition. I hypothesized that during wet periods, resource

space is broader, suggesting reduced overlap of resource use. My results indicate that low-flow conditions constrain resources in isotopic space, and wet conditions increase diversity of available resources. During wet conditions, native and non-native groups have more varied resource use. SIA of museum specimens offered the potential to test key hypotheses about the impact of non-native species on a native fauna, and provided understanding of the environmental context that non-native species negatively impact native fishes. Such understanding is important for conservation of the fishes of the Gila River, where climate change and pending water diversion could lead to further imperilment of native fish abundance.

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Chapter 1 INTRODUCTION

The introduction of non-native fishes often contributes to the decline of native fishes (Minckley 1982; Douglas *et al.* 1994; Moyle & Light 1996; Carey & Wahl 2010; Jackson & Britton 2014; Whitney *et al.* 2014)). Negative interactions, primarily competition and predation, are hypothesized to be the predominant mechanisms contributing to the displacement and loss of native species (Moyle & Light 1996). However, the introduction of non-native species does not always coincide with the extirpation of native fishes because the outcome of invasions can be mediated by environmental variability (Lodge 1993; Moyle & Light 1996). Drought conditions, flow regulation, and diversions are common in the arid Southwest and can have major impacts on native and non-native fish assemblages (Propst *et al.* 2008; Turner *et al.* 2015). While rivers are an important resource throughout the world, rivers serve a particularly critical function for the ecology of this region due to scarcity of water that has strongly limited diversity and distribution of biota. Furthermore, the climate change projections for this region indicate less water availability (Gutzler 2013), which could ultimately exacerbate biotic effects of harsh conditions. This study attempts to disentangle the biotic interactions (non-native species) and abiotic influences (variable flow conditions) that may be affecting native fish abundance and assemblage structure in the Gila River, New Mexico.

Reductions in surface water availability and alterations to the natural flow regime of the Gila River could potentially have adverse effects on native fish abundance and diversity. Drought conditions are likely to intensify in this region as evaporative water losses in the Gila River basin increase with climate change (Gutzler 2013). Climatic fluctuations in arid regions, such as the southwest United States, can severely constrain resource abundance and availability (through effects on primary production and water availability), intensifying selection processes on competitors (Wiens 1977). Perhaps most importantly, a proposed diversion (built under the authority of the Arizona Water Settlement Act) could modify the natural flow regime in ways that significantly transform ecosystem function (Gori *et al.* 2014). By characterizing the effects of predation and competition of non-native fishes on the native fish community under various hydrologic conditions, the trajectory of change to the system could be revealed, allowing for more effective management and conservation of this system.

Competition and Invasion Theory

Ecological theory provides fundamental insight into interspecific interactions such as competition and predation. As defined by Connell (1983), competition is any negative interaction between two or more species that results from competing over the same limited resource. Interactions can be largely summarized as indirect competition (e.g. resulting from environmental variables that affect species overlap, such as drought reducing habitat availability and concentrating fishes) or direct competition (e.g. where species interact closely for the same resources) (Schoener 1974). A full interpretation of competitive interactions can be challenging in the field because environmental factors can alter interactions. Moreover, other factors like evolutionary background (Douglas *et*

al. 1994) and non-native species effects on habitat through ecosystem engineering (Hölker *et al.* 2015) can appreciably alter the intensity of interspecific interactions.

The establishment of non-native species is a key driver of ecosystem change (Elton 1958, Mack *et al.* 2000; Lockwood *et al.* 2007) and frequently does so by altering the number and intensity of biotic interactions (Walsworth *et al.* 2013). Effects of non-natives are dependent on the structure of the native community (Carey & Wahl 2010), and the ecology of invading non-native species (i.e., Bøhn & Amundsen 2001). Impacts of non-natives within a community that is not saturated (i.e., all niches aren't occupied) can be highly variable (Carey & Wahl 2010) and depauperate native communities often experience the greatest declines in native fish abundance (Moyle & Light 1996; Whitney *et al.* 2014). Competitive interactions can be intensified, causing niche overlap, or mitigated, causing niche divergence, when non-natives are in sympatry (Jackson & Britton 2014). Divergence of niche space between sympatric non-natives once established can result in successful coexistence (Jackson & Britton 2014), and systems sustaining multiple non-native species are common (i.e., Propst & Gido 2004; Olden *et al.* 2006; Gido *et al.* 2013; Turner *et al.* 2015). Additionally, invading species have the ability to alter habitat, and change competitive interactions in an indirect manner (Hölker *et al.* 2015). For instance, carp (*Cyprinus* carpio) can eliminate aquatic vegetation, increasing turbidity, and decrease habitat complexity (Douglas *et al.* 1994). Non-natives can indirectly compete with natives by inducing predator avoidance behaviors in native fishes, causing smaller bodied individuals to move out of preferred habitat or resource space (Harvey 1991; Magoulick 2000). Nevertheless, direct evidence for competitive exclusion of natives by non-natives is limited (Moyle & Light 1996).

The Colorado River basin has undergone many species invasions that have changed native fish communities (Minckley 1982; Douglas *et al.* 1994; Propst *et al.* 2008; Pilger *et al.* 2010) and non-native fishes appear to have directly excluded native species through competition in many parts of the basin (Minckley 1982; Douglas *et al.* 1994; Moyle & Light 1996; Carey & Wahl 2010; Jackson & Britton 2014). Native species in the arid-southwest are particularly vulnerable due to the evolutionary processes that led to diversification of these unique fauna; habitats fragmented by geological and climatic events in the last millennia created isolated populations that evolved independently (Douglas *et al.* 1994). Fishes from this evolutionary background often lack predator avoidance behaviors effective against introduced species and cannot compete with fishes recently introduced from more species-rich waters (Moyle *et al.* 1986; Douglas *et al.* 1994).

Unlike in other parts of the basin, native fishes of the upper Gila River basin have persisted under a changing competitive regime with additional non-native species present in the food web. The natural flow regime of the Gila River has been hypothesized to ameliorate negative effects of non-native species on natives (Poff 1997; i.e., Propst & Gido 2004; Propst *et al.* 2008; Gido *et al.* 2013; Whitney *et al.* 2014), which could be explained in part by the adaptations of native species to local hydrologic variability (Gido *et al.* 2013; Whitney *et al.* 2014).

Importance of the Natural Flow Regime

The largely unmodified flow regime of the Gila River in New Mexico sets this system apart from other rivers in the arid Southwest and could be the mechanism by

which native fishes are sustaining populations (Stefferud *et al.* 2011; Gori *et al.* 2014; Whitney *et al.* 2014). A natural flow regime involves seasonal high flow (i.e., spring snowmelt) and dry down periods (i.e., summer low flows). In unmodified river channels, high flows promote lateral interactions of the river channel and floodplain (Ward & Stanford 1995). A productive floodplain is an essential element of a functioning river ecosystem (Junk *et al.* 1989) and is disturbance-dependent, requiring the kinetic energy of flooding to maintain connectivity to aquatic environments (Ward & Stanford 1995). Inundated floodplain habitat is critical for spawning behavior, larval nursery habitat (Pease *et al.* 2006), litter decomposition, recruitment of riparian vegetation (Rood *et al.* 2005), sediment mobilization, and channel heterogeneity (Ellis *et al.* 1999; Bunn & Arthington 2002; Gori *et al.* 2014). At the beginning of spring snowmelt, flooding flushes the river of old debris and initiates decomposition of leaf litter that ultimately releases critical nutrients into the system and promotes increased primary production (Ellis *et al.* 1999). High peak flows connect systems to floodplain habitats, remove fine sediment from spawning habitats, and stimulate ecosystem productivity via nutrient transportation (Junk *et al.* 1989; Hill *et al.* 1991; Poff 1997; Gido *et al.* 2013; Gori *et al.* 2014). The spring snowmelt recession period is especially important for the 'moving littoral' zone that is created, producing diverse habitats and mobilizing nutrients (Ward & Stanford 1995; Yarnell *et al.* 2010). Thus, the natural flow regime of the Gila River is serving diverse functions for the health of the overall system, and especially the native fish community. A loss of any given flow attribute (either climatic or human induced) could severely alter the Gila River ecosystem, ultimately to the detriment of native fishes.

Impacts of Low-flow Conditions and Flow Modification

Low-flow conditions (whether natural (i.e., drought), or human-imposed through water extraction) have immediate effects on aquatic systems, including decreased surface water availability and lowered water quality (Magoulick & Kobza 2003). Documented effects of low-flow conditions on fish include population decline, loss of habitat, changes in community composition, negative impacts due to poor water quality, reduced movement within catchments, and crowding of fish in microhabitats (Matthews & Marsh-Matthews 2003; Gori *et al.* 2014; Turner *et al.* 2015). Changes in flow regime resulting from climatic warming can alter the timing of flows and decrease the magnitude of spring snowmelt recession, which can result in altered species composition and increased non-native species abundance (Yarnell *et al.* 2010). River regulation often changes the gradual decline of spring snowmelt to a rapid shift from flood-flow to base-flow, which homogenizes channel morphology and decreases the diversity of aquatic and riparian species (Yarnell *et al.* 2010). In regulated rivers, the frequency and size of floods is reduced by flood control management (Molles *et al.* 1995), the frequency of floodplain inundation is reduced (Ward & Stanford 1995), and riparian plant recruitment and abundance is diminished (Poff 1997; Ellis *et al.* 1999). Persistent low flows, while different then drought, could also increase with climate change, and are expected to reduce habitat and food resources available to fishes and other aquatic consumers (Bunn & Arthington 2002; Magoulick & Kobza 2003).

Native and non-native species respond differently to changes in natural flow regimes (Meffe 1985; Moyle & Light 1996; Poff 1997; Bunn & Arthington 2002; Propst & Gido 2004; Propst *et al.* 2008), and decoupling environmental factors from negative

impacts of introduced fishes (i.e., competition and predation) is particularly difficult (Bunn & Arthington 2002). In the Gila River when low flow conditions cause variation to the natural flow regime, fishes are physically constrained in reduced habitat (Gido *et al.* 2013; Gori *et al.* 2014) and predation and competition among the species present will increase (Magoulick & Kobza 2003). Stefferud *et al.* (2011) determined that disruption of natural flow regime in the Gila River can jeopardize persistence of native fishes, especially when flows are low and non-native predator density is high. Low-flows can reduce recruitment success because most native species in the Gila River spawn during elevated flows, either snowmelt or storm-induced (Propst *et al.* 2008). Small-bodied cyprinid (Cyprinidae) and age-0 catostomid (Catostomidae) densities respond positively to increased discharge (Stefferud *et al.* 2011). While the Gila River currently maintains a natural flow regime, with little human modification, a proposed diversion would induce major alterations that include decreased variability of flow events and decreased base flow conditions (Gori *et al.* 2014).

Niche Theory

The primary focus of this research was to evaluate the nature and potential intensity of biotic interactions between native and non-native fishes under low- and high-flow conditions. In order to examine how abiotic (flow conditions) and biotic (species interaction opportunities) factors might be interdependent I used a framework based on the niche concept (Hutchinson 1957; Leibold 1995). Evaluating the resources available and assimilated provides information that allows the potential for negative interactions between non-native and native species to be determined.

An extension of the niche concept is the 'isotopic niche', which has become an effective tool to assess an organism's ecological characteristics that make up a niche (Bearhop *et al.* 2004; Newsome *et al.* 2007). Isotopic ratios of elemental carbon and nitrogen in consumers reflect the isotopic ratios of their prey and the sources of primary production that fuel higher trophic level, respectively (Layman *et al.* 2007a; Gonzalez-Bergonzoni *et al.* 2014). The proportion of light isotopes of carbon, for example, $\delta^{13}C$, can be used to track carbon source movement through food webs because it undergoes a small natural trophic fractionation relative to differences in isotopic signatures of food resources (Fry 2007; Layman *et al.* 2007a; Gonzalez-Bergonzoni *et al.* 2014). Primary production $\delta^{13}C$ signatures have significant variation due to different photosynthetic pathways, thus $\delta^{13}C$ can be used in determining dietary carbon sources in consumers (Fry 2007; Layman *et al.* 2007a; Gonzalez-Bergonzoni *et al.* 2014). Similarly, $\delta^{15}N$ varies predictably between 3-5 ‰ (the ratio of heavy to light isotope relative to standard, expressed as per mil) from source to consumer, and thus can be used to estimate trophic level (Layman *et al.* 2007a, b; Gonzalez-Bergonzoni *et al.* 2014). As $\delta^{15}N$ values increase in consumer tissues, it indicates higher trophic levels and greater trophic diversity of consumers (Layman *et al.* 2007b)

The interpretation of stable isotope analysis (SIA) in the context of resource use, trophic position, and overlap/divergence of resource use among species is key to utilizing SIA to better understand food web dynamics. Stable isotope analysis is an important tool for evaluating the dynamics of food webs in river systems in the arid Southwest that have experienced increased levels of human modification and drought (Turner & Edwards 2012). Stable isotope ratios have been compared to gut contents analysis, and are an

excellent indicator of trophic position for Gila River fishes (Pilger *et al.* 2010). By determining the isotopic niches of the Gila River fish community occurring under a variety of hydrologic conditions, I can assess trophic responses of native and non-native fishes to changes in resource availability associated with reduced flow conditions.

Research Objectives

In this thesis, I retrospectively evaluated the effects of non-native fishes and drought on the native fish assemblage in the Gila River, New Mexico. While the Gila River has remained relatively unmodified compared to other rivers in the American Southwest, native species ranges and abundances have declined since the introduction of non-native fishes in the early 20th century (Propst *et al.* 2008; Pilger *et al.* 2010; Stefferud *et al.* 2011; Whitney *et al.* 2014). Drought and the presence of non-native fish species are threats to the native fish assemblage in this system (Stefferud *et al.* 2011; Gido *et al.* 2013; Whitney *et al.* 2014). If native fishes have thus far persisted in the presence of non-natives in the Gila River, do extreme environmental conditions (i.e., drought) provide opportunities for non-natives to have greater negative effects? Alternatively, is it possible that drought decreases the effects of nonnative species, by decreasing the success of all fishes equally?

In order to further understand trophic relationships between native and non-native fishes in the Gila River, I tested hypotheses based on stable isotope analysis of a time series of museum-preserved-fishes, spanning the early 1980s to present. I predicted that abiotic factors could be the driving force behind non-native interactions with natives. I also hypothesized that during low-flow conditions, resources in the system would be constrained due to lack of interaction with the floodplain and diminished inundated

habitat and that isotopic niches of native and non-native species would overlap. These conditions could lead to increased competition during drought. During 'wet' conditions, I predicted an increase in resource availability and diversity, resulting from increased interaction with riparian sources and increased inundated habitat. These conditions would result in a broader range of $\delta^{13}C$ values because more diverse carbon resources are available. In addition, in 'wet' years, species can specialize on particular food resources (i.e. niche partitioning) and avoid competition among other species, which is expressed as distinct niches in isotopic space. These results will not only provide evidence for natives and non-natives competing for similar resources, but offer a mechanism by which non-natives could displace natives in the Gila River if drought conditions worsen.

Chapter 2 MATERIALS AND METHODS

Study Area and Site Selection

From its origins in the Mogollon Rim of southwestern New Mexico, the Gila River flows 1044 km through New Mexico and Arizona to join the Colorado River on the California border. The Gila Basin is an arid-land watershed that encompasses nearly 155,000 km^2. Land-use in the upper Gila River basin consists mostly of outdoor recreation, dispersed livestock grazing, and scattered human developments (Pilger *et al.* 2010). In the lower reaches of the Gila River in New Mexico, human development increases, but is limited to livestock grazing, small-scale irrigation diversion, and limited community development (Pilger *et al.* 2010). Annual discharge of the system is generally characterized by strong seasonal and inter-annual variability, including spring snowmelt

inflow from February to May, and sporadic monsoonal inputs from July to September (Propst *et al.* 2008; Whitney *et al.* 2014)**.** Climate change is projected to diminish stream flow and increase dry surface conditions for this system (Gutzler 2013). The annual hydrograph of the Gila River can be broken down into four distinct periods, each serving different biological and ecological purposes for the system: Snowmelt Runoff, Summer Low Flow, Monsoon, and Fall-Winter Base Flow (Gori *et al.* 2014).

Vegetation and morphology of the Cliff-Gila valley of the Gila River was characterized by Gori *et al.* (2014)**.** The Cliff-Gila valley (Figure 1) is a 30 km segment of the Gila River and is an alluvial floodplain reach with characteristic riparian vegetation and braided river channel morphology that supports the most diverse fish community in the upper Gila Basin (Propst *et al.* 2008). There are canyon-bound river reaches immediately upstream and downstream of the Cliff-Gila Valley that lack extensive floodplain habitat and have much lower fish abundance and diversity (Whitney *et al.* 2014). Tree species that make up the majority of riparian forests include Fremont cottonwood (*Populus fremontii),* Goodding's willow (*Salix goodingii*), seep willow (*Baccharis salicifolia),* and coyote willow (*Salix exigua*). Side channels are dominated by rushes (*Juncus torryii*), cattails (*Typha latifolia)*, and rice cutgrass (*Leersia oryzoides*). Xeric upland areas are dominated by rabbitbrush (*Hymenoclea monogyra)* and desert broom (*Baccharis sarathroides)*. The Cliff-Gila valley bottom spans 1,200 -2,400 m in total width, but the active floodplain is 200-500 m. The riverbed consists mostly of medium to coarse gravel, but larger cobbles exist in higher-velocity areas. The rivers main channel was measured along the Cliff-Gila Valley reach in 2013, and an average width (57 m) and depth (2.2 m) were determined.

The Cliff-Gila Valley (Figure 1) has been consistently sampled by ichthyologists starting in the early 1980s, and specimens of the entire fish assemblage were deposited in natural history collections in New Mexico. Annual monitoring data indicates that non-native fishes are consistently present in the fish assemblage (Propst *et al.* 2008). The majority of museum specimens were used from two sites: Riverside and Bird Area (Figure 1), although collections from other sites within the Cliff-Gila Valley were also used.

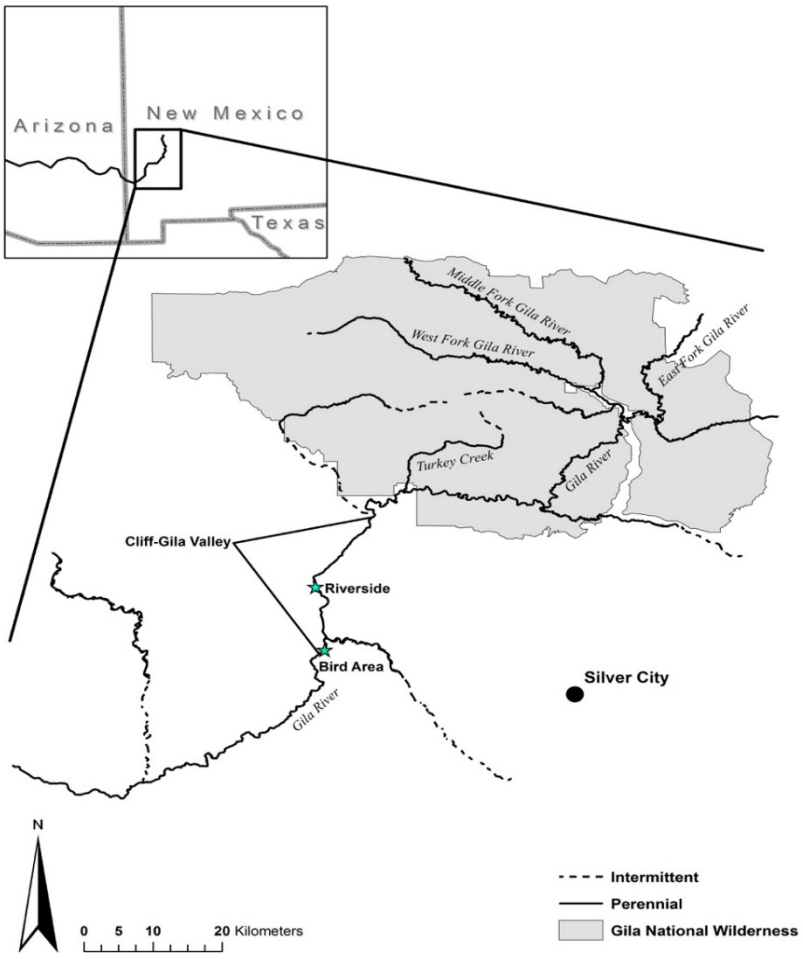

Figure 1. Map of the headwaters and Cliff-Gila valley reach of the Gila River in New Mexico. Riverside and Bird area are indicated with stars, and are the upper and lower bounds of the study reach, respectively.

Hydrologic Data

The study reach, the Cliff-Gila Valley (Figure 1), was selected based on hydrologic patterns of 'wet' and 'drought' conditions, which undergo natural periodic fluctuation, and museum specimen availability. This project focuses on both the timing and magnitude of flow as potential factors affecting fish assemblage stability and

structure. Discharge data was obtained from the U.S. Geological Service (USGS) website (http://waterdata.usgs.gov/) for the Gila River near Gila, NM gauge (USGS 09430500). Mean discharge at base flow is approximately 0.63 m^3/s (Whitney *et al.* 2014). Mean annual discharge (MAD), based on calendar year, was computed and used to classify years as 'wet', 'dry', or 'average' (e.g., Propst *et al.* 2008). MAD is a an overall measure of how much water the system received in a given year. The Q50 date was calculated for all years of analysis, as an indicator of what time of year the system was receiving the majority of flow inputs. The Q50 is the Julian date at which the river system has received 50% of the total annual discharge (Stewart *et al.* 2004; Krabbenhoft *et al.* 2014). Spring snowmelt can constitute up to 70% of the annual stream flow for streams with mountainous headwaters (Hauer *et al.* 1997). Likewise, years with a very low mean annual discharge, tend to have little to no spring snowmelt, and Q50 dates come later in the year due to monsoonal flows dominating the hydrograph.

The Palmer Drought Severity Index (PDSI) (Palmer 1965) was used to assess regional flow conditions for our sample years. Wet years have a PDSI of 2 in 1983 and 6 in 1985, indicating moderately wet conditions in 1983 and extremely wet conditions in 1985 (Figure 2). Drought years have a PDSI of nearly -3 in 1990 and nearly -4 in 1996, which indicates severe drought and extreme drought, respectively (Figure 2). Intermediate flow years, 2007, 2008, and 2015 exhibit values near zero, indicating near normal conditions (Figure 2).

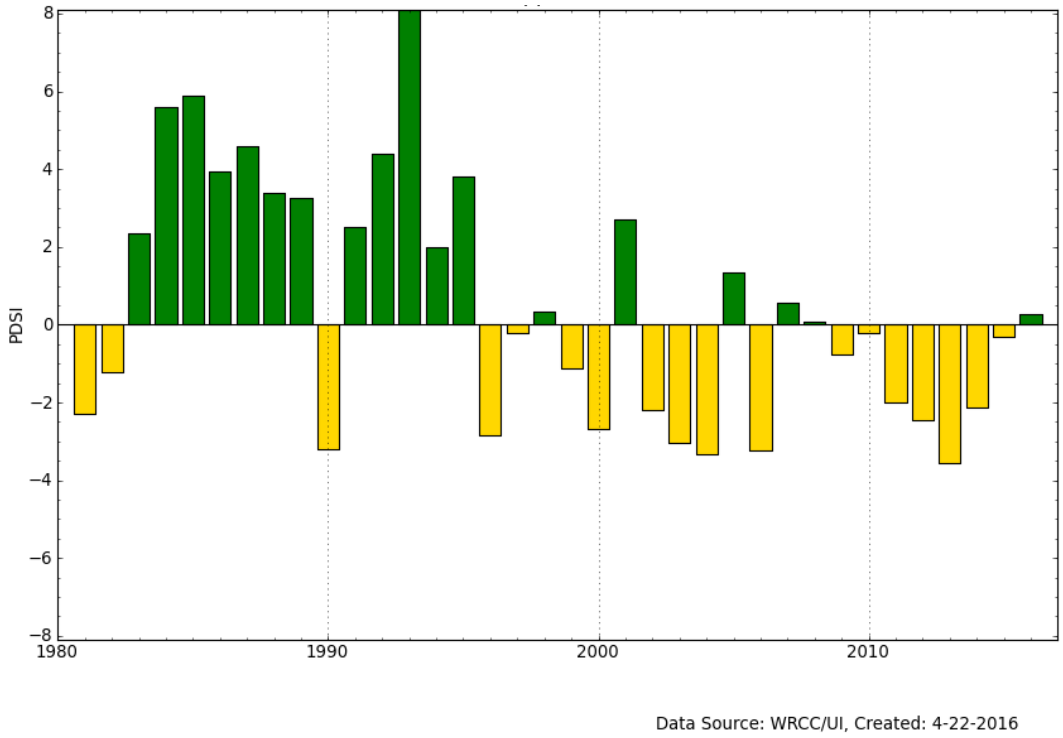

Figure 2. Palmer Drought Severity Index (PDSI) for the Upper Gil Region from 1980 to 2016.

Specimen Selection and Sample Sizes

The native fish assemblage of the Cliff-Gila valley includes seven species; Longfin Dace *Agosia chrysogaster* , Gila Chub *Gila intermedia*, Roundtail Chub *Gila robusta,* Spikedace *Meda fulgida*, Loach Minnow *Tiaroga cobitis* , Sonoran Sucker *Catostomus insignis,* Desert Sucker *Pantosteus clarkii*, Gila Topminnow *Poeciliopsis occidentalis* (Gori *et al.* 2014). Of these, the two *Gila* species and Gila Topminnow are rarely captured in this reach and are presumed to be extirpated. In the last 65 years, 12 non-native fish species have been introduced into this reach. Beginning in 1949, four non-native fishes were sampled in the Cliff-Gila Valley: Smallmouth bass *Micropterus dolomieu.* Largemouth bass *Micropterus salmoides,* Black bullhead *Ameiurus natalis,*

and Channel catfish *Ictalurus punctatus* (Gori *et al.* 2014). Eight more non-native species have been introduced since that time (Gori *et al.* 2014).

Our study aimed to characterize resource use of the Gila River fish assemblage using stable isotope analysis (SIA) of preserved museum specimens and included both native and non-native representatives for all size classes. Stable isotope analysis has been compared to gut content analysis in Gila River fishes, and is an effective method of assessing food web relationships (Pilger *et al.* 2010). Specimens were obtained from the Museum of Southwestern Biology (MSB) and Western New Mexico University (WNMU), according to the IACUC protocol 13-101019-TR-MC. This analysis includes fishes collected in years that span a range of hydrological conditions: 1983 (wet), 1985 (wet), 1990 (dry), and 1996 (dry). Smaller-bodied specimens were proportionally more available than larger specimens in museum records, but adult individuals were sampled when available. In total, 599 specimens were sampled and analyzed for $\delta^{13}C$ and $\delta^{15}N$ (Table 1). Additional $\delta^{13}C$ and $\delta^{15}N$ data was available from 2007 and 2008 (Pilger *et al.* 2010), and was included in this analysis. We also sampled fishes and other food web constituents at Riverside and Bird Area in 2015 and included isotopic ratios into the comparative analysis. Years 2007, 2008, and 2015 are considered 'average' years. Details are provided below.

Table 1. Number of specimens used in study of each species, in each year. Status: N= Native, I=Introduced

Species	Status	1983	1985	1990	1996	2007	2008	2015
Agosia chrysogaster	N	20	20	20	20	6	8	10
Gila robusta	N	20	0	0	0	0	0	0
Meda fulgida	N	20	20	20	3	4	4	0
Tiaroga cobitis	N	20	20	20	0	4	4	0

Catostomus insignis	N	20	20	20	21	12	14	17
Pantosteus clarkii	I	20	20	20	5	2	8	13
Micropterus salmoides	I	0	0	1	0	0	0	0
Micropterus dolomieu	I	5	0	0	0	0	5	0
Cypinus carpio	I	3	1	0	3	0	0	7
Cyprinella lutrensis	I	20	20	0	10	3	0	1
Lepomis cyanellus	I	10	0	0	1	0	0	5
Pimephales promelas	I	20	0	0	0	0	0	5
Ameirus melas	I	2	0	0	0	0	0	0
Ameiurus natalis	I	5	0	0	1	0	0	0
Ictalurus punctatus	I	20	0	0	0	0	3	7
Pylodictus olivarus	I	0	1	0	0	0	2	6
Ictalurus punctatus	I	20	0	0	0	0	3	7
Gambusia affinis	I	20	0	0	8	4	0	9
Totals		**225**	**122**	**101**	**72**	**35**	**51**	**44**

Contemporary food web sampling

Fish sampling took place at Riverside and Bird Area on Oct. 7th-8th, 2015, using a backpack electrofisher (Model B Smith-Root POW Electrofisher) and a seine (3 x 1.8 m, ½ cm mesh) to obtain specimens. Pools, riffles and other mesohabitats were sampled with similar intensity following a standard protocol (Propst *et al.* 2008; Whitney *et al.* 2014). Macroinvertebrate samples were taken from fish seine halls, including specimens from Baetidae (swimming mayflies), Corydalinae (dobson fly larvae), Belostomatidae (diant water bugs), Hydrophilidae (water scavenger beetles), Naucoridae (creeping water bugs), and Libellulidae (dragonfly larvae) (Table 2). Predominate riparian vegetation types were sampled, including trees (i.e. *Populus fremontii*, *Salix sp.*, *Tamarix sp*), grasses, forbs, and rushes. Algae and biofilms were scraped from rocks using a razor blade. Aquatic (submerged or emergent) macrophytes were sampled as available. All samples were placed in a cooler on ice, until they could be stored in a -20 C freezer. Samples from 2015

were collected to understand current baseline conditions, and compare two locations in the Cliff-Gila Valley, Bird Area to Riverside, in isotopic values to assess whether museum samples could be pooled from these locations. Primary production values are critical as baseline isotopic data for the system (Grey 2006; Boecklen *et al.* 2011).

Table 2. Macroinvertebrate samples for SIA from Riverside and Bird Area in 2015.

Classification	Sample size (n)
Oronectes virilis	4
Baetidae	10
Belostomatidae	12
Corydalinae	5
Chironomidae	2
Hydrophilidae	1
Libellulidae	1
Naucoridae	1

Stable Isotope Analysis

A 3-mm diameter white-muscle tissue plug was taken from the right dorsal area of each fish. Tissue samples were vacuum freeze-dried in a Labconco 2.5 L FreeZone for approximately 3 hours, and 0.9-1.0 mg of each sample was packed into tin capsules. Samples were combusted in a Costech Elemental Analyzer and transported to a mass spectrometer (either a Thermo Delta V Plus or a Thermo Delta Plus) at the Center for Stable Isotope Analysis, University of New Mexico. Data were reported in parts per thousand in delta (δ) notation, and were computed utilizing: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard})-1] \times 1000$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Fry 2006). Laboratory standards (calibrated to international standards) were used for carbon, and the standard for nitrogen was air.

Museum specimens were originally fixed in 10% formalin at the time of preservation, before being washed in water, and stored in 70% EtOH for long term storage. The effects of museum fixation with formalin and preservation with ethanol have been examined for impacts to stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$. Museum preserved specimens are depleted an average of 1.1 ‰ in $\delta^{13}C$ signatures (SD=0.8) and enriched on average of 0.5 ‰ in $\delta^{15}N$ values (SD=0.3) regardless of time spent in preservation (Edwards *et al.* 2002). The preservation effects on $\delta^{13}C$ values are of greater significance, because 1 ‰ depletion surpasses natural trophic fractionation (Gonzalez-Bergonzoni *et al.* 2014). The estimation of community-wide food web metrics was not affected by preservation (Edwards *et al.* 2002; Gonzalez-Bergonzoni *et al.* 2014), validating stable isotope analysis as an effective method for comparison of food web dynamics across temporal scales.

Statistical Methods

Our primary objective was to compare isotopic niche space occupied by native and non-native fishes across sample years different in hydrological conditions from high to low discharge. We hypothesized that under low flow conditions, native and non-native fishes would converge on resource use as they retreated to wetted refugia (Magoulick & Kobza 2003; Propst *et al.* 2008). Native fishes and non-natives fishes were pooled in each year. Statistical analyses of stable isotope ratios were conducted using the framework presented in Turner *et al.*(2010). This analysis generates centroids (bivariate mean $\delta^{13}C$ and $\delta^{15}N$) for each species or functional group of interest, which can then be measured for dispersion in isotopic space among species or groups. Centroid Distance (CD) is the

Euclidean distance between centroids of two groups, in this case native and non-native fishes. The $\delta^{13}C$ distance is the difference between the mean $\delta^{13}C$ values for these two groups. Whole-community dispersion in isotopic space was assessed for each year using the mean distance to the group centroid (MDC) and the mean nearest neighbor distance (MNND). The MDC compares the mean of the Euclidean distances of individual observations to the sample centroid, and thus the dispersion of individual observations within species or groups in isotopic space. The MNND compares the mean of Euclidean distances of individual observations to the mean of the Euclidean distances of each observations' nearest neighbor in isotopic space. Whole-community isotopic niche space is represented by the MDC when all samples are pooled (Bearhop *et al.* 2004; Layman *et al.* 2007a; Newsome *et al.* 2007; Turner *et al.* 2015). Larger MDC values indicate a greater proportion of isotopic space is being utilized (Turner *et al.* 2010)

The MNND can be interpreted as how strongly the isotopic values group together (Layman *et al.* 2007a; Turner *et al.* 2015). If values of MNND decrease, this is indicative of convergence of species or functional groups on the same resource (Turner *et al.* 2015). These measures take into consideration centroid location and dispersion around the centroid, which converts raw SIA results into a measure of trophic niche breadth and resource use. This analysis was used to compare natives to non-natives as functional groups, and among individual species within the Gila River fish community. Analyses were performed with R scripts written by Turner et al. 2010, using R version 3.0.2 (R Development Core Team 2013). In all cases, a residual permutation process was applied to generate null distributions of test statistics (Turner et al. 2010).

Additional statistical comparisons included Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson *et al.* 2011). Multivariate ellipse-based metrics are used in place of traditional convex hull methods, because ellipses are unbiased by sample size; thus allow comparison of communities with different sample sizes (Jackson *et al.* 2011). Ellipse overlap between natives and non-natives, and among different species, was used to examine niche partitioning in a qualitative fashion, as is often done with ordination techniques like Principle Components Analysis (PCA). Standard ellipses contain 40% of the data, regardless of sample size (Jackson *et al.* 2011). Analyses were performed using R version 3.0.2 (R Development Core Team 2013).

Finally, ordinary least-squares regression was conducted to evaluate relationships of centroid distance (CD) and $\delta^{13}C$ distance as dependent variables to MAD and Q50 independent variables. Separate regressions were performed to determine if the MAD or Q50 could explain the variation seen in CD and $\delta^{13}C$ distance.

Abundance Metrics

Fish collection records, available for the study reach from 1983 to present, were compiled and tabulated to estimate abundance of all species. Additional abundance data from Propst *et al.* (2008) were included in abundance analysis and the interpretation of SIA results. Relative abundance of non-natives was calculated as a proportion of the sum of all non-native individuals divided by the total number of fishes collected in each sampling event.

Chapter 3 RESULTS

Interpretation of community change over time

In order to effectively assess community change in this system, several issues regarding sampling had to be addressed. These included determining that different types of primary production (i.e., autochthonous vs. allochthonous) can be distinguished by isotopic signatures, that baseline isotopic values for the Cliff-Gila Valley are relatively constant among seasons, and that SIA values at all trophic levels in the Cliff-Gila Valley was relatively homogenous among sites in isotopic signatures.

Baseline data from previous SIA and food web research in the upper Gila Basin (Pilger et al 2010) found that single-celled algae ($\delta^{13}C$ =-24.3 ± 2.3) and emergent macrophytes ($\delta^{13}C$ =-22.9 ± 2.2) had larger $\delta^{13}C$ values then riparian sourced inputs, including willow ($\delta^{13}C$ =-27.8 ± 1.3), detritus (-$\delta^{13}C$ =-27.6 ± 1.6), FPOM ($\delta^{13}C$ =-28.4 ± 6.9), and grass (-26.9 ± 3.4).. The differences of note between the 2010 baselines (collected in 2007-08) and the 2015 baselines occur in macrophytes and filamentous algae, which had $\delta^{13}C$ averages of -22.9 ± 2.2 and -27.4 ± 7.1 in 2007-08 and -29.86 ± 0.48 and -30.05 ± 1.91 in 2015.

Table 3. Mean values (±SE) of $\delta^{13}C$ and $\delta^{15}N$ from 2015 sampling.

Type	Sample Size (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Fish	77	-25.30 ± 1.43	10.70 ± 1.39
Macroinvertebrates	35	-27.37 ± 1.06	7.60 ± 1.33
Smartweed	2	-30.38 ± 1.40	4.45 ± 0.63
Algae	6	-30.05 ± 1.91	5.06 ± 1.08
Grass	2	-13.73 ± 0.23	6.14 ± 1.07
Macrophytes	3	-29.86 ± 0.48	5.03 ± 1.03
Trees	5	-29.27 ± 0.65	2.32 ± 1.29
Crayfish	9	-24.29 ± 0.40	8.12 ± 1.11

Sampling considerations

Field-collections of fishes and associated environmental data from the Cliff-Gila Valley have occurred regularly since the 1960s and specimens and data are housed in the Museum of Southwestern Biology and natural history collections at Western New Mexico University. Until 1983, collections were usually sporadic in time and space, and conducted without explicit experimental design. Specimens examined in this project were pooled across all seasons within years, and combined across sampling areas defined by a geomorphically contiguous 19-km reach of the river. We tested for seasonal effects by generating dispersion statistics for collections made in 1983 among spring, summer, and fall. Figure 2 shows an isotopic bi-plot of these data which highlight the even distribution of points throughout all the seasons, indicating minimal differences among seasons.

Table 3 gives the centroid locations and standard deviations for each season. Within season variation is proportionally larger than among-season variation.

Table 4. Centroids and standard deviations for seasonal $\delta^{13}C$ and $\delta^{15}N$ values in 1983.

Type	**Sample Size (n)**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**
Summer	84	-24.48 ± 1.24	11.22 ± 1.05
Fall	98	-24.88 ± 1.53	12.14 ± 1.47
Winter	26	-25.18 ± 1.75	11.68 ± 1.33

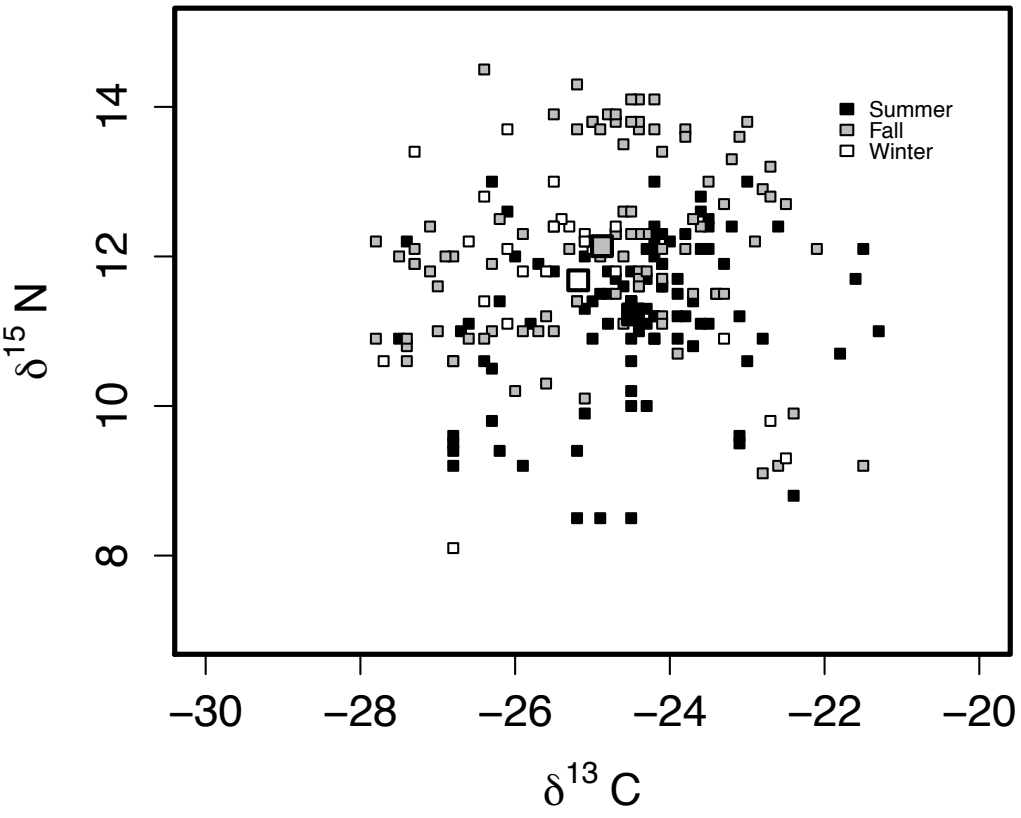

Figure 3. Isotopic bi-plot comparing summer, fall, and winter in 1983 sampling. No significant seasonal variation in fish isotopic signatures were detected.

We assessed effects of combining samples across localities by plotting variation in isotopic ratios of collections taken at Riverside and Bird Area in 2015. Centroids are

marginally significantly different (*p=0.048*) across sites, but plot very close to each other in isotopic space. Cross-site differences are amplified by differences in $\delta^{15}N$. The centroid for Riverside was (-26.35, 8.48) and the centroid for Bird Area was (-25.83, 9.45). For all other metrics, the null hypothesis was not rejected. Dispersion around the centroids at Riverside and Bird Area were similar (*p=0.073*) and mean nearest neighbor was also similar between the two sites (*p=0.614*). Comparisons across trophic levels including fish, macroinvertebrates, riparian vegetation, and algae were not significantly different between Riverside and Bird Area (Figure 3.) The most enriched $\delta^{15}N$ fishes in Bird Area are highlighted with a circle. These fish are likely more enriched in $\delta^{15}N$ because the fish collected at Bird Area were larger, on average, than specimens collected at Riverside. Inputs from Mangas Creek, a tributary entering the Gila River directly above Bird Area, could be contributing to elevated $\delta^{15}N$ levels.

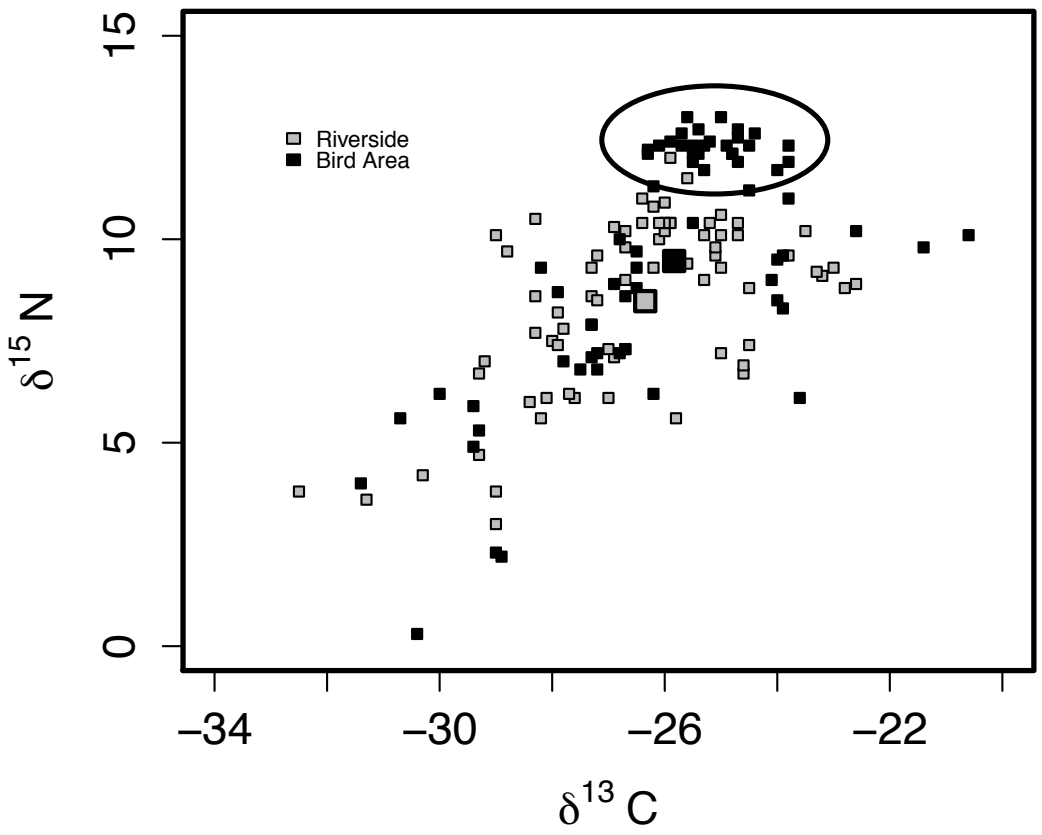

Figure 4. Isotopic bi-plot comparing $\delta^{13}C$ and $\delta^{15}N$ isotopic niche space of fishes in Riverside to Bird Area.

Hydrologic Analysis

Generally, a year with a high MAD, corresponds with having a low Q50 (Figure 5). This is due to years that have a high MAD receiving a large snowmelt. Likewise, years that have a very low MAD, typically have received little to no spring snowmelt, and the majority of flow is associated with late summer monsoonal flows. However, these relationships are not always maintained. The Q50 is more informative for the timing of flow, than the actual flow that the system receives.

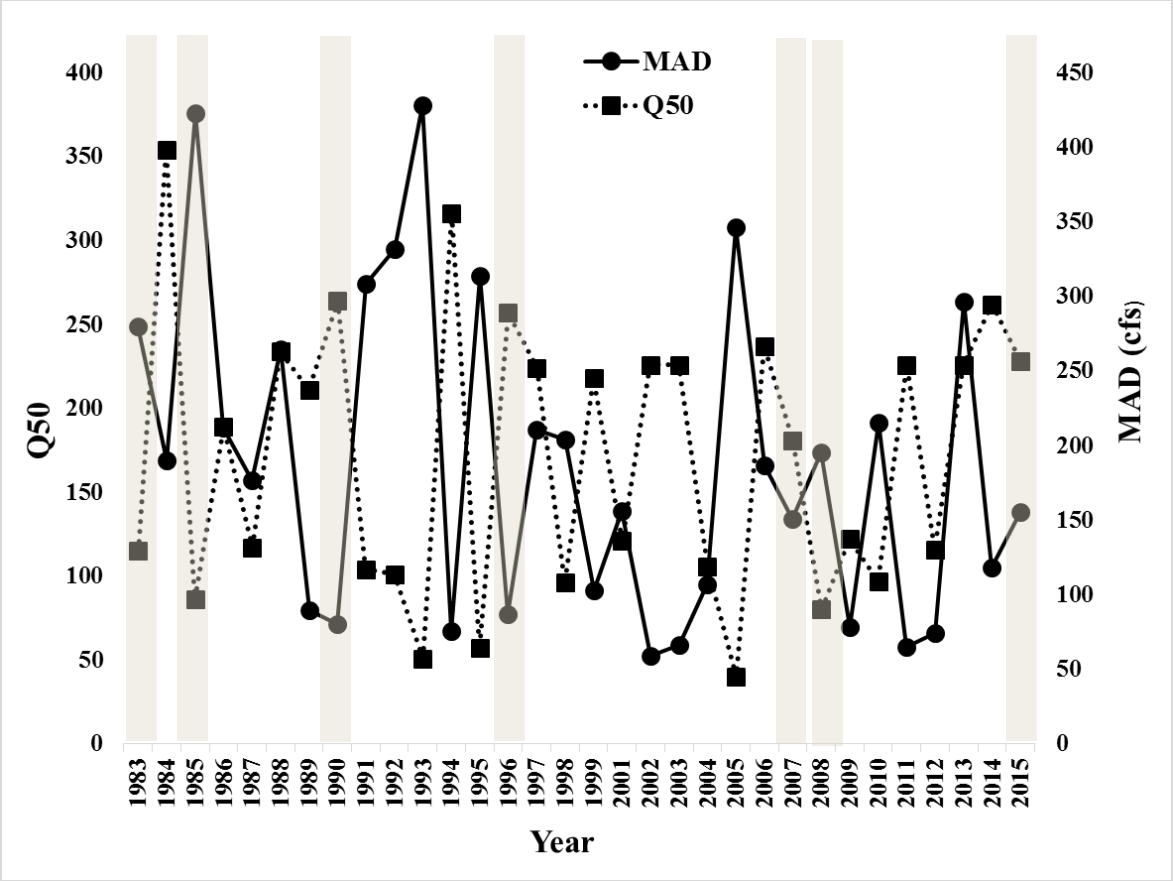

Figure 5. Mean Annual Discharge (MAD) and Q50 date through time, with years of SIA highlight in grey bars.

Non-native fish populations respond to flow conditions, as seen through the fluctuation of non-native proportions in the fish assemblage in relation to hydrologic conditions (Figure 6). In most of the very low flow years, the percentage of non-natives tend to increase (i.e., years 1994, 2003, 2011). Additionally, certain low flow events appear to show the same trend, but with a lag effect; the proportion of non-natives increases directly following a low-flow year (i.e., years 1998, 1999).

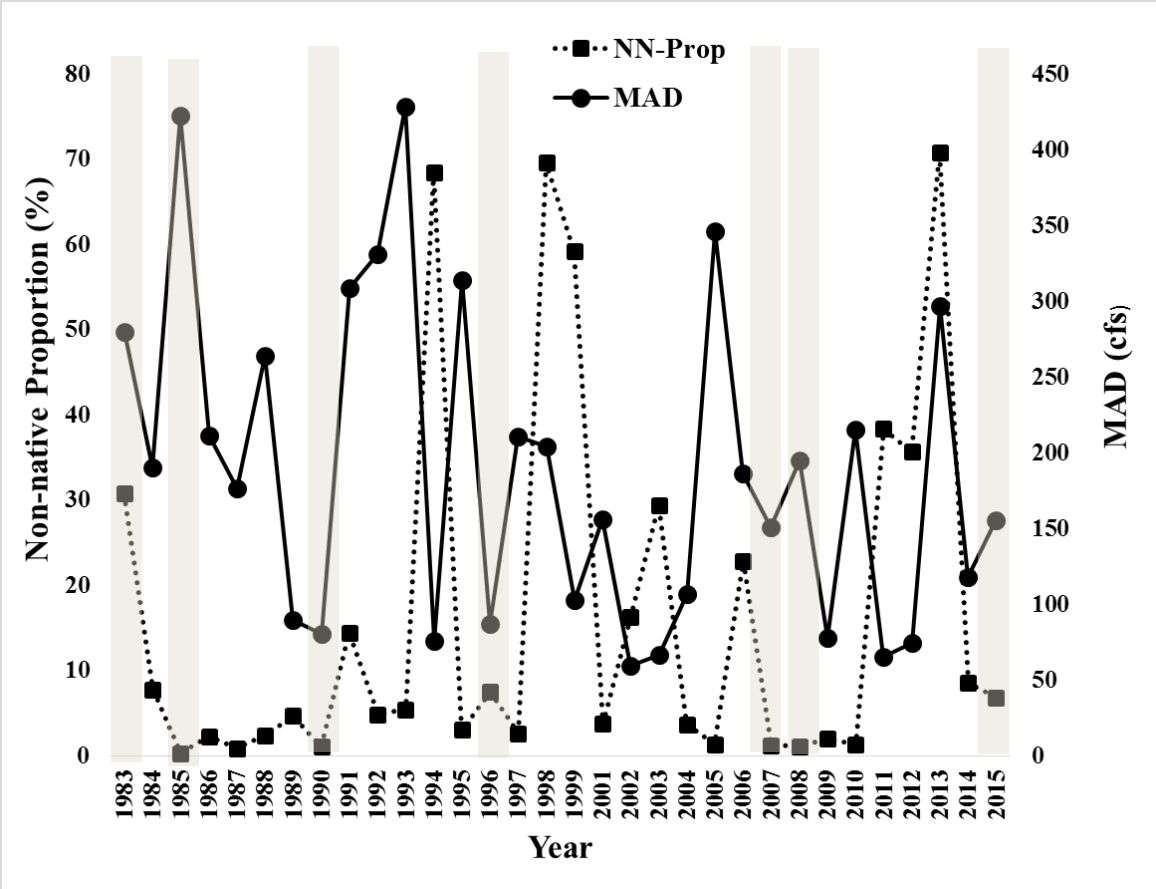

Figure 6. Mean annual discharge and non-native proportion plotted through time, with years of SIA highlighted by grey bars.

Isotopic Analysis by Origin

Fishes were pooled by origin, native and non-native fishes, to assess how resource use changed between groups across sample years that varied in hydrological conditions. Sample years included 'wet' (1983, 1985), 'dry' (1990, 1996), and 'average' years (2007, 2008, 2015). The average MAD for 1983-2015 was 189.08 cfs and the median was 86 cfs. The average Q50 was 171.5 Julian days and the median was 185 Julian days**.** Centroid distances between natives and non-natives are generally larger during wet years,

and smaller during drought conditions (Table 5). This trend is even more pronounced when just looking at $\delta^{13}C$ distance (Table 5).

Table 5. Mean values of $\delta^{13}C$ and $\delta^{15}N$ of natives and non-natives for each year of analysis. Centroid distance is computed as described in the text. In 1990 only contained one non-native sample, which was used as the centroid for comparisons. * denotes the centroids are significantly different between natives and non-natives where $p < 0.01$.

Year	Status	Sample Size (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Centroid Distance (CD) (‰)	$\delta^{13}C$ Distance (‰)
1983	*Natives*	121	-25.4 ± 1.24	11.9 ± 0.95	1.46*	1.40
	Non-Natives	105	-24.0 ± 1.28	11.5 ± 1.48		
1985	*Natives*	99	-27.0 ± 1.31	11.0 ± 0.85	2.30*	2.30
	Non-Natives	22	-24.7 ± 0.50	11.0 ± 0.76		
1990	*Natives*	100	-23.6 ± 1.81	12.4 ± 1.64	1.80	0.0
	Non-Natives	1	-23.6	10.6		
1996	*Natives*	49	-24.6 ± 1.02	12.1 ± 0.75	0.32	0.3
	Non-Natives	26	-24.3 ± 1.67	12.0 ± 1.14		
2007	*Natives*	28	-27.1 ± 0.92	10.9 ± 0.81	2.15*	1.9
	Non-Natives	7	-25.2 ± 0.86	9.9 ± 1.56		
2008	*Natives*	41	-27.3 ± 0.91	10.7 ± 0.70	1.27*	0.9
	Non-Natives	10	-26.4 ± 0.61	11.6 ± 1.14		
2015	*Natives*	39	-25.9 ± 1.18	10.6 ± 1.56	1.12*	1.1
	Non-Natives	40	-24.8 ± 1.47	10.8 ± 1.22		

Table 6. Comparison of native fishes to non-native fishes by Distance between Centroids (CD), Mean distance to the Centroid (MDC), Mean Nearest Neighbor (MNN), and Eccentricity (ECC) for all years of analysis. A single * denotes a significant p value ($p<0.05$). A double ** denotes a marginally significant p value ($p<0.01$). Dispersion metrics for 1990 are unavailable due to lack of non-native samples.

Year	Group	MDC (‰)	MNN (‰)	ECC (‰)
1983	Native	1.40**	0.20**	0.51
	Non-native	1.61**	0.27**	0.27
1985	Natives	1.41*	0.17	0.58
	Non-Natives	0.67*	0.17	0.74
1990	Natives	-	-	-
	Non-Natives	-	-	-
1996	Natives	1.06**	0.32	0.52
	Non-natives	1.46**	0.51	0.78
2007	Natives	1.09	0.32**	0.44
	Non-natives	1.32	1.07**	0.87
2008	Natives	1.02	0.24	0.48
	Non-natives	1.03	0.62	0.75
2015	Natives	1.75	0.37	0.81
	Non-natives	1.74	0.41	0.58

Significant differences in centroid locations were observed when comparing natives to non-natives ($p=0.001$), except for 1996 ($p=0.622$). In all year of analysis, the non-native centroid had larger $\delta^{13}C$ values. Natives and non-natives have similar centroid locations in 1996, one of the driest years on record. In dry conditions, natives and non-natives converge on the same $\delta^{13}C$ and $\delta^{15}N$ signatures, indicating very similar resource use (Figure 6) where centroids plot in marginally identical positions. Differences in MDC of natives compared to non-natives was significant only in 1985 ($p=0.002$), a comparatively wet year. Non-native MDC (0.67) was significantly smaller than the native MDC (1.41). Differences in MDC were marginally significant in two years: 1983 ($p=0.094$) and 1996 ($p=0.091$). Mean nearest-neighbor distance was marginally

significant in two years: 1983 (p=0.066) and 2007 (p=0.066). Eccentricity of natives compared to non-natives was not significantly different in any year of analysis.

The two 'wet' years of analysis are 1983 and 1985, and have large $\delta^{13}C$ space between the native and non-native centroids, as well as a substantial distance between centroids (Table 5). The distance in $\delta^{13}C$ space is 1.4‰ in 1983 (Figure 6) and 2.3‰ in 1985 (Figure 7). These two years have the largest separation in native and non-native groups for this data set.

The years 1990 and 1996 are the two 'dry' years of analysis, and both have very small $\delta^{13}C$ distance between natives and non-natives (Table 5). The distance in $\delta^{13}C$ space is 0.0‰ in 1990 (Figure 8) and 0.3‰ in 1996 (Figure 9). These are the smallest distances in $\delta^{13}C$ space for this data set.

The modern samples included in the analysis are all 'average' hydrology years. While the $\delta^{13}C$ distance for 2007 is very large (1.9 ‰) (Figure 10), the other two years have $\delta^{13}C$ distances (1.1‰ in 2008 (Figure 11) and 0.9‰ in 2015 (Figure 12)) that are intermediate to the 'wet' and 'dry' years (Table 5).

SIBER analysis indicated that in every year, except 1985, the SEA of the non-native community was larger than the native SEA. However, this pattern was predominantly caused by outliers in the data. Outliers were identified as points in the data set that had overly large effects on the location of the centroid. In 1996 (Figure 7), 2007 (Figure 8), and 2008 (Figure 9), outliers in the non-native fish community appear to have a large effect on the calculation of the SEA. The removal of the extreme outliers causes

large decreases in the SEA of non-native fishes in these years, and decreases the overlap between natives and non-natives in two of the three years.

Table 7. The standard ellipse areas of natives and non-natives in each year of SIA, the ratio of the Native SEA to the Non-native SEA, and the overlap between the native ellipse and the non-native ellipse. *Non-native SEA is not available for 1990 because only

Year	**Native SEA**	**Non-native SEA**	**Overlap**
1983	3.64	6.00	1.42
1985	3.53	1.10	0
*1990**	-	-	-
1996	2.42	5.05	2.35
1996-Outliers removed	2.42	3.14	1.89
2007	2.35	3.75	0
2007-Outliers removed	2.35	1.82	0
2008	2.00	2.37	0.22
2008-Outliers removed	2.00	1.53	0.08
2015	4.52	5.37	2.32

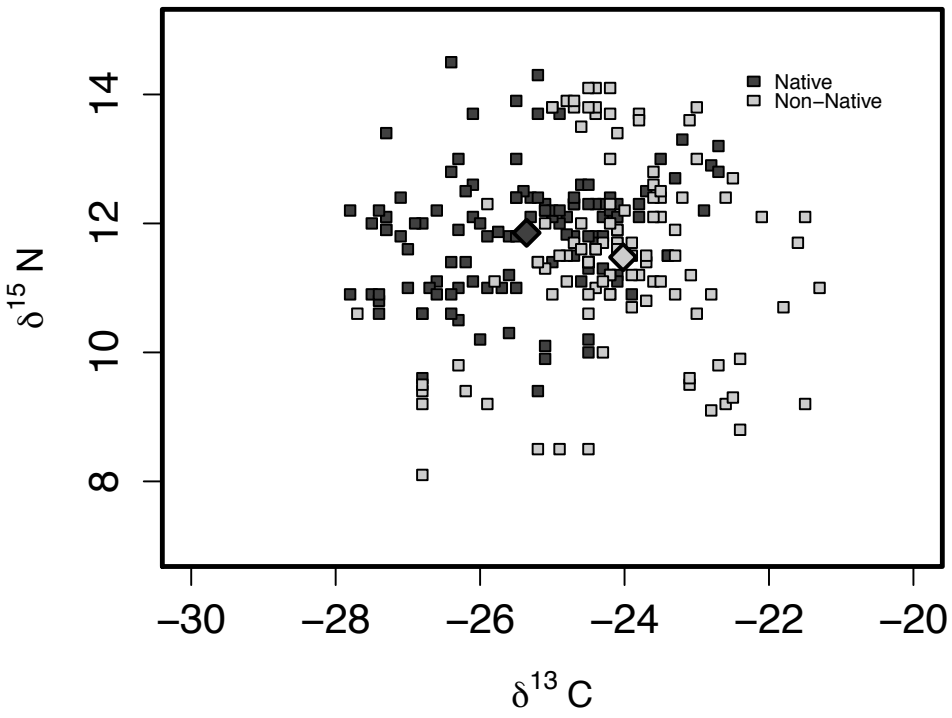

Figure 7. Natives and non-natives compared in 1983. Diamonds indicate centroids.

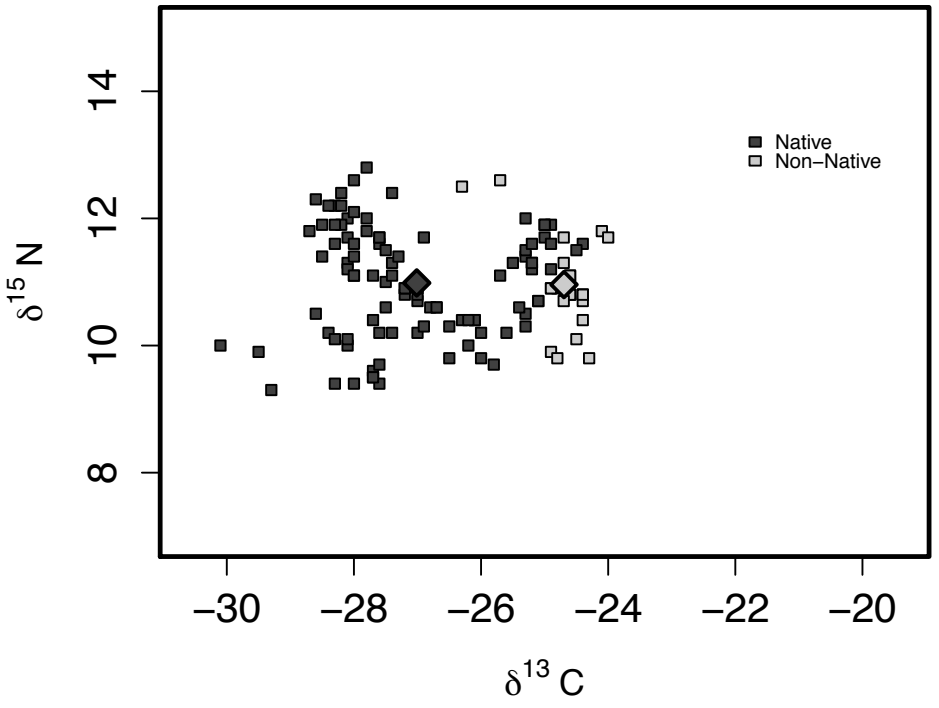

Figure 8. Natives and non-natives compared in 1985. Diamonds indicate centroids.

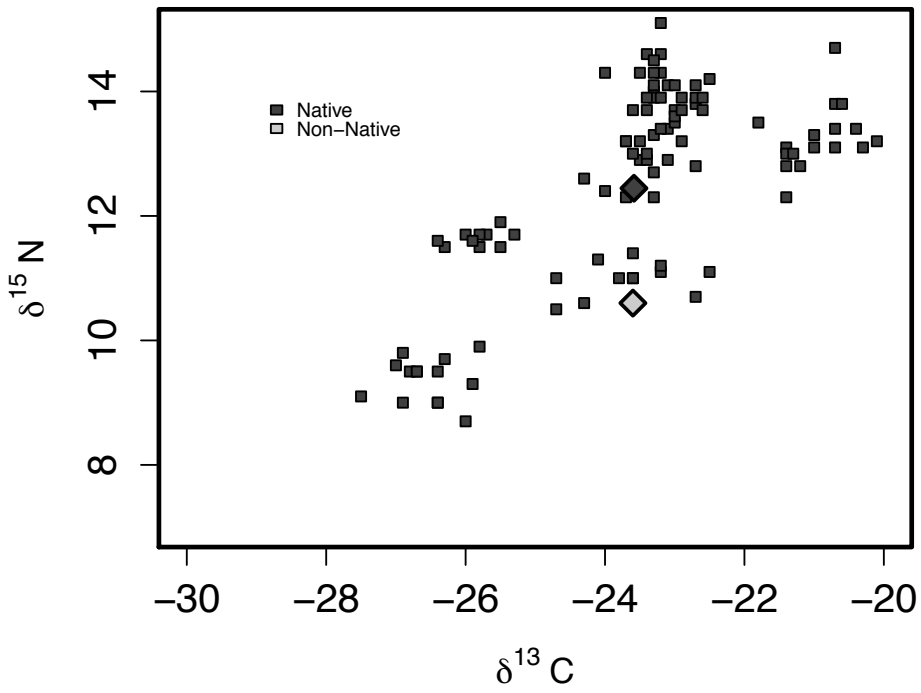

Figure 9. Natives and non-natives compared in 1990. Diamonds indicate centroids.

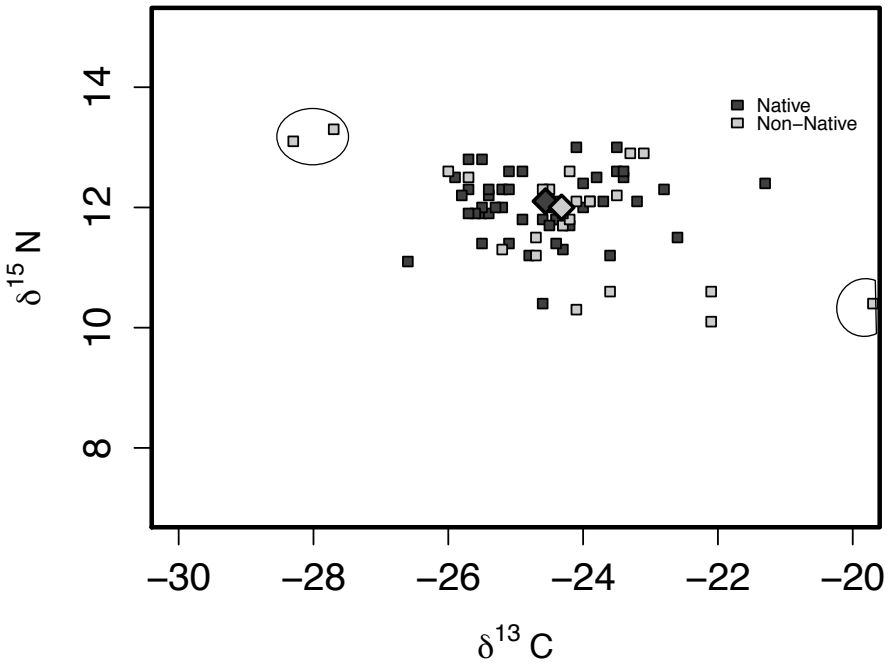

Figure 10. Natives and non-natives compared in 1996. Diamonds indicate centroids. Outliers are indicated with circles.

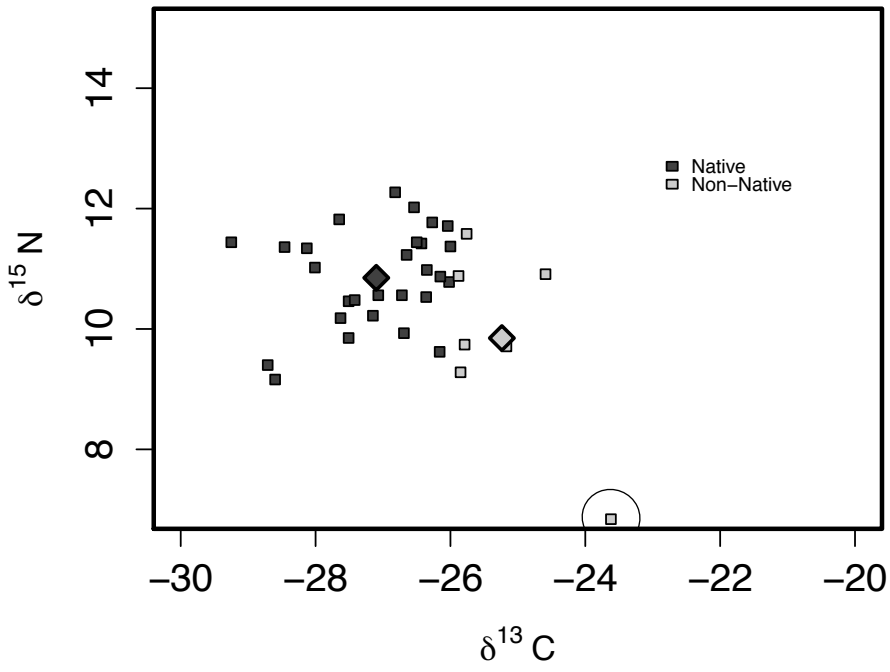

Figure 11. Natives and non-natives compared in 2007. Diamonds indicate centroids. Outliers are indicated with circles.

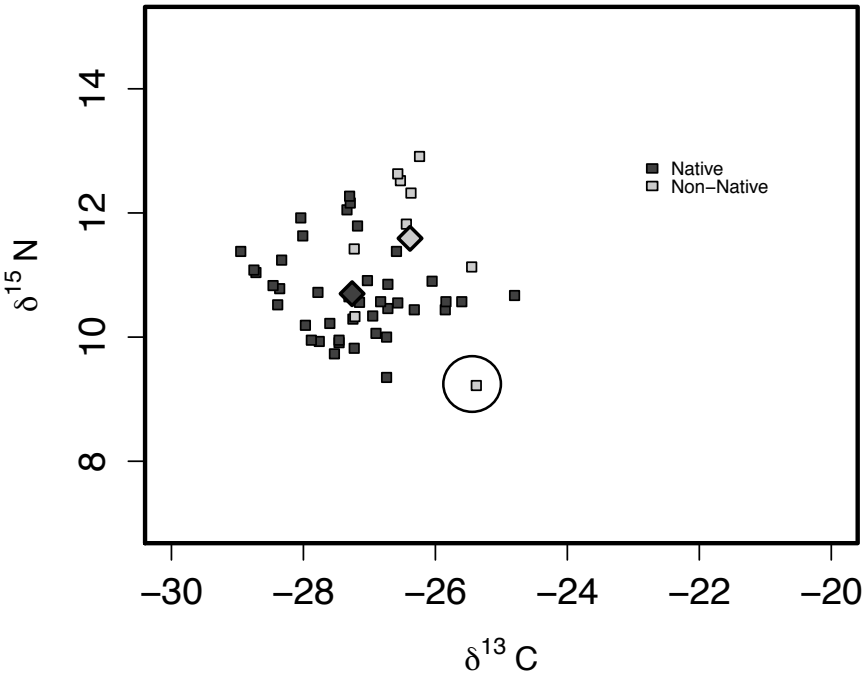

Figure 12. Natives and non-natives compared in 2008. Diamonds indicate centroids. Outliers are indicated with circles.

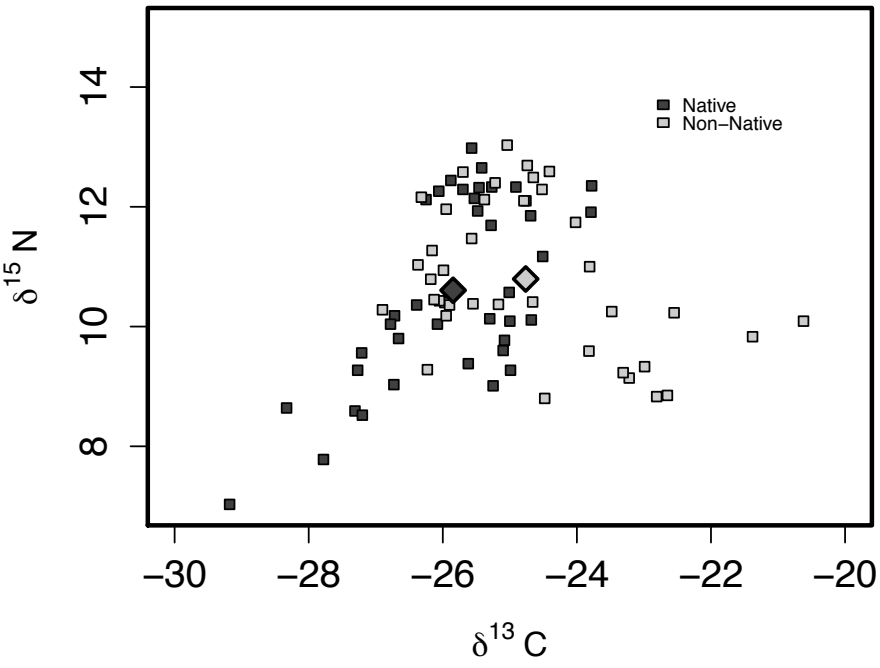

Figure 13. Natives and non-natives compared in 2015. Diamonds indicate centroids.

Centroid Distance Relationships with Hydrology

The relationship of distance between native and non-native centroids and hydrologic conditions was examined to relate resource use to hydrologic parameters in the Gila River. Linear regressions were performed between centroid distance and carbon distance between natives and non-natives against the Q50 day and the MAD. The Q50 day showed a correlation with centroid distance (R^2= 0.171) and carbon distance (R^2= 0.453) (Figure 13). Mean annual discharge showed a stronger correlation with both centroid distance (R^2= 0.279) and carbon distance (R^2=0.640) then the Q50 day results (Figure 14). However, the only relationship with a significant p-value was between MAD and carbon distance (p = 0.03, R^2=0.640). This indicates that as water in the system increases (higher MAD), the average distance in $\delta^{13}C$ values between natives and non-natives also increases. This means that resource use is more varied between these two

groups in ‘wet’ conditions. Furthermore, this also means that in drier conditions, natives and non-natives are more similar in their resource utilization.

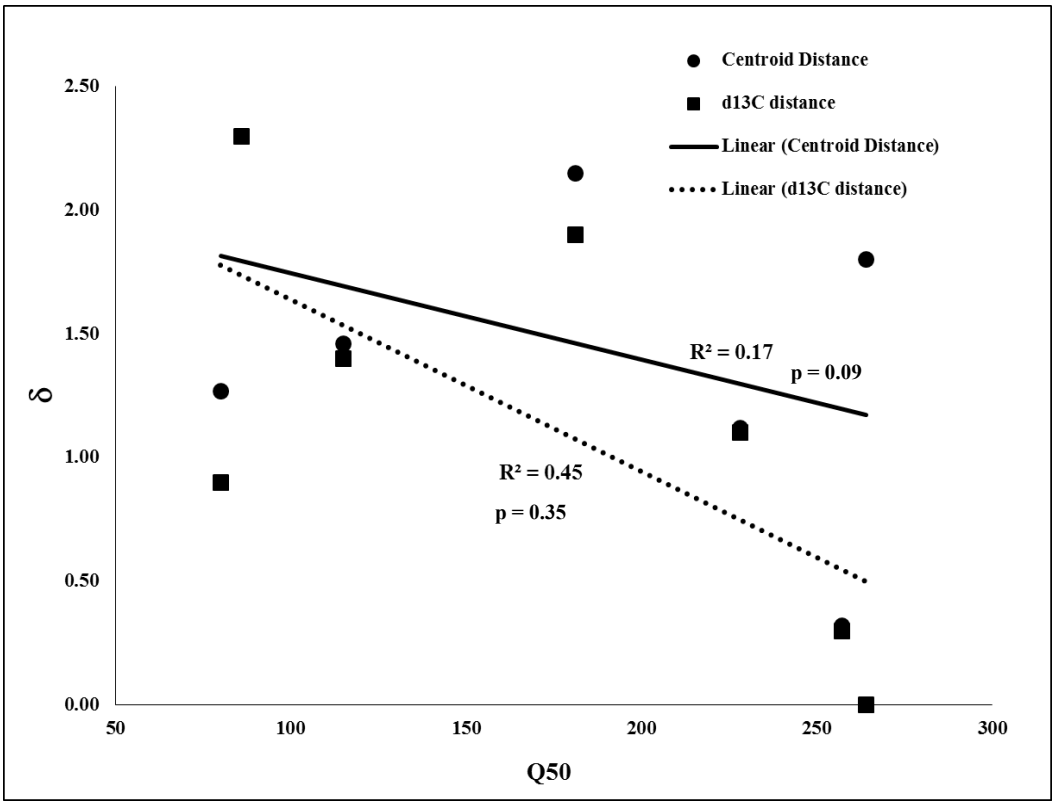

Figure 14. Carbon distance and centroid distance of natives to non-natives regressed against the Q50 date.

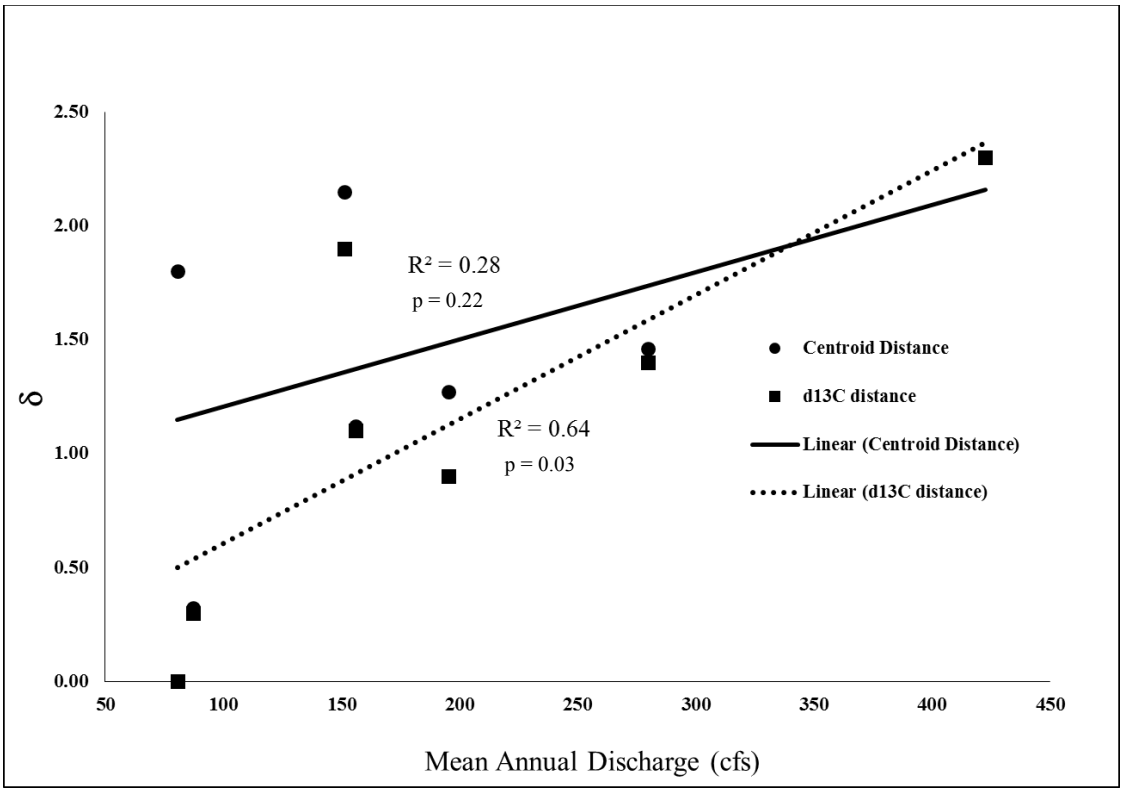

Figure 15. Centroid distance and $\delta^{13}C$ distance of natives compared to non-natives against mean annual discharge (MAD).

Isotopic Niche Space of Individual Species

Fishes were grouped by species to assess how resource use changed among individual species across sample years that varied in hydrological conditions (Figure 16-22). Sample sizes, centroid locations, standard deviation of species groups, Euclidean distances among all species, and p-values indicating significantly different centroid locations were used to assess differences among species groups (Table 8-21).

In 1983, 8.57% species had similar centroid locations (9 of 105 pairwise comparisons) (Table 9) and in 1985, all species had significantly different centroid locations (Table 11). The year 1996 follows the trend we expected, but 1990 resulted in values that appear more closely to wet conditions. In 1996, 21.43% of species had similar

centroid locations (6 of 28 pairwise comparisons) (Table 15), whereas in 1990, all species had significantly different centroid locations. In the 'average' years of analysis, two years (2007, 2008) showed intermediate values to the 'wet' and 'dry' years, but 2015 had the greatest amount of centroid overlaps proportionally. In 2007, 10.71% of species had significant overlap in centroid locations (3 of 28 pairwise comparisons) (Table 17) and in 2008, 11.11% of species had significant overlap in centroid locations (4 of 36 pairwise comparisons) (Table 19). In 2015, the trend of the 'average' years breaks down, and 24.44% of species had significant overlap of centroids (11 of 45 pairwise comparisons) (Table 21).

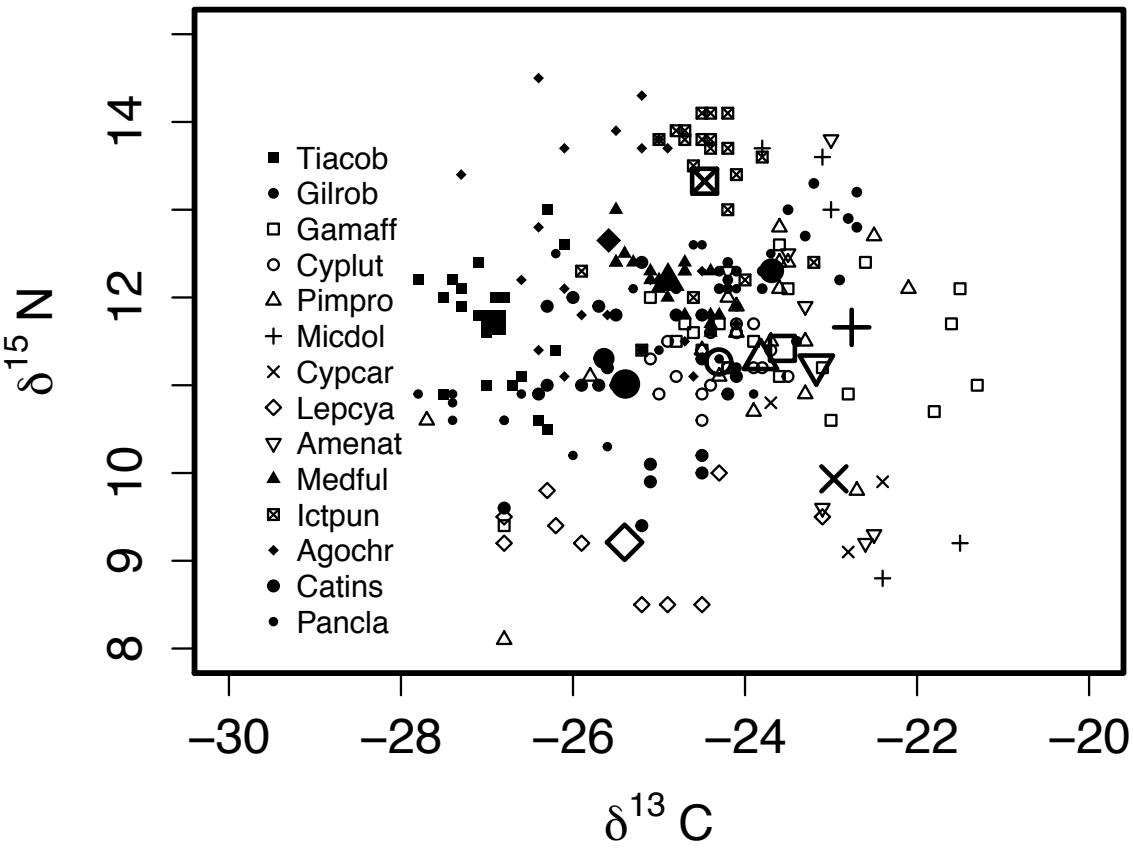

Figure 16. Isotopic bi-plot of 1983 fishes.

Table 8. Sample sizes and centroid locations with standard deviations of 1983 species groups.

Species	Sample Size	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰
Tiacob	20	-26.93 ± 0.49	11.71 ± 0.68
Gilrob	20	-23.69 ± 0.62	12.31 ± 0.56
Gamaff	20	-23.57 ± 1.40	11.42 ± 0.72
Cyplut	20	-24.31 ± 0.44	11.27 ± 0.31
Pimpro	20	-23.82 ± 1.75	11.30 ± 1.19
Micdol	5	-22.76 ± 0.86	11.66 ± 2.45
Cypcar	3	-22.97 ± 0.67	9.93 ± 0.85
Lepcya	10	-25.40 ± 1.21	9.21 ± 0.55
Amenat	7	-23.17 ± 0.58	11.23 ± 1.86
Medful	20	-24.90 ± 0.41	12.19 ± 0.33
Ictpun	20	-24.47 ± 0.55	12.33 ± 0.81
Agochr	20	-25.59 ± 0.84	12.65 ± 1.12
Catins	20	-25.39 ± 0.74	11.01 ± 0.86
Pancla	20	-25.64 ± 1.34	11.31 ± 0.80

Table 9. Euclidean distances among all species centroids in 1983, and p-values indicating significance.

Species	*Tiacob*	*Gilrob*	*Gamaff*	*Cyplut*	*Pimpro*	*Micdol*	*Cypcar*
Tiacob	X	0.001	0.001	0.001	0.001	0.001	0.001
Gilrob	3.29	X	0.011	0.001	0.005	0.050	0.002
Gamaff	2.38	0.89	X	0.028	0.604	0.167	0.025
Cyplut	2.66	1.21	0.76	X	0.245	0.006	0.011
Pimpro	3.14	1.02	0.28	0.49	X	0.060	0.029
Micdol	4.17	1.13	0.84	1.59	1.12	X	0.033
Cypcar	4.34	2.48	1.60	1.89	1.61	1.74	X
Lepcya	2.93	3.54	2.87	2.33	2.62	3.60	2.54
Amenat	3.79	1.19	0.44	1.13	0.65	0.60	1.31
Medful	2.09	1.21	1.53	1.09	1.40	2.20	2.96
Ictpun	2.94	1.28	2.11	2.07	2.13	2.39	3.71
Agochr	1.64	1.93	2.37	1.89	2.23	2.99	3.77
Catins	1.69	2.13	1.87	1.11	1.60	2.71	2.65
Pancla	1.35	2.19	2.08	1.34	1.82	2.90	3.00

Species	*Lepcya*	*Amenat*	*Medful*	*Ictpun*	*Agochr*	*Catins*	*Pancla*
Tiacob	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Gilrob	0.001	0.017	0.001	0.001	0.001	0.001	0.001
Gamaff	0.001	0.508	0.001	0.001	0.001	0.001	0.001
Cyplut	0.001	0.022	0.001	0.001	0.001	0.001	0.001
Pimpro	0.001	0.249	0.001	0.001	0.001	0.001	0.001
Micdol	0.001	0.507	0.001	0.001	0.001	0.001	0.001
Cypcar	0.001	0.105	0.001	0.001	0.001	0.001	0.001
Lepcya	X	0.001	0.001	0.001	0.001	0.001	0.001
Amenat	3.01	X	0.001	0.001	0.001	0.001	0.001
Medful	3.02	1.97	X	0.001	0.013	0.001	0.001
Ictpun	4.22	2.47	1.22	X	0.001	0.001	0.001
Agochr	3.44	2.80	0.83	1.30	X	0.001	0.001
Catins	1.80	2.23	1.27	2.49	1.65	X	0.397
Pancla	2.11	2.47	1.15	0.33	1.35	0.38	X

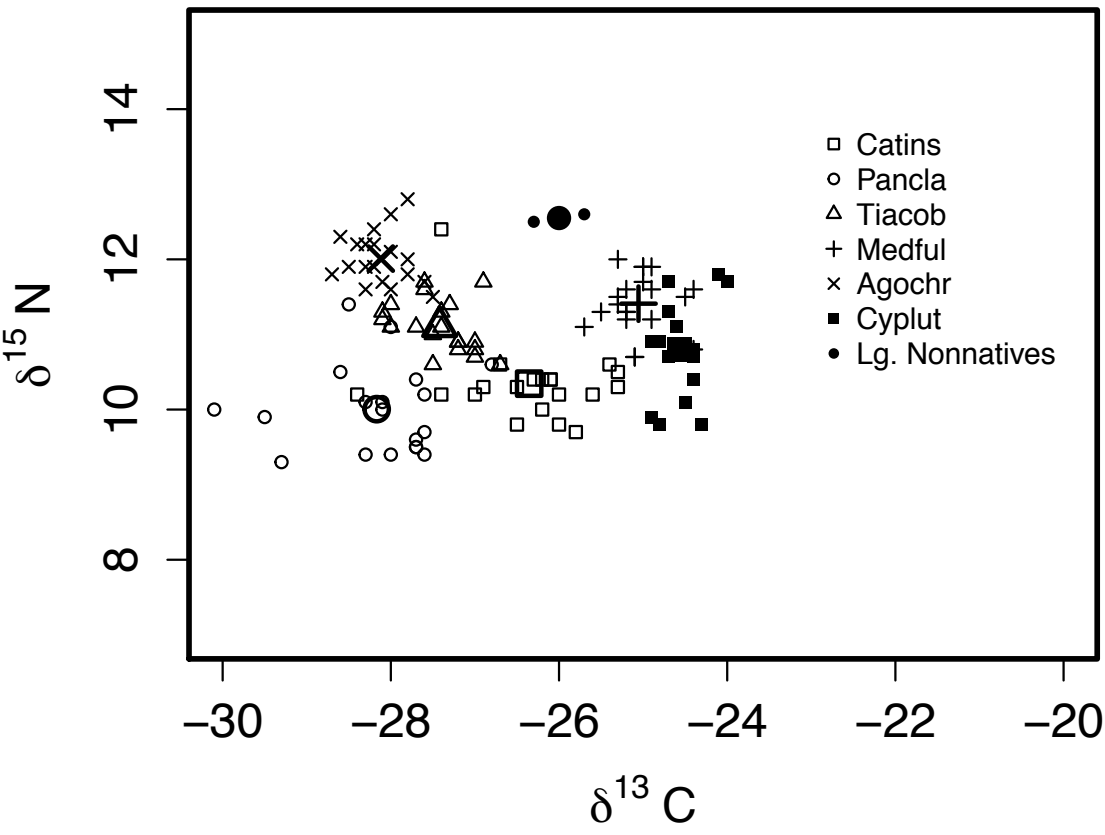

Figure 17. Isotopic bi-plot of 1985 fishes.

Table 10.Sample sizes and centroid locations with standard deviations of 1985 species groups.

Species	Sample Size (n)	δ^{13}C (‰)	δ^{15}N (‰)
Catins	20	-26.36 ± 0.78	10.35 ± 0.54
Pancla	20	-28.17 ± 0.78	10.01 ± 0.59
Tiacob	20	-27.42 ± 0.41	11.11 ± 0.34
Medful	20	-25.06 ± 0.33	11.41 ± 0.39
Agochr	20	-28.12 ± 0.32	12.01 ± 0.34
Cyplut	20	-24.57 ± 0.25	10.80 ± 0.59
Lg. Non-natives	2	-26.00 ± 0.42	12.55 ± 0.07

Table 11. Euclidean distances among all species centroids in 1985, and p-values indicating significance. NN = non-natives

Species	*Catins*	*Pancla*	*Tiacob*	*Medful*	*Agochr*	*Cyplut*	*Lg. NN*
Catins	X	0.001	0.001	0.001	0.001	0.001	0.001
Pancla	1.84	X	0.001	0.001	0.001	0.001	0.001
Tiacob	1.31	1.33	X	0.001	0.001	0.001	0.001
Medful	1.68	3.42	2.38	X	0.001	0.001	0.005
Agochr	2.43	2.01	1.14	3.12	X	0.001	0.001
Cyplut	1.85	3.69	2.87	0.78	3.76	X	0.001
Lg. NN	2.23	3.34	2.03	1.48	2.19	2.26	X

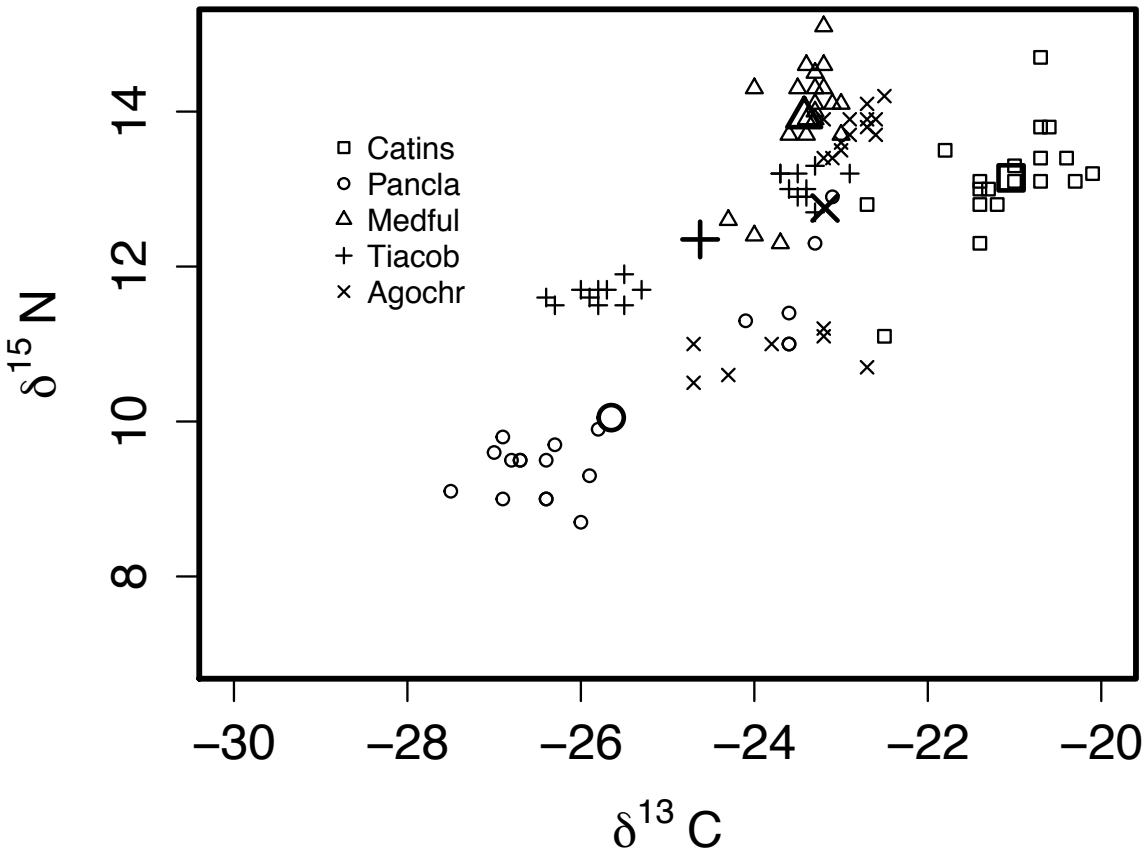

Figure 18. Isotopic bi-plot of 1990 fishes.

Table 12. Sample sizes and centroid locations with standard deviations of 1990 species groups.

Species	**Sample Size**	**δ^{13}C ‰**	**δ^{15}N ‰**
Catins	20	-21.04 ± 0.76	13.15 ± 0.69
Pancla	20	-25.65 ± 1.47	10.05 ± 1.18
Medful	20	-23.43 ± 0.34	13.93 ± 0.73
Tiacob	20	-24.63 ± 1.26	12.35 ± 0.75
Agochr	20	-23.19 ± 0.67	12.76 ± 1.44

Table 13. Euclidean distances among all species centroids in 1990, and p-values indicating significance.

Species	*Catins*	*Pancla*	*Medful*	*Tiacob*	*Agochr*
Catins	X	0.001	0.001	0.001	0.001
Pancla	5.55	X	0.001	0.001	0.001
Medful	2.51	4.47	X	0.001	0.005
Tiacob	3.67	2.52	1.98	X	0.001
Agochr	2.18	3.66	1.19	1.50	X

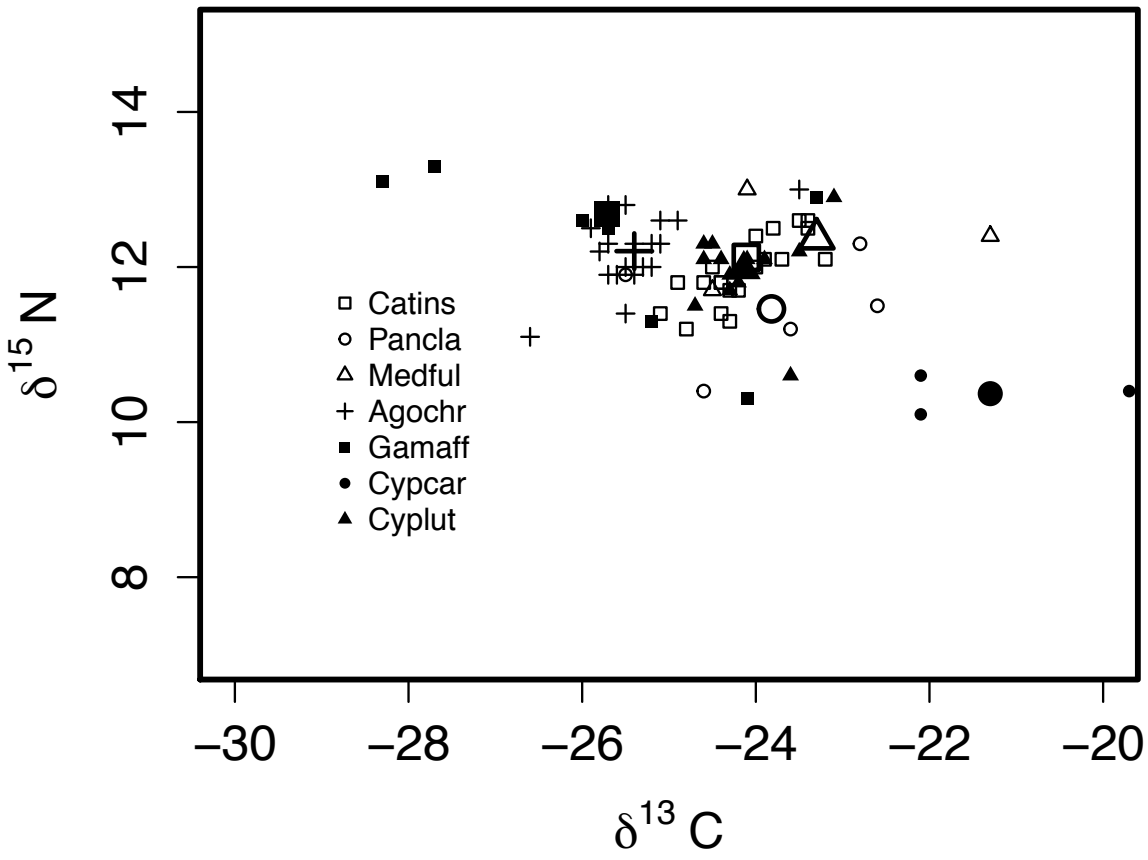

Figure 19. Isotopic bi-plot of 1996 fishes

Table 14. Sample sizes and centroid locations with standard deviations of 1996 species groups.

Species	Sample Size	δ^{13}C ‰	δ^{15}N ‰
Catins	21	-24.11 ± 0.53	12.12 ± 0.94
Pancla	5	-23.82 ± 1.23	11.46 ± 0.72
Gamaff	8	-25.71 ± 1.67	12.69 ± 1.52
Medful	3	-23.30 ± 1.74	12.37 ± 0.65
Cypcar	3	-21.30 ± 1.39	12.37 ± 0.25
Cyplut	13	-24.12 ± 0.49	11.97 ± 0.53
Agochr	20	-25.40 ± 0.58	12.25 ± 0.46

Table 15. Euclidean distances among all species centroids in 1996, and p-values indicating significance.

Species	*Catins*	*Pancla*	*Gamaff*	*Medful*	*Cypcar*	*Cyplut*	*Agochr*
Catins	X	0.218	0.001	0.242	0.001	0.853	0.001
Pancla	0.72	X	0.001	0.197	0.001	0.381	0.001
Gamaff	1.70	2.26	X	0.003	0.001	0.242	0.003
Medful	0.85	1.05	2.43	X	0.003	0.207	0.003
Cypcar	3.31	2.75	4.99	2.83	X	0.001	0.001
Cyplut	0.16	0.60	1.73	0.93	3.26	X	0.001
Agochr	1.29	1.75	0.57	2.11	4.49	1.28	X

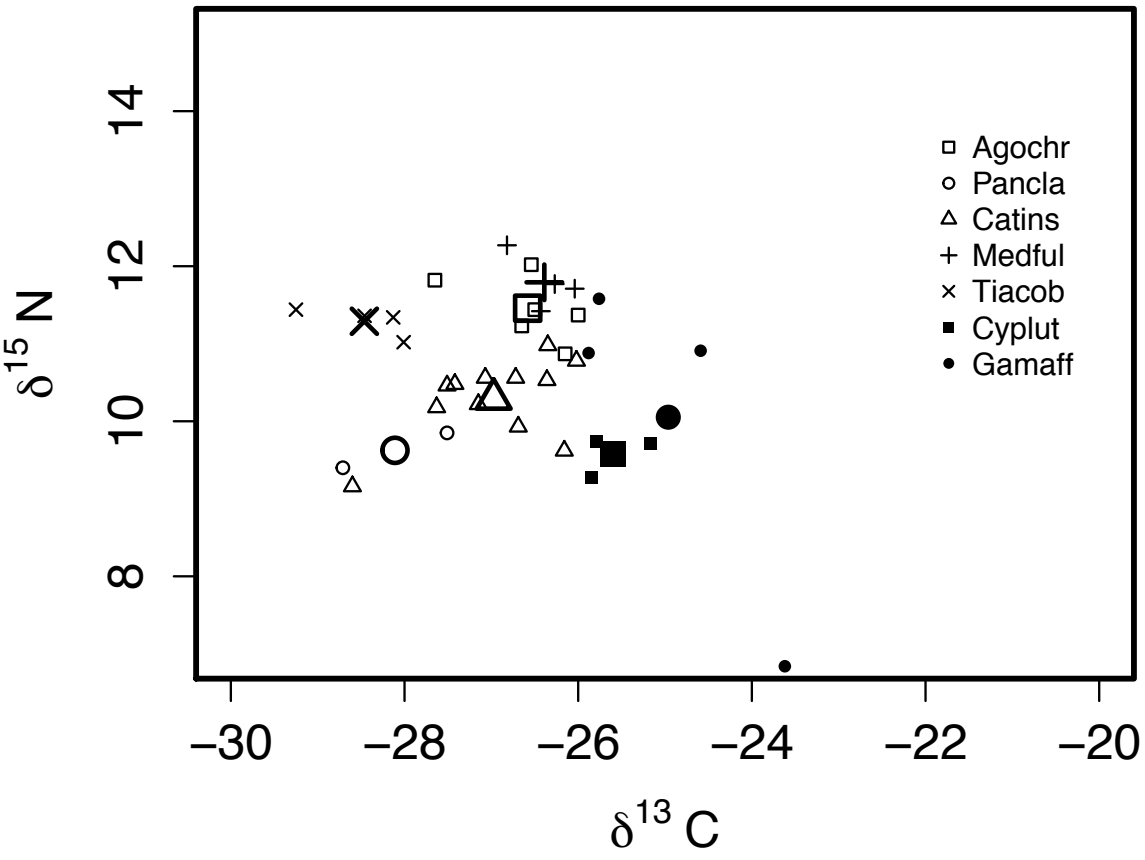

Figure 20. Isotopic bi-plot of 2007 fishes.

Table 16.Sample sizes and centroid locations with standard deviations of 2007 species groups.

Species	**Sample Size**	**δ^{13}C ‰**	**δ^{15}N ‰**
Agochr	6	-26.58 ± 0.58	11.46 ± 0.41
Pancla	2	-28.11 ± 0.85	9.63 ± 0.32
Catins	12	-26.97 ± 0.57	10.29 ± 0.51
Medful	4	-25.60 ± 0.33	9.58 ± 0.35
Tiacob	4	-24.96 ± 0.56	10.05 ± 0.19
Cyplut	3	-26.39 ± 0.38	11.79 ± 0.26
Gamaff	4	-28.46 ± 1.08	11.29 ± 2.17

Table 17. Euclidean distances among all species centroids in 2007, and p-values indicating significance.

Species	*Agochr*	*Pancla*	*Catins*	*Medful*	*Tiacob*	*Cyplut*	*Gamaff*
Agochr	X	0.003	0.001	0.001	0.001	0.639	0.001
Pancla	2.39	X	0.083	0.002	0.001	0.001	0.048
Catins	1.23	1.32	X	0.01	0.001	0.001	0.001
Medful	2.12	2.51	1.54	X	0.268	0.001	0.001
Tiacob	2.14	3.18	2.02	0.80	X	0.001	0.001
Cyplut	0.39	2.77	1.61	2.35	2.25	X	0.001
Gamaff	1.89	1.70	1.79	3.33	3.71	2.13	X

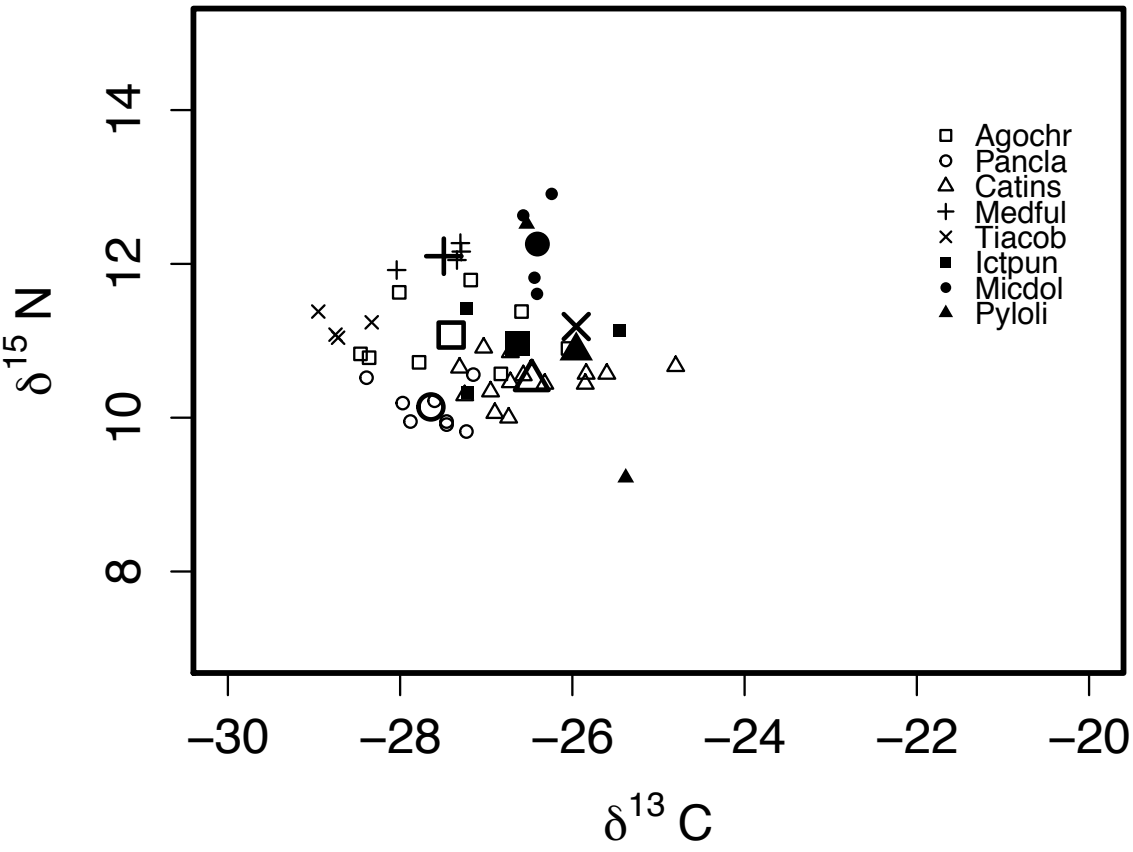

Figure 21. Isotopic bi-plot of 2008 fishes.

Table 18. Sample sizes and centroid locations with standard deviations of 2008 fish species

Species	Sample size	δ^{13}C ‰	δ^{15}N ‰
Agochr	8	-27.41 ± 0.88	11.08 ± 0.46
Pancla	8	-27.64 ± 0.41	10.14 ± 0.28
Catins	14	-26.47 ± 0.71	10.49 ± 0.26
Ictpun	3	-26.63 ± 1.02	10.96 ± 0.56
Medful	4	-27.49 ± 0.37	12.10 ± 0.15
Micdol	5	-26.41 ± 0.12	12.26 ± 0.54
Pyloli	2	-25.96 ± 0.81	10.87 ± 2.33
Tiacob	4	-28.69 ± 0.26	11.19 ± 0.16

Table 19. Euclidean distances among all species centroids in 2008, and p-values indicating significance.

Species	*Agochr*	*Pancla*	*Catins*	*Ictpun*	*Medful*	*Micdol*	*Pyloli*	*Tiacob*
Agochr	X	0.001	0.001	0.107	0.004	0.001	0.003	0.001
Pancla	0.96	X	0.001	0.002	0.001	0.001	0.001	0.001
Catins	1.11	1.22	X	0.364	0.001	0.001	0.274	0.001
Ictpun	0.78	1.30	0.50	X	0.003	0.005	0.395	0.001
Medful	1.03	1.97	1.91	1.43	X	0.011	0.001	0.001
Micdol	1.55	2.45	1.77	1.32	1.10	X	0.005	0.001
Pyloli	1.47	1.84	0.64	0.68	1.97	1.46	X	0.001
Tiacob	1.28	1.48	2.32	2.07	1.51	2.52	2.75	X

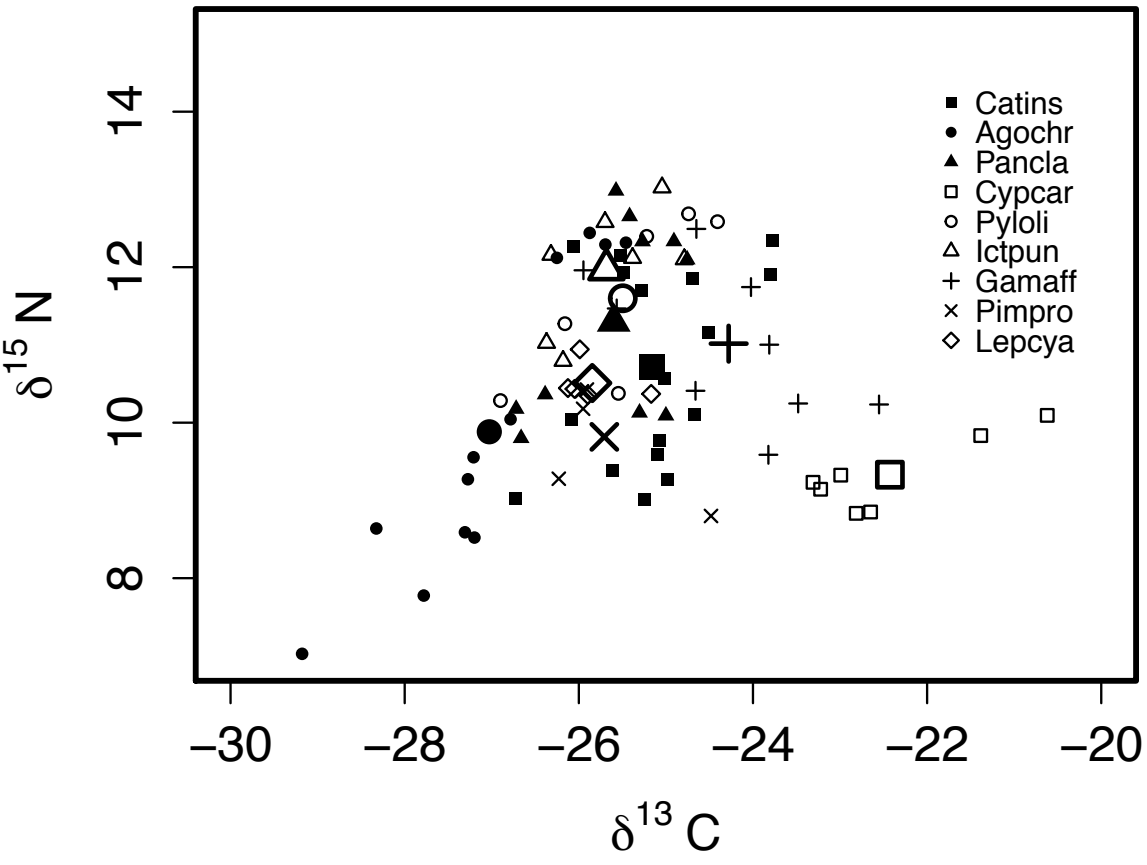

Figure 22. Isotopic bi-plot of 2015 fishes.

Table 20. Sample sizes and centroid locations with standard deviations of 2015species groups.

Species	Sample Size	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰
Catins	17	-25.16 ± 0.76	10.71 ± 1.25
Cypcar	7	-22.43 ± 1.02	9.33 ± 0.48
Pancla	12	-27.03 ± 1.10	9.88 ± 1.94
Pyloli	6	-25.50 ± 0.92	11.60 ± 1.11
Ictpun	7	-25.68 ± 0.64	11.97 ± 0.80
Gamaff	9	-24.28 ± 1.05	11.02 ± 0.96
Agochr	10	-25.60 ± 0.73	11.30 ± 1.28
Pimpro	5	-25.71 ± 0.70	9.82 ± 0.74
Lepcya	5	-25.85 ± 0.39	10.51 ± 0.25

Table 21. Centroid distances among all species in 2015, and p-values indicating significant differences.

Species	*Catins*	*Cypcar*	*Pancla*	*Pyloli*	*Ictpun*	*Gamaff*	*Agochr*	*Pimpro*	*Lepcya*
Catins	X	0.001	0.001	0.133	0.020	0.098	0.194	0.122	0.345
Cypcar	3.06	X	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Pancla	2.05	4.63	X	0.001	0.001	0.001	0.001	0.055	0.052
Pyloli	0.95	3.82	2.30	X	0.718	0.048	0.791	0.018	0.170
Ictpun	1.37	4.19	2.48	0.42	X	0.008	0.381	0.001	0.044
Gamaff	0.93	2.50	2.97	1.35	1.70	X	0.027	0.006	0.024
Agochr	0.73	3.73	2.01	0.32	0.68	1.35	X	0.036	0.324
Pimpro	1.05	3.32	1.32	1.80	2.15	1.86	1.48	X	0.510
Lepcya	0.72	3.62	1.34	1.15	1.47	1.65	0.82	0.71	X

Chapter 4 DISCUSSION

This study evaluated how variation in hydrological conditions (abiotic factors) affects the potential of interactions between native and non-native species (biotic factors) in an unregulated river fish community in the arid southwestern United States. Introductions of non-native fish have occurred over the last century and have coincided with native fish declines and transformation of river ecosystems through large-scale water management (Minckley 1982; Meffe 1985; Turner *et al.* 2015). Many studies have evaluated effects of non-native introductions and habitat modification separately, but usually implicate interactions of abiotic and biotic factors in native fish declines (Propst *et al.* 2008; Pilger *et al.* 2010; Whitney *et al.* 2014). Here, I retrospectively analyzed stable isotope signatures from fishes present in the Cliff-Gila valley fish assemblage across years that differed in hydrologic conditions to examine how trophic interactions between native and non-native species respond to changes in flow regime.

My analysis revealed that natives and non-natives differ in isotopic signatures according to hydrologic conditions. During 'wet' conditions (high MAD), native and non-native fishes diverge in centroid distance ($\delta^{13}C, \delta^{15}N$) (Figure 13) and to an even greater extent in $\delta^{13}C$ distance (Figure 14). Centroid- and $\delta^{13}C$-distances diminish, and isotopic niches overlap substantially in years with low MAD. Regression analysis revealed that MAD explained up to 64% of the variance in $\delta^{13}C$ values. Changes in $\delta^{13}C$-values indicate significant shifts in the availability and perhaps abundance of primary producers that are fueling the food web as hydrological conditions change (Figure 8 vs. Figure 10). As a consequence, native and non-native isotopic ratios overlap substantially

in isotopic niche space during years with low mean discharge (Figure 10). Natives and non-natives occupy distinct resource niches (and longer centroid- and $\delta^{13}C$-distances) in 'wet' conditions, as the availability of resources and habitat allow fishes to partition resources (Figure 7-8). Flow regime thus affects the availability of resources, which influence isotopic signatures in consumers (Werner & Hall 1979; Walsworth *et al.* 2013).

Natural flow regimes that include regularly-timed seasonal flow pulses promote abundance and diversity of native fishes. For example, Gido *et al.* (2013) determined that discharge from spring snowmelt induced a positive response in native fish abundance in both altered and natural systems. Previous research has determined that native fishes in the Gila prefer shallower habitats and greater spring discharge (Propst *et al.* 2008; Stefferud *et al.* 2011; Whitney *et al.* 2014). The density of native fishes has been found to be greatest in years of elevated discharge, and non-native predators decreased in these years (Propst *et al.* 2008). Spring flow pulses are also critical for connecting aquatic environments to the floodplain (Ward & Stanford 1995). When floodplains become inundated numerous essential ecosystem functions are induced: spawning behavior of native fishes is cued, sediment is cleared from spawning habitat, larval nursery habitat is created, litter decomposition is accelerated, riparian vegetation is recruited, and nutrients are mobilized (Ellis *et al.* 1999; Bunn & Arthington 2002; Gori *et al.* 2014). Connection of floodplains makes heterogeneous resources available to fish consumers, and our study revealed coincident increases in isotopic space in 'wet' and 'intermediate' conditions. In 'wet' (Figure 7-8) and 'intermediate' (Figure 11-13) conditions, native fishes shift towards depleted $\delta^{13}C$ ratios, which originate from riparian vegetation and filamentous algae that occurs in inundated riffle habitats. Additionally, in 'wet' years individual

species have increased habitat space and types (*i.e.*, habitats become more heterogeneous) and have opportunity to more finely partition these newly created habitats (Figure 16-17). Such partitioning, especially in food resources, can lead to differences in isotopic signatures.

Several native fishes, especially Loach Minnow and Spikedace, prefer swift habitat, with highly aerated water (Douglas *et al.* 1994; Propst 1999). Centroid locations of these species during 'wet' conditions are indicative of inputs of riparian production and instream production from shallow riffles into the fish food web. Instream production from shallow riffles is likely to have $\delta^{13}C$ signatures that appear similar to riparian production because the aeration of shallow riffles decreases fractionation processes that give algae lighter $\delta^{13}C$ values (Finlay *et al.* 1999). Thus, Loach Minnow has a centroid location of -26.93 ± 0.49 in 1983 and -27.42 ± 0.41 in 1985, both wet years. In dry conditions these centroid locations shift: -24.63 ± 1.26 in 1990 (1996 Loach Minnow was not sampled). Similarly, Spikedace shows the same change from 'wet' to 'drought' conditions. In 1983 the centroid location of Spikedace is -24.90 ± 0.41 and in 1985 it is -25.60 ± 0.33. But when in 'drought', the centroid locations are -23.43± 0.34 in 1990 and -23.30 ± 1.74 in 1996. Isotopic shifts suggest that during drought these two species are sharing similar food resources with non-native species, which is likely due to prey itmes (insects) shifting resource use from riparian sources to algae. Fishes become concentrated during low flow conditions, because available habitat is reduced (Walsworth *et al.* 2013). However, if their preferred habitat persists throughout the year, these species could be able to avoid co-occurrence and possible resource overlap with other species that remain

in pool habitat, and specialize on the different resources available in riffles, as their centroids indicate.

Overlap in isotopic niches does not prove that non-natives are negatively affecting natives through competition (or perhaps predation) during low-flow years. Low-flow conditions (i.e., drought, diversion) have variable effects on isotopic signatures of fishes in the Cliff-Gila Valley. The two drought years of analysis, 1990 and 1996, show different relationships between natives and non-natives, and among species. In 1996, natives and non-natives have marginally the same centroid, and experience complete overlap of isotopic niche space (Figure 9). Likewise, all native species experience high levels of overlap (Figure 18, Table 14). This could indicate that all species are using similar resources, resulting in similar isotopic signatures in dry conditions. The other dry year, 1990, shows much less overlap among species. This could be due to the less severe drought conditions experienced in 1990 (PDSI-moderate drought) compared to 1996 (PDSI-extreme drought). Natives and non-natives are difficult to compare in this year, as non-native specimens were not available for sampling. Fluctuation of baseline primary production values is a possibility, although evidence of this was not present in any other year of analysis. Baseline values assessed in 2007, 2008, and 2015 revealed that isotopic ratios of primary producers and primary consumers (macroinvertebrates) are relatively homogenous in terms of primary production signatures between Riverside and Bird Area sites.

It does appear that species overlap in isotopic space can be intensified during drought (i.e., 1996, Figure 19), perhaps dependent on how severe drought conditions are. Sonoran Sucker, Desert Sucker, Spikedace, and Red Shiner all have similar centroid

locations in 1996, signifying comparable resource use (Table 15). These four species typically occupy different food and habitat niches (i.e., suckers are detritivores, dace are insectivores, and shiners are considered both detritivores and insectivores (Pilger *et al.* 2010). The entire fish community in 1996 returned $\delta^{13}C$ values within a 4 ‰ range, indicating that overall resource heterogeneity was limited. When water contracts during drought, habitat and resources become more homogeneous (Magoulick & Kobza 2003), which could force diverse species into similar habitat and resource space.

Non-native fishes became more abundant in low flow years. For example, proportions from 1983 to 2015 (Figure 4) show similar patterns to previous analysis on the Gila (Propst *et al.* 2008; Gido *et al.* 2013; Whitney *et al.* 2014). Non-native proportions increased in response to low flow years (e.g., 1994, 2003, 2011). Certain low flow years showed the same trend, but suggested some lag time (e.g., 1998, 1999) where non-natives become more abundant in years that follow a low-flow year. Reduction in flow decreases the availability and quality of spawning habitat for native fishes and reduces abundance and heterogeneity of food resources, which can reduce abundance and recruitment native fishes (Bunn & Arthington 2002; Poff *et al.* 2007; Yarnell *et al.* 2010; Gido *et al.* 2013), perhaps allowing non-native fishes to make up a larger proportion of the fish community. Additionally, non-native fishes in the Gila River prefer lotic, slower moving waters (Whitney *et al.* 2014), and this habitat type persists even during low flow conditions. Non-native fishes obtain dietary carbon from instream production (probably microalgae) regardless of hydrologic conditions as reflected in enriched $\delta^{13}C$ ratios in their tissues. Thus, during low flow conditions, non-natives preferred habitat type (pools) and preferred resource (in-stream production) are still available, and allow their

populations to persist and grow. While Propst *et al.* (2008) found that over time drought had no influence on long-term native fish density, our results show that low MAD does control the fluctuation of non-native proportions of the fish community via a re-structuring of resource availability in low flow conditions. Propst *et al.* (2008) concluded that other factors including thermal regime, turbidity, and habitat diversity could be mediating competitive interactions. However, these factors are interrelated with flow regime and could act synergistically during low flows.

Non-native fishes have the ability to partition resources and habitat space as well, which could be allowing for co-utilization of habitats (Werner & Hall 1979). Jackson and Britton (2014) found that niche partitioning was utilized to avoid the overlap in trophic space between multiple invading species. Thus, the presence of multiple invading species plays a role in determining the trophic niche space of each individual invader. The Cliff-Gila Valley consistently has a non-native component of the fish assemblage (Propst *et al.* 2008), but non-natives don't appear to be partitioning niche space in all years of analysis. In 1983, the centroids of Red shiner, Fathead minnow, Western mosquito fish, and Yellow bullhead were not significantly different in isotopic space location (Fig. 15, Table 8). However, in 1985, Red shiner and large bodied non-natives have significantly different centroid locations (Table 10), but many of the non-natives sampled in 1983 were not available in the 1985 sample. The number of non-native species likely impacts how the food web is impacted (i.e., Walsworth *et al.* 2013). In 1996, Red Shiner's centroid is only significantly different from 2 of the 6 other species (Table 14). Non-native fishes may be partitioning resources at times to avoid competition, but frequently overlap with other non-natives and with natives.

Predation on natives by non-natives is another factor that could reduce abundance and diversity of native species. Walsworth *et al.* (2013) found that three non-native fishes in the San Rafael River (channel catfish, black bullhead, and green sunfish) all had trophic positions indicating at least partial piscivory. The Cliff-Gila valley maintains populations of large-bodied piscivores, including Channel Catfish, Yellow Bullhead Catfish, Green Sunfish, and other Centrarchids (Propst *et al.* 2008). Increased productivity of flathead catfish and common carp were strongly associated with decreased native fish productivity in canyon bound reaches of the Gila River (Whitney *et al.* 2014). When 'drought' conditions concentrate fishes in refuge habitat, predators can exert greater influence on abundance and interactions by consuming prey (direct effects) or altering the behaviors of prey (indirect effects). In refugia cover is sparse and predator avoidance can cause prey species to experience resource use changes (Magoulick & Kobza 2003). As fish resource use is altered by the presence of novel predators in limited habitats during drought, a decrease in energy intake can lead to less favorable growth patterns or decreased fitness, and ultimately smaller populations (Quinn & Peterson 1996; Mills *et al.* 2004; Davey *et al.* 2006; Walsworth *et al.* 2013). In the Middle Fork of the Gila River, non-native predators were observed to have almost eliminated native fishes, in only a few years, likely confounded by the stress on the native fishes due to drought conditions (Propst *et al.* 2008).

Assumptions and Considerations

I chose the Cliff-Gila valley reach of the Gila River as my study site because it met some key assumptions and parameters necessary to compare data from many years. From 1988 to 2006, Propst et al (2008) found that fish assemblage composition at

Riverside was stable. Within the 6 study sites throughout the Gila basin, the Riverside site was the only site at which no native fish species experienced an overall decline. However, a greater number of non-native species were collected at Riverside than any other side in the Gila Basin. Having a stable fish assemblage and a relatively homogenous reach of the river to study allowed for the least amount of extraneous variation to be induced into the project.

Additionally, the presence of non-natives in the Cliff-Gila valley reach is well documented and had been previously assessed. The presence of non-natives in Propst *et al.* (2008) was determined by density during sampling events, whereas the proportion of non-natives calculated here is a percentage of non-natives present in the entire fish community for all sampling events in a given year. The two metrics give a slightly different picture of the presence of non-natives in the Cliff-Gila valley. Throughout the 1980s, the non-native proportion was less the 10% (Figure 6**)** except for 1983, in which the high percentage of non-natives was driven by the presence of ~1000 western mosquito fish.

Finally, in order to achieve an effective comparison of isotopic values through time, the availability of pervious isotopic work for the Cliff-Gila valley was critical. Overall, the baseline values in Pilger *et al.* (2010) showed similar distribution in isotopic values to the baseline samples collected in 2015, with few exceptions. This indicates that among years the trophic structure of the Gila River is relatively constant. The major difference in baselines between 2010 and 2015 is the $\delta^{13}C$ signature in submerged macrophytes. We would expect macrophytes and algae to both plot ~-22 to -24 ‰ in the $\delta^{13}C$ dimension due to fractionation processes of CO_2 diffusion in aquatic environments

(Finlay *et al.* 1999). However, these sources of primary production are likely plotting more similar to riparian production in the data we collected in 2015 due to the areas that they were collected from; algae production was very limited and could only be found in very shallow, riffle habitats. These types of habitats are so highly aerated that they are not limited in light isotope carbon supply by CO_2 diffusion (Finlay *et al.* 1999). Likewise, the macrophytes collected were in shallow environments and very little of their foliage was actually under the water. The trophic break down found by Pilger et al (2010) is similar to the results from 2015. Three base trophic levels are functioning in this food web. Algae, smartweed, grass, macrophytes, and trees all have $\delta^{15}N$ signatures that are low, ranging from 2.32 ± 1.29 to 6.14 ±1.07, and make up the primary production for the system. Macroinvertebrates are one trophic step up from the primary producers, with $\delta^{15}N$ signatures of 7.60 ± 1.33. The top of the food chain is made up of fishes and crayfish, with $\delta^{15}N$ signatures of 10.70 ± 1.39 and 8.12 ± 1.11.

Chapter 5 CONCLUSION

The Gila River in New Mexico is one of the few remaining unregulated rivers in the American Southwest that maintains a relatively intact native fish assemblage. Thus, it is a valuable system to study, especially before a pending diversion is implemented, and the hydrology changed toward lower flow conditions associated with regulated rivers (Gori *et al.* 2014). This analysis spans 27 years, and captures a range of flow conditions and non-native abundances in the system. My results suggest that non-natives have great potential to impose increased competitive pressures on native fishes, especially during

low-flow conditions. While these data do not prove increased competition (Newsome *et al.* 2007), this study as well as many others in lower Colorado River Basin provide substantial evidence that non-native fishes are negatively impacting native fishes (Minckley 1982; Douglas *et al.* 1994; Propst & Gido 2004; Turner & Edwards 2012). The isotopic results from this project provide additional evidence of the negative impacts of non-native species on natives. I propose that the mechanism for the displacement of natives by non-natives begins with low flow conditions, causing a reduction in habitat and food resources, increasing competition and predator effects, which ultimately leads to reduced abundances of native fishes. Human-induced low flows, by diversion, extraction, and/or climate change, could facilitate a shift from a native to a non-native dominated community over the next few decades.

The interaction between hydrologic conditions and non-native fish abundance is critical for the management and conservation of the Gila River. The Cliff-Gila Valley is the most productive, diverse, and stable (from a community composition perspective) reach of the Upper Gila River. Other areas of the Gila River that are less stable could experience more pronounced impacts of drought and non-natives, such as canyon reaches where native fish success was lowest, and non-native fishes are highly productive (Whitney *et al.* 2014). As the Gila River faces increasing threats of diversion and climate change, synergistic negative effects of drought and non-natives could significantly reduce native fish in the Gila River. Non-native removal efforts and restoration of natural flow regimes have been recognized as the main efforts needed to support native fish conservation (Propst & Gido 2004) and these results provide further evidence for the need of these measures.

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APPENDIX

Table 22. Appendix of all museum specimens sampled.

Sample ID	Species	Length	MSB	Field-Note
83-1	T. cobitis	46 SL, 57 TL	MSB 62788	DLP83-423
83-2	T. cobitis	44 SL, 52 TL	MSB 62788	DLP83-423
83-3	T. cobitis	45 SL, 53 TL	MSB 62788	DLP83-423
83-4	T. cobitis	40 SL, 50 TL	MSB 62788	DLP83-423
83-5	T. cobitis	46 SL, 55 TL	MSB 63194	DLP83-512
83-6	T. cobitis	48 SL, 60 TL	MSB 63194	DLP83-512
83-7	T. cobitis	50 SL, 59 TL	MSB 63194	DLP83-512
83-8	T. cobitis	50 SL, 60 TL	MSB 63194	DLP83-512
83-9	T. cobitis	50 SL, 61 TL	MSB 63194	DLP83-512
83-10	T. cobitis	48 SL, 59 TL	MSB 63194	DLP83-512
83-11	T. cobitis	47 SL, 57 TL	MSB 63194	DLP83-512
83-12	T. cobitis	45 SL, 55 TL	MSB 63194	DLP83-512
83-13	T. cobitis	43 SL, 53 TL	MSB 63194	DLP83-512
83-14	T. cobitis	38 SL, 46 TL	MSB 63194	DLP83-512
83-20	T. cobitis	37 SL, 45 TL	MSB 63194	DLP83-512
83-15	T. cobitis	49 SL, 58 TL	MSB 62953	DLP83-454
83-16	T. cobitis	40 SL, 50 TL	MSB 62953	DLP83-454
83-17	T. cobitis	46 SL, 54 TL	MSB 62953	DLP83-454
83-18	T. cobitis	44 SL, 54 TL	MSB 62929	DLP83-449
83-19	T. cobitis	46 SL, 55 TL	MSB 62929	DLP83-449
83-21	G. robusta	104 SL, 128 TL	MSB 63150	DLP83-505
83-22	G. robusta	106 SL, 132 TL	MSB 63150	DLP83-505
83-23	G. robusta	70 SL, 82 TL	MSB 63150	DLP83-505
83-24	G. robusta	57 SL, 70 TL	MSB 63150	DLP83-505
83-25	G. robusta	56 SL, 69 TL	MSB 63150	DLP83-505
83-26	G. robusta	54 SL, 65 TL	MSB 63150	DLP83-505
83-27	G. robusta	60 SL, 73 TL	MSB 63150	DLP83-505
83-28	G. robusta	50 SL, 61 TL	MSB 63150	DLP83-505
83-29	G. robusta	87 SL, 106 TL	MSB 62928	DLP83-449
83-30	G. robusta	78 SL, 96 TL	MSB 63245	DLP83-445
83-31	G. robusta	66 SL, 81 TL	MSB 63245	DLP83-445

83-32	G. robusta	87 SL, 105 TL	MSB 63245	DLP83-445
83-33	G. robusta	80 SL, 96 TL	MSB 63245	DLP83-445
83-34	G. robusta	87 SL, 102 TL	MSB 63245	DLP83-445
83-35	G. robusta	83 SL, 97 TL	MSB 63245	DLP83-445
83-36	G. robusta	75 SL, 88 TL	MSB 63245	DLP83-445
83-37	G. robusta	145 SL, 165 TL	MSB 63161	DLP83-506
83-38	G. robusta	50 SL, 61 TL	MSB 63161	DLP83-506
83-39	G. robusta	91 SL, 110 TL	MSB 63161	DLP83-506
83-40	G. robusta	110 SL, 135 TL	MSB 63161	DLP83-506
83-41	G. affinis	38 SL, 44 TL	MSB 74895	DLP83-449
83-42	G. affinis	35 SL, 41 TL	MSB 74895	DLP83-449
83-43	G. affinis	36 SL, 44 TL	MSB 74895	DLP83-449
83-44	G. affinis	35 SL, 43 TL	MSB 74895	DLP83-449
83-45	G. affinis	33 SL, 40 TL	MSB 62818	DLP83-428
83-46	G. affinis	35 SL, 40 TL	MSB 62818	DLP83-428
83-47	G. affinis	36 SL, 45 TL	MSB 62818	DLP83-428
83-48	G. affinis	34 SL, 40 TL	MSB 62818	DLP83-428
83-49	G. affinis	33 SL, 39 TL	MSB 62818	DLP83-428
83-50	G. affinis	39 SL, 46 TL	MSB 62908	DLP83-445
83-51	G. affinis	38 SL, 45 TL	MSB 62908	DLP83-445
83-52	G. affinis	40 SL, 47 TL	MSB 62908	DLP83-445
83-53	G. affinis	38 SL, 45 TL	MSB 62908	DLP83-445
83-54	G. affinis	39 SL, 47 TL	MSB 62908	DLP83-445
83-55	G. affinis	37 SL, 44 TL	MSB 62908	DLP83-445
83-56	G. affinis	38 SL, 45 TL	MSB 62908	DLP83-445
83-57	G. affinis	37 SL, 45 TL	MSB 62791	DLP83-423
83-58	G. affinis	34 SL, 39 TL	MSB 62791	DLP83-423
83-59	G. affinis	33 SL, 38 TL	MSB 62791	DLP83-423
83-60	G. affinis	31 SL, 37 TL	MSB 62791	DLP83-423
83-61	C. lutrensis	53 SL, 62 TL	MSB 62902	DLP83-445
83-62	C. lutrensis	55 SL, 62 TL	MSB 62902	DLP83-445
83-63	C. lutrensis	55 SL, 66 TL	MSB 62902	DLP83-445
83-64	C. lutrensis	57 SL, 66 TL	MSB 62902	DLP83-445
83-65	C. lutrensis	53 SL, 62 TL	MSB 62902	DLP83-445
83-66	C. lutrensis	48 SL, 57 TL	MSB 62902	DLP83-445
83-67	C. lutrensis	47 SL, 56 TL	MSB 62902	DLP83-445
83-68	C. lutrensis	50 SL, 61 TL	MSB 62902	DLP83-445
83-69	C. lutrensis	46 SL, 55 TL	MSB 62902	DLP83-445
83-70	C. lutrensis	43 SL, 50 TL	MSB 62902	DLP83-445

83-71	C. lutrensis	57 SL, 67 TL	MSB 62902	DLP83-445
83-72	C. lutrensis	56 SL, 65 TL	MSB 62902	DLP83-445
83-73	C. lutrensis	64 SL, 73 TL	MSB 62902	DLP83-445
83-74	C. lutrensis	55 SL, 64 TL	MSB 62902	DLP83-445
83-75	C. lutrensis	56 SL, 63 TL	MSB 62902	DLP83-445
83-76	C. lutrensis	47 SL, 56 TL	MSB 62902	DLP83-445
83-77	C. lutrensis	60 SL, 68 TL	MSB 62902	DLP83-445
83-78	C. lutrensis	55 SL, 64 TL	MSB 62902	DLP83-445
83-79	C. lutrensis	47 SL, 55 TL	MSB 62902	DLP83-445
83-80	C. lutrensis	46 SL, 56 TL	MSB 62902	DLP83-445
83-81	P. promelas	54 SL, 62 TL	MSB 62904	DLP83-445
83-82	P. promelas	52 SL, 61 TL	MSB 62904	DLP83-445
83-83	P. promelas	47 SL, 56 TL	MSB 62904	DLP83-445
83-84	P. promelas	49 SL, 57 TL	MSB 62904	DLP83-445
83-85	P. promelas	47 SL, 56 TL	MSB 62904	DLP83-445
83-86	P. promelas	40 SL, 48 TL	MSB 62904	DLP83-445
83-87	P. promelas	45 SL, 52 TL	MSB 62904	DLP83-445
83-88	P. promelas	40 SL, 48 TL	MSB 62904	DLP83-445
83-89	P. promelas	44 SL, 51 TL	MSB 62904	DLP83-445
83-90	P. promelas	49 SL, 57 TL	MSB 63152	DLP83-505
83-91	P. promelas	40 SL, 47 TL	MSB 63152	DLP83-505
83-92	P. promelas	45 SL, 51 TL	MSB 63152	DLP83-505
83-93	P. promelas	44 SL, 53 TL	MSB 63152	DLP83-505
83-94	P. promelas	42 SL, 51 TL	MSB 63152	DLP83-505
83-95	P. promelas	36 SL, 45 TL	MSB 63152	DLP83-505
83-96	P. promelas	28 SL, 35 TL	MSB 63222	DLP83-517
83-97	P. promelas	36 SL, 44 TL	MSB 63222	DLP83-517
83-98	P. promelas	40 SL, 50 TL	MSB 63222	DLP83-517
83-99	P. promelas	35 SL, 42 TL	MSB 63222	DLP83-517
83-100	P. promelas	35 SL, 43 TL	MSB 63222	DLP83-517
83-101	M. dolomieu	135 SL, 152 TL	MSB 62909	DLP83-445
83-102	M. dolomieu	148 SL, 164 TL	MSB 62909	DLP83-445
83-103	M. dolomieu	55 SL, 66 TL	MSB 62833	DLP83-432
83-104	M. dolomieu	142 SL, 159 TL	MSB 62927	DLP83-449
83-105	M. dolomieu	156 SL, 173 TL	MSB 63175	DLP83-507
83-106	C. carpio	112 SL, 145 TL	MSB 63080	DLP83-492
83-107	C. carpio	127 SL, 148 TL	MSB 63080	DLP83-492
83-108	C. carpio	164 SL, 177 TL	MSB 62927	DLP83-449
83-109	L. cyanellus	137 SL, 163 TL	MSB 62832	DLP83-432

83-110	L. cyanellus	86 SL, 106 TL	MSB 62832	DLP83-432
83-111	L. cyanellus	70 SL, 86 TL	MSB 62832	DLP83-432
83-112	L. cyanellus	74 SL, 86 TL	MSB 62832	DLP83-432
83-113	L. cyanellus	56 SL, 67 TL	MSB 62832	DLP83-432
83-114	L. cyanellus	67 SL, 80 TL	MSB 62832	DLP83-432
83-115	L. cyanellus	65 SL, 78 TL	MSB 62832	DLP83-432
83-116	L. cyanellus	80 SL, 96 TL	MSB 62832	DLP83-432
83-117	L. cyanellus	65 SL, 78 TL	MSB 62832	DLP83-432
83-118	L. cyanellus	67 SL, 82 TL	MSB 62832	DLP83-432
83-119	A. natalis	60 SL, 71 TL	MSB 62832	DLP83-432
83-120	A. natalis	91 SL, 106 TL	MSB 63172	DLP83-507
83-121	A. natalis	87 SL, 99 TL	MSB 62932	DLP83-449
83-122	A. natalis	85 SL, 95 TL	MSB 62932	DLP83-449
83-123	A. natalis	110 SL, 131 TL	MSB 62907	DLP83-445
83-124	M. fulgida	40 SL, 49 TL	MSB 63192	DLP83-512
83-125	M. fulgida	57 SL, 65 TL	MSB 63192	DLP83-512
83-126	M. fulgida	44 SL, 51 TL	MSB 63192	DLP83-512
83-127	M. fulgida	44 SL, 52 TL	MSB 63192	DLP83-512
83-128	M. fulgida	41 SL, 50 TL	MSB 63192	DLP83-512
83-129	M. fulgida	54 SL, 54 TL	MSB 63081	DLP83-492
83-130	M. fulgida	45 SL, 53 TL	MSB 63081	DLP83-492
83-131	M. fulgida	38 SL, 46 TL	MSB 63081	DLP83-492
83-132	M. fulgida	40 SL, 50 TL	MSB 63081	DLP83-492
83-133	M. fulgida	39 SL, 49 TL	MSB 63081	DLP83-492
83-134	M. fulgida	38 SL, 47 TL	MSB 63216	DLP83-516
83-135	M. fulgida	45 SL, 52 TL	MSB 63216	DLP83-516
83-136	M. fulgida	46 SL, 54 TL	MSB 63216	DLP83-516
83-137	M. fulgida	45 SL, 55 TL	MSB 63216	DLP83-516
83-138	M. fulgida	40 SL, 46 TL	MSB 63216	DLP83-516
83-139	M. fulgida	48 SL, 60 TL	MSB 63221	DLP83-517
83-140	M. fulgida	44 SL, 53 TL	MSB 63221	DLP83-517
83-141	M. fulgida	46 SL, 54 TL	MSB 63221	DLP83-517
83-142	M. fulgida	38 SL, 47 TL	MSB 63221	DLP83-517
83-143	M. fulgida	43 SL, 53 TL	MSB 63221	DLP83-517
83-144	I. punctatus	~300 ml	MSB 77374	DLP83-449
83-145	I. punctatus	~400 ml	MSB 77374	DLP83-449
83-146	I. punctatus	~200 ml	MSB 77374	DLP83-449
83-147	I. punctatus	66 SL, 78 TL	MSB 63085	DLP83-492
83-148	I. punctatus	71 SL, 84 TL	MSB 63156	DLP83-505

83-149	I. punctatus	137 SL, 167 TL	MSB 63156	DLP83-505
83-150	I. punctatus	66 SL, 83 TL	MSB 63166	DLP83-506
83-151	I. punctatus	65 SL, 78 TL	MSB 63166	DLP83-506
83-152	I. punctatus	56 SL, 70 TL	MSB 63166	DLP83-506
83-153	I. punctatus	55 SL, 73 TL	MSB 63166	DLP83-506
83-154	I. punctatus	56 SL, 70 TL	MSB 63166	DLP83-506
83-155	I. punctatus	57 SL, 70 TL	MSB 63166	DLP83-506
83-156	I. punctatus	60 SL, 70 TL	MSB 63166	DLP83-506
83-157	I. punctatus	70 SL, 82 TL	MSB 63166	DLP83-506
83-158	I. punctatus	67 SL, 80 TL	MSB 63166	DLP83-506
83-159	I. punctatus	64 SL, 76 TL	MSB 63166	DLP83-506
83-160	I. punctatus	55 SL, 68 TL	MSB 63166	DLP83-506
83-161	I. punctatus	56 SL, 69 TL	MSB 63166	DLP83-506
83-162	I. punctatus	57 SL, 68 TL	MSB 63166	DLP83-506
83-163	I. punctatus	57 SL, 70 TL	MSB 63166	DLP83-506
83-164	A. natalis	65 SL, 76 TL	MSB 63020	DLP83-474
83-165	A. natalis	160 SL, 190 TL	MSB 63239	DLP83-520
83-166	A. chrysogaster	56 SL, 65 TL	MSB 63220	DLP83-517
83-167	A. chrysogaster	54 SL, 65 TL	MSB 63220	DLP83-517
83-168	A. chrysogaster	50 SL, 58 TL	MSB 63220	DLP83-517
83-169	A. chrysogaster	49 SL, 58 TL	MSB 63220	DLP83-517
83-170	A. chrysogaster	45 SL, 55 TL	MSB 63220	DLP83-517
83-171	A. chrysogaster	47 SL, 56 TL	MSB 63190	DLP83-512
83-172	A. chrysogaster	47 SL, 56 TL	MSB 63190	DLP83-512
83-173	A. chrysogaster	48 SL, 55 TL	MSB 63190	DLP83-512
83-174	A. chrysogaster	43 SL, 52 TL	MSB 63190	DLP83-512
83-175	A. chrysogaster	44 SL, 51 TL	MSB 63190	DLP83-512
83-176	A. chrysogaster	50 SL, 60 TL	MSB 63231	DLP83-519
83-177	A. chrysogaster	48 SL, 57 TL	MSB 63231	DLP83-519
83-178	A. chrysogaster	45 SL, 54 TL	MSB 63231	DLP83-519
83-179	A. chrysogaster	44 SL, 55 TL	MSB 63231	DLP83-519
83-180	A. chrysogaster	44 SL, 55 TL	MSB 63231	DLP83-519
83-181	A. chrysogaster	48 SL, 56 TL	MSB 63079	DLP83-492
83-182	A. chrysogaster	57 SL, 68 TL	MSB 63079	DLP83-492
83-183	A. chrysogaster	46 SL, 55 TL	MSB 63079	DLP83-492
83-184	A. chrysogaster	46 SL, 55 TL	MSB 63079	DLP83-492
83-185	A. chrysogaster	41 SL, 50 TL	MSB 63079	DLP83-492
83-186	C. insignis	121 SL, 140 TL	MSB 62931	DLP83-449
83-187	C. insignis	94 SL, 110 TL	MSB 62931	DLP83-449

83-188	C. insignis	80 SL, 91 TL	MSB 62931	DLP83-449
83-189	C. insignis	109 SL, 124 TL	MSB 62931	DLP83-449
83-190	C. insignis	76 SL, 89 TL	MSB 62931	DLP83-449
83-191	C. insignis	75 SL, 87 TL	MSB 63084	DLP83-492
83-192	C. insignis	58 SL, 66 TL	MSB 63084	DLP83-492
83-193	C. insignis	75 SL, 90 TL	MSB 63084	DLP83-492
83-194	C. insignis	63 SL, 74 TL	MSB 63084	DLP83-492
83-195	C. insignis	67 SL, 82 TL	MSB 63084	DLP83-492
83-196	C. insignis	92 SL, 106 TL	MSB 62817	DLP83-428
83-197	C. insignis	65 SL, 76 TL	MSB 62817	DLP83-429
83-198	C. insignis	66 SL, 77 TL	MSB 62817	DLP83-430
83-199	C. insignis	59 SL, 70 TL	MSB 62817	DLP83-431
83-200	C. insignis	54 SL, 65 TL	MSB 62817	DLP83-432
83-201	C. insignis	142 SL, 158 TL	MSB 63019	DLP83-474
83-202	C. insignis	59 SL, 70 TL	MSB 63019	DLP83-474
83-203	C. insignis	104 SL, 119 TL	MSB 63019	DLP83-474
83-204	C. insignis	46 SL, 60 TL	MSB 63019	DLP83-474
83-205	C. insignis	63 SL, 73 TL	MSB 63019	DLP83-474
83-206	P. clarkii	119 SL, 132 TL	MSB 63153	DLP83-505
83-207	P. clarkii	46 SL, 54 TL	MSB 63153	DLP83-505
83-208	P. clarkii	61 SL, 72 TL	MSB 63153	DLP83-505
83-209	P. clarkii	52 SL, 60 TL	MSB 63153	DLP83-505
83-210	P. clarkii	55 SL, 64 TL	MSB 63153	DLP83-505
83-211	P. clarkii	116 SL, 128 TL	MSB 62930	DLP83-449
83-212	P. clarkii	75 SL, 87 TL	MSB 62930	DLP83-449
83-213	P. clarkii	80 SL, 93 TL	MSB 62930	DLP83-449
83-214	P. clarkii	89 SL, 103 TL	MSB 62930	DLP83-449
83-215	P. clarkii	73 SL, 81 TL	MSB 62930	DLP83-449
83-216	P. clarkii	66 SL, 75 TL	MSB 63195	DLP83-512
83-217	P. clarkii	61 SL, 68 TL	MSB 63195	DLP83-512
83-218	P. clarkii	65 SL, 76 TL	MSB 63195	DLP83-512
83-219	P. clarkii	45 SL, 53 TL	MSB 63195	DLP83-512
83-220	P. clarkii	68 SL, 80 TL	MSB 63195	DLP83-512
83-221	P. clarkii	59 SL, 69 TL	MSB 63083	DLP83-492
83-222	P. clarkii	40 SL, 46 TL	MSB 63083	DLP83-492
83-223	P. clarkii	67 SL, 76 TL	MSB 63083	DLP83-492
83-224	P. clarkii	45 SL, 53 TL	MSB 63083	DLP83-492
83-225	P. clarkii	49 SL, 58 TL	MSB 63083	DLP83-492
85-1	C. insignis	59 SL, 68 TL	MSB 73468	DLP85-736

85-2	C. insignis	52 SL, 60 TL	MSB 73468	DLP85-736
85-3	C. insignis	63 SL, 74 TL	MSB 73468	DLP85-736
85-4	C. insignis	61 SL, 73 TL	MSB 73468	DLP85-736
85-5	C. insignis	68 SL, 77 TL	MSB 73468	DLP85-736
85-6	C. insignis	75 SL, 87 TL	MSB 73468	DLP85-736
85-7	C. insignis	74 SL, 86 TL	MSB 73468	DLP85-736
85-8	C. insignis	78 SL, 87 TL	MSB 73468	DLP85-736
85-9	C. insignis	76 SL, 87 TL	MSB 73468	DLP85-736
85-10	C. insignis	36 SL, 45 TL	MSB 73482	DLP85-759
85-11	C. insignis	37 SL, 46 TL	MSB 73482	DLP85-759
85-12	C. insignis	35 SL, 45 TL	MSB 73482	DLP85-759
85-13	C. insignis	36 SL, 44 TL	MSB 73482	DLP85-759
85-14	C. insignis	36 SL, 45 TL	MSB 73482	DLP85-759
85-15	C. insignis	41 SL, 49 TL	MSB 73482	DLP85-759
85-16	C. insignis	36 SL, 44 TL	MSB 73482	DLP85-759
85-17	C. insignis	36 SL, 45 TL	MSB 73482	DLP85-759
85-18	C. insignis	38 SL, 47 TL	MSB 73482	DLP85-759
85-19	C. insignis	35 SL, 44 TL	MSB 73482	DLP85-759
85-20	C. insignis	38 SL, 47 TL	MSB 73482	DLP85-759
85-21	P. clarkii	42 SL, 47 TL	MSB 73467	DLP85-736
85-22	P. clarkii	43 SL, 52 TL	MSB 73468	DLP85-736
85-23	P. clarkii	53 SL, 61 TL	MSB 73469	DLP85-736
85-24	P. clarkii	51 SL, 58 TL	MSB 73470	DLP85-736
85-25	P. clarkii	63 SL, 70 TL	MSB 73471	DLP85-736
85-26	P. clarkii	48 SL, 55 TL	MSB 73472	DLP85-736
85-27	P. clarkii	55 SL, 64 TL	MSB 73473	DLP85-736
85-28	P. clarkii	66 SL, 74 TL	MSB 73474	DLP85-736
85-29	P. clarkii	67 SL, 75 TL	MSB 73475	DLP85-736
85-30	P. clarkii	61 SL, 72 TL	MSB 73476	DLP85-736
85-31	P. clarkii	61 SL, 69 TL	MSB 73477	DLP85-736
85-32	P. clarkii	77 SL, 86 TL	MSB 73481	DLP85-759
85-33	P. clarkii	41 SL, 47 TL	MSB 73481	DLP85-759
85-34	P. clarkii	38 SL, 45 TL	MSB 73481	DLP85-759
85-35	P. clarkii	46 SL, 55 TL	MSB 73529	DLP85-788
85-36	P. clarkii	49 SL, 58 TL	MSB 73529	DLP85-788
85-37	P. clarkii	56 SL, 65 TL	MSB 73529	DLP85-788
85-38	P. clarkii	42 SL, 50 TL	MSB 73529	DLP85-788
85-39	P. clarkii	54 SL, 64 TL	MSB 73529	DLP85-788
85-40	P. clarkii	46 SL, 55 TL	MSB 73529	DLP85-788

85-41	T. cobitis	45 SL, 56 TL	MSB 73466	DLP85-736
85-42	T. cobitis	43 SL, 50 TL	MSB 73466	DLP85-736
85-43	T. cobitis	40 SL, 49 TL	MSB 73466	DLP85-736
85-44	T. cobitis	44 SL, 55 TL	MSB 73466	DLP85-736
85-45	T. cobitis	37 SL, 46 TL	MSB 73466	DLP85-736
85-46	T. cobitis	47 SL, 56 TL	MSB 73466	DLP85-736
85-47	T. cobitis	40 SL, 47 TL	MSB 73466	DLP85-736
85-48	T. cobitis	38 SL, 48 TL	MSB 73466	DLP85-736
85-49	T. cobitis	40 SL, 49 TL	MSB 73466	DLP85-736
85-50	T. cobitis	45 SL, 53 TL	MSB 73466	DLP85-736
85-51	T. cobitis	40 SL, 49 TL	MSB 73466	DLP85-736
85-52	T. cobitis	46 SL, 54 TL	MSB 73466	DLP85-736
85-53	T. cobitis	40 SL, 47 TL	MSB 73466	DLP85-736
85-54	T. cobitis	38 SL, 46 TL	MSB 73466	DLP85-736
85-55	T. cobitis	45 SL, 52 TL	MSB 73466	DLP85-736
85-56	T. cobitis	50 SL, 60 TL	MSB 73466	DLP85-736
85-57	T. cobitis	35 SL, 44 TL	MSB 73466	DLP85-736
85-58	T. cobitis	37 SL, 46 TL	MSB 73466	DLP85-736
85-59	T. cobitis	41 SL, 50 TL	MSB 73466	DLP85-736
85-60	T. cobitis	37 SL, 42 TL	MSB 73466	DLP85-736
85-61	M. fulgida	39 SL, 43 TL	MSB 73465	DLP85-736
85-62	M. fulgida	42 SL, 51 TL	MSB 73465	DLP85-736
85-63	M. fulgida	41 SL, 48 TL	MSB 73465	DLP85-736
85-64	M. fulgida	39 SL, 49 TL	MSB 73465	DLP85-736
85-65	M. fulgida	44 SL, 52 TL	MSB 73465	DLP85-736
85-66	M. fulgida	42 SL, 50 TL	MSB 73465	DLP85-736
85-67	M. fulgida	41 SL, 48 TL	MSB 73465	DLP85-736
85-68	M. fulgida	41 SL, 48 TL	MSB 73465	DLP85-736
85-69	M. fulgida	43 SL, 50 TL	MSB 73465	DLP85-736
85-70	M. fulgida	44 SL, 52 TL	MSB 73465	DLP85-736
85-71	M. fulgida	42 SL, 50 TL	MSB 73465	DLP85-736
85-72	M. fulgida	41 SL, 51 TL	MSB 73465	DLP85-736
85-73	M. fulgida	54 SL, 67 TL	MSB 73465	DLP85-736
85-74	M. fulgida	38 SL, 46 TL	MSB 73465	DLP85-736
85-75	M. fulgida	45 SL, 54 TL	MSB 73465	DLP85-736
85-76	M. fulgida	40 SL, 50 TL	MSB 73465	DLP85-736
85-77	M. fulgida	41 SL, 52 TL	MSB 73465	DLP85-736
85-78	M. fulgida	45 SL, 54 TL	MSB 73465	DLP85-736
85-79	M. fulgida	38 SL, 45 TL	MSB 73465	DLP85-736

85-80	M. fulgida	39 SL, 46 TL	MSB 73465	DLP85-736
85-81	A. chrysogaster	45 SL, 54 TL	MSB 73566	DLP85-796
85-82	A. chrysogaster	49 SL, 60 TL	MSB 73566	DLP85-796
85-83	A. chrysogaster	59 SL, 70 TL	MSB 73566	DLP85-796
85-84	A. chrysogaster	54 SL, 69 TL	MSB 73566	DLP85-796
85-85	A. chrysogaster	45 SL, 55 TL	MSB 73566	DLP85-796
85-86	A. chrysogaster	44 SL, 51 TL	MSB 73566	DLP85-796
85-87	A. chrysogaster	43 SL, 51 TL	MSB 73566	DLP85-796
85-88	A. chrysogaster	53 SL, 61 TL	MSB 73566	DLP85-796
85-89	A. chrysogaster	40 SL, 50 TL	MSB 73566	DLP85-796
85-90	A. chrysogaster	44 SL, 54 TL	MSB 73566	DLP85-796
85-91	A. chrysogaster	55 SL, 66 TL	MSB 73566	DLP85-796
85-92	A. chrysogaster	38 SL, 46 TL	MSB 73566	DLP85-796
85-93	A. chrysogaster	40 SL, 49 TL	MSB 73566	DLP85-796
85-94	A. chrysogaster	46 SL, 55 TL	MSB 73566	DLP85-796
85-95	A. chrysogaster	64 SL, 76 TL	MSB 73566	DLP85-796
85-96	A. chrysogaster	49 SL, 59 TL	MSB 73566	DLP85-796
85-97	A. chrysogaster	47 SL, 55 TL	MSB 73566	DLP85-796
85-98	A. chrysogaster	45 SL, 54 TL	MSB 73566	DLP85-796
85-99	A. chrysogaster	48 SL, 57 TL	MSB 73566	DLP85-796
85-100	A. chrysogaster	47 SL, 56 TL	MSB 73566	DLP85-796
85-101	C. lutrensis	50 SL, 60 TL	MSB 73464	DLP85-736
85-102	C. lutrensis	39 SL, 48 TL	MSB 73464	DLP85-736
85-103	C. lutrensis	44 SL, 54 TL	MSB 73464	DLP85-736
85-104	C. lutrensis	49 SL, 58 TL	MSB 73464	DLP85-736
85-105	C. lutrensis	40 SL, 49 TL	MSB 73464	DLP85-736
85-106	C. lutrensis	41 SL, 49 TL	MSB 73464	DLP85-736
85-107	C. lutrensis	39 SL, 50 TL	MSB 73464	DLP85-736
85-108	C. lutrensis	42 SL, 53 TL	MSB 73464	DLP85-736
85-109	C. lutrensis	42 SL, 51 TL	MSB 73464	DLP85-736
85-110	C. lutrensis	41 SL, 49 TL	MSB 73464	DLP85-736
85-111	C. lutrensis	51 SL, 60 TL	MSB 73464	DLP85-736
85-112	C. lutrensis	38 SL, 47 TL	MSB 73464	DLP85-736
85-113	C. lutrensis	47 SL, 58 TL	MSB 73464	DLP85-736
85-114	C. lutrensis	41 SL, 50 TL	MSB 73464	DLP85-736
85-115	C. lutrensis	45 SL, 55 TL	MSB 73464	DLP85-736
85-116	C. lutrensis	40 SL, 49 TL	MSB 73464	DLP85-736
85-117	C. lutrensis	43 SL, 52 TL	MSB 73464	DLP85-736
85-118	C. lutrensis	40 SL, 50 TL	MSB 73464	DLP85-736

85-119	C. lutrensis	39 SL, 48 TL	MSB 73464	DLP85-736
85-120	C. lutrensis	38 SL, 47 TL	MSB 73464	DLP85-736
85-121	C. carpio	67 SL, 83 TL	MSB 73567	DLP85-796
85-122	P. olivaris	257 SL, 291 TL	MSB 73469	DLP85-736
90-1	P. insignis	53 SL, 61 TL	MSB 77114	DLP90-1826
90-2	P. insignis	60 SL, 70 TL	MSB 77114	DLP90-1826
90-3	P. insignis	50 SL, 60 TL	MSB 77114	DLP90-1826
90-4	P. insignis	56 SL, 66 TL	MSB 77114	DLP90-1826
90-5	P. insignis	62 SL, 74 TL	MSB 77114	DLP90-1826
90-6	P. insignis	60 SL, 71 TL	MSB 77114	DLP90-1826
90-7	P. insignis	55 SL, 66 TL	MSB 77114	DLP90-1826
90-8	P. insignis	54 SL, 66 TL	MSB 77114	DLP90-1826
90-9	P. insignis	47 SL, 58 TL	MSB 77114	DLP90-1826
90-10	P. insignis	40 SL, 50 TL	MSB 77114	DLP90-1826
90-11	P. insignis	51 SL, 62 TL	MSB 77092	DLP90-1728
90-12	P. insignis	63 SL, 72 TL	MSB 77092	DLP90-1728
90-13	P. insignis	43 SL, 54 TL	MSB 77092	DLP90-1728
90-14	P. insignis	67 SL, 76 TL	MSB 77092	DLP90-1728
90-15	P. insignis	52 SL, 62 TL	MSB 77092	DLP90-1728
90-16	P. insignis	48 SL, 57 TL	MSB 77092	DLP90-1728
90-17	P. insignis	50 SL, 61 TL	MSB 77092	DLP90-1728
90-18	P. insignis	53 SL, 63 TL	MSB 77092	DLP90-1728
90-19	P. insignis	58 SL, 71 TL	MSB 77092	DLP90-1728
90-20	P. insignis	47 SL, 58 TL	MSB 77092	DLP90-1728
90-21	P. clarkii	66 SL, 74 TL	MSB 77109	DLP90-1825
90-22	P. clarkii	62 SL, 70 TL	MSB 77109	DLP90-1825
90-23	P. clarkii	44 SL, 53 TL	MSB 77109	DLP90-1825
90-24	P. clarkii	47 SL, 55 TL	MSB 77109	DLP90-1825
90-25	P. clarkii	59 SL, 68 TL	MSB 77109	DLP90-1825
90-26	P. clarkii	55 SL, 66 TL	MSB 77109	DLP90-1825
90-27	P. clarkii	46 SL, 55 TL	MSB 77109	DLP90-1825
90-28	P. clarkii	50 SL, 57 TL	MSB 77109	DLP90-1825
90-29	P. clarkii	51 SL, 60 TL	MSB 77109	DLP90-1825
90-30	P. clarkii	47 SL, 55 TL	MSB 77109	DLP90-1825
90-31	P. clarkii	103 SL, 120 TL	MSB 77113	DLP90-1826
90-32	P. clarkii	74 SL, 86 TL	MSB 77113	DLP90-1826
90-33	P. clarkii	77 SL, 94 TL	MSB 77113	DLP90-1826
90-34	P. clarkii	117 SL, 133 TL	MSB 77113	DLP90-1826
90-35	P. clarkii	64 SL, 75 TL	MSB 77113	DLP90-1826

90-36	P. clarkii	48 SL, 60 TL	MSB 77113	DLP90-1826
90-37	P. clarkii	51 SL, 61 TL	MSB 77113	DLP90-1826
90-38	P. clarkii	54 SL, 66 TL	MSB 77113	DLP90-1826
90-39	P. clarkii	54 SL, 61 TL	MSB 77113	DLP90-1826
90-40	P. clarkii	46 SL, 55 TL	MSB 77113	DLP90-1826
90-41	M. fulgida	57 SL, 66 TL	MSB 77107	DLP90-1825
90-42	M. fulgida	52 SL, 60 TL	MSB 77107	DLP90-1825
90-43	M. fulgida	52 SL, 60 TL	MSB 77107	DLP90-1825
90-44	M. fulgida	52 SL, 60 TL	MSB 77089	DLP90-1728
90-45	M. fulgida	54 SL, 60 TL	MSB 77089	DLP90-1728
90-46	M. fulgida	55 SL, 64 TL	MSB 77089	DLP90-1728
90-47	M. fulgida	50 SL, 59 TL	MSB 77089	DLP90-1728
90-48	M. fulgida	50 SL, 59 TL	MSB 77089	DLP90-1728
90-49	M. fulgida	51 SL, 60 TL	MSB 77089	DLP90-1728
90-50	M. fulgida	47 SL, 56 TL	MSB 77089	DLP90-1728
90-51	M. fulgida	51 SL, 62 TL	MSB 77089	DLP90-1728
90-52	M. fulgida	46 SL, 54 TL	MSB 77089	DLP90-1728
90-53	M. fulgida	50 SL, 57 TL	MSB 77089	DLP90-1728
90-54	M. fulgida	48 SL, 55 TL	MSB 77089	DLP90-1728
90-55	M. fulgida	51 SL, 59 TL	MSB 77089	DLP90-1728
90-56	M. fulgida	46 SL, 55 TL	MSB 77089	DLP90-1728
90-57	M. fulgida	49 SL, 59 TL	MSB 77089	DLP90-1728
90-58	M. fulgida	53 SL, 61 TL	MSB 77089	DLP90-1728
90-59	M. fulgida	50 SL, 57 TL	MSB 77089	DLP90-1728
90-60	M. fulgida	52 SL, 61 TL	MSB 77089	DLP90-1728
90-61	T. cobitis	50 SL, 60 TL	MSB 77153	DLP90-1826
90-62	T. cobitis	47 SL, 56 TL	MSB 77153	DLP90-1826
90-63	T. cobitis	45 SL, 56 TL	MSB 77153	DLP90-1826
90-64	T. cobitis	44 SL, 51 TL	MSB 77153	DLP90-1826
90-65	T. cobitis	46 SL, 53 TL	MSB 77153	DLP90-1826
90-66	T. cobitis	46 SL, 54 TL	MSB 77153	DLP90-1826
90-67	T. cobitis	45 SL, 52 TL	MSB 77153	DLP90-1826
90-68	T. cobitis	44 SL, 52 TL	MSB 77153	DLP90-1826
90-69	T. cobitis	50 SL, 59 TL	MSB 77153	DLP90-1826
90-70	T. cobitis	44 SL, 52 TL	MSB 77153	DLP90-1826
90-71	T. cobitis	51 SL, 57 TL	MSB 77108	DLP90-1825
90-72	T. cobitis	46 SL, 52 TL	MSB 77108	DLP90-1825
90-73	T. cobitis	51 SL, 58 TL	MSB 77108	DLP90-1825
90-74	T. cobitis	37 SL, 44 TL	MSB 77108	DLP90-1825

90-75	T. cobitis	47 SL, 56 TL	MSB 77108	DLP90-1825
90-76	T. cobitis	46 SL, 54 TL	MSB 77108	DLP90-1825
90-77	T. cobitis	50 SL, 58 TL	MSB 77108	DLP90-1825
90-78	T. cobitis	55 SL, 64 TL	MSB 77108	DLP90-1825
90-79	T. cobitis	47 SL, 53 TL	MSB 77108	DLP90-1825
90-80	T. cobitis	48 SL, 56 TL	MSB 77108	DLP90-1825
90-81	M.salmoides	55 SL, 66 TL	MSB 77110	DLP90-1825
90-82	A. chrysogaster	38 SL, 46 TL	MSB 77106	DLP90-1825
90-83	A. chrysogaster	35 SL, 45 TL	MSB 77106	DLP90-1825
90-84	A. chrysogaster	37 SL, 45 TL	MSB 77106	DLP90-1825
90-85	A. chrysogaster	36 SL, 44 TL	MSB 77106	DLP90-1825
90-86	A. chrysogaster	34 SL, 43 TL	MSB 77106	DLP90-1825
90-87	A. chrysogaster	40 SL, 47 TL	MSB 77106	DLP90-1825
90-88	A. chrysogaster	39 SL, 47 TL	MSB 77106	DLP90-1825
90-89	A. chrysogaster	64 SL, 76 TL	MSB 77088	DLP90-1728
90-90	A. chrysogaster	62 SL, 71 TL	MSB 77088	DLP90-1728
90-91	A. chrysogaster	55 SL, 66 TL	MSB 77088	DLP90-1728
90-92	A. chrysogaster	63 SL, 72 TL	MSB 77088	DLP90-1728
90-93	A. chrysogaster	62 SL, 73 TL	MSB 77088	DLP90-1728
90-94	A. chrysogaster	58 SL, 67 TL	MSB 77088	DLP90-1728
90-95	A. chrysogaster	57 SL, 66 TL	MSB 77088	DLP90-1728
90-96	A. chrysogaster	59 SL, 66 TL	MSB 77088	DLP90-1728
90-97	A. chrysogaster	60 SL, 67 TL	MSB 77088	DLP90-1728
90-98	A. chrysogaster	59 SL, 70 TL	MSB 77088	DLP90-1728
90-99	A. chrysogaster	61 SL, 70 TL	MSB 77088	DLP90-1728
90-100	A. chrysogaster	55 SL, 67 TL	MSB 77088	DLP90-1728
90-101	A. chrysogaster	63 SL, 75 TL	MSB 77088	DLP90-1728
96-1	P. clarkii	44 SL, 54 TL	Coll. #30	N/A
96-2	P. clarkii	43 SL, 55 TL	Coll. #30	N/A
96-3	P. clarkii	38 SL, 46 TL	Coll. #30	N/A
96-4	P. clarkii	34 SL, 41 TL	Coll. #30	N/A
96-5	P. clarkii	71 SL, 83 TL	Coll. #26b	N/A
96-6	C. insignis	45 SL, 53 TL	Coll. #26b	N/A
96-7	C. insignis	42 SL, 50 TL	Coll. #26b	N/A
96-8	C. insignis	44 SL, 51 TL	Coll. #26b	N/A
96-9	C. insignis	41 SL, 49 TL	Coll. #26b	N/A
96-10	C. insignis	41 SL, 48 TL	Coll. #26b	N/A
96-11	C. insignis	40 SL, 47 TL	Coll. #26b	N/A
96-12	C. insignis	39 SL, 46 TL	Coll. #26b	N/A

96-13	C. insignis	39 SL, 47 TL	Coll. #26b	N/A
96-14	C. insignis	40 SL, 47 TL	Coll. #26b	N/A
96-15	C. insignis	39 SL, 46 TL	Coll. #26b	N/A
96-16	C. insignis	41 SL, 49 TL	Coll. #28	N/A
96-17	C. insignis	41 SL, 49 TL	Coll. #28	N/A
96-18	C. insignis	40 SL, 47 TL	Coll. #28	N/A
96-19	C. insignis	37 SL, 45 TL	Coll. #28	N/A
96-20	C. insignis	37 SL, 47 TL	Coll. #28	N/A
96-21	C. insignis	37 SL, 44 TL	Coll. #28	N/A
96-22	C. insignis	35 SL, 43 TL	Coll. #28	N/A
96-23	C. insignis	36 SL, 46 TL	Coll. #28	N/A
96-24	C. insignis	34 SL, 42 TL	Coll. #28	N/A
96-25	C. insignis	35 SL, 43 TL	Coll. #28	N/A
96-26	C. insignis	76 SL, 93 TL	Coll. #30	N/A
96-27	G. affinis	34 SL, 40 TL	Coll. #30	N/A
96-28	G. affinis	29 SL, 33 TL	Coll. #30	N/A
96-29	G. affinis	27 SL, 32 TL	Coll. #30	N/A
96-30	G. affinis	27 SL, 31 TL	Coll. #30	N/A
96-31	G. affinis	23 SL, 28 TL	Coll. #30	N/A
96-32	G. affinis	22 SL, 27 TL	Coll. #30	N/A
96-33	G. affinis	23 SL, 27 TL	Coll. #30	N/A
96-34	G. affinis	22 SL, 26 TL	Coll. #30	N/A
96-35	L. cyanellus	59 SL, 71 TL	Coll. #30	N/A
96-36	M. fulgida	43 SL, 52 TL	Coll. #26b	N/A
96-37	M. fulgida	41 SL, 48 TL	Coll. #26b	N/A
96-38	M. fulgida	40 SL, 50 TL	Coll. #32	N/A
96-39	C. carpio	103 SL, 130 TL	Coll. #30	N/A
96-40	C. carpio	43 SL, 54 TL	Coll. #26b	N/A
96-41	C. carpio	33 SL, 43 TL	Coll. #26b	N/A
96-42	C. lutrensis	46 SL, 57 TL	Coll. #28	N/A
96-43	C. lutrensis	44 SL, 55 TL	Coll. #28	N/A
96-44	C. lutrensis	40 SL, 50 TL	Coll. #28	N/A
96-45	C. lutrensis	41 SL, 50 TL	Coll. #28	N/A
96-46	C. lutrensis	39 SL, 47 TL	Coll. #28	N/A
96-47	C. lutrensis	39 SL, 46 TL	Coll. #28	N/A
96-48	C. lutrensis	37 SL, 47 TL	Coll. #28	N/A
96-49	C. lutrensis	42 SL, 50 TL	Coll. #28	N/A
96-50	C. lutrensis	40 SL, 51 TL	Coll. #28	N/A
96-51	C. lutrensis	47 SL, 55 TL	Coll. #28	N/A

96-52	A. chrysogaster	59 SL, 70 TL	Coll. #28	N/A
96-53	A. chrysogaster	53 SL, 61 TL	Coll. #28	N/A
96-54	A. chrysogaster	54 SL, 65 TL	Coll. #28	N/A
96-55	A. chrysogaster	54 SL, 65 TL	Coll. #28	N/A
96-56	A. chrysogaster	49 SL, 59 TL	Coll. #28	N/A
96-57	A. chrysogaster	56 SL, 65 TL	Coll. #28	N/A
96-58	A. chrysogaster	50 SL, 59 TL	Coll. #28	N/A
96-59	A. chrysogaster	59 SL, 67 TL	Coll. #28	N/A
96-60	A. chrysogaster	52 SL, 62 TL	Coll. #28	N/A
96-61	A. chrysogaster	56 SL, 67 TL	Coll. #28	N/A
96-62	A. chrysogaster	50 SL, 60 TL	Coll. #28	N/A
96-63	A. chrysogaster	53 SL, 62 TL	Coll. #28	N/A
96-64	A. chrysogaster	53 SL, 64 TL	Coll. #28	N/A
96-65	A. chrysogaster	57 SL, 67 TL	Coll. #28	N/A
96-66	A. chrysogaster	53 SL, 62 TL	Coll. #28	N/A
96-67	A. chrysogaster	50 SL, 59 TL	Coll. #28	N/A
96-68	A. chrysogaster	52 SL, 64 TL	Coll. #28	N/A
96-69	A. chrysogaster	50 SL, 59 TL	Coll. #28	N/A
96-70	A. chrysogaster	53 SL, 63 TL	Coll. #28	N/A
96-71	A. chrysogaster	58 SL, 70 TL	Coll. #28	N/A
96-72	A. natalis	69 SL, 80 TL	MSB 77228	DLP96-4143
96-73	C. lutrensis	47 SL, 56 TL	MSB 77227	DLP96-4143
96-74	C. lutrensis	27 SL, 32 TL	MSB 77226	DLP96-4143
96-75	C. lutrensis	39 SL, 48 TL	MSB 77225	DLP96-4143