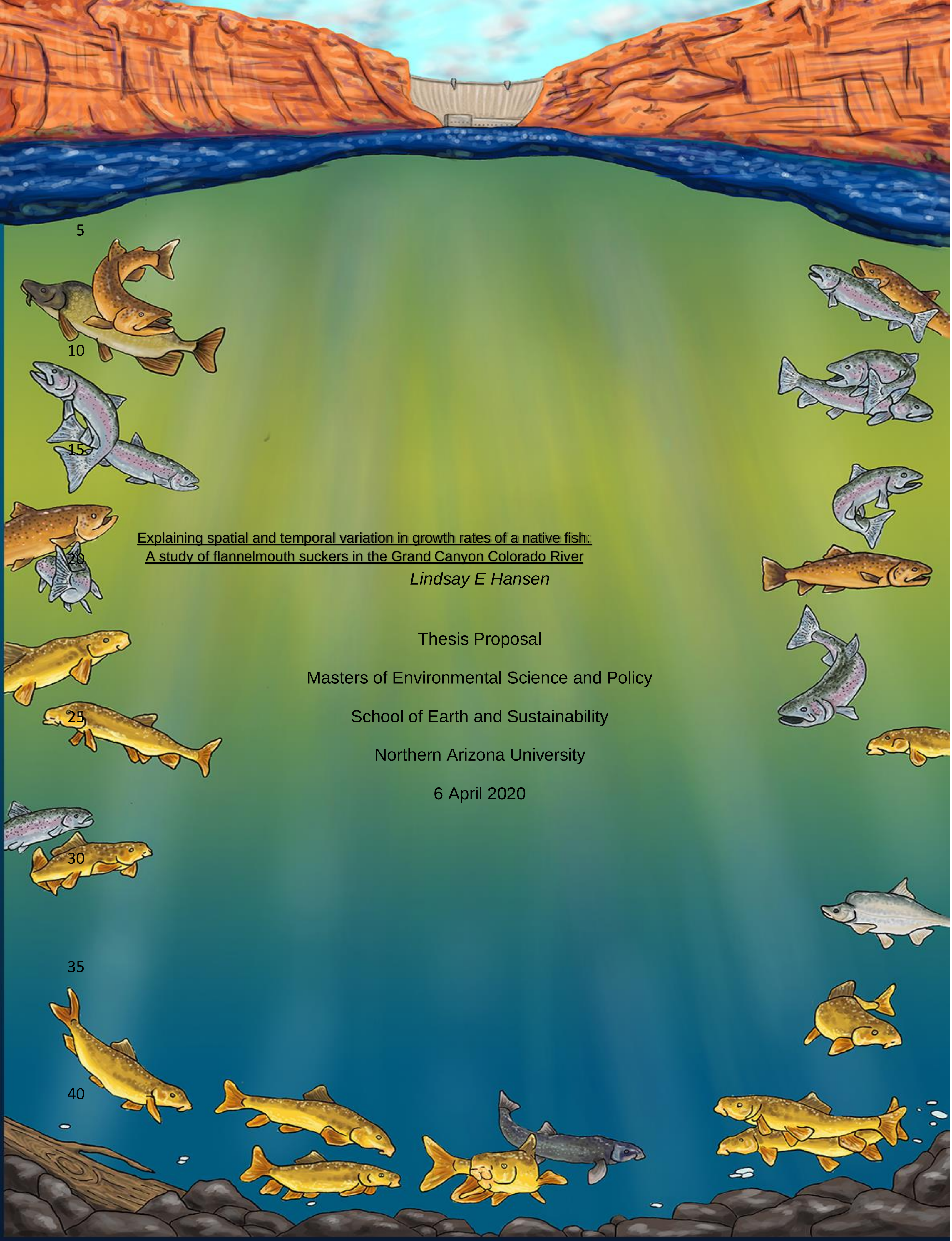

Explaining spatial and temporal variation in growth rates of a native fish: A study of flannelmouth suckers in the Grand Canyon Colorado River

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Contents

Abstract

The flannelmouth sucker (*Catostomus latipinnis)* (hereafter FMS) is currently the most abundant native fish in the Grand Canyon reaches of the Colorado River, but because it has a higher abundance than other native fish in this river system limited research has been conducted to assess the drivers of individual growth and reproduction that might underlie its high abundance. In this study, I will determine variation of FMS growth over time (1990's-present) and space (from Glen Canyon Dam to Lake Mead), and what habitat features, including temperature, turbidity, and primary productivity, explain those trends in growth. Using a 25-year mark-recapture dataset on flannelmouth weight, length, and distribution in the Grand Canyon, I will create a model to test the impacts of habitat characteristics, including water temperature, turbidity, and primary productivity, on growth. This research is important because Catostomidae are a widely distributed but understudied family of freshwater fishes in the Colorado River Basin and determining factors leading to their increased growth may add to understanding of habitat features that may be important to other native fish in the system. Because so little is known about how FMS find ample food for survival in this food-limited ecosystem, more research is recommended in this area to uncover how and what these fish are eating to more robustly predict future change.

Introduction

The flannelmouth sucker (*Catostomus latipinnis)* is currently the most abundant native fish in the Grand Canyon reaches of the Colorado River, but during the 1990's, the population was in such low numbers that the species was on the verge of being listed on the Endangered Species Act (Makinster et al. 2010). However, beginning in the mid aughts, the species population has increased dramatically, coincident with the start of a two-decades long drought that began in 2000 (Makinster et al. 2010, Schmidt et al. 2011). No research has been published that tests the correlation between the habitat conditions created by this drought and FMS growth or abundance. Currently the FMS makes up a significant portion of the fish biomass within the Grand Canyon, but because it has such a stable population, limited research has been conducted to assess its life history.

Flannelmouth suckers in the Grand Canyon portion of the Colorado River are split from upstream populations by Glen Canyon Dam. Flow releases from the dam cause water in the river to exhibit less seasonal variability, and is colder in the summer and warmer in the winter compared to pre-dam conditions (Schmidt et al. 1998). Drought during the past 20 years has lowered the water level in Lake Powell. Due to lower water surface elevation in the reservoir, warmer surface waters are close to the elevation of the penstocks, hence warmer water is entrained into releases from GCD (Dibble *in review*). The volume of water in the reservoir determines the velocity of water releases, and thus determines the speed of the river and thermal inertia (how much water is available to be warmed). This volume paired with solar insolation, and to a lesser degree air temperature in the system, contribute to warming water within the canyon (Yard et al. 2005, Wright et al. 2009, Ward et al. 2017). Fifty to eighty percent of production comes from autochthony, although this varies depending on location in the canyon and whether tributaries are flooding (Kennedy 2013). Upstream of tributaries to the mainstem of the Colorado River (i.e. Paria, Little Colorado River), the river food chain is macrophyte dominated, but tributaries bring higher flows and an influx of a small number of allochthonous inputs, including terrestrial subsidies and detritus(Cross et al. 2011, Sabo et al. 2018). However, because the ecosystem is a desert habitat, these inputs are minimal, and the high concentration of fine sediment from tributary inflow limits autochthonous production downstream due to light attenuation (Kennedy 2013, Hall et al. 2015).

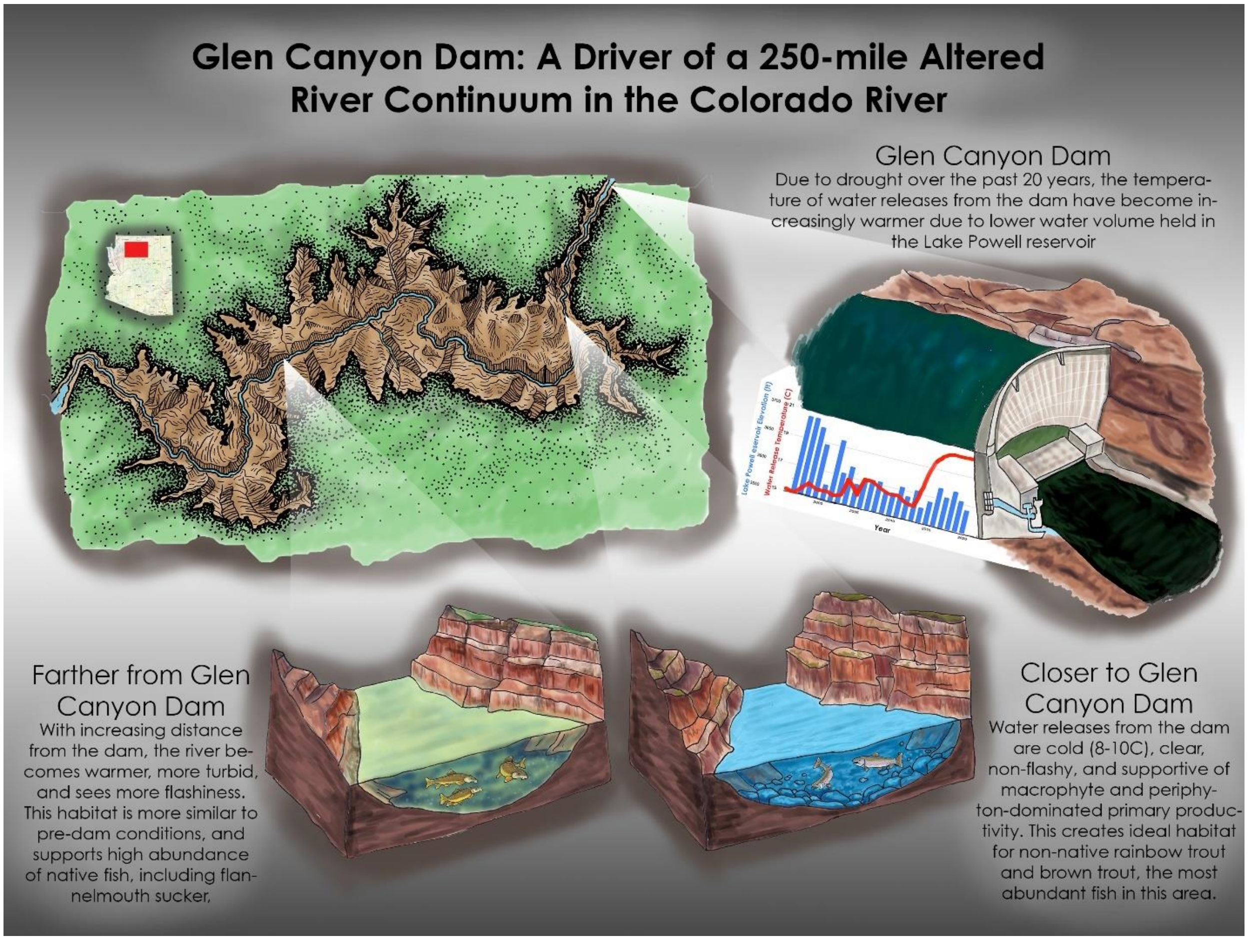


Figure 1: An illustration of the habitat continuum created by Glen Canyon dam and tributary river inputs in the Colorado River in the Grand Canyon. Tributary inputs make water warmer farther from Glen Canyon Dam, and a drought in the past 20 years has led to warming of water releases from Glen Canyon Dam, as well as warmer water inputs into the system from tributaries due to increased solar insolation, lower precipitation, and warmer air temperatures. In this proposal, I hypothesize that warmer temperatures lead to increased growth in FMS.

The large biomass of FMS is surprising given known limitations on fish growth and abundance in the Grand Canyon, including basal energy inputs (there is barely enough primary productivity to explain the secondary productivity we have observed), water temperature, altered discharge and flow (resulting from Glen Canyon Dam hydropeaking), and turbidity. A better understanding of how growth rates vary over time and space and how that variation is driven by things like temperature and resource availability could help explain trends in FMS somatic growth, fish condition and secondary production.

Research Questions/ Proposed Chapters

PROJECT GOAL: determine growth trends of FMS over time (1990's-present) and space (from Glen Canyon Dam to Lake Mead), and what habitat features, including temperature, turbidity, and primary productivity, explain those trends in growth

Chapter 1 - Growth of FMS over time and space

- H_{N1}: Growth of FMS is higher in areas of the Grand Canyon further from Glen Canyon Dam
- H_{N2}: Growth of FMS has increased coincident with the ongoing drought since 2000

Chapter 2 - Modeling explanations of FMS growth

- H_{N3}: FMS growth trends follow trends in increased water temperature as a result of drought conditions
- H_{N4}: Flannelmouth sucker condition will follow a graph of seasonal primary productivity within Grand Canyon
- H_{N5}: Growth of FMS is higher in areas of the canyon further from Glen Canyon Dam, as caused by water temperature increases and increased turbidity

Literature Review

Introduction

Freshwater fishes represent one of the most globally imperiled groups of animals and exhibit some of the highest rates of extinction (Cooke et al. 2005). In the southwestern United States, one of the threats to native fish is the combination of regulated rivers and declining flows. FMS have declined in their native range, but maintain a relatively large population in the Grand Canyon compared to other native fishes. Here, I explore habitat characteristics of the Grand Canyon Colorado River and synthesize understandings of fish growth. This literature review serves as background information to begin understanding trends in growth for FMS within the Grand Canyon over the past 30 years.

The Colorado River hosts a small richness of morphologically unique native fish species adapted for life in turbid and flood-prone water. The river drains eight percent of the continental United States and flows through eleven national parks and monuments, including the Grand Canyon (American Rivers n.d.). Although known for being iconic and remote, the Colorado River is fragmented by large hydroelectric dams, such as the Glen Canyon Dam that separates the Grand Canyon portion of the river from all upstream reaches (Schmidt et al. 1998). This limits fish movement, blocks sediments from the upper basin from reaching the Grand Canyon, and creates cold and stable water temperatures, dramatically altering natural habitat for native fish in the system.

This literature review will synthesize the current understanding of Flannelmouth Sucker biology in the Grand Canyon and impacts of dams and human uses of the Colorado River on native fish growth.

Flannelmouth Sucker Biology

Physical and taxonomic description

The flannelmouth sucker (*Catostomus latipinnis)* are bony freshwater fish of the family Catostomidae, 'suckers', that are found almost exclusively in North America (Bureau of Reclamation 2016). Like other fishes in this group, FMS have fleshy lips located on the underside of their faces, adapted for scraping food from benthic substrates, as the name 'sucker' suggests. FMS specifically are identified by lips covered in nodules, a thicker lower lip, and dark brown-green on their dorsal side and yellow or orange fading to white on their ventral size (Bureau of Reclamation 2016). FMS can live up to 30 years, and have a maximum recorded size of 700 mm (Bureau of Reclamation 2016).

Habitat, native range and distribution

FMS are the most abundant native sucker in the Colorado River (Bureau of Reclamation 2016). FMS are endemic to the Colorado River Basin, historically spanning the entire basin (Bureau of Reclamation 2016), but now occur in about half of their historic range (Bezzerides and Bestgen 2002, Dauwalter et al. 2011). FMS is a river obligate species which is most often found in deep and slow sections of swift streams and in runs of large rivers (Bureau of Reclamation 2016). These fish prefer sand and cobble substrates with overhead cover, such as undercut banks and overhanging vegetation (Bureau of Reclamation 2016). The FMS population of the Colorado River Basin has a notable lack of genetic variation likely due to a recent period of low population size toward the end of the Pleistocene epoch (Douglas et al. 2003).

FMS are mobile fish, and have been known to travel hundreds of miles upriver (Chart and Bergersen 1992). Since the completion of Glen Canyon Dam, FMS have been known to conglomerate within about 5km downstream of the dam, which is theorized to reflect a blockage of historic migration routes upstream (McKinney et al. 1999). This fish was believed to have been on the verge of extirpation in the 1970's (Mueller and Wydoski 2004), but has had a notable increase in abundance since this period, with a significantly higher abundance in river reaches further downstream from Glen Canyon Dam in comparison with reaches close to the Dam (Counihan et al. 2018). FMS abundance increases notably just downstream of the confluence of the Little Colorado River and the mainstem of the Colorado River, likely because the Little Colorado River is a major spawning ground for FMS (Douglas and Marsh 1998). This spectrum of abundance suggests that the dam has created a habitat gradient that benefits different parts of the Colorado River fish assemblage (Counihan et al. 2018).

Understanding Fish Growth

Fish growth, both in length and weight, is an important predictor of survival, reproductive capacity, and recruitment success of juvenile fish (Poff et al. 1997). Understanding growth and survival rates in fish is an important aspect of understanding fish population dynamics and is vital for preparing effective recovery and management plans for endangered, threatened, or susceptible species (Osmundson 1997). In most species, growth slows during the onset of maturity, as the fish begins investing more energy into reproduction rather than into length or weight gain (Roff 1983, Mommsen 2001). Unlike most other vertebrate taxa, however, fishes are unique in that they have indeterminate growth: the size of adult fish is never fixed, and some growth continues throughout the entire life of a fish regardless of this reapportionment of energy into reproduction, especially if habitat conditions are amenable (Mommsen 2001). Growth in many fish species is further complicated by water temperature and winter conditions. Fish condition declines as length of exposure to winter conditions increases, likely due to decreased riverine food base (Thompson et al. 1991), and humpback chub in the Colorado River do not grow in length in too-cold water temperatures (Dzul et al. 2017).

As a family, Catostomidae are among the most widespread and ecologically important families of freshwater fishes in North America, but are one of the least understood fishes in regards to factors that influence survival, reproduction, and growth (Quist and Spiegel 2012). Many Catostomid species, particularly those endemic to single river basins such as FMS, are believed to have seen significant population declines during the past two centuries (Gilbert 1993). Species of this family show a range of life-history strategies, and understanding these difference is important in evaluating susceptibility to disturbance and creating effective conservation plans (Eberhardt and Ricker 1977, Hubert and Quist 2010, Grabowski et al. 2012).

Temperature, turbidity, and primary production influences on fish growth

Flannelmouth suckers have a higher temperature tolerance, reflecting the natural variability in water temperatures seen in the pre-impoundment Colorado River (~2°C to 30°C) (Bureau of Reclamation 2016). However, warmer in-river temperatures are important for FMS survival and successful recruitment (Holden and Stalnaker 1975, Minckley 1991, Ward et al. 2002). Juveniles show reduced swimming ability in colder waters, which may make them susceptible to predation by nonnative trout, and mainstem dams and their cool tailwaters may reduce survival of FMS (Holden and Stalnaker 1975, Ward et al. 2002). Drought conditions from 2000 to today may be part of the reason for an increase in FMS abundance during the same time period. However, this hypothesis is complicated by research conducted on FMS recruitment in small streams outside of the Grand Canyon that shows a decline in juvenile survival during drought years as a result of diminished backwater nursery habitat and exogenous nutrient depletion when there are limited floodwaters that bring terrestrial subsidies into the wetted river (Douglas and Marsh 1998).

During the 1990's, the population of FMS was stable in the Grand Canyon, but this may have been due to a higher amount of long-lived adult fish, rather than a result of successful recruitment (Douglas and Marsh 1998). Low numbers of FMS and simultaneous low recruitment in the Grand Canyon during this time has been attributed to cold releases from hydroelectric dams (Weiss et al. 1998). Females are mature between ages 4-6, fecund for over two decades, and have the ability to produce large cohorts of eggs annually (3,000-30,000 eggs) (Mueller and Wydoski 2004, Bureau of Reclamation 2016). However, adults may skip multiple years of spawning at a time if physiological or environmental conditions are not conducive to procreation, such as lack of accrued fat storage, lack of suitable breeding habitat due to flow, or inaccessible tributary or backwater spawning habitat (Douglas and Marsh 1998, Mueller and Wydoski 2004, Fraser et al. 2017). Historically FMS made significant spawning migrations, but this has been altered since the completion of dam impoundments (Bureau of Reclamation 2016).

Fish in the Colorado River are unique in their wide temperature tolerance – many fish in other systems have a low lethal maximum temperature, but because the waters of the Colorado River naturally fluctuate to ~30˚C, FMS and other native fish to this river are adapted to, and perhaps reliant on, these higher temperatures for survival, reproduction, and growth. FMS optimal growth is thought to occur between 14˚C and 26˚C, and lethal temperatures are as high as 35˚C (Nevada Division of Environmental Protection 2016). Water releases from Glen Canyon Dam were fixed at a stable 10˚C until 2003, and now fluctuates between 9-15 ˚C (Ward et al. 2002, Dibble et al. 2018). Because fish are ectotherms (so-called 'cold blooded' animals), they rely on adequate water temperature in order to develop and grow (Boeuf and Le Bail 1999). Clarkson and Childs (1998) show that FMS growth rates are lower at 14˚C compared to 20˚C, based on lab experiments. In the Grand Canyon, water warms as it moves downstream from Glen Canyon Dam due to solar insolation and atmospheric heat exchange (Yard et al. 2005). FMS abundance follows a similar trend in water temperature warming with distance from Glen Canyon Dam, which may suggest warmer areas are more conducive to juvenile growth (Rogowski and Boyer 2019).

Growth influence on fish survival and reproduction

The body size of a fish determines its total reproductive output and fecundity; larger mature females produce disproportionately more eggs than smaller females (Barneche et al. 2018). As a result, fecundity generally increases as a function of body size (Wootton 1979, Roff 1983). However, there is a direct tradeoff between growth and reproduction; as a fish reaches maturity and approaches spawning season, energy will be reapportioned from increasing individual fish size to supporting gonad growth (Jones and Johnston 1977). This loss of energy to reproductive activities can reduce future fecundity, lead to post-reproductive decrease in growth rate, and in some cases can increase mortality in reproductive individuals (Hutchings et al. 1999). Bigger fish may be more fecund, but bigger fish are also more likely to lose weight if conditions are not right for maintaining that weight during winter (Hutchings et al. 1999).

For juvenile fish, the ability to grow quickly has a direct impact on survival and mortality. Those fry born earlier in the spawning season show higher survivorship (50% larger after one year) compared to later-born individuals as a result of increased access to food from being alive for more of the growing season (Cargnelli and Gross 1996). Inadequate fat storage within tissues increases mortality during winter seasons in age-0 fish (likely as a result from hypothermia), insufficient energy to evade predators, and starvation (Seelbach 1987, Cargnelli and Gross 1996). To survive the winter, fish either need to accumulate enough fats and lipids during high-productivity seasons, or be able to find enough food during the winter to offset the drain on fat stores during the colder season (Thompson et al. 1991).

Food Resources: Limitations to Fishes in the Grand Canyon

Food is the major limiting resource for all fish species in the Grand Canyon Colorado River. Within the river, there is a low amount of high quality invertebrate prey available; the invertebrate food sources that are available, midge and black fly larvae, are consumed almost to totality by fishes (Kennedy 2013). There are limited additional food sources in the Grand Canyon, both autochthonous (algae) and allochthonous (terrestrial insects, detritus), but these food sources combined are impoverished and too depauperate to support large fish biomass (Lechleitner 1992). Periods of particularly low food availability leads to substantial weight loss and poor fish condition (actual weight compared to expected weight based on average fish of that species given a certain length), which leads to slower maturation rates, lower survival, and decrease in abundance (Korman et al. 2019).

Before the construction of Glen Canyon Dam, autochthonous inputs were limited in the river due to the massive quantities of sand that moved along the river bottom, disrupting holdfasts for periphyton (Carothers 2000). High turbidity from suspended sediments blocked light penetration and disrupted phytoplankton production (Carothers 2000). Although minimal, pre-dam food bases were mostly reliant on terrestrial insect subsidies (Carothers 2000).

Dam construction brought changes to food web structure within the river. Just below Glen Canyon Dam, food webs are now dominated from the bottom-up by invasive New Zealand mudsnails and algae due to cold water temperatures and clear water that allows solar radiation to reach the substrate (Cross et al. 2013). This increase in sunlight penetration has increased primary production within the upper 75 mile reach of the river (Carothers n.d.). The most abundant fish in this part of the system is the invasive rainbow trout, which is managed at Lee's Ferry for sport fishing (Korman et al. 2015).

Food webs in the Grand Canyon shift steeply immediately downstream of the first tributary confluence with the mainstem of the river. With the input of turbid, warm water from tributaries, there is a marked increase in detritus-based food webs with an increase in omnivory and invertebrate production, but a decrease in primary production (Carothers n.d., Cross et al. 2013). The further downstream from the dam and with increasing tributary input, food webs become more complex and fish assemblages at the top of the food chain become native species-dominated (Cross et al. 2013, Sabo et al. 2018). The combination of allochthonous inputs from tributaries with local autochthony generated during periods of clear water may be alleviating some of the historic food limitation on native fishes.

Flannelmouth suckers are omnivorous and opportunistic feeders, known to consume planktonic algae, aquatic insect larvae (chironomidae, simuliidae, etc.) , terrestrial invertebrates and vegetation, and other organic and inorganic matter (Seegert et al. 2014, Bureau of Reclamation 2016). Possible intercohort cannibalism and predation by older FMS on young of year of both FMS and other fish species is suggested (Walters and Martell 2004).

On average, mature FMS grow in length ~5.5mm per year (Bureau of Reclamation 2016). Somatic growth is strongly linked with warmer water temperatures, especially for young fish; juveniles that move from the warm Little Colorado River into the cold mainstem of the Colorado River show very little growth in their first few months of life compared to their counterparts that stay in the Little Colorado River (Robinson and Childs 2001). Paukert and Rogers (2004) suggest that the mean weight of FMS was highest during pre-spawning periods, and lowest in the summer and fall, with the highest fish condition at intermediate distances from Glen Canyon Dam. These trends are believed to follow temperature trends: warmer river reaches will support larger fish, and growth of fish will follow seasonal fluctuations in water temperature (Paukert and Rogers 2004). However, this has not been proven for fish of the family Catostomidae.

River systems with higher amounts of primary productivity in the form of algae growth and terrestrial subsidies, as well as those with relatively high secondary production through ample invertebrate communities, often support fish populations that show higher rates of growth than rivers with limited production have on the same fish species (Tanentzap et al. 2014). For benthic scraping adapted catostomid species, the type of substrate often determines growth, because some species prefer aquatic invertebrates and algae that grow in silty substrates, while others specialize in consuming food sources on rockier substrates (Quist and Spiegel 2012). FMS prefer sand and fine cobble substrates, which are more common further downstream of Glen Canyon Dam as a result of tributary inputs bringing finer sediments into the river than those that pass through the dam (Bureau of Reclamation 2016).

Major Threats to Grand Canyon Fish

Beyond food limitation, native fish face two major threats: nonnative fish and habitat degradation (Campos 2005). Fish declines have been noted as early as 1900, which correlates with the start of diverting water from the river for agriculture and the introduction of non-native fish such as carp and catfish in the 1880's (Minckley 1991). However, Glen Canyon Dam is the major driver of habitat degradation, which has changed a flashy system characterized by a wide seasonal temperature variation and high turbidity into a sediment-starved cold water river (Campos 2005). The installation of dam impoundments is compounded by blockage of migration routes and changes in water temperature, flow regime, and food base that result from the collection of water and sediment in reservoirs stopped by large hydropower dams (Cooke et al. 2005). Beyond habitat degradation, fish in the Grand Canyon experience direct predation and indirect competition for resources from non-native fish invaders, and disease and parasitism from non-native vector organisms (Cooke et al. 2005, Walters et al. 2015).

Glen Canyon Dam

The Colorado River is the most prominent source of freshwater for the southwestern United States, but it is a river system characterized by flooding, drought, and impressive movement of sediment. Pre-dam flows of the Colorado river were notably flashy; between 1884 to 1963, peak discharge varied from ~25,000 cubic feet per second (cfs) to ~300,000 cfs, and fell to ~7,000 cfs during the fall and winter on average (Campos 2005). However, given the size of the basin, mean annual discharge has been relatively small compared to other river systems, both before and after dam construction (Schmidt et al. 1998). Annual pre-dam river temperature varied greatly between seasons, between 0˚C and 29˚C, but now river temperature is determined by the temperature of the reservoir, which varies with depth. Releases fluctuate between 8-15˚C depending on the elevation of the reservoir (Schmidt et al. 1998, National Parks Service 2018).

Relevant Policy and Management

Legal Status

Although not federally listed, flannelmouth sucker is sufficiently at-risk to warrant multi-state conservation agreements and are considered species of special concern (labeled imperiled and vulnerable, respectively) in Arizona by the Arizona Department of Fish and Game (Arizona Game & Fish 2019). They are included in the Lower Colorado River Multi-Species Conservation Plan due to potential of the species being listed under the ESA or CESA, or becoming protected under Nevada or Arizona law (Bureau of Reclamation 2016). Although these sucker species currently occupy less than half of their historical ranges, due to the hierarchical ranking of extinction risk they receive far fewer monitoring resources and attention than the federally endangered fishes (Dauwalter et al. 2011).

FMS is not listed as threatened or endangered, but has been given special status by non-federal agencies because it is an extremely isolated species and its habitat is declining (Rees et al. 2005). In Arizona, FMS are listed as a species of special concern by the state, and are included on the LCR MSCP due to their declining population across their native range and the resulting likelihood of being listed on the Endangered Species Act (Bureau of Reclamation 2004). As a response to low abundance of FMS and other native fish in the Grand Canyon, federal and state agencies began monitoring and restoration efforts with the explicit goal of improving fisheries success and habitat during the 1990’s (Bureau of Reclamation 2004). There are currently no FMS-specific conservation plans for FMS within the Grand Canyon.

Although Catostomid conservation in general has been limited due to a lack of ecology and life history understanding about these species, the belief that catostomids are resilient and tolerant to degraded habitat, and the lack of value as an economic or sport fishery species, there are some accepted conservation strategies that will likely lead to population stability or growth (Cooke et al. 2005). Small tributary systems are of high conservation value for FMS because they are both spawning and nursery habitat as well as areas of manageable conservation efforts where habitat protection and invasive species removal is feasible (Bower et al. 2008). In tributaries, FMS abundance is improved by increased floodplain areas and improved wetted width refugia connectivity during drought conditions, abundance of rocky substrate and submerged aquatic vegetation and algae, and a variety of habitat complexity such as pools, runs and riffles (Holden and Stalnaker 1975, Fraser et al. 2017). For FMS specifically, thermal cues indicate spawning migrations, when FMS will move from mainstem waters into tributaries (Fraser et al. 2017). Although they are rare within Grand Canyon, conserving ample refuge habitat made of large, deep pools and floodplain or backwater habitat can be important to FMS as well as other native species in the Grand Canyon (Mueller 2005, Bower et al. 2008).

Further conservation management efforts that have been proven to support abundance of native fishes beyond FMS are many. They removal or reduction of invasive fish community density can significantly increase native fish success (Mueller 2005), and the ‘field of dreams hypothesis’, that if habitat and flow is restored in a river, the appropriate organisms will recolonize and correct ecosystem functioning will resume (Fuller and Death 2018). The choice of management goals, for FMS, the Grand Canyon, and all aquatic organisms within, is a complex decision-making process that includes economics, societal values, logistics, tradition and ecosystem services, and should include specific mention of those non-human users of rivers that rely on freshwaters (Schmidt et al. 1998).

Modern river policy: water demand

The Colorado River has the most complete allocation of water of any river in the world, and is one of the most heavily regulated (US Department of the Interior 2014). A significant amount of the demand for water within the Colorado River Basin is from sources outside of the basin, notably arid agricultural areas and metropolitan areas of California and Arizona (Bureau of Reclamation 2004). The mean annual discharge at Lee's Ferry is only 505 m^3/s, which is small given the size of the basin, and is compounded by the high human demand for this water (Schmidt et al. 1998). The lower Colorado River is projected to be one of the few places in the American Southwest where surface water will remain as the globe warms, so aggressive and ongoing management and reallocation of water resources in this area is important for human livelihood as well as fish wellbeing (Minckley et al. 2003).

With climate change, water temperatures are expected to increase, which may enable the spread of invasive non-native species or diseases (Ray and Hoerling 2008). Earlier snow melts and lower precipitation as a result of climate change is expected to lower the already scarce flow, which may complicate prior appropriations of water rights and compacts (Ray and Hoerling 2008).

Current management of the Colorado River within Grand Canyon is influenced by a number of stakeholders from many management and regulatory agencies and local communities. These groups include federal agencies (US Bureau of Reclamation, National Park Service, US Fish and Wildlife Service, USGS GCMRC), power companies (Western Area Power Administration), state agencies (Arizona Game and Fish), tribes and indigenous nations (Navajo Nation, Hualapai Tribe, Hopi Tribe), agriculture, national and regional environmental groups, river running companies, trout fishing groups, and others (Schmidt et al. 1998).

Conclusion

The flannelmouth sucker is believed to have the highest abundance of any native fish in the Grand Canyon Colorado River from anecdotal findings from sampling efforts. Beginning in the mid aughts, the species population has increased dramatically, coincident with the start of a two-decades long drought. Major limitations on growth and abundance for this fish in the Grand Canyon reaches include habitat alteration from Glen Canyon Dam, including altered temperature and turbidity, as well as a naturally food-limited ecosystem. Limited research has been conducted to assess its population stability, abundance, and growth. A better understanding of how FMS growth rates respond to temperature and/or fluctuations in resource availability, and a more robust understanding of benthic productivity and prey availability, could help explain population and individual growth.

Methods and Approach

Study Area:

The study area for this research extends from Glen Canyon Dam (river mile 0) to the Colorado River confluence with Diamond Creek (mile 225). Glen Canyon Dam creates a specific nonnatural aquatic habitat in water temperature, primary productivity, and turbidity. With every tributary input to the mainstem river, temperature and turbidity increases when waters mix. For this project, data will be binned based on these tributary inputs: the river will be split into six reaches, each beginning on the downstream end at the confluence of the mainstem river with major tributaries and ending just upstream of the next closest tributary input (Figure 1).

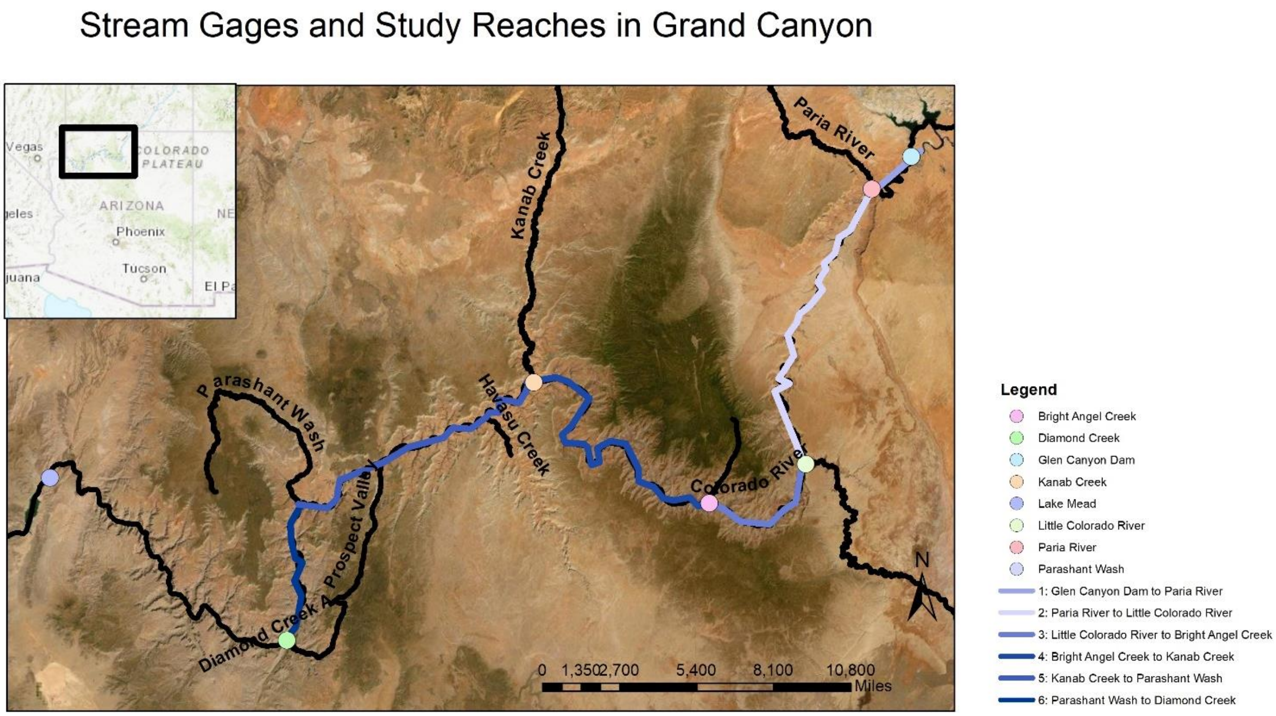


Figure 2: Study reaches and stream gages within the Grand Canyon.

Field Sampling:

Mark-recapture data used in this project was collected as a collaborative effort by USGS, Arizona Fish and Game, US Fish and Wildlife, and the National Parks Service over a 27 year period beginning in 1993. Nighttime boat electrofishing and hoop netting were used to opportunistically catch fish. Multiple downstream sampling trips were conducted per year. New FMS to the project were administered a unique PIT (passive integrated transponder) tag, weighed, lengthened, and sexed before being returned to the water. For every time a fish was recaptured, the individual’s specific tag was recorded, and the new weight and length of the fish was added to the data. Because each agency uses different methods and has different project lengths, some of the data is complicated by inaccurate weight and length measurements for FMS.

Statistical modeling:

I will calculate growth rates for FMS for each reach and year, then will use statistical models to test how growth depends on covariates. The covariates I will use are water temperature, turbidity, primary productivity (dissolved oxygen), and discharge. I will use a linear mixed-effects model to predict growth using R. The importance of the covariates used to predict growth, and the most parsimonious growth model with the best predictive power, will be determined based on parameter values, multi-level R2 statistics.

Datasets:

The following tables describe the two main datasets for this project. The first, Dataset 1, includes all FMS-specific data collected between 1993-2020 by USGS, Arizona Game and Fish, and National Parks Service Electrofishing and Hoop-Netting efforts. Dataset 2 is data collected by remote stream gages located along the mainstem of the Colorado River.

Dataset 1: FMS recapture data

Item	Datasheet Code	Data Type	Number of Datapoints	Description
Trip ID	FISH_T_SAMPLE.TRIP_ID	Categorical	77128	
Trip Start Date	FISH_T_SAMPLE.START_DATETIME	Categorical	77110	April 1990 to October 2018
River	RIVER_CODE	Categorical	LCR(19162), COR (55784), BAC 5), DRC (1), HAV (1135), KAN (805), PAR(150)	LCR – Little Colorado River COR – Colorado River BAC – Bright Angel Creek DRC – Diamond Creek HAV – Havasu Creek KAN – Kanab Creek PAR – Paria River
River Mile	START_RM	Numerical	55482	Will need to convert these values into River Kilometer
River Kilometer	START_RKM	Numerical	34393	
Species	SPECIES_CODE	Categorical	77128	All entries are FMS
Total Length (mm)	TOTAL_LENGTH	Numerical	77128	Length of fish from snout to the outermost part of the dorsal fin
Weight (grams)	WEIGHT	Numerical	28755	Total weight of the fish, in grams
PIT tag number	PITTAG	Categorial	77109	Each fish has a unique tag number that will not change

Dataset 2: Stream Gage Data

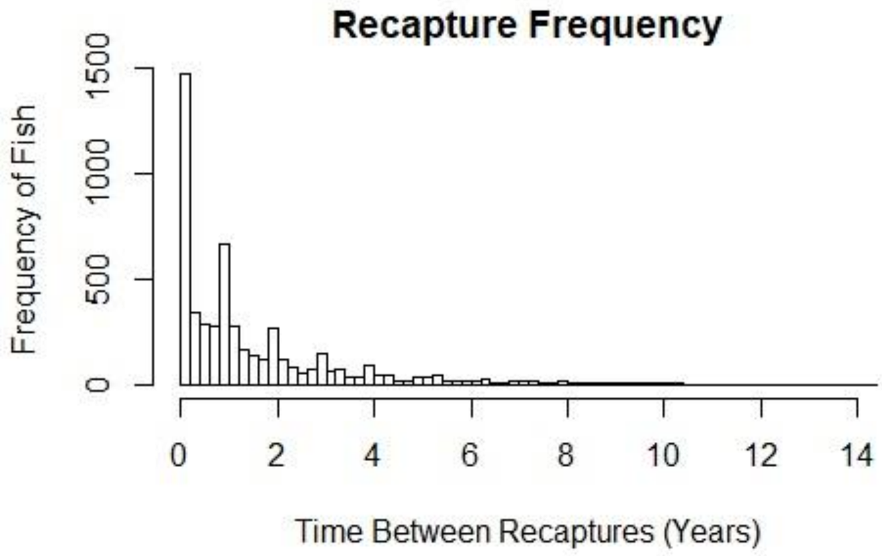
Gage Name	USGS Gage Number	River Mile	Data Type	Start Date	End Date	Notes
Lake Powell at Glen Canyon Dam	9379900	-15	Reservoir water surface elevation	2019	2020	
Mainsteam Near Lee's Ferry	9380000	0	Temperature	1986	2020	Data recorded daily - some
			Discharge	1921	2020	

			Suspended Sediment	1928	1965	dates are missing
Mainstem Near Phantom Ranch	9402500	88.1	Temperature	1983	2003	
			Discharge	1922	2020	
			Specific Conductance	1986	2003	
Mainstem near Diamond Creek	9404200	225	Temperature	1990	2007	Upstream of Diamond Creek
			Discharge	1983	2020	
			Specific Conductance	1990	2007	

Step-wise Action Plan and Preliminary Data Analysis:

<u>**Step 1**: Data organization for Dataset 1 (FMS Data)</u>

- Remove duplicate entries
    - Entries with all the same data
    - Entries with all the same data, but different trip ID numbers
- Convert river mile to kilometer. Remove data with no kilometer data.
- Remove data points caught with too little time between recaptures (not enough time interval to demonstrate fish growth).
    - **need to determine an appropriate minimum interval between recaptures
    - Use quick recaptures to constraining observation error in models.



    - **Figure 3**: This histogram shows that there is a significant number of FMS that are recaptured during the same surveying trip. These data points may not be suitable for this growth modeling, because there will not be enough time between captures for a fish's weight or length to change. Most FMS are recaught within two years of initial capture, with the highest incidence of recapture occurring within the same sampling trip. Few individuals were recaptured with up to 10 years between captures.
- Remove FMS data points captured in tributaries (for the initial analysis at least)
    - Length and weight are positively correlated, which reflects normal trends in growth: larger individuals in length weigh more than shorter individuals.

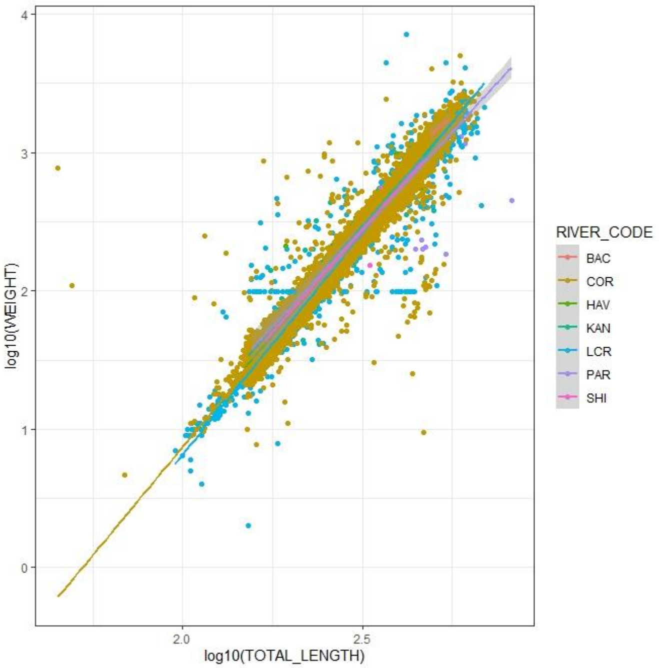


Figure 4: Plot comparing trends in fish condition based on capture in different rivers and tributaries within the Grand Canyon.

- Remove data points that represent fish that have never been recaptured (the PIT tag shows up in the dataset only once)

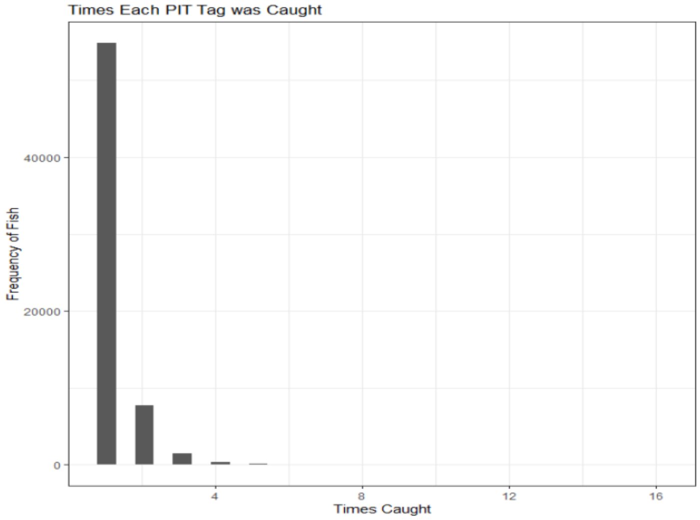


Figure 5: Most PIT tagged individual FMS were only seen one time. These never-recaptured fish will not demonstrate trends in growth, because there is no time interval between recaptures.

  - For fish caught multiple times, they range from being caught a maximum of 2-9 times.
    - I will need to determine a way to compare growth between fish caught a different number of times. Will I only look at trends between first and second capture? Or between first and last capture? Or, should we determine growth based on maximum time interval between captures?
  - An additional question here may be, can we compare growth between growing periods? For example, bin those fish caught after one year, compared to fish caught after five years?

- Calculate fish condition

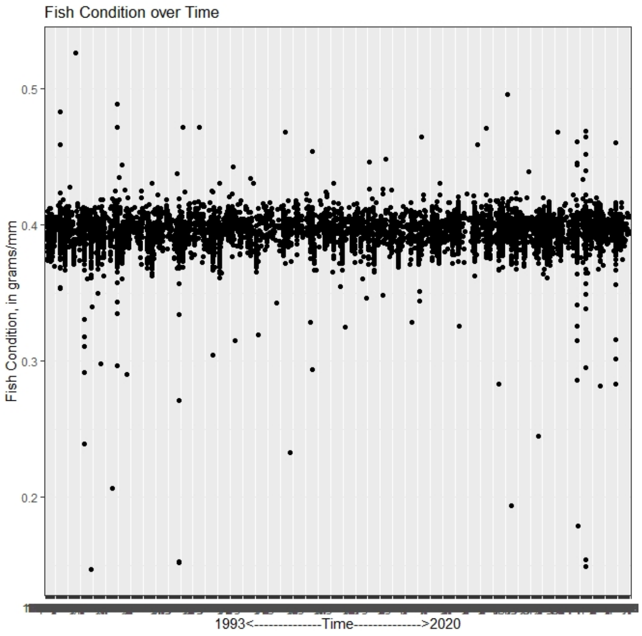


Figure 6: Here I have looked at growth along the river coarsely over time based off of residuals in fish condition, using the entire dataset (before it is subset). There is no apparent trend between fish condition and time.

  - Fish condition is calculated as a ratio of fish weight to length
    - log-log regression and exponentiate residuals.
- The next step is to break up data into reaches based on tributary inputs. This will I will isolate recaptured fish in six reaches, each corresponding with a stream gage that report temperature, turbidity, and dissolved oxygen.
  - Properly correlate growth over time to correlate with what is going on in that part of the river over time
- Remake these preliminary figures after subsetting the data to see trends

<u>**Step 2**: Data Collection and organization for Dataset 2 (stream gage data)</u>

- Source data from all gages
- Based on Dataset 2, river temperatures are consistently cooler closer to Glen Canyon Dam (Lee’s Ferry) compared to further distances from the dam (Diamond).

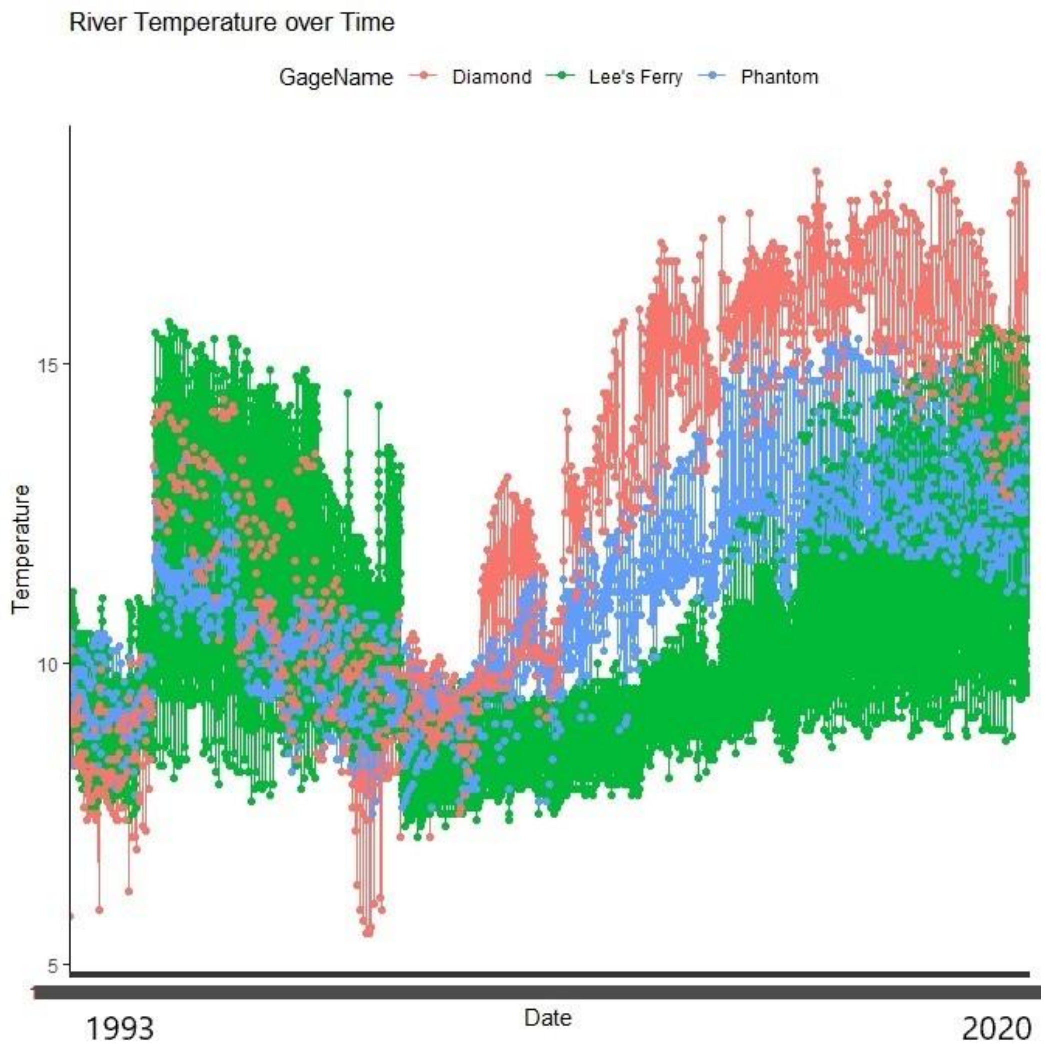


Figure 7: There is a notable shift in temperature between the stream gages at about 2000.

  - Did dam releases change during this time? This likely could have ecological consequences. We may be able to use this date of temperature switch as a question for growth of fish.

- Visualize trends in temperature from releases from Glen Canyon Dam

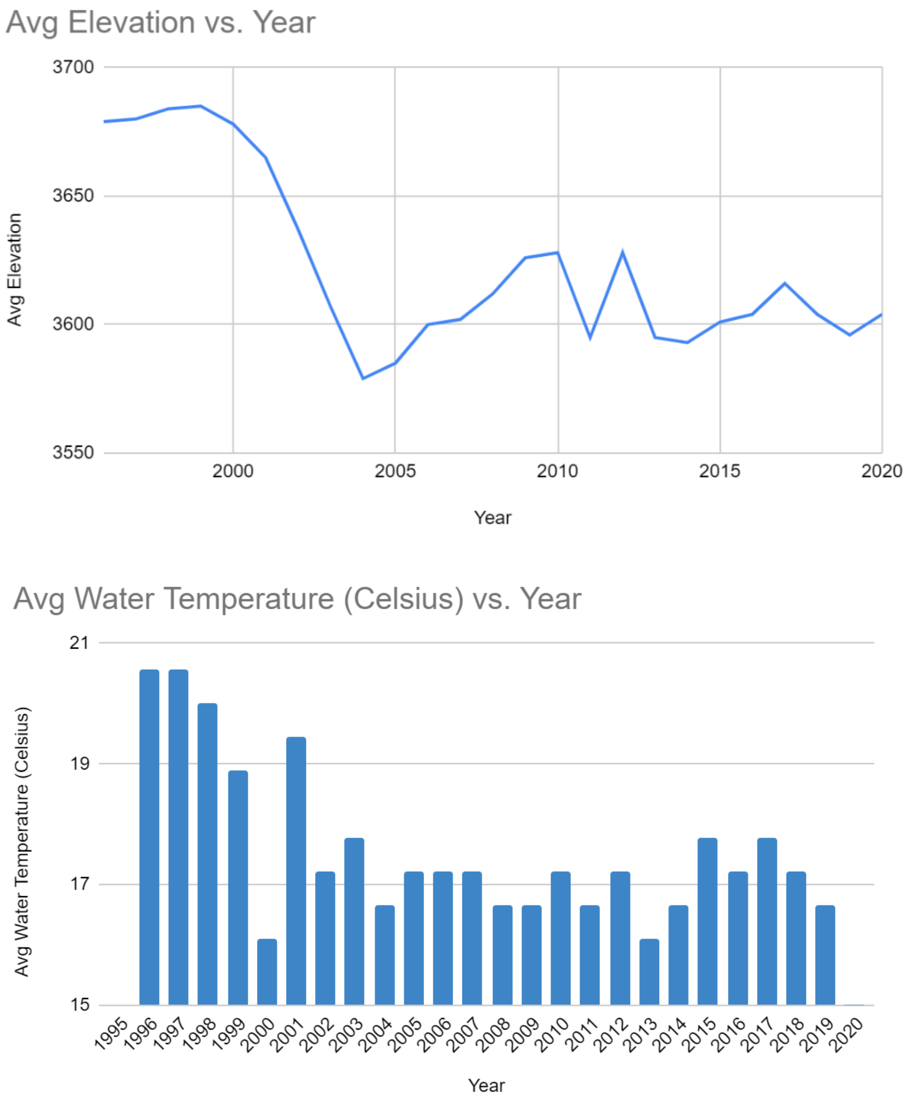


Figure 8: Temperature of dam releases has decreased since 2001, and height of water stored in Lake Powell Reservoir has decreased beginning in 2000 (data from http://lakepowell.water-data.com/index2.php).

- Make initial plots to visualize gage data based on the following covariates:
  - Temperature
  - Turbidity
  - Dissolved oxygen
- Subset data as necessary, determined by location and time
  - By reach – will we be using the upstream or downstream gage for each of the covariates listed above?
  - By time – for any additional primary productivity data, we will need to subset both the FMS dataset and data for other covariates to correlate with the available time series for the data with the lowest range in collection dates
- Remake these preliminary figures after subsetting the data to see trends

Step 3: Analyzing Research Questions: create regression models

- Between length, weight, and fish condition (Log of length, weight)
- Complex ideas to keep in mind
    - Fish may put on weight, but if water isn't warm enough, may not convert this weight into length
    - Once a fish grows in length, it cannot decrease. However, a fish can continually put on and slough off weight throughout its life

Chapter 1 - Growth of FMS over time and space

- H_{N1}: Growth of FMS is higher in areas of the Grand Canyon further from Glen Canyon Dam
    - Explore trends in fish weight and length over the course of the river

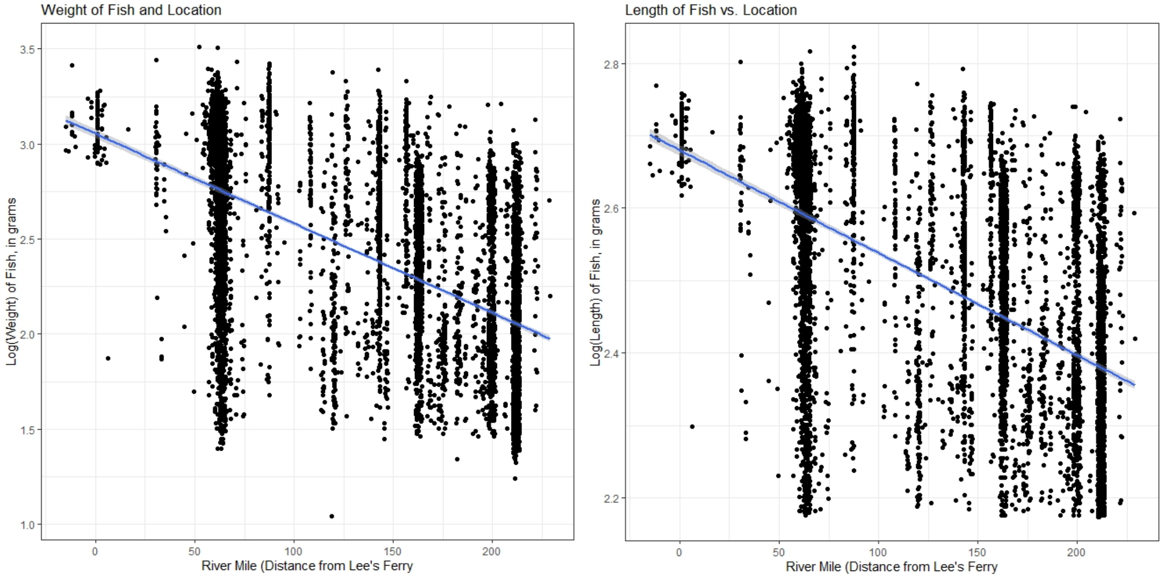


Figure 6: Weight and length of fish decreases with increased distance from Glen Canyon Dam. The trend in this data could be explained due to the few large FMS caught close to the dam.

    - These figures were created using the entire dataset. FMS are believed to move upstream as they mature. mainstem water is still too cold for growth of early life stages above the Lower Colorado River, and most of the FMS likely are reared in a tributary for part of their life – including reproduction in Paria River. However, recreating these figures with subset data may show different trends.
- H_{N2}: Growth of FMS has increased between 2000 and 2010, but has decreased over time since 2010
    - I will test if fish growth has increased over time, using pre-drought and post drought time periods, as well as binned time periods during the drought

Chapter 2 - Modeling explanations of FMS growth

- H_{N3}: FMS growth trends follow trends in increased water temperature as a result of drought conditions
    - I will test if fish growth is correlated with temperature (also, turbidity?)
- H_{N4}: Flannelmouth sucker condition will follow a graph of seasonal primary productivity within Grand Canyon
    - I will test if fish growth is correlated with productivity
    - I will test is productivity has increased with temperature
- H_{N5}: Growth of FMS is higher in areas of the canyon further from Glen Canyon Dam, as caused by water temperature increases and increased turbidity
    - I will test if fish growth is correlated with temperature and turbidity along the river continuum with distance from the dam

Step 4: Additional data comparisons or models to consider

- Timing of growth
  - Seasonality
  - Yearly trends
  - Drought years vs. pre drought
- Location of growth
  - Mainstem reaches
  - Tributaries
- Stable fish (that remain in the same reach between recaptures) vs. highly mobile fish

Step 5: Evaluate Correlations in Predictors and Interpret models

- Univariate correlations and multicollinearity
- Additional abiotic or biological data that may complicate data?
- Interpret model output

Anticipated Results and Significance

This study will test how much variation in growth seems to be explained by changes in temperature and productivity. I anticipate that growth has increased as a result of drought conditions. I expect that warmer water temperatures from the drought in the Grand Canyon since 2000 that pushes warm surface water through Glen Canyon Dam, and warms inputs from tributaries, has led to an increase in food base in an otherwise food-limited system. This warmer water paired with a lack of warm-water adapted invasive species due to fish barriers like Pearce Ferry Rapid in the south and Glen Canyon Dam in the north, recession of Lake Mead that has created 60 more miles of river habitat, and a potential increase in primary productivity within the river may have contributed to the increase in abundance and growth of FMS. Additional factors might include changing species interactions, such as the extirpation of the Colorado Pikeminnow or introduction of rainbow trout and brown trout, both in the 1970's.

This research will inform management to ensure that FMS doesn't experience another population crash. Further, understanding where one fish in the canyon is getting its food can be extrapolated to understanding the food base of the other native fish species that represent the top of the Grand Canyon aquatic food web.

Timeline and Work Plan

	2020									2021				
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Chapter 1: Growth of FMS over time and space (analysis)	■■■	■■■	■■■	■■■	■■■	■■■	■■■	□□□	□□□	□□□	□□□	□□□	□□□	□□□
Chapter 1: Growth of FMS over time and space (writing)	□□□	□□□	□□□	□□□	□□□	□□□	□□□	■■■	■■■	■■■	■■■	□□□	□□□	□□□
Field work with USGS	□□□	■■□	□□□	■■■	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□
Internship with USGS (Wyss Funded)	□□□	■■■	■■■	■■■	■■■	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□
Chapter 2: Modeling explanations of FMS growth (analysis)	□□□	□□□	□□□	□□□	■■■	■■■	■■■	■■■	■■■	■■□	□□□	□□□	□□□	□□□
Chapter 2: Modeling explanations of FMS growth (writing)	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	■■■	■■■	■■■	■□□	□□□
Thesis Defense	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□■□	□□□
Publishing Chapters	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□□	□□■	■■■
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