DETECTING ECOSYSTEM RESPONSE TO RESTORATION EFFORTS WITH

IMPLICATIONS FOR RECOVERY OF THE THREATENED JUNE SUCKER

(*CHASMISTES LIORUS*) IN A SHALLOW,

EUTROPHIC, UTAH LAKE

by

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A thesis submitted in partial fulfillment
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ABSTRACT

Detecting Ecosystem Response to Restoration Efforts with Implications for Recovery of the

Threatened June Sucker (*Chasmistes liorus*) in a Shallow,

Eutrophic, Utah Lake

by

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Ecosystem degradation associated with the growing human population will increase globally without active management. Active restoration can promote recovery, yet often fails to produce desired results and may require decades to achieve noticeable benefits. Detecting incremental responses to restoration is imperative in these difficult situations. Here, I demonstrate that restoration focused on fish biomanipulation triggers incremental responses in aquatic communities. Removing common carp (*Cyprinus carpio*) is expected to encourage recovery of macrophyte diversity and abundance, increasing habitat heterogeneity, resulting in higher macroinvertebrate biomass, richness, and predator abundance. Carp removal should also increase water clarity, improving the visual environment for fishes, thus increasing prey acquisition. I examined the response of aquatic macrophyte and macroinvertebrate communities and fishes' body condition to carp removal in Utah Lake, UT, to demonstrate that these metrics can serve as indicators of incremental response to restoration. Submerged, native, herbaceous, and mixed-macrophyte communities were most common at low carp biomass. Macroinvertebrate predators, richness, and biomass varied among macrophyte habitat types, where, in general, all were higher in macrophyte habitats than bare sediment. Macroinvertebrate predators were primarily associated with mixed macrophytes, and biomass and richness were both significantly higher in

mixed macrophytes than bare sediment. Neither macroinvertebrate richness nor biomass were significantly related to carp biomass, but white bass (*Morone chyrsops*) body condition was significantly greater at low carp biomass. However, other environmental drivers can also influence the biotic community, and may counteract desirable benefits from carp removal. Indeed, I found that the benefits of carp removal are reduced if water levels are not maintained. Macrophyte relative abundance decreased as the lake level declined and macrophyte habitat was completely absent at very low lake levels. Additionally, macroinvertebrate richness and walleye (*Sander vitreus*) body condition both decreased with lower lake levels. Water clarity did not respond to changes in carp biomass, nor did it influence fishes' body condition. Quantifying relationships between carp removal, the biotic community, and other environmental drivers provides a useful framework for detecting incremental restoration responses while simultaneously capturing the effects of multiple environmental drivers including drought.

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PUBLIC ABSTRACT

Detecting Ecosystem Response to Restoration Efforts with Implications for Recovery of the

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Environmental damage associated with a growing human population will increase globally without active management. Restoration can promote ecosystem recovery, yet often fails to produce desired results and may require decades to achieve noticeable benefits. Detecting small, incremental changes is imperative in these difficult situations. Here, I demonstrate that restoration focused on fish removal triggers incremental responses in aquatic plants and animals. Removing common carp is expected to encourage recovery of aquatic plants, increasing animal habitat, resulting in more macroinvertebrates (e.g., aquatic insects, snails). Carp removal should also increase water clarity, improving visibility for fishes, thus increasing their ability to find food. I examined the response of aquatic plants, macroinvertebrates, and fishes' weight to carp removal in Utah Lake, UT, to demonstrate that plants and animals can serve as indicators of incremental changes following restoration. Submerged, native, non-woody, and mixed-plant communities were most common when carp were reduced. Macroinvertebrate predators, total unique types, and total weight varied among plant habitat types, where, in general, all were higher in plant habitats than bare sediment. Macroinvertebrate predators were highest in mixed plants, and total weight and total unique types were both much higher in mixed plants than bare sediment. Neither total unique macroinvertebrate types nor total weight were influenced by carp population changes, but white bass (*Morone chysops*) weight was much greater when carp were reduced. However, other environmental conditions can also influence aquatic plants and animals, and may limit the benefits achieved with carp removal. Indeed, I found that the benefits of carp removal are reduced if water levels are not maintained. Aquatic plants decreased as lake level

declined and plant habitat was completely absent at very low lake levels. Additionally, the total unique types of macroinvertebrates and walleye (*Sander vitreus*) weight both decreased with lower lake levels. Water clarity did not respond to carp population changes, nor did it influence fishes' weight. Identifying relationships between carp removal, aquatic plants and animals, and other environmental conditions provides a useful framework for detecting incremental changes caused by restoration, while simultaneously capturing the effects of multiple environmental conditions including drought.

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Ryan D. Dillingham

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CHAPTER I

INTRODUCTION

Human activities have altered natural ecosystems globally, causing degradation including desertification, climate change, regime shifts, and irreversible loss of biological diversity (Helldén 1991, Vitousek et al. 1997, Chapin Iii et al. 2000, Sala et al. 2000, Folke et al. 2004). Natural ecosystems are typically resilient to disturbance and respond by reorganizing, enabling them to absorb the disturbance while retaining essentially the same functions, structure, identity, and feedbacks (Holling 1973, Gunderson 2000, Carpenter et al. 2001, Folke et al. 2004). However, as disturbances continue to stress an ecosystem, resilience mechanisms such as reorganization of biodiversity, functional redundancy, and habitat connectivity may be eroded, reducing an ecosystem's ability for self-repair (Nyström et al. 2000, Scheffer et al. 2001, Davis et al. 2003, Carpenter 2005, Moretti et al. 2006). Often anthropogenic in nature, extraordinary (e.g., persistent, novel, extreme, compounding, synergistic) disturbances can cause resilience mechanisms to collapse, potentially triggering a shift to a less desirable, degraded state (Holling 1973, Aronson et al. 1993, Scheffer et al. 2001, Davis et al. 2003, Gao et al. 2011, Batt et al. 2013). Reduction and loss of resilience can negatively influence ecological structure and function while simultaneously reducing ecosystem services including resource production, ecotourism and recreation opportunities, and inherent and spiritual value (Aronson et al. 1993, Clewell and Aronson 2006, Primack 2006). Fortunately, ecological restoration can encourage recovery from degraded conditions (Clewell and Aronson 2013, Hobbs 2013), and in some cases, may reestablish resilience in the desirable state (Carpenter and Cottingham 1997, Meijer et al. 1999, Carpenter et al. 2001, Ripple and Beschta 2003, Benayas et al. 2009, Benson and Garmestani 2011, Bullock et al. 2011, Ritchie et al. 2012, Reynolds et al. 2013, Newton and Cantarello 2015, Kaiser-Bunbury et al. 2017).

While ecological restoration provides a means to recover degraded ecosystems, restoration efforts may require decades to achieve noticeable benefits and often fail to produce desired results (Rapport and Whitford 1999, Zedler and Callaway 1999, Suding et al. 2004, Palmer et al. 2010, Moreno-Mateos et al. 2012), making careful definition of monitoring protocols and restoration targets imperative (Ehrenfeld 2000, Ruiz-Jaen and Aide 2005, Wortley et al. 2013). For example, some ecosystems revert back to degraded conditions after years of active management (Søndergaard et al. 2007, Beklioglu and Tan 2008, Angeler et al. 2020), while others may follow alternate trajectories resulting in novel or hybrid ecosystems (Hobbs et al. 2009). In extreme cases, ecosystems stabilize in the degraded state and may not respond to restoration efforts, making restoration from the degraded state extremely challenging (Zedler 2000, Hobbs and Harris 2001, Clewell and Aronson 2013). However, even when ecosystems are resistant to full restoration or slow to recover, incremental improvement of desirable conditions may still occur (Carpenter et al. 2001, Benayas et al. 2009, Thomasen and Chow-Fraser 2012). Incremental responses are especially important in systems where those small changes may slow or reverse the decline of endangered species. Long-term monitoring, adaptive management, and selection of proper response indicators are imperative in these challenging situations where detecting incremental changes may be the only way to determine if restoration efforts are working (Thomasen and Chow-Fraser 2012).

Selecting proper indicators of restoration response requires sound ecological theory and, ideally, multiple indicators representing a suite of ecological processes and ecosystem components (Hobbs and Harris 2001, Ruiz-Jaen and Aide 2005, Doren et al. 2009, Wright et al. 2009, Bullock et al. 2011, Kaiser-Bunbury et al. 2017). Changes in community composition (e.g., diversity, size of dominant taxa, and abundance of sensitive species) and statistical early warning signals, are examples of indicators used to detect incremental change during early stages of ecosystem stress and approaching tipping points (Rapport et al. 1985, Schindler 1987, Gray 1989, Rapport and Whitford 1999, Scheffer et al. 2009, Carpenter et al. 2011, Wilkinson et al. 2018).

Each of these indicators reflect changes triggered by modification of ecosystem structure and function. For example, reduction or extirpation of sensitive species can indicate environmental abnormalities that exceed those species' environmental tolerances and can indicate habitat degradation (Hilsenhoff 1988, Rehn 2009, EPA 2017). Decreased diversity or rising statistical variance can indicate changes in food web structure and may reflect reduced ecosystem resilience (Chapin Iii et al. 2000, Carpenter et al. 2011). Changes in the mean size of dominant taxa could indicate changes in predator size selectivity, ecosystem productivity, or competition for limited resources (Crowder and Cooper 1982, Mittelbach 1988, Capellini and Gosling 2007). Similar to early warning signals of ecosystem stress, restoration indicators can be selected to detect and monitor incremental response of desirable characteristics (Desender et al. 2007, Thomasen and Chow-Fraser 2012). These indicators should capture structural and functional responses (Ruiz-Jaen and Aide 2005, Wright et al. 2009), such as changes in food web structure (e.g., increased primary production and predator abundance) and ecosystem resilience (e.g., increased diversity and reappearance of sensitive species). Using ecological theory to guide selection of restoration indicators may be the most expedient way to detect functional, structural, and incremental response, particularly during the early stages of restoration and in severely degraded ecosystems (Hobbs 2013).

Utah Lake, UT, is a severely degraded lentic ecosystem with a legacy of anthropogenic disturbances which have modified habitat, altered the fish community, and imperiled native species, triggering a need for conservation and restoration efforts (USFWS 1999). Historic records describe Utah Lake as a mesotrophic lake with extensive aquatic macrophyte beds, a diverse fish assemblage dominated by cutthroat trout *(Salmo clarki)* and lake suckers (Utah sucker *Catostomus ardens*, webug sucker *Catostomus fecundus*, mountain sucker *Catostomus playtrhynchus*, and June sucker *Chasmistes liorus*), and water much clearer than today (Cottam 1926, Heckmann et al. 1981, Janetski 1990, USFWS 1999, Miller 2004). However, human activities including excessive nutrient loading, watershed development, commercial fishing, and

the introduction of non-native fish species have degraded habitat and caused native fishes to decline (Heckmann et al. 1981, Keleher et al. 1998, USFWS 1999, Miller 2004, Billman 2008). Common carp (*Cyprinus carpio*; hereafter "carp") were introduced in 1886 and appear to be a leading driver in the loss of macrophyte habitat (Heckmann et al. 1981, Miller 2004, King 2019). Carp are notorious for their benthic feeding behavior which causes sediment resuspension and damages aquatic macrophytes (Roberts et al. 1995, Miller and Crowl 2006, Lin and Wu 2013). Watershed development and agricultural practices increased as the carp population grew, exacerbating the loss of submerged macrophytes due to increased sedimentation and nutrient-induced eutrophication (Keleher et al. 1998, USFWS 1999, King 2019). The declining aquatic macrophyte diversity and cover caused a reduction in refuge habitat and food production for many native species (Thomas 1998, USFWS 1999, Miller 2004). Meanwhile, commercial fishing operations and the introduction of other non-native fishes altered community composition and predator-prey interactions (Heckmann et al. 1981, Landom 2010). The synergistic effects resulting from these anthropogenic stressors altered native ecosystem structure and function, resulting in the decline and extirpation of many native species (Heckmann et al. 1981, Landom 2010).

Of the thirteen fish species native to Utah Lake, only the Utah sucker, Utah chub (*Gila atraria*), and the endemic June sucker remain (Reynolds 2017). The June sucker was listed as endangered in 1986, with an estimated wild population of fewer than 1,000 individuals. The population continued to decline until reaching an estimated adult spawning population of only 311-515 individuals in 1998 (Keleher et al. 1998, USFWS 1999). The U.S. Fish and Wildlife Service contracted the Utah Division of Wildlife Services and Utah State University to develop the June sucker Recovery Plan, which outlined ecosystem restoration as a leading conservation priority and biomanipulation of the fish community as the primary restoration method (USFWS 1999).

Large-scale restoration actions began in 2009 with intensive removal of carp, providing an opportunity to investigate ecosystem response to restoration efforts. Carp removal was expected to provide multiple benefits to the Utah Lake ecosystem. For example, reduced carp biomass should decrease benthic foraging pressure and disturbance, allowing sediments to stabilize and macrophytes to recover. Aquatic macrophytes increase structural complexity and habitat heterogeneity, which can increase food production, refuge availability, and breeding sites for aquatic animals including macroinvertebrates (Engel 1985, Hargeby et al. 1994, Jeppesen et al. 2012). Therefore, incremental changes in the macrophyte and macroinvertebrate communities could serve as useful indicators of early response to restoration. Additionally, as carp represented the vast majority of fish biomass in the lake at the onset of removal efforts (Heckmann et al. 1981, SWCA 2002, Landom et al. 2014), carp removal could also reduce interspecific competition for prey resources. Reduced sediment disturbance by carp may also increase water clarity, potentially improving foraging conditions for visually-foraging fishes (Gardner 1981, Breitburg 1988, Vogel and Beauchamp 1999). Therefore, decreasing interspecific competition and improving foraging conditions could increase resource acquisition by other fishes, which may be reflected in increased body condition.

Since 2009, carp control efforts have removed more than 15,000 tons of carp from Utah Lake, and model estimates indicate a reduction in carp biomass greater than 75% was achieved by 2016 (Walsworth et al. 2020). However, other environmental conditions such as water temperature and lake levels could also influence the ecological community and should be considered. Utah Lake entered an ongoing drought cycle in 2011, potentially masking impacts of carp removal but providing the additional opportunity to study restoration during multiyear drought. As the lake level declines during multi-year drought, the shoreline recedes rapidly, exposing large areas of previously inundated habitats. Decreasing water volume can also influence thermal conditions and concentrate biota, nutrients, and suspended materials (Robel 1961, Wetzel 1983, Bozelli 1994, Beklioglu and Tan 2008, Özen et al. 2010, Atwood et al. 2018).

Therefore, ecosystem changes caused by drought may also be reflected in indicators such as macrophyte and macroinvertebrate assemblages or fishes' body condition. Monitoring indicators that reflect changes in ecosystem structure and function throughout the restoration process, rather than simply setting end-goal targets, may enable detection of subtle responses to restoration while simultaneously detecting changes triggered by other environmental drivers such as water temperature, or reduced lake levels caused by anthropogenic withdrawals or drought.

In Chapter 2, I investigated the effects of carp removal and changing lake level on (1) macrophyte diversity and abundance, and (2) macroinvertebrate assemblages among different macrophyte habitats. My objective was to test for differences in macroinvertebrate assemblages among habitat types, and to test for incremental changes in macrophyte and macroinvertebrate communities triggered by carp removal.

In Chapter 3, I investigated (1) the effect of carp biomass and lake level on water clarity and (2) the effects of changing environmental conditions on fishes' body condition. My objective was to use the body condition (a metric of relative weight-at-length) of three fish species (June sucker, walleye – *Sander vitreus*, and white bass – *Morone chrysops*) to test for potential changes to the visual foraging environment triggered by carp removal. While carp removal could improve visual foraging conditions and reduce interspecific competition for prey, prey acquisition is not the only factor influencing fishes' body condition. Thus, I also examine the influence of lake level, temperature, and reproductive cycles for the three fish species. Incremental increases in fishes' body condition may indicate improved foraging conditions for these species in the presence of reduced carp biomass.

The results of my research can help steer restoration efforts on Utah Lake, while simultaneously contributing to ecosystem restoration projects worldwide. Selecting and testing indicators of incremental changes will help ensure resource managers have the tools they need to determine whether carp removal is contributing to desirable ecosystem characteristics. Additionally, establishing multiple incremental indicators enables restoration specialists to detect

not only desirable structural and functional responses, but adds the additional opportunity to detect unintended effects of restoration. Furthermore, changes triggered by synergistic and antagonistic (e.g., drought during carp removal) ecological drivers may also be monitored. Detecting incremental response has been explicitly employed to detect early warning signals to ecosystem stress in numerous studies (Rapport et al. 1985, Schindler 1987, Gray 1989, Rapport and Whitford 1999, Scheffer et al. 2009, Wilkinson et al. 2018), but remains poorly studied, though it is sometimes implied, in ecosystem restoration (*see* Desender et al. 2007, Carpenter et al. 2011, Thomasen and Chow-Fraser 2012). By developing an approach to detect incremental response to restoration, my research will also contribute to the rapidly growing field of ecosystem restoration. Establishing ecosystem monitoring frameworks based on sound ecological theory and ability to detect desired changes over long-time frames will provide valuable tools for evaluation of restoration success worldwide.

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CHAPTER II

DETECTING ECOSYSTEM RESPONSES TO RESTORATION EFFORTS USING AQUATIC

MACROPHYTE AND MACROINVERTEBRATE COMMUNITIES

INTRODUCTION

Aquatic macrophytes serve as important habitat for animals by providing structural complexity, food production, refuge, and breeding sites (Engel 1985, Hargeby et al. 1994, Papas 2007, Jeppesen et al. 2012). Macrophytes increase total available niche space by providing spatial heterogeneity at the ecosystem scale (Crowder and Cooper 1982, Werner and Hall 1988, Papas 2007), while increasing colonizable surface area and microhabitat diversity at the individual plant scale (Cyr and Downing 1988, Cheruvelil et al. 2002, Balci and Kennedy 2003a, Balci and Kennedy 2003b). Many animals depend on aquatic macrophytes for food, where some consume plant tissue directly (Engel 1985, Newman 1991, Merritt and Cummins 1996) and others consume epiphytic algae (Cattaneo and Kalff 1980, Downing 1981, Hoyer et al. 1998) or macrophyte detritus (Engel 1988, Newman 1991, Kornijów 1992). Aquatic macrophytes can also provide refuge for prey species (Engel 1985, Diehl 1988, Mittelbach 1988, Scheffer 2004), and increasing macrophyte complexity can reduce predator efficiency when compared to more simplified habitat (Crowder and Cooper 1982). Furthermore, many animals depend on aquatic macrophytes to complete their life cycles (Gower 1967, James 1970, Keast 1984, Werner and Hall 1988, Merritt and Cummins 1996, Egan and Paton 2004, Scheffer 2004). Consequently, reduction or loss of aquatic macrophytes can influence the structure and function of aquatic ecosystems.

Anthropogenic disturbances can decrease aquatic macrophyte abundance and biomass, causing degradation of the structure and functions they support. Excessive nutrient additions can drive eutrophication and encourage the production of floating and suspended algae, which can block light to submerged macrophytes and inhibit growth (Scheffer et al. 1993, Carpenter and

Kinne 2003, Folke et al. 2004, Carpenter 2005, Scheffer and van Nes 2007). Non-native and invasive animals, such as common carp (*Cyprinus carpio*; Cahoon 1953, Threinen and Helm 1954, King and Hunt 1967, Crivelli 1983, Roberts et al. 1995, Miller and Crowl 2006) and rusty crayfish (*Orconectes rusticus*; Hein et al. 2006, Hein et al. 2007, Hansen et al. 2013), can consume, destroy, and uproot aquatic macrophytes. Additionally, lake-level declines during multiyear droughts, particularly when exacerbated by water withdrawals for human uses, may leave aquatic macrophytes stranded and desiccating along shorelines (Blindow et al. 1993, Coops and Hosper 2002, Keeton 2019). Degraded habitat caused by loss of macrophytes may require restoration efforts to encourage reestablishment. However, restoration that simply increases aquatic macrophytes may not fully indicate restoration of the processes they support. For example, if aquatic macroinvertebrates do not recolonize the restored macrophytes, then even though structure has been restored, some desired ecological functions such as habitat, prey production, and increased ecosystem resilience may still be lacking. By simultaneously monitoring macroinvertebrate diversity, biomass, and predator assemblages we gain insight into desirable ecological responses including recovery of food web structure and reestablishment of ecosystem resilience. Therefore, monitoring metrics such as macroinvertebrate production, diversity, and predator abundance, in conjunction with monitoring macrophyte recovery, may improve detection of a more complete functional restoration, rather than recovery of macrophytes alone.

As restoration often influences multiple components of an ecosystem, indicators of ecosystem responses to restoration should represent a suite of processes (Scheffer 2004, Ruiz-Jaen and Aide 2005, Søndergaard et al. 2007, Søndergaard et al. 2008). Aquatic macroinvertebrate assemblages are ideal for monitoring ecosystem condition as they can serve as indicators of multiple processes simultaneously. For example, macroinvertebrate assemblages are frequently used as indicators of water quality (Hawkins et al. 1982, Hilsenhoff 1987, Johnson et al. 1993, Merritt and Cummins 1996, Smith et al. 1999, Hawkins et al. 2000, Pond et al. 2008)

and increases in macroinvertebrate abundance and diversity can reflect an expansion of total niche space (Crowder and Cooper 1982, Papas 2007). Increasing macroinvertebrate density and biomass increases food supply for upper trophic levels, which can increase community complexity and expand ecosystem-wide trophic structure. Such increases in macroinvertebrate densities can have effects that propagate through food webs to fishes and even waterfowl (Hargeby et al. 1994). The ability of macroinvertebrate assemblages to indicate changes to numerous functions of an ecosystem make them an ideal indicator to employ in conjunction with other metrics, such as macrophyte abundance, when monitoring restoration efforts.

Utah Lake, UT, is a highly degraded lentic ecosystem with a legacy of eutrophication, introduction of many non-native and invasive species including common carp (hereafter, "carp"), and altered hydrology due to water development, water withdrawals, and multiyear drought cycles, all of which have impaired water quality and drastically reduced macrophyte abundance and diversity. Altered water quality and macrophyte composition are thought to be leading drivers in the decline of an endemic, threatened June sucker population (USFWS 1999), and are thus the focus of restoration efforts. Reduction of benthivorous fish, such as carp, has been successfully applied to several turbid shallow lakes to improve water clarity and promote recovery of aquatic macrophytes (Meijer et al. 1990, Scheffer et al. 1993, Søndergaard et al. 2008). Therefore, a whole-lake carp removal effort to improve June sucker habitat was initiated by the June Sucker Recovery Implementation Program (JSRIP) in 2009. However, the region entered into a drought cycle in 2011, potentially limiting any response from carp removal. Ongoing carp removal during multiyear drought provides an ideal opportunity to investigate potential relationships between carp removal, multiyear drought, and the macrophyte and macroinvertebrate communities as indicators of changes in ecosystem health.

In this chapter, I investigate the effects of lake level change and carp removal on (1) macrophyte diversity and abundance, and (2) macroinvertebrate richness and biomass among different macrophyte habitats. Through these investigations, I aim to develop a more complete

understanding of how restoration efforts affect ecological communities and whether we can detect

an ecosystem response in the absence of full recovery and in the continued presence of multiple

stressors.

METHODS

General approach

I collected macrophyte and macroinvertebrate data during the growing seasons of 2011

and 2012, and then again from 2014 through 2018, which I combined with lake-wide estimates of

carp biomass and lake level. I used a lake-wide sampling design by dividing Utah Lake into 9

strata from which I recorded macrophyte composition and collected macroinvertebrate samples

from standardized sites within each stratum (Fig. 1). I combined these site-level data with annual

carp biomass estimates from Walsworth et al. (2020), which were derived from an age-structured

population model incorporating both commercial harvest and standardized carp survey data. I

used relative lake surface elevation (hereafter, "lake level"), measured daily by the Bureau of

Reclamation (Bureau of Reclamation 2021), as a surrogate for drought conditions given that lake

level is the dominant mechanism through which multiyear drought influences Utah Lake. The

Bureau of Reclamation measures lake level relative to an elevation locally referred to as

"compromise" (1,368 m; 4,489 ft. above sea level), a management-accepted maximum level

considered full pool, which when exceeded begins to flood private property. Once exceeded, the

Jordan River (which transports water from Utah Lake to the Great Salt Lake downstream) pumps

and gates are left open to avoid flooding. As such, I reported all lake level data relative to

compromise. I averaged all daily lake level data for the month prior to macroinvertebrate

sampling to account for community and physiological responses to environmental conditions

prior to sampling, rather than at the time of sampling, allowing time for integration of

environmental conditions.

Macrophyte sampling design and identification

We collected macrophyte and macroinvertebrate community data as part of two independent surveys: 1) a course resolution, but lake-wide macrophyte-macroinvertebrate survey starting in 2011 where we collected macrophyte and macroinvertebrate data from nine sites, one in each of the nine lake strata, and 2) a higher resolution, macrophyte transect survey starting in 2016 from three additional sites within strata 2E and Provo Bay (Fig. 1).We collected course resolution, lake-wide macrophyte data each May and September (Sept. 2011 & May 2012 as part of a pilot study, & each May and Sept 2014-2018 as an established annual monitoring protocol). The lake-wide survey was designed to document the localized influence of different macrophyte habitat types on the macroinvertebrate community, which could then be used to document and infer any lake-wide changes present in both communities due to carp removal. We randomly selected one site within each of the nine strata where macrophytes were present in 2011 (Fig. 1). Sites were defined as a region of littoral shoreline where sufficient macrophytes were present to collect 10 (1 meter) D-frame sweep net macroinvertebrate samples (see *Macroinvertebrate Sampling Design and Identification* below). Sites ranged in size, but typically required shoreline macrophytes covering at least 300 m^2 (e.g., 30 m long by 10 m wide, 20 meters long by 15 meters wide, etc.). In some cases, macrophytes were limited in spatial extent, forcing us to collect macroinvertebrate samples from a smaller area. We recorded qualitative habitat descriptions at each site by documenting the macrophyte species composition present from which macroinvertebrate samples were collected. Subsequently, I grouped all macrophyte habitats into four qualitative classifications based on project goals, dominant macrophyte types, and ecological function. Sago pondweed (*Stuckenia pectinata*) and curly leaf pondweed (*Potamogeton crispus*) were the only submerged macrophytes observed during my survey period and so I classified them as "submerged." Common reed (*Phragmites australis*), hardstem bulrush (*Schoenoplectus acutus*), broadleaf cattail (*Typha latifolia*), and alkali bulrush (*Schoenoplectus maritimus*) formed homogeneous stands in Utah Lake and when sampled as homogenous stands, I classified each as

"emergent." When macrophyte taxa were sampled together (whether multiple emergent taxa, multiple submerged taxa, or a mix of emergent and submerged), I grouped these mixed-macrophyte communities into a "mixed" classification. Finally, we collected bare sediment control samples lacking macrophytes adjacent to each of our lake-wide and macrophyte transect sampling sites. I classified these bare sediment samples as "open." Initially, our goal was to sample the same nine locations identified in 2011 and 2012 each year. However, receding lake levels forced us to adjust some of our initial southern (4E & 4W) and Provo Bay site locations. Furthermore, prolonged lake level declines draw water from existing macrophytes in Utah Lake, and when the lake level declined below 1.5 meters relative to compromise, no sites contained inundated macrophytes. When low water-level conditions prevented sampling of macrophytes from a stratum, we collected three nearshore bare sediment samples in place of macrophyte samples.

We collected higher resolution macrophyte transect data monthly from 2016-2018 (June and August in 2016 as part of a pilot study, and May-October 2017-2018 as an established annual monitoring protocol). The macrophyte transect survey was implemented separate from the lake-wide survey and was designed to quantify changes in the littoral macrophyte community, with the secondary objective of augmenting data for habitat types lacking from the lake-wide macrophyte survey. The transect surveys were designed with an emphasis on monitoring changes in submerged macrophytes (Landom et al. 2019); therefore, we selected macrophyte transect survey sites with the highest densities of submerged macrophytes in 2016 (Fig. 1). Macrophyte transect surveys were conducted by recording the macrophyte species present along transects oriented perpendicular to the shoreline (Landom et al. 2019). However, to fulfill the secondary objective of augmenting the lake-wide survey, we also collected macroinvertebrate samples from these additional sites and recorded the qualitative habitat descriptions by documenting the macrophyte species composition from which macroinvertebrates were collected. To maintain consistency with the lake-wide survey, I classified the macrophyte type, or macrophyte community into the same

four qualitative categories as the lake-wide macrophyte survey (submerged, emergent, mixed, and open). Consequently, the macrophyte transect survey provided additional qualitative macrophyte samples for habitat types that were lacking from the lake-wide macrophyte survey, particularly mixed and submerged macrophyte habitats. I used only the qualitative categories from both surveys to describe the habitat for the macroinvertebrate samples we collected in conjunction with all macrophyte samples.

Macroinvertebrate sampling design and identification

We collected macroinvertebrate samples during each standardized, lake-wide macrophyte survey, and during each supplemental macrophyte transect survey. Each macrophyte sampling event included three macroinvertebrate samples: two samples from littoral macrophyte habitats, when available, and one bare sediment sample approximately 30 meters from the sampled macrophytes and farther from shore. When macrophytes were absent at any of our sites, we collected three nearshore bare sediment samples, one of which was sampled approximately 30 meters farther from shore. We collected macroinvertebrate samples using a conventional D-frame sweep net (mesh size = 500 µm, 12-inch wide, 10-inch high; Turner and Trexler 1997). Each sample consisted of 10, 1m long sweeps. Sweep net contents were sieved (U.S. standard NO. 35, 500 µm) in the field to remove fine sediments prior to preservation, then preserved in 70% ethanol, and transported to the laboratory for enumeration and identification.

Macroinvertebrate samples were sorted and identified to taxa in the laboratory following protocols outlined in Miller and Judson (2011), Cuffney et al. (1993), and Moulton et al. (2000). We divided each sample into four equivalent subsamples using a straight-edge ruler, then labeled and stored them independently. Subsamples were processed sequentially where macroinvertebrates were counted and sorted into taxonomic categories (usually to order) while removing vegetation and debris under binocular dissecting microscope (Vinson and Hawkins 1996). Once sorted, we identified, counted, and grouped macroinvertebrates into the lowest

feasible taxonomic level (Table 1, Leslie et al. 1997). We identified Nematoda to phylum, while

Oligochaeta, Hirudinea, and Collembola were identified to subclass. We identified

Ephemeroptera, Isopoda, Lepidoptera, Plecoptera, and Trombidiformes to order. All other

macroinvertebrate taxa, except for Chironomidae and Coleoptera were identified to family

(Table 1). Chironomidae and Coleoptera are the most diverse insect taxa worldwide and in Utah

Lake (Merritt and Cummins 1996), thus Chironomidae were identified to subfamily and

Coleoptera to genus to account for this added diversity. Total abundance was recorded and the

body length measured for up to 20 randomly selected individuals per taxa. I applied length-

weight regression equations to calculate the biomass of each taxa per sample (Burgherr 1997,

Benke et al. 1999).

Statistical analyses

I used linear mixed effects models to test for relationships between macroinvertebrate

biomass and richness with carp biomass and lake level among macrophyte categories. I modeled

macroinvertebrate biomass (log10 transformed) and richness per sample (log10 transformed)

independently as a function of the fixed effects carp biomass (centered and scaled), lake level,

and habitat type, with random effects of year, survey method, and strata. I also explored season as

a random effect but found little variation among seasons, and thus, discarded season from the

models. I performed all linear mixed models following procedures described in Gelman and Hill

(2006) and Zuur et al. (2009).

I used multivariate techniques to compare macroinvertebrate community composition

from each sample collected with all other samples to test for dissimilarity between samples and

among habitat classifications. I used non-metric multidimensional scaling (NMDS) to visualize

differences among samples and colored each sample point according to the habitat type from

which it was collected. I used permutational multivariate analysis of variance (PERMANOVA) to

test for a significant difference in macroinvertebrate community composition between samples

collected from different habitat types. Subsequently, I used pairwise comparisons to test for

significant differences in macroinvertebrate community composition between macrophyte

classifications by comparing each macrophyte classification to all other macrophyte

classifications independently. I removed taxa with fewer than five individuals sampled before

performing NMDS, PERMANOVA, and pairwise comparisons. After removing rare taxa, I

calculated a Bray-Curtis matrix of community dissimilarity which I used as the input for the

NMDS, PERMANOVA, and pairwise comparisons, and I adjusted pairwise comparison p-scores

using a Bonferroni correction to avoid Type 1 errors.

I conducted all statistical analyses using the R Statistical Computing Environment (R

Core Team 2020, version 3.6.3, 2020-2-29). I fit the mixed effects models using the "lme4"

(Bates et al. 2015, version 1.1-23) and the "effects" (Fox and Weisberg 2019, version 3.6.3)

packages, and determined mixed effects model significance values and degrees of freedom using

the packages "nlme" (Pinheiro et al. 2020, version 3.1-151), and "lmerTest" (Kuznetsova et al.

2017, version 3.1-3). I used package "multcomp" (Hothorn et al. 2008, version 1.4-13) for mixed-

effects multiple pairwise comparisons, package "vegan" (Oksanen et al. 2019, version 2.5-6) for

NMDS and PERMANOVA, and package "pairwiseAdonis" (Arbizu 2017, version 0.0.1) for

multivariate pairwise comparisons.

<div align="center">RESULTS</div>

<div align="center">*Macrophyte community*</div>

The macrophyte community was limited to the shoreline of Utah Lake and dominated by

emergent taxa with rare occurrences of submerged species (Fig. 2). Invasive common reed and

native hardstem bulrush were the most abundant macrophyte species observed at our study sites.

Native sago pondweed and non-native curly leaf pondweed were the only submerged

macrophytes observed and were both rare. Other uncommon aquatic and semi-aquatic

macrophyte taxa at our study sites included broadleaf cattail (native), curly dock (*Rumex crispus*;

non-native), water plantain (*Alisma* sp.; native), alkali bulrush (native), and smallflower tamarisk (*Tamarix parviflora*; non-native), all of which were only observed during the later years of my study. Sample size varied among macrophyte groups with 223 open, 166 emergent, 55 mixed, and 11 submerged at all of our study sites.

The number of unique macrophyte habitat types at our standardized, lake-wide, study sites increased as carp biomass declined (Fig. 2a). Sites with macrophytes (opposed to bare sediment) were primarily limited to homogenous stands of hard-stemmed, stalk-like macrophytes (common reed and hardstem bulrush) during the first five years of carp removal (except one site containing sago pondweed in 2011). However, as carp biomass declined, submerged sago pondweed and curly leaf pondweed, as well as herbaceous curly dock became more common. Additionally, native species including alkali bulrush and broadleaf cattail recolonized, and mixed macrophyte communities composed of multiple species at the same site established (Fig. 2a). Indeed, submerged, and mixed macrophytes were only available to sample when carp biomass was less than 20 M kg, except for one submerged sample in 2011, when carp biomass was above 60 M kg (60,000 tons; Fig. 2a) and the lake level was above compromise (Fig. 2b). Despite the apparent relationship between low carp biomass and the number of unique macrophyte habitat types, lake level also appeared to influence the number of unique macrophyte habitat types and macrophyte relative abundance (Fig. 2b). The number of unique macrophyte habitat types was also higher at low lake levels, though drastic reductions in lake level in 2015 and 2016 (1.95 m and 2.46 m below compromise, respectively) were associated with a complete lack of macrophytes at any of our sites, leaving only bare sediment as available macroinvertebrate habitat (Fig. 2b). Mixed macrophytes were only available to sample when the lake level was approximately 1.5 to 1.0 m below compromise, which coincided with carp biomass less than 20 M kg (20,000 tons). Submerged vegetation was also most common between 1.5 and 1.0 meters below compromise (Fig. 2b).

Macroinvertebrate community composition

I identified 57 unique macroinvertebrate taxa in Utah Lake during this study (Table 1), 52 of which were from standardized sweep nets and used to calculate richness, while the other 5 were observed during other sampling efforts. Oligochaeta were the most abundant taxa (n=212,869) and occurred in 92% of all sweep net samples, followed by Corixidae (n=102,371) which occurred in 64% of samples. Chironomidae occurred in the greatest percentage of samples (95%) and were the third most abundant taxa (n=74,503). Three subfamilies of Chironomidae were identified and used to calculate richness: Chironominae, Orthocladiinae, and Tanypodinae. Chironominae were the most abundant Chironomidae subfamily (n= 56,567 individuals), making up 80% of all Chironomids. Richness was highest in the predator functional feeding group (n=22); however, all predators combined only accounted for 26% of individuals counted, 20% of which were Corixidae. The heightened predator diversity is partially because Coleoptera were sorted to genus, and within each genus, adults were classified as distinct taxa from larva. Larvae within Coleoptera genera were sometimes the same functional feeding group as adults (e.g., Dytiscidae *hygrotus*); whereas, sometimes adults and larva within genera were different functional feeding groups (e.g., Hydrophilidae *Tropisternus,* Hydrophilidae *Berosis*; Merritt and Cummins 1996). Coleoptera, Odonata, and Hemiptera comprised most of the predacious macroinvertebrates. Collector-gatherers were the most abundant functional feeding group (n=284,236), comprising the greatest percentage of individuals (56%), but only accounted for 10 unique taxa. Oligochaeta were the most abundant collector-gatherer accounting for 42% of all individuals, and 75% of all collector-gatherers. Scrapers (n=4,491) accounted for 0.9% of all individuals. I observed five taxa during other sampling efforts (light traps & minnow traps) but not in standardized sweep samples (Gomphidae, Gyrinidae, Nepidae, Dytiscidae *Dytiscinae*, & Dytiscidae. *Rhantus*). I identified two genera of Corixidae (*Corisella* and *Hesperocorixa*), and three families of Collembola (Poduridae, Sminthuridae, & Isotomidae) during this study, but this finer taxonomic resolution was not confirmed until 2016. Since Corixidae and Collembola were

not identified to genera and family, respectively, before 2016, the samples after 2016 could not be directly compared for the finer resolution and were therefore left at family and class, respectively, for purposes of calculating richness.

Macrophyte and macroinvertebrate interactions

Macroinvertebrate community composition varied among macrophyte classes in Utah Lake (Fig. 3a). Non-metric dimensional scaling demonstrated significant separation between macroinvertebrate assemblages from emergent, mixed, and bare sediment habitats (stress = 0.199, non-metric $R^2 = 0.961$, linear $R^2 = 0.72$, k = 3, PERMANOVA p < 0.01). Pairwise comparison further indicated that macroinvertebrate assemblages in bare sediment were significantly different from emergent, submerged, and mixed macrophyte assemblages (p<0.05; Table 2), and assemblages in mixed macrophytes were significantly different from emergent macrophytes (p<0.05). However, macroinvertebrate assemblages in submerged macrophytes were only marginally different from mixed macrophytes (p<0.1) and did not differ from emergent macrophytes (Table 2).

Many macroinvertebrate taxa demonstrated strong associations with a particular macrophyte habitat (Fig. 3b). Large (> 5mm), mobile (Merritt and Cummins 1996), predators (Dytiscidae, Hydrophilidae, Notonectidae, Libellulidae, Aeshnidae, Coenagrionidae) were most strongly associated with mixed macrophytes, whereas, the smaller, more sedentary predators (Hydridae and Trombidiformes) were most strongly associated with bare sediment and emergent macrophytes. The three most common taxa (Oligochaeta, Corixidae, and Chironominae) were all associated with bare sediment. Hydropsychidae, Polycentropidae, and Planorbidae loaded most strongly towards the negative side of NMDS1, and Tanypodinae, Nematoda, and Dolichipodidae loaded most strongly on the positive side of NMDS1, suggesting that these six species explain most of the differences in samples along the primary axis (NMDS1). Trombidiformes, Chironominae, and Polycentropidae loaded most strongly toward the negative side of NMDS2,

and Syrphidae, Mesoveliidae, and Psychodidae loaded most strongly on the positive side of NMDS2, explaining most of the differences among samples on the second most important axis (NMDS2).

Carp and lake level effects on macroinvertebrate-macrophyte relationships

Carp biomass was not a significant predictor of macroinvertebrate biomass (Table 3) or richness (Table 4). Linear mixed-effects analysis predictions revealed no significant effect between macroinvertebrate biomass and carp biomass ($p = 0.31$, $t = 1.05$), nor macroinvertebrate richness and carp biomass ($p = 0.13$, $t = -1.61$).

Lake level was a significant predictor of macroinvertebrate biomass (Table 3) and a weak predictor of macroinvertebrate richness (Table 4; Fig. 4). Linear mixed-effects analysis revealed that macroinvertebrate biomass per sample was highest when the lake level was low, and decreased as the lake level rose ($p = 0.02$; Table 3). Although only marginally significant ($p = 0.09$; Table 4), macroinvertebrate richness increased with lake level.

Macroinvertebrate richness and biomass varied among habitat types, as both were generally lowest in bare sediment, increased in homogenous emergent and submerged macrophytes, and were highest in mixed-macrophyte communities (Fig. 4). Macroinvertebrate biomass was significantly lower in bare sediment than in mixed macrophyte habitat types (Table 3; $p < 0.01$). Macroinvertebrate biomass in submerged ($p = 0.78$) and emergent ($p = 0.26$) habitats did not differ significantly from biomass in mixed macrophyte habitat. Macroinvertebrate richness was also significantly lower in bare sediment than in mixed macrophyte habitats (Table 4; mixed effects $p < 0.01$). Richness in submerged habitat did not differ significantly from mixed vegetation ($p = 0.78$), but richness in emergent habitat was marginally lower than mixed habitat ($p = 0.07$). However, mixed-effects model estimates indicate that both mean richness and mean biomass were highest in mixed macrophytes, decreased in submerged macrophytes, decreased further in emergent macrophytes, and were lowest in bare sediment (Fig. 4).

DISCUSSION

Introduction of non-native fishes can threaten native species by triggering many changes to aquatic ecosystems, including altering food web structure (Carpenter et al. 1985, Spencer et al. 1991, Maezono and Miyashita 2003, Weyl et al. 2010, Sepulveda et al. 2013) and degrading habitats (Roberts et al. 1995, Zambrano et al. 2001, Scheffer 2004, Walsworth et al. 2020). As such, invasive fishes have become the focus of control and removal efforts in many ecosystems globally (Pinto et al. 2005, Søndergaard et al. 2008, Zelasko et al. 2016, Marsden and Siefkes 2019, Budy et al. 2021). However, synergistic disturbances can limit the ecosystem response to such efforts (Beklioglu and Tan 2008), and severely degraded ecosystems may take decades to manifest a restoration response (Rapport and Whitford 1999, Clewell and Aronson 2013). My results suggest a response in aquatic macrophytes to a large-scale carp removal program, which appears to provide an indirect benefit to the macroinvertebrate community, indicating a positive ecosystem response to carp removal. As carp biomass declined, the expansion of native, non-native, submerged, and mixed macrophyte communities increased macrophyte richness. Macroinvertebrate community structure varied among macrophyte habitat types, with macroinvertebrate biomass, richness, and predators being much more prevalent in mixed macrophyte habitats than other habitat types. Macroinvertebrate biomass and richness was higher in all vegetated macrophyte habitats types when compared to bare sediment. However, persistent lake level declines caused by multiyear drought likely limited the magnitude of these responses, and may have prevented additional community level responses such as increased macrophyte abundance, and macroinvertebrate biomass and richness with carp removal. Despite the challenges presented by declining lake levels, my results suggest that the carp removal program on Utah Lake is successfully reestablishing desired ecosystem conditions expected to be beneficial to both native species conservation and recreational users.

Fish removal programs often target benthivorous fishes to reduce their impacts on aquatic macrophyte abundance and diversity (Robel 1961, King and Hunt 1967, Crivelli 1983, Roberts et

al. 1995). In Utah Lake, proportional cover of submerged and herbaceous aquatic macrophytes, including curly leaf pondweed, sago pondweed, water plantain, and curly dock, increased as carp biomass declined, consistent with previous research (Black 1946; Robel 1961; Roberts et al. 1995; *but see* Moyle and Kuhn 1964). Thick-stemmed emergent macrophytes, such as hardstem bulrush and common reed may be more resistant to carp disturbance because of their robust stalks and deep roots, whereas submerged taxa have smaller stems and less intricate root zones (Fletcher et al. 1985, Miller 2004). Encouraging the reestablishment of submerged and herbaceous macrophytes, especially native species, can provide additional refuge from predators and expand total niche space by increasing habitat heterogeneity and surface architecture for food production, fish and macroinvertebrate reproduction sites, and colonizable surface area (Crowder and Cooper 1982, Papas 2007). Submerged vegetation also grows in deeper water farther from shore which may help stabilize sediments and buffer wave action (Hamilton and Mitchell 1996, Scheffer 2004). While care should be taken to avoid expansion of non-native macrophytes, successfully maintaining low carp biomass may allow for further establishment and expansion of submerged vegetation, thus enhancing habitat for aquatic animals and providing desirable ecosystem services by improving water clarity.

While submerged and herbaceous macrophyte cover increased as carp biomass declined, the proportion of vegetated sites relative to bare sediment decreased. This decline in macrophyte availability was likely a result of common reed control efforts and prolonged lake level declines experienced during my study. Light typically reaches more substrate in shallow lakes during lake level declines resulting in increased macrophyte growth (Blindow 1992, Beklioglu and Altinayar 2006), which can buffer wave action and stabilize sediment (Hamilton and Mitchell 1996, Scheffer 2001, Blindow et al. 2002), further increasing light penetration and macrophyte growth (Coops and Hosper 2002, Scheffer 2004). However, the extreme paucity of macrophytes combined with very high turbidity caused by waves, anthropogenic eutrophication, and chronic carp disturbance limits light penetration in Utah Lake, restricting the expansion of submerged

littoral vegetation (Buelow 2006, Landom and Walsworth 2021). Prolonged lake level declines draw water from existing macrophytes and strand their seed banks, exacerbating the effects of wave action on turbidity and further limiting macrophyte establishment and growth. Maintaining a low carp population during a period of stable lake levels would likely allow shoreline macrophytes to expand, stabilizing sediment and slowing wave action, which would increase light penetration and amplify submerged and emergent macrophyte growth. Increased macrophyte abundance would increase seed production and the seedbank, further promoting growth and expansion of the macrophyte community and increasing habitat and food for animals.

Restoring macrophytes in degraded lakes should increase habitat diversity and niche space (Crowder and Cooper 1982, Papas 2007), which can restore the animal community (Engel 1985, Hargeby et al. 1994, Jeppesen et al. 2012) and increase ecosystem resilience and resistance (Hairston et al. 1968, Chapin et al. 1997, Nyström et al. 2000, Folke et al. 2004). Vegetated habitats typically yield higher macroinvertebrate diversity, a common metric used to quantify aquatic ecosystem integrity (Barbour et al. 1996, Pond et al. 2008, Rehn 2009, Awal and Svozil 2010, Stranko et al. 2012, EPA 2017), than bare sediment. In Utah Lake, macroinvertebrate diversity was higher in macrophyte habitats than bare sediment, and was highest in diverse macrophyte habitats. Additionally, submerged macrophytes generally exhibit more leaf dissectedness, surface texture, and surface area than emergent taxa, characteristics that have been shown to support higher macroinvertebrate abundance and diversity (Humphries 1996, Papas 2007). Contrary to previous research (Krecker 1939, Cheruvelil et al. 2002, Balci and Kennedy 2003b), macroinvertebrate diversity in submerged macrophytes was only superficially higher than in emergent macrophytes and was not significantly different than in more diverse macrophyte communities. My inability to detect higher biomass and richness in submerged macrophytes may be caused by low submerged macrophyte sample size (n=11), the poor condition of observed submerged macrophytes in Utah Lake, or the use of qualitative rather than quantitative macrophyte classifications (e.g., emergent and mixed macrophyte communities were usually

more dense and extensive than submerged macrophytes when sampled). The limited abundance and meager condition of submerged macrophytes in Utah Lake is likely limiting macroinvertebrate habitat quality. However, sustained carp removal should increase the abundance of submerged macrophytes, and decreased foraging pressure should promote healthier plants, both of which should provide more habitat and greater macroinvertebrate diversity and biomass. The increased macroinvertebrate diversity in vegetated habitats implies that restoration of macrophyte habitats, especially diverse, and likely submerged, macrophyte habitats will aid recovery of ecosystem resistance and resilience.

Macroinvertebrates are important prey for most of the animal community in Utah Lake during at least one life stage, including both prized sport fishes as well as the threatened June sucker (Heckmann et al. 1981, Miller and Crowl 2006, Landom 2010, May et al. 2021). Complex macrophyte habitats provide predator refuge and breeding habitats for macroinvertebrates, which can promote prey production for higher trophic levels (Crowder and Cooper 1982, Hargeby et al. 1994, Merritt and Cummins 1996, Papas 2007). In Utah Lake, macroinvertebrate biomass was significantly higher in vegetated habitats compared to bare sediment and appeared to increase with habitat complexity. Submerged and mixed macrophyte communities appeared to maintain the highest levels of macroinvertebrate biomass, but were only present at low carp densities, suggesting that maintaining low carp biomass in Utah Lake should promote recovery of these high-quality habitats and the diverse and abundant macroinvertebrate communities they support. Increasing the abundance and condition of macrophytes, especially submerged and mixed macrophyte communities should restore habitat and increase the food supply for higher trophic levels.

Macroinvertebrate predator richness and the percent of the macroinvertebrate community represented by predator species are frequently used metrics of the biological integrity of aquatic ecosystems (Barbour et al. 1996, Chen et al. 2014, Fierro et al. 2018). In Utah Lake, predacious macroinvertebrate abundance and diversity, especially large predacious macroinvertebrates (>

5mm), increased in submerged macrophyte habitats, and was highest in mixed macrophyte communities. Three potential mechanisms may explain this result: 1) Macrophytes, especially mixed macrophytes, provide refuge from fish predators, increasing macroinvertebrate survival and augmenting the food supply to bigger and more diverse macroinvertebrate predators, 2) fish predators select for large macroinvertebrates before small ones; therefore, increased refuge releases larger macroinvertebrates from predation, or 3) greater habitat complexity in mixed and submerged macrophyte communities provides more diverse habitats and available ecological niches for macroinvertebrate predators and prey species to occupy. Indeed, predators often preferentially select large prey (Brooks and Dodson 1965, Li et al. 1985, Tate and Hershey 2003, Buria et al. 2007), but complex habitat can buffer that relationship by providing refuge and reducing predator efficiency (Crowder and Cooper 1982, Diehl 1988, 1992). The exact relationship between large macroinvertebrate predators, macrophyte communities, and carp removal needs further investigation. Regardless of the exact mechanism, increased macroinvertebrate richness and abundance, including predatory species, indicates a positive response to carp removal.

Ecosystems are rarely impacted by a single stressor, and the effects of multiyear drought likely limited the benefits realized through carp removal efforts in Utah Lake (Beklioglu and Tan 2008). Macroinvertebrate richness appeared to increase with lake level; however, biomass significantly declined. Increased richness may simply be a result of habitat availability, as inundated macrophytes were completely absent at lake levels more than 1.5 m below compromise in Utah Lake, and became more available as lake levels increased. However, despite lower macroinvertebrate richness at low lake levels, macroinvertebrate biomass increased, which may represent a concentration effect. As lake levels decline, aquatic prey are forced into a smaller water volume (Atwood et al. 2018) and macroinvertebrates are drawn from their macrophyte refuge into smaller areas of macrophyte habitat and into open water where sampling is most efficient. Reduction of carp was simultaneous with lake level declines in Utah Lake. The

simultaneous concentration of prey alongside benthivorous carp reductions may have allowed

detection of increased macroinvertebrate biomass at low lake levels. Alternatively, increased lake

levels correlate with greater lake volume, and despite detecting lower biomass per unit volume at

high lake levels, biomass in the lake as a whole may have actually increased. Despite the

challenges presented by multiyear drought, biotic communities within Utah Lake responded to

carp removal either directly (macrophytes) or indirectly (macroinvertebrates via macrophyte

habitats).

 Ecosystem degradation is challenging native biodiversity and the provision of ecosystem

services worldwide (Vitousek et al. 1997, Chapin Iii et al. 2000, Sala et al. 2000, Folke et al.

2004, Dudgeon et al. 2006, Bullock et al. 2011, Pereira et al. 2012, Reid et al. 2019), and

restoration is increasingly being used to reverse this degradation (Hobbs and Harris 2001, Ritchie

et al. 2012, Aronson and Alexander 2013, Clewell and Aronson 2013). My study provides a

framework to monitor and detect ecosystem response to restoration efforts when achieving full

restoration targets (e.g., eradication of carp) may not be possible or may take a very long time. By

monitoring multiple components of an ecosystem that represent a suite of ecosystem processes,

we gain a more complete understanding of the functional ecosystem response (Hobbs and Norton

1996, Ruiz-Jaen and Aide 2005, Moreno-Mateos et al. 2012, Stranko et al. 2012). While full

restoration may not be possible in many cases (Carpenter et al. 1999, Zedler 2000, Hobbs and

Harris 2001, Hobbs et al. 2009, Clewell and Aronson 2013, Green et al. 2014) including Utah

Lake, rehabilitation and continued maintenance may improve the value of these ecosystems for

native species, valuable sport animals, and other recreational purposes such as ecotourism.

Improving ecosystem conditions despite the inability to achieve restoration to a pristine state is

also imperative for aiding conservation efforts such as recovery of threatened and endangered

species worldwide (Webb and Shine 2000, Young 2000, Hobbs et al. 2009, Santos 2009, Glen et

al. 2013), including the threatened June sucker in Utah Lake. Establishing ecosystem monitoring

frameworks based on sound ecological theory and ability to detect desired changes over long-

time frames will provide valuable tools for evaluation of restoration success.

TABLES AND FIGURES

TABLE 1. Macroinvertebrate taxa observed in Utah Lake from 2011-2018, including the taxonomic level to which each was identified, NMDS ID, taxa Order, functional feeding group, and community composition. 'Taxa' were the taxa found during this study, and those used to calculate richness (except for Chironomidae, Dytiscidae, and Hydrophilidae which were sorted to subfamily, genus, and genus, respectively. ID is the short code used to identify taxa in the NMDS (Fig. 3). An (*) indicates superfamily rather than order. Functional feeding groups: predator (PR), shredder-herbivore (SH), collector-gatherer (CG), scraper (SC), collector-filterer (CF), parasite (PA), piercer-herbivore (PH), piercer (PI), shredder-detritivore (SD).

Taxa	ID (NMDS)	Order	Functional Feeding Group	Sum	Mean	Median	Max	Min	Samples	Percent occurance	Relative abundance
Taxa Sorted to Phylum											
Nematoda	Nem	NA	PA	8,077	17	0	670	0	196	41.60	1.86
Taxa Sorted to Subclass											
Oligochaeta	Oli	NA	CG	212,869	452	63	16,824	0	431	91.50	48.97
Hirudinea	Hir	NA	PA	57	0	0	14	0	19	4.00	0.01
Collembola	Col	NA	CG	2,688	6	0	829	0	113	24.00	0.62
Taxa Sorted to Order											
Ephemeroptera	Eph	NA		171	0	0	26	0	33	7.00	0.04
Isopoda	Iso	NA	CG	93	0	0	24	0	21	4.50	0.02
Lepidoptera	NA	NA		7	0	0	2	0	5	1.10	< 0.01
Plecoptera	NA	NA		1	0	0	1	0	1	0.20	< 0.01
Trombidiformes	Tro	NA	PR	7,357	16	3	372	0	332	70.50	1.69
Taxa Sorted to Family											
Aeshnidae	O. Aes	Odonata	PR	81	0	0	24	0	19	4.00	0.02
Ancylidae	P. Anc	Planorboidea*	SC	360	1	0	109	0	38	8.10	0.08
Ceratopogonidae	D. Cer	Diptera	PR	427	1	0	73	0	41	8.70	0.1
Chironomidae	subfamilies	Diptera	CG/PR	74,503	158	34	6,432	0	445	94.50	subfamilies
Coenagrionidae	O. Coe	Odonata	PR	840	2	0	101	0	87	18.50	0.19
Corixidae	H. Cor	Hemiptera	PR	102,371	217	2	10,936	0	301	63.90	23.55
Culicidae	NA	Diptera	CG/CF	2	0	0	2	0	1	0.20	< 0.01
Dixidae	NA	Diptera	CG	3	0	0	3	0	1	0.20	< 0.01
Dolichopodidae	D. Dol	Diptera	PR	82	0	0	37	0	10	2.10	0.02
Dugesiidae	T. Dug	Tricladida		1,945	4	0	333	0	67	14.20	0.45
Dytiscidae	C. Dyt	Coleoptera	PR	286	1	0	48	0	29	6.20	genus
Elmidae	NA	Coleoptera	CG/SC	1	0	0	1	0	1	0.20	< 0.01
Ephydridae	D. Eph	Diptera	CG/SH/SC/PR	15	0	0	8	0	6	1.30	< 0.01
Gerridae	H. Ger	Hemiptera	PR	72	0	0	33	0	8	1.70	0.02
Glossiphoniidae	R. Glo	Rhynchobdellida	PA	15	0	0	6	0	9	1.90	< 0.01
Gomphidae	NA	Odonata	PR	not found in sweep samples							
Gyrinidae	NA	Coleoptera	PR	not found in sweep samples							
Haliplidae	NA	Coleoptera	SH/PH/PR	1	0	0	1	0	1	0.20	< 0.01
Hyalellidae	A. Hya	Amphipoda	CG	6,850	15	1	565	0	236	50.10	1.58
Hydridae	H. Hyd	Hydroida	PR	12,391	26	0	3,388	0	121	25.70	2.85
Hydrophilidae	C. Hyd	Coleoptera	PR/CG	785	2	0	200	0	25	5.30	genus
Hydropsychidae	T. Hyd	Trichoptera	CF	45	0	0	9	0	19	4.00	0.01
Hydroptilidae	T. Hyt	Trichoptera	PH/SC/CG	291	1	0	77	0	34	7.20	0.07
Libellulidae	O. Lib	Odonata	PR	6	0	0	2	0	5	1.10	< 0.01
Lymnaeidae	L. Lym	Lymnaeoidea*	SC	49	0	0	8	0	18	3.80	0.01
Mesoveliidae	H. Mes	Hemiptera	PR	25	0	0	8	0	10	2.10	0.01
Nepidae	NA	Hemiptera	PR	not found in sweep samples							
Notonectidae	H. Not	Hemiptera	PR	251	1	0	36	0	28	5.90	0.06
Physidae	P. Phy	Planorboidea*	SC	3,585	8	0	544	0	184	39.10	0.82
Pisidiidae	V. Pis	Sphaeriida	CF	575	1	0	116	0	77	16.30	0.13
Planorbidae	P. Pla	Planorboidea*	SC	497	1	0	139	0	36	7.60	0.11
Polycentropidae	T. Pol	Trichoptera	PR	47	0	0	21	0	10	2.10	0.01
Psychodidae	D. Psy	Diptera	SC/CG	17	0	0	8	0	5	1.10	< 0.01
Simuliidae	NA	Diptera	CF	1	0	0	1	0	1	0.20	< 0.01
Stratiomyidae	D. Str	Diptera	CG	25	0	0	8	0	7	1.50	0.01
Syrphidae	D. Syr	Diptera	CG	11	0	0	5	0	3	0.60	< 0.01
Tabanidae	D. Tab	Diptera	PR	15	0	0	10	0	4	0.80	< 0.01
Tipulidae	D. Tip	Diptera	SD/CG	14	0	0	3	0	8	1.70	< 0.01
Taxa Sorted to Subfamily											
Chironominae	D. Chi	Diptera	CG	56,567	120	20	6,068	0	420	89.20	13.01
Orthocladiinae	D. Ort	Diptera	CG	5,056	11	0	608	0	225	47.80	1.16
Tanypodinae	D. Tan	Diptera	PR	9,823	21	0	1,432	0	175	37.20	2.26
Taxa Sorted to Genus											
D. Dytiscinae (adult)	NA	Coleoptera	PR	not found in sweep samples							
D. Dytiscus (larva)	family	Coleoptera	PR	57	0	0	32	0	4	0.80	0.01
D. Hygrotus (adult)	family	Coleoptera	PR	43	0	0	24	0	9	1.90	0.01
D. Hygrotus (larva)	family	Coleoptera	PR	145	0	0	39	0	20	4.20	0.03
D. Laccophilus (adult)	family	Coleoptera	PR	10	0	0	8	0	2	0.40	< 0.01
D. Liodessus (adult)	family	Coleoptera	PR	10	0	0	8	0	3	0.60	< 0.01
D. Rhantus	NA	Coleoptera	PR	not found in sweep samples							
H. Berosus (adult)	family	Coleoptera	PH/CG	52	0	0	16	0	6	1.30	0.01
H. Berosus (larva)	family	Coleoptera	PR	218	0	0	80	0	10	2.10	0.05
H. Hydrophilus (larva)	family	Coleoptera	PR	48	0	0	32	0	3	0.60	0.01
H. Peltodytes (adult)	family	Coleoptera	PI/SH/PR	1	0	0	1	0	1	0.20	< 0.01
H. Phaenonotum (adult)	family	Coleoptera	CG	8	0	0	8	0	1	0.20	< 0.01
H. Tropisternus (adult)	family	Coleoptera	CG/PH	74	0	0	16	0	8	1.70	0.02
H. Tropisternus (larva)	family	Coleoptera	PR	359	1	0	88	0	9	1.90	0.08

TABLE 2. Pairwise comparisons for macroinvertebrate community composition between macrophyte classifications. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

pairwise comparison	df	sum of squares	F-model	R2	p-value	p-adjusted
emergent vs open	1.00	3.90	11.57	0.03	0.00	0.006*
emergent vs potamogeton	1.00	0.56	1.62	0.01	0.07	0.40
emergent vs mixed	1.00	3.20	9.68	0.04	0.00	0.006*
open vs submerged	1.00	1.09	3.30	0.01	0.00	0.006*
open vs mixed	1.00	5.60	17.34	0.06	0.00	0.006*
submerged vs mixed	1.00	0.91	3.12	0.05	0.01	0.04 .

TABLE 3. Linear mixed effects model results for macroinvertebrate biomass response to carp biomass, lake level, and habitat type. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	estimate	std. error	df	t-value	p-value
mixed (intercept)	2.68	0.60	21.17	4.48	0.000204 ***
open	-1.52	0.30	437.87	-5.15	3.97e-07 ***
submerged	-0.16	0.57	447.87	-0.28	0.78
emergent	-0.36	0.31	430.61	-1.14	0.26
carp biomass	0.31	0.29	15.29	1.05	0.31
lake level	-0.89	0.37	247.74	-2.41	0.02 *

TABLE 4. Linear mixed effects model results for macroinvertebrate richness response to carp biomass, lake level, and habitat type. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	estimate	std. error	df	t-value	p-value
mixed (intercept)	2.42	0.12	30.76	20.30	< 2e-16 ***
open	-0.59	0.07	238.22	-8.79	3.06e-16 ***
submerged	-0.04	0.13	404.84	-0.27	0.78
emergent	-0.13	0.07	202.39	-1.77	0.08 .
carp biomass	-0.10	0.06	17.61	-1.61	0.12
lake level	0.14	0.09	185.25	1.69	0.09 .
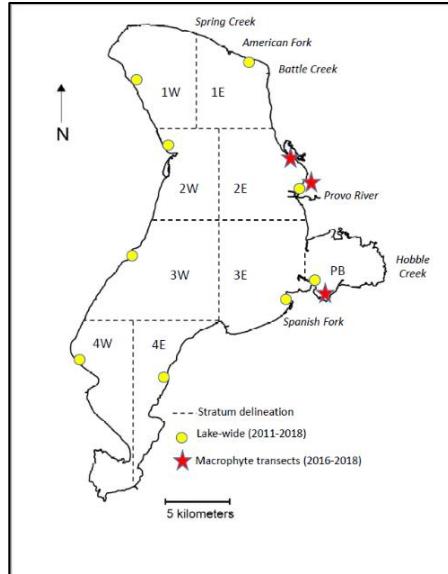
FIG. 1. Map of Utah Lake showing strata delineation and macrophyte-macroinvertebrate sampling locations. Dotted lines indicate strata delineation. Yellow circles indicate standardized lake-wide macrophyte sampling locations (2011–2018). Red stars indicate macrophyte transect locations (2016–2018).
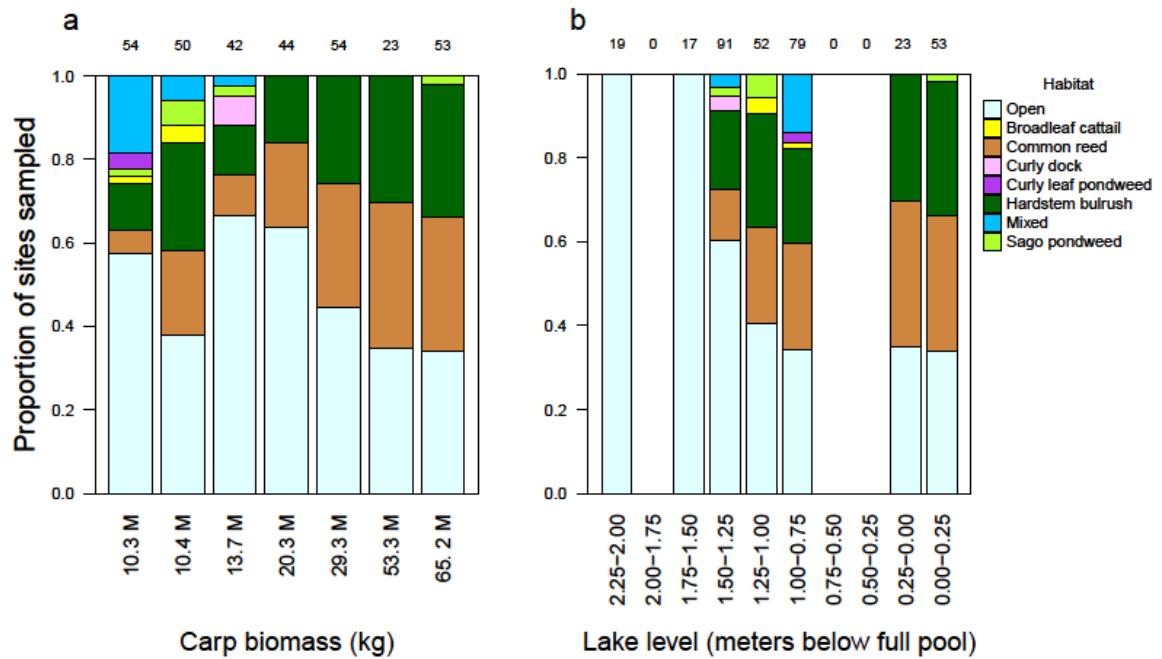
FIG. 2. Proportion of habitat types sampled from our standardized, lake-wide sites only, at varying carp densities (a), and at varying lake levels (b), observed in Utah Lake, UT from 2011 to 2018. Numbers above bars indicate total number of samples collected at each carp biomass (a) and at each lake level interval (b). The data used in panel a and panel b are the same, but aggregated by annual carp biomass estimates in panal (a), and by 0.25 m lake level increments in panal (b).
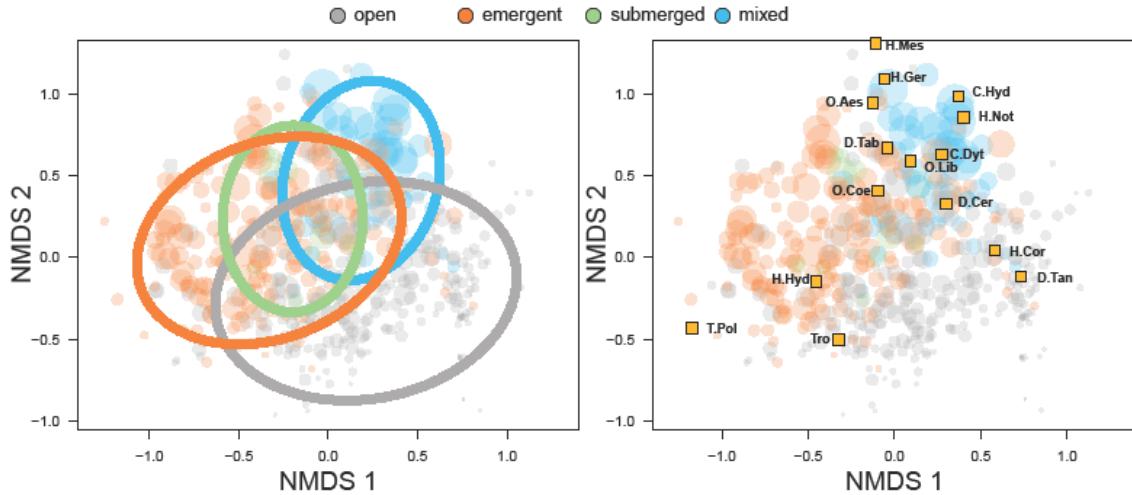
FIG. 3. NMDS results for macroinvertebrate samples, using taxa abundances, among macrophyte classes in Utah Lake, UT from 2011 to 2018 (n=454). Each point represents a sample collected from a particular habitat type, indicated by color, and the size of each point is scaled to richness per sample, where large points are taxa rich, and small points are taxa poor. Standard deviation confidence ellipses in panel (a) were set to 0.8 to encompass the 80% confidence interval for each habitat type. Orange squares in panel (b) are species centroids for all macroinvertebrate predators included in the multivariate analyses, used to visualize predator associations with specific macrophyte habitats.
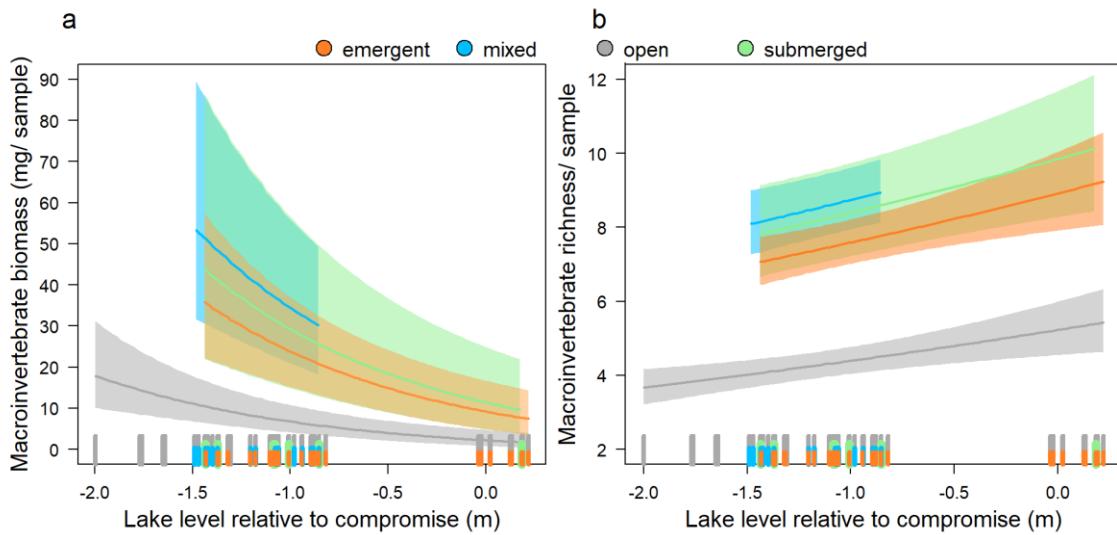
FIG. 4. Linear mixed-effects model predictions for macroinvertebrate biomass (a), and richness (b) within habitat classes, across lake levels. The dark colored lines are grand mean model predictions for each habitat class, and shaded regions indicates 1 standard error. The rug along the bottom illustrates at which lake levelseach habitat type was available to sample, and was actually sampled.

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CHAPTER III

USING FISHES' BODY CONDITION TO DETECT ECOSYSTEM RESPONSE TO
RESTORATION EFFORTS AND ANTHROPOGENTIC DISTURBANCE

INTRODUCTION

Fishes' survival, health, and reproductive fitness are largely dependent on their intra- and inter-annual growth, which are constrained by physiological factors and environmental conditions (Jobling 1995). Fishes' ability to detect and consume prey determines potential growth, but water temperature regulates the metabolic processes that convert food into energy and mass, as digestion, respiration, and waste production are all temperature dependent (Kitchell et al. 1977, Brandt and Hartman 1993, Hanson 1997, Reynolds 2017). Other environmental conditions including prey density and water clarity can influence fishes' ability to detect, capture, and consume prey. Generally, more abundant prey are easier to find and capture (Holling 1966, Mittelbach 1988, Ives et al. 1993, Salamolard et al. 2000, Turesson and Brönmark 2007), and reduced water clarity can limit prey detection by restricting visibility (Gardner 1981, Breitburg 1988, Vogel and Beauchamp 1999, Davies-Colley and Smith 2001, Turesson and Brönmark 2007). As such, fishes' ability to acquire energy via predation can be limited by both physical constraints, such as their ability to detect and capture prey, as well as by environmental conditions, including temperature and water clarity. Thus, changes to the biotic and abiotic conditions experienced by a fish population may impact their growth rates and therefore survival, health, and reproductive output.

Anthropogenic disturbances including establishment of invasive species, excessive nutrient inputs, and lake level modifications can separately, and synergistically, drive substantial changes to the biotic community and decrease water clarity in lentic ecosystems (Folke et al. 2004, Scheffer 2004). For example, introduced benthivorous fishes such as common carp (*Cyprinus carpio*) and bream (*Abramis brama*) disturb benthic sediments during foraging, which can destroy aquatic vegetation and reduce water clarity by resuspension (Meijer et al. 1990,

Breukelaar et al. 1994, Beklioglu and Tan 2008, Lin and Wu 2013). Likewise, excess phosphorus inputs to lakes, usually from sewage, industrial discharges, and runoff from agriculture, construction sites, and urban areas, can increase phytoplankton in the water column, decreasing water clarity and shading out submerged macrophytes (Schindler 1977, Carpenter 2005). Altered hydrology due to water development, water withdrawals, and multiyear droughts can encourage establishment of invasive plant species (Lesica and Miles 2004, Tulbure et al. 2007, Tulbure and Johnston 2010, Zohary and Ostrovsky 2011) and cause water levels to decline, reducing the availability of complex littoral habitat important for food production, refuge, and nursery grounds (Gaeta et al. 2014, Glassic and Gaeta 2019, Keeton 2019). Lower water levels can also reduce water clarity as decreased water volume concentrates suspended materials and sediments become more vulnerable to resuspension by wave action (Robel 1961, Bozelli 1994, Jeppesen et al. 1997, Roozen et al. 2003, Scheffer 2004, Özen et al. 2010). Increasing suspended materials in the water column can limit light penetration, decreasing subsurface photosynthesis and macrophyte growth (Scheffer 2004). The resultant loss of vegetation further exacerbates turbidity by destabilizing benthic sediments, rendering them even more vulnerable to wave action and resuspension (Phillips et al. 1978, Gerbeaux and Ward 1986, Scheffer et al. 1993, Lin and Wu 2013). Consequently, habitat degradation caused by human activities can influence associated lentic biota by negatively influencing physiological function, decreasing primary production in food webs, and by decreasing water clarity, resulting in diminished health of biota, and reduced visual foraging conditions.

Decreasing water clarity has ecological consequences that propagate through lentic food webs from macrophytes to invertebrates to fishes (Spence 1982, Bruton 1985, Hargeby et al. 1994, Henley et al. 2000, Scheffer 2004). Excessive suspended materials can cause direct mortality and reduce physiological function of lentic animals (Moore and Moore 1976, Vinyard and O'brien 1976, Gardner 1981, Breitburg 1988, Vogel and Beauchamp 1999), and indirectly impact food webs by decreasing primary production and macrophyte growth (Peddicord 1979,

Newcombe and MacDonald 1991, Henley et al. 2000). Macrophyte losses associated with

reduced light penetration can diminish animal habitat, reducing macroinvertebrate and forage fish

availability for predators at higher trophic levels (Crowder and Cooper 1982, Beckett et al. 1992,

Blindow et al. 1993, Hargeby et al. 1994). Suspended particles also decrease visibility, which can

impede reaction distance and prey acquisition in visually-feeding fishes (Moore and Moore 1976,

Vinyard and O'brien 1976, Gardner 1981, Breitburg 1988, Vogel and Beauchamp 1999, Davies-

Colley and Smith 2001). Decreased feeding efficiency, degraded habitat, and limited food supply,

can all negatively influence fish health and limit growth (Sykora et al. 1972, McLeay et al. 1984,

Bruton 1985, Newcombe and MacDonald 1991), which manifests in their body condition (a

relative measure of weight at length; Murphy and Willis 1996). Therefore, changes in fishes'

body condition may be a useful metric to monitor the effects of changing ecosystem conditions,

especially during ecosystem manipulations intended to improve habitat quality, such as

ecosystem restoration projects. For example, when water clarity is high, potentially indicating

improved ecosystem conditions, increased resource acquisition may improve fishes' body

condition. Conversely, when turbidity is high, resource acquisition may slow, and poor fish body

condition may indicate degraded ecosystem conditions.

Utah Lake is a large, shallow, eutrophic lake in central Utah which has experienced over

a century of persistent anthropogenic stressors including establishment of invasive species,

nutrient inputs, and lake level modifications. Human exploitation of water and fishery resources

in Utah Lake and the surrounding watershed has caused degradation of habitat and negatively

influenced the native plant and animal communities. Historic records of Utah Lake describe a

pristine lake with extensive aquatic macrophyte beds, a very different fish community, and water

much clearer than it is today (Cottam 1926, Heckmann et al. 1981, Janetski 1990, USFWS 1999,

Miller 2004). The native fish community, once dominated by trout, suckers, and minnows, is now

composed mostly of introduced species including common carp, white bass (*Morone chrysops*),

and black bullheads (*Ameiurus melas*; Arnold 1960, Heckman et al. 1981). Commercial fisheries,

water development, nearby agricultural practices, pollution, and the establishment of non-native species have caused extirpations of many native species (Heckmann et al. 1981). Of the thirteen fish species native to Utah Lake, only the Utah sucker (*Catostomus ardens)*, Utah chub (*Gila atraria*), and the endemic June sucker (*Chasmistes liorus*) remain, all of which are rare (Reynolds 2017, Heckman et al. 1981, USFWS 1999, Carter and Stevenson 2003, Anderson et al. 2007). Anthropogenic impacts such as eutrophication, shoreline development, altered hydrology, and introduced species continue to threaten desired sport and native fishes alike (USFWS 1999). In 2010, predaceous northern pike were detected in Utah Lake, adding yet another threat to native species (Fonken 2017, Reynolds 2017), and carp, introduced in 1886 (Heckman 1981), continue to degrade aquatic habitat by destroying aquatic vegetation and decreasing water clarity by resuspending lake bottom sediments (USFWS 1999).

A whole-lake common carp removal was initiated by the June Sucker Recovery Implementation Program in 2009, intended to aid recovery of the threatened (endangered at the time) June sucker by increasing aquatic macrophyte abundance and improving water clarity (USFWS 1999). Carp control efforts have removed more than 15,000 tons of carp from Utah Lake, and model estimates indicate a reduction in carp biomass greater than 75% by 2016 (Walsworth et al. 2020). However, Utah Lake entered a drought cycle in 2011, causing lake level and inundated vegetated habitat to decline. Ongoing Carp removal and a reduced carp population through time offer an ideal opportunity to examine the impact of a major restoration action on both water clarity and fishes' health, using fishes' body condition as a potential indicator of ecosystem response. Simultaneous drought provides the additional opportunity to investigate interactions between varying lake levels, carp biomass, and water clarity, but may mask the effects of carp removal if the effect of lake level is antagonistic to that of carp removal.

Here, I investigate two ecosystem responses to restoration: 1) the effect of carp biomass and lake level on water clarity, and 2) the effects of changing environmental conditions on fishes' body condition. I examined the relationships among fishes' body condition, carp density, Secchi

depth, temperature, and reproductive cycles for three fish species (June sucker, walleye - *Sander vitreus*, and white bass). June sucker were selected because they are endemic to Utah Lake, were listed as endangered at the beginning of the study (though they were down-listed to threatened in 2021; Federal Register 2021), and due to their zooplanktivorous position in the food web (USFWS 1999). Non-native walleye were selected because they are managed as a valuable sport fish in Utah Lake, consume prey fish such as young June sucker, and have evolved a light-gathering layer in their eyes (tapetum lucidum) which may benefit prey acquisition in low clarity conditions (Vandenbyllaardt et al. 1991). White bass are also managed as a sport fish, are visual feeders, and are one of the most abundant fish species in Utah Lake (Heckmann et al. 1981, Landom et al. 2014). Through these investigations, I aim to understand how restoration efforts affect fishes' health and whether we can use fishes' body condition to detect an ecosystem response to restoration in the presence of multiple stressors and in the absence of full ecosystem recovery. Improving our understanding of fishes' response to ecosystem manipulations will advance fishery management, endangered species recovery, and ecosystem restoration practices and strategies.

METHODS

Environmental data

Broadly, Secchi depth and water temperature were collected from 9 standardized, lake-wide sampling sites distributed throughout Utah Lake, with one site located in each of 9 strata (Fig. 5). The Utah Division of Water Quality (UDWQ) has maintained eight primary water quality sampling locations within Utah Lake since 1995 (Landom et al. 2019). I used a subset of UDWQ water quality data (2009 - 2016) which were, in general, collected monthly throughout the growing season (May - October) each year during my study period (2009 - 2018). However, some sample events were missed and, in some cases, sampling was conducted outside of the growing season. To facilitate standardization, data supplementation, and comparisons between

UDWQ data and Utah State University (USU) data, we focused our water quality data collection efforts at the same sites as UDWQ sites (Landom et al. 2019; Fig.). USU collected Secchi depth and water temperature data once monthly from six standardized sites in strata 3E and PB from 2002 - 2005, and 2008 - 2010 (2 of which were the same locations as the standardized, lake-wide sites for those strata), and then from all 9 standardized lake-wide sites from 2011 - 2018 (Fig. 5). I combined the USU and UDWQ Secchi depth and water temperature data for those years when data were collected during my study period (2009-2018). Generally, USU sample events occurred once monthly during the growing season, but in some cases additional sampling events were performed outside of the growing season. Both the UDWQ and USU collected one Secchi depth measurement during each sample event, and the temperature was recorded from the water surface and at 0.5m increments throughout the water column. The shallow condition, and frequent mixing due to wave action, prevent stratification in Utah Lake, so I averaged the profile temperature measurements from each site, resulting in one Secchi depth and one temperature measurement for each sampling event. I then averaged Secchi depth and water temperature by day and stratum resulting in one observation each per day and stratum on days either agency collected water quality samples. As fishes are mobile and may not exhibit site fidelity at the scale of my sampling strata, I assumed they were not constrained within the limits of each stratum, and were more likely influenced by condition in multiple strata, or lake-wide conditions. Therefore, I averaged Secchi depth and temperature from all strata for each day to yield one average, lake-wide Secchi depth and temperature value for each day either agency collected water quality samples from Utah Lake.

Hourly estimates of Utah Lake surface elevation throughout my study period (2009–2018) were collected and made available by the Central Utah Water Conservancy District (Landom et al. 2019). The Central Utah Water Conservancy District measures lake level relative to an elevation locally referred to as "compromise" (1,368 m; 4,489 ft. above sea level) above which the Jordan River (which transports water from Utah Lake to the Great Salt Lake

downstream) pumping plant gates and pumps are left open to avoid flooding and allow excess

water to flow freely into the Jordan River. I averaged lake elevation for each day and then

averaged daily Secchi depth, temperature, and lake level data for 30, 60, and 90 days prior to

every day from 2009 - 2018 to examine different lagged effects.

I used annual carp population biomass estimates from Walsworth et al. (2020), which

were derived from an integrated age-structured population model incorporating commercial

fishing harvest, standardized seining, and lake level data. Carp biomass was estimated to be

highest in 2009 (73,117,405kg) before declining throughout the entire study period, reaching the

lowest level (10,316,458kg) in 2018 (Fig. 6a; Walsworth et al. 2020).

Fish body condition data

I used fish count, weight, and length data collected during four independent net sampling

efforts: 1) standardized, lake-wide seine samples, 2) fyke net samples, 3) trammel net samples,

and 4) commercial observer seine samples (Landom et al. 2019). Commercial carp fishermen

(Loy Fisheries), the Utah Division of Wildlife Resources (UDWR), and USU personnel pulled

the standardized, lake-wide seine nets by boat from approximately 300m to 600m offshore

towards the shoreline each August from 2012–2018. Typically, Loy Fisheries and USU personnel

performed three to five seine hauls per strata, though low lake levels prohibited standardized

seine sampling in Provo Bay in 2014, 2015, 2016, 2018. The UDWR and USU collected near-

shore fyke net samples (n=586) as part of annual fyke-net fish community monitoring efforts and

opportunistically to either catch June sucker near tributary mouths, or to obtain fish specimens for

stomach content and stable isotope analyses in other studies (Watson et al. 2013, Landom et al.

2019). Fyke net samples were usually collected during the growing season from 2009 - 2017,

primarily on the east side of the lake (n=394), and predominantly during the first four study years

(2009-2012, n=476). The UDWR and USU also collected trammel net samples (n=1,891)

opportunistically, primarily during the growing seasons from 2009-2018, mostly from strata 2E

and 3E (n=1,216), and almost entirely from the east side of Utah Lake (n =1,868). Typically, trammel-nets were deployed during USU research and UDWR monitoring activities as a targeted approach to capture June sucker near river mouths during the spring spawning run (Fonken 2017b). The UDWR, in collaboration with Loy Fisheries, collected commercial observer seine samples each month from 2009–2018 (n=298) across all 9 strata (Fonken 2019, Landom et al. 2019). UDWR personnel accompanied Loy Fisheries during carp removal efforts, counting all fish and measuring length and weight from a subset of each species caught per net. The goal of the commercial observer effort was for UDWR to observe at least 10% of all removal seine hauls per year (Fonken 2019, Landom et al. 2019).

I used dates from the scientific literature and linear modeling to approximate day of the reproductive year for three fish species in Utah Lake (June sucker, walleye, and white bass). I was able to approximate the end of the spawning period for each fish species by dividing each fish's weight by its length (a measure of body condition) and then plotting the weight-length relationship as a function of time. Visual inspection of each plot revealed a drop in body condition at the termination of each species' spawning period. I was able to assign day 1 of each species' reproductive cycle by adjusting the first day towards the end of the spawning period until I reached the best linear model fit (p-value and R^2) for each species. June sucker are endemic to Utah Lake and spawn during June. Linear models best fit the body condition data with June 8th as day 1 of the reproductive year for June sucker. Walleye usually begin spawning during ice-off from mid-April to mid-May (Bozeketal 2011, Schneider 1980), but in Utah Lake walleye are documented to spawn primarily from mid-March to mid-April (Heckman 1981). My linear model fit was optimized with April 1st as day 1 of the reproductive year for walleye. White bass generally spawn during March and April when temperatures are above 45°F (Berlinsky 1995, Webb 1968) and have been documented spawning in Utah Lake from mid-April to mid-June (Heckman 1981). Linear model fit was best with May 30th as day 1 of the reproductive year for white bass.

Statistical analyses

I used linear regression and multiple linear regression to examine the relationships among temperature, Secchi depth, carp biomass, lake level, and year. I used linear regression to investigate temporal trends in Secchi depth ($\log_{10}$ transformed) and temperature throughout my study period from 2009-2018. I also used linear regression to explore potential relationships among temperature, Secchi depth, and lake level. Additionally, I examined the relationship between Secchi depth ($\log_{10}$ transformed) and both carp biomass and lake level using multiple linear regression, to identify relationships between these potential drivers of fish body condition.

I fit linear mixed effects models to explore relationships among fish body condition, carp biomass, the environment, and each fish species' reproductive cycles. Each fish's body condition was determined by plotting its weight relative to length. Weight ($\log_{10}$ transformed) for each of the three fish species was modeled as a function of length ($\log_{10}$ transformed), Secchi depth ($\log_{10}$ transformed), lake level, water temperature, carp biomass (centered and scaled), and day of reproductive year (starting with the end of the spawning period). I fit the models using different lags (30, 60, and 90 days) to examine the impact of preceding conditions on fishes' current body condition for each of the environmental variables. Year and gear type were modeled as random effects. Linear mixed effects models were performed following procedures described in Gelman and Hill (Gelman and Hill 2006) and Zuur et al. (Zuur et al. 2009).

I used model Bayesian information criterion (BIC) to compare the influence of environmental lags and to remove variables with little or no influence on fishes' body condition, and variable t-values to determine which variables had the strongest influence on fishes' body condition. None of the lag periods demonstrated a marked improvement in BIC over any other lag period. However, as the data were most abundant and consistent when using 30-day lags, I focus on the results from the models incorporating environmental predictors with a 30-day lag. Using backwards selection from the full model, I removed dependent variables with the lowest t-value in sequence. The model with the lowest BIC score was selected as the final model. I considered

those variables remaining in the final model as those that had a significant influence on each fish

species body condition. I then used model t-values to determine the sequence of variable

importance for those remaining in the final model, where the highest t-value indicated the most

influential variable, and the lowest t-value indicated the least influential variable.

All statistical analyses were conducted using the R Statistical Computing Environment (R

Core Team 2020, version 3.6.3, 2020-2-29, "Holding the Windstock"). Mixed effects models

were fit using R packages "lme4" (Bates et al. 2015, version 1.1-23), and "effects" (Fox and

Weisberg 2019, version 3.6.3), and mixed effects model significance values and degrees of

freedom were determined using R packages "nlme" (Pinheiro et al. 2020, version 3.1-151), and

"lmerTest" (Kuznetsova et al. 2017, version 3.1-3).

RESULTS

Environmental conditions

Lake level fluctuated annually, with the highest levels peaking during spring (April-May)

and the lowest levels in late fall (October- November). Generally, the annual average lake level

declined throughout the study period, except in spring 2011 when the lake level rose to its

maximum height of 0.72m above compromise, and in 2017-2018 when the lake rose

approximately 0.5 meters from its lowest level (-2.54m below compromise) in October 2016

(Fig. 6b).

Secchi depth decreased throughout the study period ($p<0.01$, $R^2 = 0.17$), with the deepest

measurement (0.59m) occurring in September, 2011, and the shallowest (0.09m) in August, 2018

(Fig. 6c). Multiple linear regression revealed a significant increase ($p < 0.01$, $R^2 = 0.24$) in Secchi

depth with increasing lake level (Fig. 7a). Secchi depth trended deeper with increasing carp

density (Fig. 7b) but the relationship was not significant ($p=0.60$, $R^2 = 0.24$).

Water temperature varied widely within years, but did not change significantly across

years ($p=0.72$) and was not significantly related to Secchi depth ($p=0.68$), lake level ($p=0.74$), or

carp biomass (p=0.95). Growing season water temperatures (May to October) ranged from approximately 8°C to 30°C throughout my study period, with the coldest temperatures recorded in October and water temperatures usually peaking during July. The highest average lake-wide temperature (29.47°C) was recorded on June 29, 2015, and the lowest (8.40°C) on October 16, 2018. Mean water temperature was approximately 19.7°C with a median of 20.4°C.

Environmental and biotic influences on fish body condition

Secchi depth did not appear to influence fishes' body condition during my study period, but fishes' length and day of reproductive year were both significant predictors for all fishes, and water temperature, lake level, and carp biomass all influenced at least one fish species (Table 5).

June sucker weight was best predicted by a model incorporating only fish length (t= 118.97, p< 0.01, est. = 2.98, std. error= 0.025) and day of reproductive year (t= 5.74, p< 0.01, est. = 0.0002, st.error = 0.00003) as predictor variables (Fig. 8a, BIC = -1175.00). The random effects estimates revealed that June sucker body condition varied between years and gear types, with gear revealing a potential gear size bias. The year random effect estimates were highest for June sucker in 2009 (0.0031) and 2016 (0.0026), indicating higher average weight at length in those years, and lowest in 2011 (-0.0034) and 2015 (-0.0035; Fig. 8b).

Walleye weight was best predicted by a model incorporating length (t= 99.31, p< 0.01, est. = 3.16, std. error = 0.032), water temperature (t= -3.91, p< 0.01, est. = -6.87, std. error = 0.0018), lake level (t= 3.15, p< 0.01, est. = 0.062, std. error = 0.020), and day of reproductive year (t= 3.90, p< 0.01, est. = 0.00064, std. error = 0.00016) as predictor variables (Fig. 9a, BIC= -667.70). The year random effect estimates were highest for walleye in 2012 (0.0067) and 2018 (0.0061), indicating higher average weight at length in those years, and lowest in 2017 (-0.0094; Fig. 9b).

White bass weight was best predicted by a model incorporating length (t= 62.02, p< 0.01, est. = 2.78, std. error = 0.045) water temperature (t= -8.82, p< 0.01, est. = -0.0049, std. error =

0.00055), carp biomass (t= -14.72, p< 0.01, est. = -0.062, std. error = 0.042), and day of

reproductive year (t= -5.37, p< 0.01, est. = -0.00011, std. error = 0.000021) as predictor variables

(Fig. 10a, BIC = -8851.6). The year random effect estimates were highest for white bass in 2010

(0.22), indicating higher average weight at length in those years, and lowest in 2018 (-0.15;

Fig. 10b).

DISCUSSION

Increasing water clarity is a common goal of shallow lake restoration activities and is

expected to generate a suite of desirable ecosystem changes, including benefitting native and

sport fishes. While increased water clarity can benefit fishes' health directly via improved prey

acquisition, and indirectly through food web effects, fish growth is also impacted by other biotic

and abiotic interacting drivers. Here, I demonstrate that while water clarity increased with

increasing lake levels, it did not demonstrate a significant response to reduced carp biomass.

Interestingly, water clarity did not appear to influence fishes' body condition, but carp density,

lake level, temperature, and day of the reproductive year did. Day of the reproductive year was a

significant predictor of body condition for all three fish species (June sucker, white bass,

walleye), where body condition increased throughout their reproductive cycle. Water temperature

was a significant predictor of walleye and white bass body condition, where both were higher in

cold temperatures. Additionally, white bass body condition was higher at low carp densities, and

walleye body condition improved with increasing lake level. June sucker body condition did not

appear to respond to lake level, carp biomass, water temperature, or water clarity. Despite

detecting no direct response in fishes' body condition to changes in water clarity, my results

indicate that carp control and lake level management may influence fishes indirectly through

competitive release, changes to prey density, and by modifying macrophyte habitat.

Suspended materials are influenced by both abiotic and biotic factors, and can regulate

the growth and distribution of aquatic vegetation (Robel 1961, Phillips et al. 1978, Henley et al.

2000). Benthivorous fishes can increase suspended materials by destroying aquatic macrophytes and resuspending lake-bottom sediments during foraging activities (King and Hunt 1967, Zambrano et al. 2001). Likewise, declining lake levels can increase sediment resuspension by exposing more of the benthos to wave action (Hamilton and Mitchell 1996, Scheffer 2004). Removal of benthivorous fishes (Meijer et al. 1990, Drenner and Hambright 1999, Lin and Wu 2013) and lake level management (Coops and Hosper 2002, Gulati and Van Donk 2002) can reverse these trends, thereby reducing turbidity and increasing water clarity. In Utah Lake, water clarity increased with rising lake levels, but was not significantly influenced by reduction in carp biomass. Typically, littoral macrophyte communities buffer wave action and stabilize sediments in shallow lakes (Jackson and Starrett 1959, Madsen et al. 2001, Scheffer 2001). Without macrophytes, waves and benthivorous fishes have an even greater effect on sediment resuspension (Madsen et al. 2001, Scheffer 2001, Jeppesen et al. 2012), especially when lake level declines concentrate benthivorous fishes and increase wave resuspension (Hamilton and Mitchell 1996). Unfortunately, both average lake level and water volume declined simultaneously with carp biomass during this study. The extreme paucity of macrophytes, combined with chronic carp disturbance and heightened wave-induced turbidity during lake level declines potentially outweighed the benefits of carp removal on water clarity. Maintaining a low carp population during elevated, and natural seasonal lake level fluctuations would likely allow shoreline macrophytes to establish and slow wave action, decreasing the impact of waves on sediment resuspension, and improving water clarity as a result of carp removal.

Reduction or exclusion of benthivorous fishes such as carp from lake ecosystems can release macroinvertebrate prey from predation, allowing prey populations to increase and reducing interspecific competition (Zambrano et al. 2001, Miller and Crowl 2006, Bonneau and Scarnecchia 2015). Additionally, reduction of benthivorous fishes can promote recovery of high quality macrophyte habitat (Drenner and Hambright 1999, Søndergaard et al. 2008, Chapter 2), providing even higher quantities of macroinvertebrate prey for fishes. While white bass body

condition was much higher at low carp biomass during this study, neither walleye nor June sucker

body condition responded to changes in carp biomass. White bass are also becoming increasingly

dominant in fish catches in Utah Lake, and are the only species whose catch rate has increased in

response to carp biomass reduction (Landom and Walsworth 2021). White bass and walleye both

consume zooplankton as young-of-year and shift to macroinvertebrates and fishes as they grow

(Bonn 1953, Voigtlander and Wissing 1974, Beck et al. 1998, Hartman 1998, Starostka 1999,

Guy et al. 2002, Ahrens et al. 2010). However, walleye become piscivorous much earlier than

white bass (Heckmann et al. 1981, Beck et al. 1998), consuming almost exclusively fish

thereafter. White bass are opportunistic predators and rely more heavily on macroinvertebrate

prey throughout the remainder of their life cycle (Voigtlander and Wissing 1974, Heckmann et al.

1981, Beck et al. 1998). Indeed, white bass in Utah Lake rely heavily on macroinvertebrates

throughout their entire life cycle, likely a result from the lack of forage fishes (Heckmann et al.

1981). June sucker are primarily zooplanktivorous throughout their life-cycle (Billman 2005,

Kreitzer et al. 2010, Kreitzer et al. 2011); however, recent research indicates they can consume

macroinvertebrates as a large part of their adult diet (Crowl et al. 1998, May et al. 2021). Prey

release during carp removal may benefit white bass most, as they are generalists who depend

heavily on macroinvertebrates throughout their life cycle; whereas, walleye depend more heavily

on forage fishes, and adult June sucker can maintain body condition by consuming zooplankton.

  Water temperature is an important determinant of fish growth, as metabolic rates are

determined by surrounding water temperature. Typically, fish growth increases with temperature

until reaching an optimal growth temperature, beyond which metabolic costs become too high for

consumption to keep pace with respiration, driving growth declines and eventually becoming

lethal (Kitchell et al. 1977, Hanson 1997, Gaeta et al. 2012). In this study, walleye and white bass

body condition were highest at lower temperatures. Walleye are classified as cool water species

and prefer summer water temperatures between 20-24°C with an upper incipient lethal limit of

29.7°C (Bozek et al. 2011). White bass prefer warmer temperatures ranging from 28-30°C and

avoid temperatures above 33°C (Barans 1973, Eaton et al. 1995). Utah Lake temperatures often exceed 24°C which may increase walleye metabolic rate and slow growth, especially at the highest temperatures which can reach 30°C during mid-summer. However, temperatures between 24-30°C are within the preferred temperature range for white bass. While a change from sub-optimal to optimal summer water temperatures could account for the increase in white bass body condition and population size throughout my study period, variation in water temperature between years was minimal, despite changes in water level, and no long-term trend in temperature was observed. Alternatively, reduced body condition at warmer temperatures may be due to increased consumption required to meet metabolic requirement as temperatures rise. If food is limited, then when it is warm walleye and white bass may not be able to consume enough prey to maintain metabolic requirements. Additionally, fish tend to grow and increase in body condition throughout the entire growing season (May-Oct in Utah Lake) in temperate regions to accumulate energy reserves for winter survival (Conover 1990, Quinn and Peterson 1996, Huss et al. 2008). Very few of the fish used for this study were captured during winter, limiting most of my data to growing season temperatures. Water temperatures were hottest in July and declined in the later, cooler months of the growing season (September and October) when fish have had more time to accumulate mass throughout the growing season. Regardless of the exact mechanism, fishes' metabolism and environmental conditions associated with water temperature appear to influence fishes' body condition.

As Utah Lake's bathymetry and immediate surrounding topography are characterized by low relief, changes in lake level can cause either the drying or inundation of extensive areas of shoreline and may influence thermal dynamics. While white bass and June sucker body condition did not respond to changing lake level conditions, walleye body condition increased significantly at higher lake levels. Vegetated habitats become increasingly available in Utah Lake as the lake level rises, providing increased macroinvertebrate biomass and richness as prey for higher trophic levels (Chapter 2). Increased prey availability may drive a bottom-up cascade, providing more

food to forage and prey fishes, thus increasing food quality and supply to apex predators like walleye. Habitat complexity also influences predator-prey interactions by providing substrate and refuge, where predators appear most successful at intermediate levels of complexity (Crowder and Cooper 1982, Mocq et al. 2021). Macrophyte use by walleye may also reflect their physiological aversion to light or provide advantageous visual foraging conditions (Bozek et al. 2011). Walleye also prefer mesotrophic conditions with low light and deep, cool water (Bozek et al. 2011). Higher lake levels in Utah Lake may provide these conditions due to increased thermal mass reducing warming throughout summer, as well as increased inflows from cold-water tributaries providing thermal refuge. Environmental conditions at varying lake levels may influence walleye in multiple ways, but the result of interacting conditions at higher lake levels appears to benefit walleye more than white bass or June sucker.

June sucker body condition was not significantly influenced by water clarity, water temperature, carp biomass, or lake level. While macroinvertebrate prey may be limited due to interspecific competition and lack of macrophytes, June sucker also prey heavily on zooplankton and can likely obtain enough zooplankton food to maintain body condition during stressful conditions. Indeed, turbid conditions may benefit planktivorous fishes such as June sucker by reducing predation mortality by piscivores and their ability to capture zooplankton prey may not be limited in the same way as visually feeding fishes (De Robertis et al. 2003). Furthermore, varying lake levels appear to have the greatest impact on littoral fishes. June sucker are stocked into Utah Lake as subadults (Ehlo et al. 2019) who appear to thrive in both littoral and pelagic zones (USFWS 1999, Buelow 2006, Billman 2008, Marsh & Associates 2016). June sucker also evolved in the arid desert environment of Utah Lake where water temperature and lake level can be highly dynamic (Buelow 2006), though exacerbated in recent years by anthropogenic uses. Adult June sucker likely evolved traits such as temperature tolerance and open water planktivory which allow them to adapt to varying environmental conditions in Utah Lake more easily than other, introduced fishes (Buelow 2006). However, juvenile June sucker may respond differently.

No juvenile June sucker were captured or analyzed during this study, and very little evidence exists for June sucker recruitment in Utah Lake since their listing as endangered in 1986 (USFWS 1999, Wolff et al. 2013). Changes to spawning habitat, the paucity of macrophyte refuge and rearing habitat, predation by non-native fishes, and decreased food production in macrophyte habitat, may be important factors limiting June sucker recruitment and recovery in Utah Lake (Keleher et al. 1998, USFWS 1999).

My ability to detect the effects of certain environmental conditions on fishes' body condition was likely limited by the data available in this study. While water clarity has been demonstrated to impact fish foraging in other studies (Vinyard and O'brien 1976, Gardner 1981, Breitburg 1988, Vogel and Beauchamp 1999, Davies-Colley and Smith 2001), I did not detect any direct responses to water clarity for the three species examined here. However, average lake-wide Secchi depths only varied by 0.5 meters (0.09m to 0.59m) in this study, and most values were observed between 0.17m to 0.37m (mean $\pm$ 1 standard deviation). The lack of contrast among water clarity conditions likely precludes my ability to detect a response in fishes' body condition to water clarity in this study. Additionally, lake level declined at the same time as carp biomass during this study, which may have masked fishes' response to either variable. Despite the potentially counteracting effects of declining lake levels during carp removal, I was still able to observe a body condition response to varying intensities of both, which would likely be heightened during naturally occurring or controlled higher lake levels. Continued carp removal during higher water years, and naturally occurring lake level fluctuations, should allow emergent and submerged macrophytes to recover and increase food and refuge for fishes such as the June sucker, as well as providing more contrast in the dataset.

Biological integration of environmental conditions by animals can provide useful metrics for monitoring ecosystem response to management and restoration actions. For example, monitoring walleye spawning date can indicate biological responses to, and impacts of, climate change (Schneider et al. 2010), macroinvertebrate assemblages can be used to indicate the

ecological condition of water bodies (Hilsenhoff 1987, Hawkins et al. 2000, Rehn 2009, Awal and Svozil 2010), and chlorophyll concentrations can indicate eutrophication and loss of apex predators in lake ecosystems (Carpenter et al. 1985, Drenner and Hambright 1999). My study provides an additional monitoring framework where fishes' body condition can indicate ecosystem response to restoration, even when achieving full restoration targets (e.g., eradication of common carp) may not be possible or may take a very long time. While full restoration of Utah Lake may not be plausible, rehabilitation and continued management will likely improve the value of the ecosystem for native aquatic species, the valuable sport fishery, and other recreational purposes. Improving desired ecological characteristics despite the inability to achieve restoration to a pristine state will be imperative for aiding recovery of imperiled species worldwide, including the threatened June sucker in Utah Lake. Establishing multiple ecosystem indicators allows for a more holistic monitoring approach to ecosystem restoration, and defining these frameworks based on sound ecological theory and ability to detect desired changes will provide valuable tools for evaluation of restoration and management success.

TABLES AND FIGURES

TABLE 5. Mixed effects model selection and parameter estimates for all three selected fish species including change in BIC from the best model (Δ BIC), and the p-values, model estimates (est.) and standard error (std.er) for each of the dependent variables at each step of the model selection procedure.

| Model Dependent Variables (Weight ~)	Δ BIC	p-length	est/st.er	p-secchi	est/st. er	p-level	est/st.er	p-temp	est/st. er	p-carp	est/st.er	p-doy	est/st.er
June sucker model selection													
length + doy		<0.01***	2.98/ 0.025									<0.01***	0.0002/ 0.00003
length + secchil + doy	6.40	<0.01***	2.98/ 0.025	0.24	0.02/ 0.02							<0.01***	0.0002/ 0.00004
length + secchi + lake level + doy	11.00	<0.01***	2.98/ 0.025	0.07 .	0.04/ 0.02	0.09 .	-0.02/ 0.01					<0.01***	0.0002/ 0.00004
length + secchi + lake level + ave.temp + doy	15.50	<0.01***	2.98/ 0.025	0.05 .	0.04/ 0.02	0.83 .	-0.02/ 0.01	0.072 .	-0.003/ 0.001			<0.01***	0.0001/ 0.00004
length + secchi + lake level + ave.temp + carp + doy	21.99	<0.01***	2.98/ 0.025	0.038 *	0.04/ 0.02	0.046 *	-0.04/ 0.02	0.095 .	-0.002/ 0.001	0.27	0.01/ 0.01	<0.01***	0.0001/ 0.00004
length	24.90	<0.01***	3.01/ 0.025										
Walleye model selection													
length + lake level + ave.temp + doy		<0.01***	3.16/ 0.032			0.009 **	0.062/ 0.020	<0.01***	-0.0069/ 0.0018			<0.01***	0.00064/ 0.00016
length + ave.temp	0.30	<0.01***	3.14/ 0.032					<0.01***	-0.0086/ 0.0017				
length + ave.temp + doy	1.30	<0.01***	3.15/ 0.031					<0.01***	-0.0074/ 0.0017			0.011 *	0.00033/ 0.00013
length + secchi + lake level + ave.temp + doy	6.50	<0.01***	3.16/ 0.032	0.66	0.015/ 0.035	0.02 *	0.057/ 0.022	<0.01***	-0.007/ 0.0018			<0.01***	0.00067/ 0.00018
length + secchi + lake level + ave.temp + carp + doy	13.10	<0.01***	3.16/ 0.032	0.65	0.016/ 0.035	0.13	0.061/ 0.039	<0.01***	-0.007/ 0.0018	0.90	-0.0028/ 0.023	0.0097 **	0.00069/ 0.00025
length	18.30	<0.01***	3.16/ 0.032										
White bass model selection													
length + ave.temp + carp + doy		<0.01***	2.78/ 0.045					<0.01***	-0.0049/ 0.00055	<0.01***	-0.62/ 0.042	<0.01***	0.00011/ 0.000021
length + secchi + ave.temp + carp + doy	6.00	<0.01***	2.78/ 0.045	0.062 .	-0.02/ 0.011			<0.01***	-0.0048/ 0.00055	<0.01***	-0.63/ 0.043	<0.01***	0.00012/ 0.000021
length + secchi + lake level + ave.temp + carp + doy	8.90	<0.01***	2.78/ 0.047	0.0044 **	-0.035/ 0.012	0.01 *	0.025/ 0.0098	<0.01***	-0.0049/ 0.00055	<0.01***	-0.66/ 0.043	<0.01***	0.00013/ 0.000022
length + ave.temp + carp	19.40	<0.01***	2.78/ 0.042					<0.01***	-0.0059/ 0.00052	<0.01***	-0.62/ 0.042		
length + carp	136.40	<0.01***	2.80/ 0.039							<0.01***	-0.55/ 0.042		
length	266.40	<0.01***	2.81/ 0.011										

FIG. 5. Map of Utah Lake showing strata delineation and water quality sampling locations. Two sampling locations (one in Provo Bay and another in 3E) were in the same location during the entire sampling period (2005–2018). The overlapping sampling locations prior to 2011 were plotted over the sampling locations post-2011 to demonstrate they were the same location.
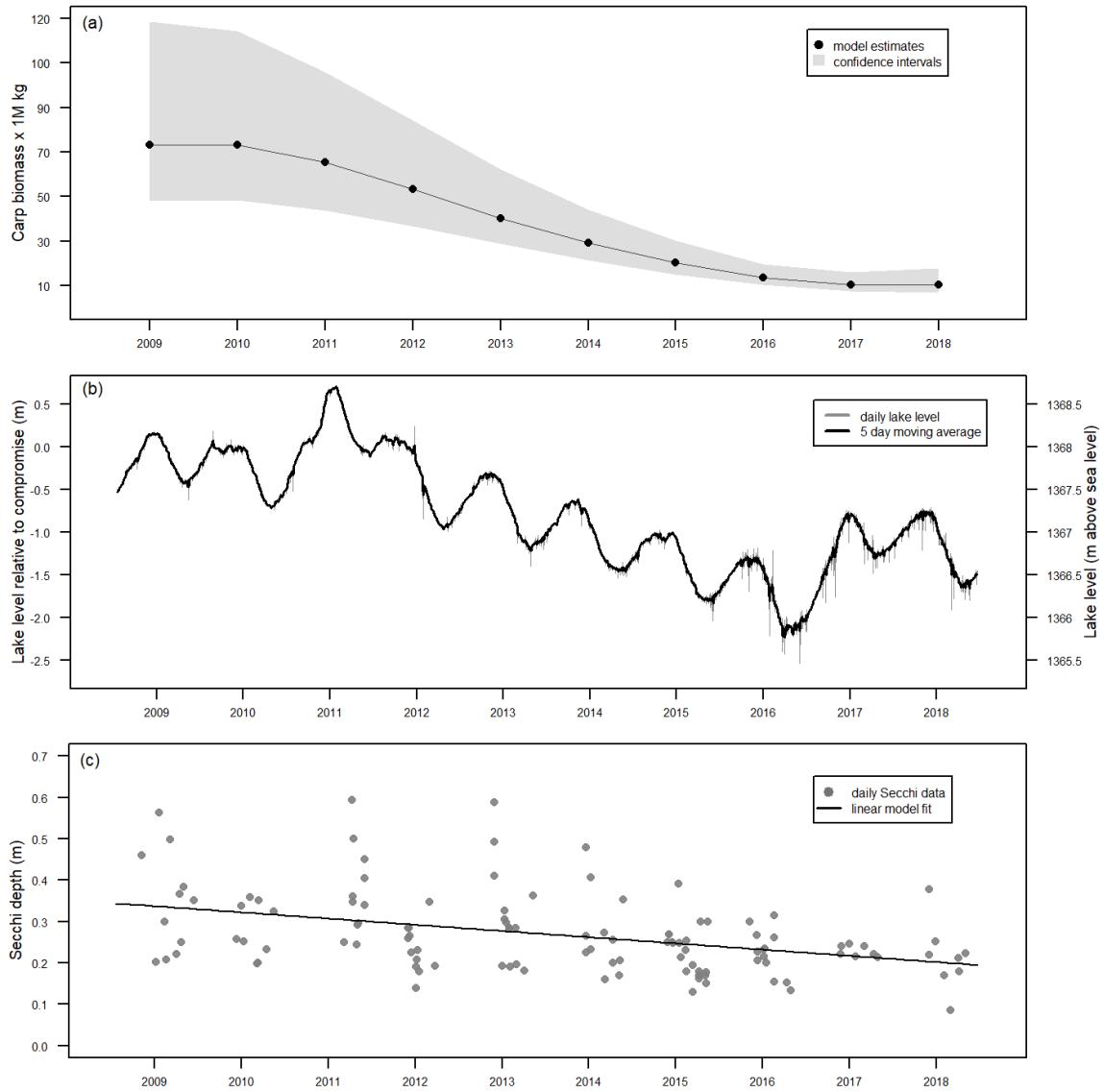
FIG. 6. Time series of a) lake-wide carp biomass model estimates (Walsworth et al. 2020), b) daily lake level, and c) average lake-wide Secchi depth measurements.
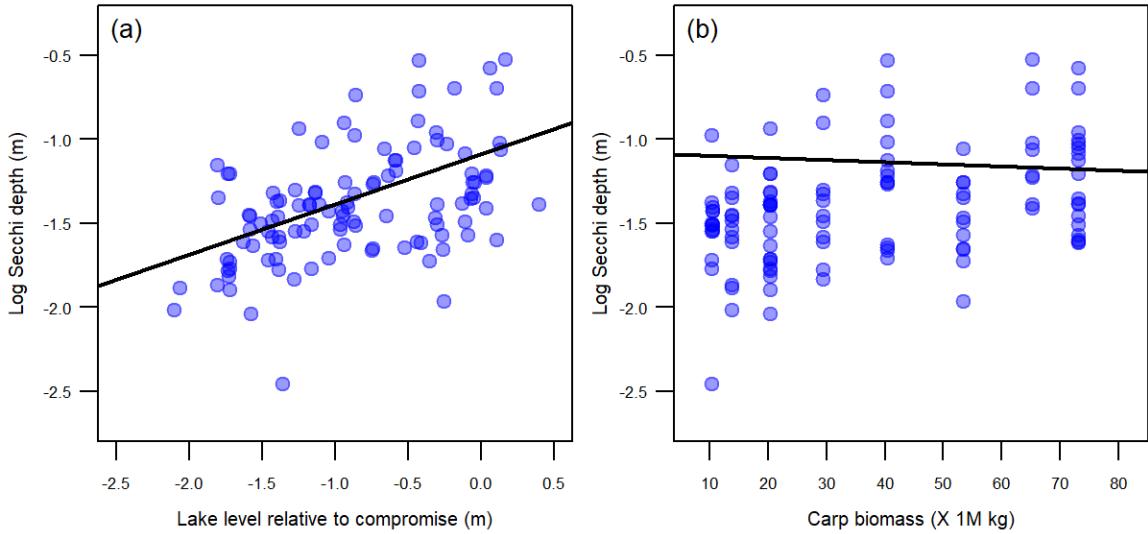
FIG. 7. Multiple linear regression model fit for a) Secchi depth at varying lake levels, and b) Secchi depth at varying carp biomass in Utah Lake from 2009–2018. The blue points are Secchi depth values measured during sampling events, and the black colored lines are model predictions showing the marginal effect after acounitng for carp in panel a, and after accounitng for lake level in panel b.
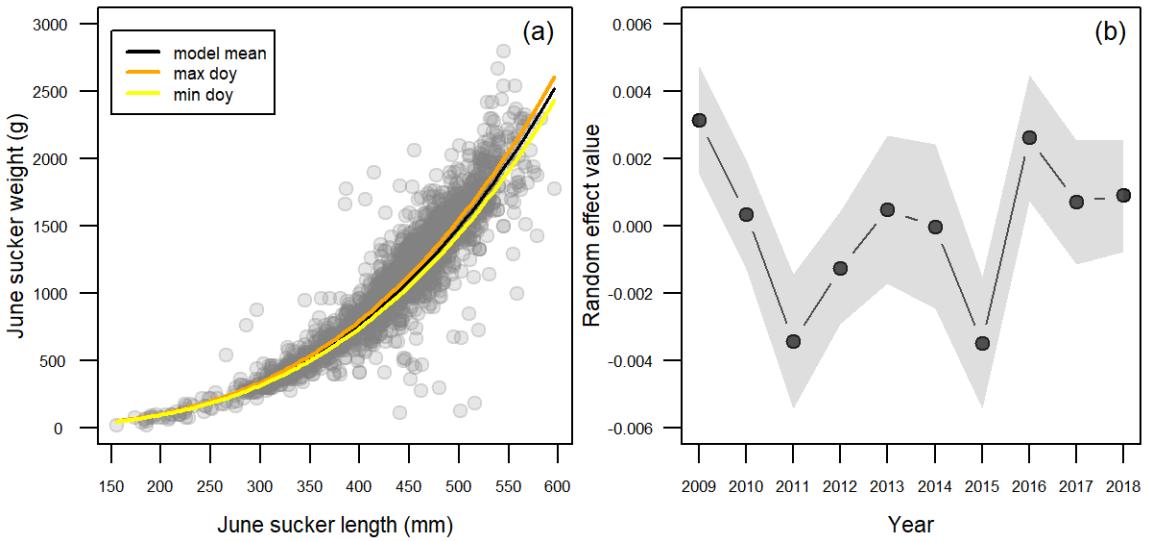
FIG. 8. Linear mixed effects model output showing the relationship between day of reproductive year and June sucker body condition (a), and the random effect values (black points) for each year showing variation in June sucker body condition among years (b). The shaded region in panel b indicates model confidence at 1 standard deviation. June sucker length and day of the reproductive year were the only significant variables in the final model.
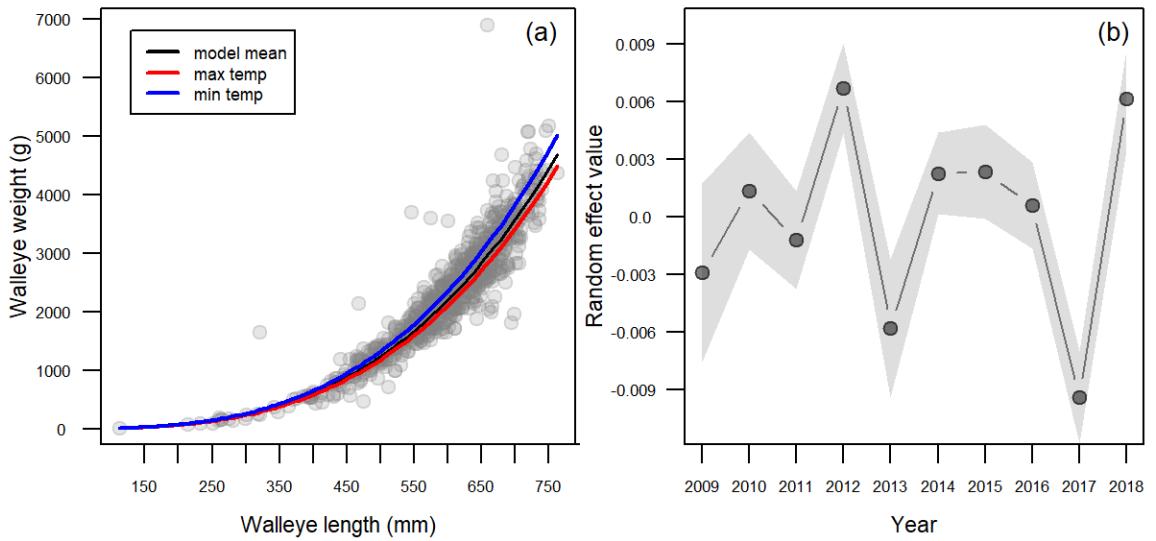
FIG. 9. Linear mixed effects model output showing the relationship between water temperature and walleye body condition (a), and the random effect values (black points) for each year showing variation in walleye body condition among years (b). The shaded region in panel b indicates model confidence at 1 standard deviation.
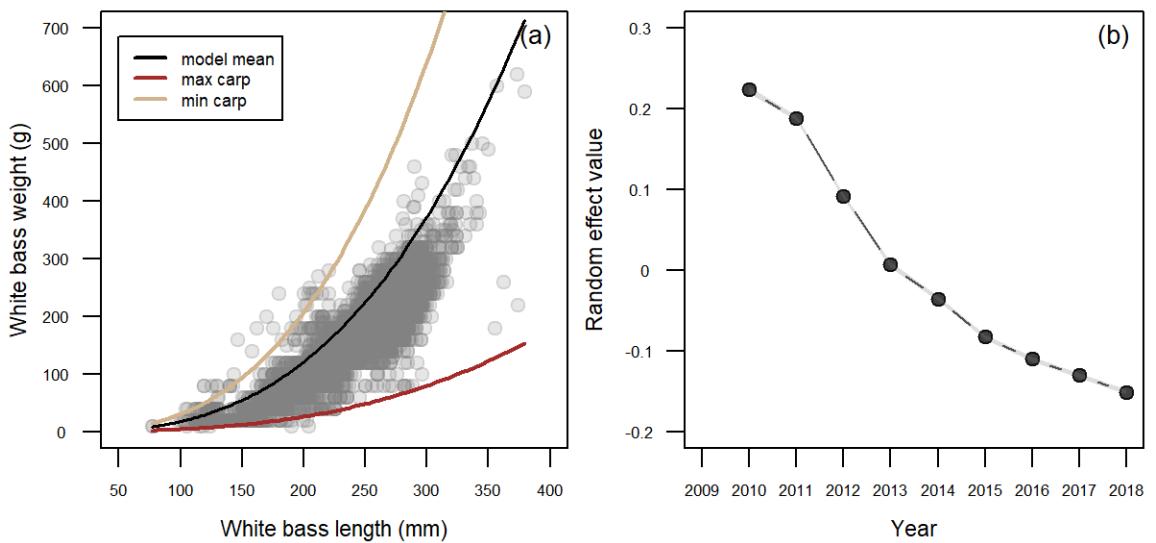

FIG. 10. Linear mixed effects model output showing the relationship between lake-wide carp bioimass and white bass body condition (a), and the random effect values for each year showing variation in white bass body condition among years (b). The shaded region in panel b indicates model confidence at 1 standard deviation.

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CHAPTER IV

CONCLUSION

Human activities can disrupt the structure and function of ecosystems, often causing

detrimental changes to native species and their environments (Vitousek et al. 1997, Sala et al.

2000, Folke et al. 2004). Ecosystem restoration efforts can encourage recovery from degraded

conditions by restoring native species interactions and habitat (Primack 2006, Clewell and

Aronson 2013, Hobbs 2013). However, restoration efforts often fail to produce desired results and

may require decades to achieve noticeable benefits, especially in severely degraded ecosystems or

where synergistic stressors promote resistance to restoration (Zedler and Callaway 1999, Palmer

et al. 2010, Thomasen and Chow-Fraser 2012, Angeler et al. 2020). Developing indicators that

can detect incremental ecosystem response is imperative for measuring restoration effectiveness

in these challenging situations and during the early stages of restoration when ecosystem response

may be occurring but limited in magnitude (Desender et al. 2007, Thomasen and Chow-Fraser

2012). An ongoing, large-scale carp removal effort aimed at restoring macrophyte habitat and

increasing water clarity in Utah Lake provided an ideal opportunity to investigate early indicators

of incremental response to restoration efforts in a severely degraded lentic ecosystem (USFWS

1999). In the preceding chapters, I tested metrics of the macrophyte, macroinvertebrate, and fish

communities as potential indicators of incremental response to restoration efforts.

Removing carp from Utah Lake should reduce macrophyte disturbance and increase

water clarity, both of which could promote recovery of aquatic macrophytes and the

macroinvertebrates that depend on them (USFWS 1999, Søndergaard et al. 2008). Therefore,

incremental changes in aquatic macrophyte and macroinvertebrate assemblages could indicate an

ecosystem response catalyzed by carp removal. In Chapter 2, I examined metrics of the

macrophyte and macroinvertebrate communities at varying carp biomass densities. Submerged,

native, herbaceous, and mixed-macrophyte communities were only present at low carp biomass,

and although not significant, macroinvertebrate richness trended upwards with reduced carp biomass. However, macrophyte relative abundance was lower at low carp biomass, and macroinvertebrate biomass trended downwards as carp biomass declined. I also found that macroinvertebrate predators, richness, and biomass varied among habitat types, where all three were lowest in bare sediment, increased in homogenous emergent and submerged macrophytes, and were highest in mixed-macrophyte communities. I hypothesize that lower carp biomass decreased macrophyte disturbance, especially of more vulnerable herbaceous plant species. The presence of these vulnerable macrophytes and mixed-macrophyte communities appears to increase habitat heterogeneity, thus providing the highest quality macroinvertebrate habitat. However, I suspect the antagonistic effects of multiyear drought may have offset some of the expected benefits of carp removal. Continuing to study the interactions between carp removal and the macrophyte and macroinvertebrate communities under a range of lake level conditions may shed further light on these relationships.

While increasing water clarity could improve foraging conditions for visually-feeding fishes, reduced carp densities could also reduce interspecific competition for prey. As prey become easier to find and more abundant with fewer carp, elevated resource acquisition by other fishes could result in improved body condition, providing another early indicator of ecosystem response to carp removal. In Chapter 3, I measured water clarity at a range of carp biomass densities to test for changes in water clarity associated with reduced carp. Additionally, I examined the effect of varying levels of carp biomass, water clarity, and other environmental conditions on the body condition of three fish species (white bass *Morone chrysops*, June sucker *Chasmistes liorus*, and walleye *Sander vitreus*) using a mixed-effects modeling approach.

Water clarity did not appear to respond to varying levels of carp biomass, nor did it appear to influence fishes' body condition. I hypothesize that decreasing lake levels during my study may have counteracted any increase in water clarity from carp removal. Alternatively, the substantial reduction in carp biomass may not have been sufficient to reduce turbidity, or carp

disturbance may not be the primary driver of turbidity in Utah Lake. In any case, the limited

range in water clarity during my study likely constrained my ability to detect a response in fishes'

body condition. Continuing carp removal could allow sediments to stabilize as lake levels rise

following drought release or as macrophytes reestablish, and the increasing water volume

commensurate with higher lake levels could dilute the current turbidity concentration.

Phytoplankton also contribute to turbidity, which can be limited by reducing nutrient inputs into

the lake, and increasing rooted macrophytes can stabilize sediments and reduce wave

resuspension. Implementing new turbidity management strategies and continuing to remove carp

could increase water clarity and expand the range of water clarity observed in Utah Lake, which

could drive stronger responses in fishes' body condition.

　　　　While no fishes' body condition responded to changes in water clarity, white bass body

condition was significantly greater at low carp biomass densities during this study, yet neither

walleye nor June sucker body condition responded to changes in carp biomass. This result agrees

with recent monitoring efforts indicating white bass are the only species whose catch rate has

increased in response to carp biomass reduction (Landom and Walsworth 2021). I hypothesize

that interspecific competition for prey was reduced as carp biomass declined, releasing

macroinvertebrate prey for other fishes. Prey release during carp removal likely benefits white

bass most, as they are generalists who depend on macroinvertebrates throughout their life cycle.

Conversely, walleye prey more heavily on forage fishes and adult June sucker can maintain body

condition by consuming zooplankton. Additionally, while carp biomass was a significant

predictor only of white bass body condition, other environmental conditions were significantly

related to body condition of other species. Specifically, white bass and walleye body condition

were both highest at lower temperatures, and walleye body condition increased with lake level.

　　　　My research provides empirical evidence that carp removal can improve desirable

characteristics of ecosystems both directly and indirectly, but ecosystem response can be slow

and complicated by other synergistic and antagonistic stressors. As demonstrated here and in

other systems (Beklioglu and Tan 2008, Lin and Wu 2013), carp removal can encourage recovery of macrophytes, but receding shorelines during drought and water withdrawals can negate the benefits of carp removal by stranding shoreline habitat. Carp removal can also improve water clarity (Beklioglu and Tan 2008, Lin and Wu 2013), but without rooted macrophytes, sediments are more vulnerable to disturbance and lower lake levels can exacerbate the resuspension characteristics of wave action (Hamilton and Mitchell 1996, Scheffer 2004, Jeppesen et al. 2012). Despite the complications presented by multiple interacting stressors, macrophyte and macroinvertebrate assemblages demonstrated associations with reduced carp biomass, where macrophyte types and assemblages most common at low carp biomass appear to provide the highest quality habitat for macroinvertebrates. Additionally, white bass body condition increased as carp declined. These changes could indicate an early ecosystem response to carp removal, potentially providing a framework for detecting ecosystem response to restoration efforts.

In addition to detecting responses to restoration efforts and multiple drivers simultaneously, incremental response indicators are useful for monitoring ecosystem responses that may follow alternate trajectories or result in novel ecosystem states. Unintended trajectories and novel ecosystems can still provide improved conditions relative to the degraded state which, in some cases, may require continual or even perpetual active management to maintain those gains (Angeler et al. 2020). For example, restoring the native fish community, stopping new land development in the watershed, and restoring the littoral fringe habitat to one without common reed (*Phragmites australis*) and other invasive vegetation is not likely in Utah Lake. Without accomplishing these tasks, Utah Lake represents a flagship novel ecosystem with a unique community assemblage and modified abiotic conditions. However, continued carp removal and water quality management could further improve the macroinvertebrate food supply, the sport fishery quality, recreational value, and macrophyte habitat in Utah Lake. Further, increasing macrophyte habitat in Utah Lake could improve food production and refuge habitat availability for the endemic and threatened June sucker. Improving refuge habitat, even without full

restoration, is a particularly important improvement in the novel Utah Lake ecosystem which is now composed primarily of non-native predator fish species. In degraded ecosystems with persistent anthropogenic influence and multiple stressors, simply improving desirable characteristics or moving towards less degraded but novel ecosystems may be the only realistic outcome. My research provides a framework for monitoring ecosystem changes that result from restoration efforts and in the absence of full recovery.

Indicators which suggest incremental improvement of desirable characteristics can provide support for continued restoration; whereas, an absent or negative response might support abandoning those efforts and pivoting focus to other restoration methods. I propose that future recommendations for monitoring restoration response on Utah Lake largely revolve around continued testing of the indictors provided here and development of additional response indicators. Continuing to monitor macrophytes, macroinvertebrates, and fishes' body condition after drought is essential for determining the full magnitude of carp removal on these indicators without the antagonistic influence of declining lake levels. Additionally, transect surveys (Cho and Poirrier 2005), sonar (Bennett et al. 2020), and infrared mapping (Ihse 2007) could provide tools for quantifying macrophyte response at a broader scale than the limited site survey conducted here. Collecting macroinvertebrates from deeper pelagic water, fish stomachs, and riparian areas could enhance our understanding of macroinvertebrate community response. Metrics of the zooplankton community, fish community assemblages, and water quality could also serve as early response indicators (Landom et al. 2019, Landom and Walsworth 2021). Continued development of the techniques tested here and establishing additional indicators could provide a more holistic monitoring approach while ensuring finer resolution in detection. While these tools provide a means to detect changes triggered by carp removal in Utah Lake, they can also be applied in other lentic ecosystems globally. Thus, my research provides a useful monitoring framework both in Utah Lake and in the rapidly growing field of ecosystem

restoration globally, while also furthering ecological understanding in the broader field of ecology as a scientific discipline.

Without active management, ecosystem disturbance associated with the growing human population will increase globally, resulting in continued degradation and loss of desirable ecosystem characteristics (Vitousek et al. 1997). Active ecosystem restoration and rehabilitation can promote recovery of desirable characteristics, but defining realistic goals within the constraints of budgets, politics, and ecological reality is imperative (Clewell and Aronson 2013, Angeler et al. 2020). Designing methods to monitor and quantify changes triggered by human intervention is increasingly important in these real-world applications to determine not only the realistic levels of improvement, but also the absence of response or responses that may further degrade an ecosystem (Clewell and Aronson 2013, Angeler et al. 2020). Knowledge gained through ecosystem restoration and response monitoring can improve scientific endeavors while simultaneously contributing to human understanding of our relationship with the natural world and the practice of environmental stewardship constrained within the context of a growing human population with an increasing influence on the natural environment.

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