The Health and Integrity of Utah Lake 2022 A Brief Ecological Evaluation

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David Richards
OreoHelix Ecological

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A Brief Ecological Evaluation

Left: One of thousands of relict snail shells that can be found on sandy beaches along the shores of Utah Lake. Right: Shell of *Helisoma newberryi newberryi*, the Great Basin Ramshorn, a former abundant resident of Utah Lake that has been extirpated.

To
Wasatch Front Water Quality Council, Salt Lake City, UT

By
David C. Richards, Ph.D.

OreoHelix Ecological, Vineyard UT 84059
Phone: 406.580.7816
Email: oreohelix@icloud.com

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Glossary

Alternative stable state ecosystems can exist under multiple "states" (sets of unique biotic and abiotic conditions). These alternative states are non-transitory and therefore considered stable over ecologically relevant timescales. Ecosystems may transition from one stable state to another, in what is known as a state shift (sometimes termed a phase shift or regime shift), when perturbed. Due to ecological feedbacks, ecosystems display resistance to state shifts and therefore tend to remain in one state unless perturbations are large enough. Multiple states may persist under equal environmental conditions, a phenomenon known as hysteresis. Alternative stable state theory suggests that discrete states are separated by ecological thresholds, in contrast to ecosystems which change smoothly and continuously along an environmental gradient.

Marten Scheffer (2009) provided a simple explanation for alternative stable states, "Suppose that you are in a canoe and gradually lean farther and farther over to one side to look as something interesting underwater. Leaning over too far may cause you to capsize and end up in an alternative stable state upside down. Although the details of the theory of alternative stable states may appear tricky, several key properties can be seen in this simple example. For instance, returning from the capsized state requires more than just leaning a bit less to the side. It is difficult to see the tipping point coming, as the position of the boat may change relatively little up until the critical point. Also, close to the tipping point resilience of the upright position is small, and minor disturbances such as a small wave can tip the balance.

Autotrophic production from complex organic compounds (such as carbohydrates, fats, and proteins) using carbon from simple substances such as carbon dioxide, generally using energy from light photosynthesis.

Benthic algae grow on the bottom sediments of fresh and salt waterbodies. Benthic algae are most commonly filamentous or colonial forms, but also may be microscopic single-celled organisms. Benthic algae perform various beneficial functions. Benthic algae provide food and habitat for many aquatic organisms. In this way they contribute to the biological productivity of aquatic systems.

Benthic invertebrates are invertebrates such as midge larvae, worms, beetles, bugs, and dragonfly larvae, etc., that live at the sediment water interface.

Biological integrity the capacity to support and maintain a balanced, integrated, adaptive biological system having the full range of elements (genes, species, assemblages) and processes (mutation, demography, biotic interactions, nutrient and energy dynamics, and metapopulation processes) expected in the natural habitat … (Angermeier and Karr 1994, Karr and Dudley 1981, Karr et al. 1986).

Detrital snow is the continuous shower of mostly organic detritus from plankton falling from the upper layers of the water column. It can be a significant means of exporting energy from the light-rich photic zone to the aphotic zone.

Ecological health implies a flourishing condition, well-being, vitality, or prosperity. An ecosystem is healthy when it performs all its vital functions normally and properly; a healthy ecosystem is resilient, able to recover from many stresses; a healthy ecosystem requires minimal outside care" (Karr 1996).

Ecological integrity is the sum of physical, chemical, and biological integrity. Integrity implies an unimpaired condition or the quality or state of being complete or undivided; it implies correspondence with some original condition. (Karr 1993, 1996).

Ecosystem engineer are species that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials, and in so doing they modify, maintain, and/or create habitats (Jones et al., 1994). Jones et al. distinguished (i) autogenic engineers, when the changes in the environment occurred via their own physical structure, living or dead tissues (e.g., coral reefs), and (ii) allogenic engineers, when they produced changes in the environment through the transformation of living or nonliving materials from one physical state to another via mechanical means (e.g., rabbits and burrows).

Ecosystem shift All ecosystems are exposed to gradual changes in climate, nutrient loading, habitat fragmentation or biotic exploitation. Nature is usually assumed to respond to gradual change in a smooth way. However, studies have shown that smooth change can be interrupted by sudden drastic switches to a contrasting state (*alternative stable state*) and, shallow lakes (Scheffer and Jeppesen 1998). Although diverse events can trigger such shifts, studies show that a loss of resilience usually paves the way for a switch to an alternative state. This suggests that strategies for sustainable management of such ecosystems should focus on maintaining resilience (Scheffer et al. 2001).

Effective number of taxa (ENT) is the number of taxa (species) that dominate the diversity of an ecological community and are most responsible for its function. It is an entropy-based idea that is often calculated as the Hillsenhoff Diversity Index exponentiated and is considered more informative than other diversity indices (Jost 2006).

Epiphytes grow on the surface of a plant and derive nutrients from the water or from debris accumulating around it. Epiphytes take part in nutrient cycles and add to both the diversity and biomass of the ecosystem in which they occur. They are an important source of food for many species

Eutrophication can be defined as the inorganic nutrient enrichment of natural waters, leading to an increased production of algae and *macrophytes* (aquatic plants). Many lakes are naturally eutrophic and often there is a progressive eutrophication as the lake matures

Heterotrophic production from other sources of organic carbon than light photosynthesis, mainly from plant or animal matter.

Microbial loop describes a trophic pathway where, in aquatic systems, dissolved organic carbon (DOC) is returned to higher trophic levels via its incorporation into bacterial biomass, and then coupled with the classic food web formed by phytoplankton-zooplankton-nekton.

Mollusks are mussels and clams (bivalves) and snails (gastropods).

Periphyton is a complex mixture of algae, cyanobacteria, heterotrophic microbes, and detritus that is attached to submerged surfaces in most aquatic ecosystems.

Phytoplankton are the autotrophic (self-feeding) components of the plankton community and a key component of freshwater ecosystems. The name comes from the Greek words φυτόν (phyton), meaning 'plant', and πλαγκτός (planktos), meaning 'wanderer' or 'drifter'. Phytoplankton obtain their energy through photosynthesis and must have light from the sun, so they live in the well-lit surface layers (euphotic zone) of lakes. In comparison with terrestrial plants, phytoplankton are distributed over a larger surface area, are exposed to less seasonal variation and have markedly faster turnover rates than trees (days versus decades). As a result, phytoplankton respond rapidly on a global scale to climate variations.

Resistance the property of communities or populations to remain "essentially unchanged" when subject to disturbance or restoration.

Resilience the capacity of a population/community of organisms or an ecosystem to respond to a perturbation or disturbance by resisting damage and recovering quickly.

River continuum is the entire watershed system as a continuously and predictable integrating series of physical gradients and associated biotic adjustments as the river flows from headwater to mouth and lakes. Within the stream system, longitudinal connectivity refers to the pathways along the entire length of a stream. As the physical gradient changes from source to mouth, chemical systems and biological communities shift and change in response. The *River Continuum Concept* can be applied to this linear cycling of nutrients, continuum of habitats, influx of organic materials, and dissipation of energy (Vannote et al. 1980).

Trophic cascade is an ecological phenomenon triggered by the addition or removal of top predators and involving reciprocal changes in the relative populations of predator and prey through a food web, which often results in dramatic changes in ecosystem structure and nutrient cycling. Trophic cascades in lakes have been well documented by Carpenter and Kitchell (1996).

Watershed connectivity is the flow and exchange of organisms, energy and materials throughout numerous pathways within a watershed ecosystem. Watershed connectivity supports the functions of the terrestrial and aquatic ecosystems and governs the interactions between the terrestrial and aquatic ecosystems in watersheds that provide ecosystem services that are vital to its health and well-being.

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Introduction

Utah Lake is a slightly saline- eutrophic to hypereutrophic- alkaline-wind and wave driven turbid-shallow-temperate lake existing in a semi-arid environment, unlike any other lake in the world. It is highly regulated and primarily managed as a reservoir with unnatural water level fluctuations that, among other things, prevent emergent aquatic native plants from becoming or remaining established, thus eliminating their much-needed contribution to ecosystem function. For well over 150 years Utah Lake has been cutoff and disconnected from its tributary arteries severing its river-lake- continuum-connection to its watershed, the life blood of its existence. Utah Lake's native biota have been completely extirpated or reduced to ecologically irrelevant levels or replaced by highly invasive analog species. Those few native ecologically effective species that remain do so under ever cumulating harsh environmental conditions that constrain their ability to self-regulate ecological interactions within the food web, including algal blooms, as they witness and respond to lopsided and anomalous trophic cascades. Uncontrolled urbanization and industrialization along with rapidly increasing desertification are exponentially deteriorating what remains of the lake's resilience and resistance to a looming ecosystem shift, potentially for the worse. Utah Lake has all but lost its ecological integrity and its health is in serious jeopardy.

Justification

There is much concern as to the future of Utah Lake and what can be done to improve its condition. We have been studying the ecology of Utah Lake for nearly a decade including all aspects of its food web including, chemistry, nutrients, primary producers, zooplankton, benthic invertebrates, fishes, trophic cascades, etc. and we are developing the most comprehensive bioenergetic mass balance food web to date. Our scientific findings combined with available other research directly related to Utah Lake and well-established concepts of lake ecology support our summary of the introduction presented here. The following discussion will provide readers with basic scientific findings of key components of Utah Lake's ecosystem in the hopes of directing future restoration of this unique body of water.

Measures of health and integrity

There are many methods (metrics) that can be used to measure the health and integrity of Utah Lake's ecosystem. Several generalized measures are presented in the following report; however, this is not an exhaustive or quantitative list. Richards and Miller (2019a) are developing a multimetric index of ecological integrity (MIEI) for Utah Lake that will include several dozen relatively easy to generate metrics that can be obtained by initiating a comprehensive and consistent monitoring program. We recommend that Richards and Miller (2019a) provisional MIEI be the starting point for further development of metrics holistically covering Utah Lake's ecosystem and necessary for evaluating changes in its health[1].

Phytoplankton Assemblages and Water Column Primary Production

Utah Lake primary production has been almost completely dominated by water column phytoplankton (algae) for at least 50 years indicating an unbalanced poorly functioning ecosystem. In a healthy state,

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[1] This MIEI will thoroughly address the unanswered question posed on multiple occasions to the DWQ Utah Lake Science Panel about the effort(s) and metric endpoints needed for improving water quality conditions in Utah Lake, "How clean is clean".

the lake should have relatively equal contributions from water column and benthic primary production given its shallow nature (Scheffer 1998, Scheffer and Jeppesen 1998). There are over 400 algal taxa reported from Utah Lake, however the effective number of phytoplankton taxa in the lake typically ranges from only 2 to 4, mainly comprised of potentially toxin producing undesirable cyanobacteria (Richards 2022a). Out of the 400 taxa, very few are ecologically relevant. In addition, we statistically analyzed chlorophyll *a* and cyanobacteria from Utah Division of Water Quality data from 1995 to 2018 and did not find any trends, either decreasing or increasing (Richards 2022b, 2022c) indicating the lake remains in its degraded resistant state.

Benthic Algae Primary Production

Benthic periphyton (algae) ecosystem functions are numerous and include significant contributions to gross primary production (Velasco et al. 2003, Vadeboncoeur et al. 2002), trophic interactions (Moulten et al. 2004), ecosystem engineering (e.g., biostabilization of sediments; Dodds 2003; Droppo et al. 2007; Spears et al. 2007b) and regulation of nutrient cycling across the sediment–water interface (Dodds 2003, Poulickova et al. 2008, Vadeboncoeur et al., 2003). Benthic algae are also vastly underappreciated contributors to pelagic fisheries (Vadeboncoeur et al. 2002) and also increase retention of nutrients. According to Dodds (2003), periphyton can:

- Remove nutrients from the water column and cause a net flux of nutrients toward the sediments,
- slow water exchange across the sediment/water column boundary thus decreasing advective transport of P away from sediments,
- intercept nutrients diffusing from the benthic sediments or senescent macrophytes,
- cause biochemical conditions that favor P deposition and can,
- trap particulate material from the water column (Adey et al. 1993).

Eutrophication is the most important determinant of shifts from benthic algal production to phytoplankton production in shallow lakes including Utah Lake, however many other factors are involved (Vadeboncoeur et al. 2002, 2003, 2008, Dodds 2003). This shift from benthic algal primary production to water column primary production is likely the single most important metric demonstrating the degradation of Utah Lake's ecosystem over the last 150 years.

Benthic (epiphytic and periphytic) algae are still present in Utah Lake but are limited by a paucity of available stable substrate attachment surfaces. The vast majority of the lake's substrate is a loose, unconsolidated mixture of silt, clay, and organic matter. We are presently conducting mesocosm experiments that will help understand epiphytic and periphytic algae growth rates in the lake. Periphyton grows rapidly on the sides of our mesocosms demonstrating that periphytic algae in the lake simply need suitable conditions to grow and potentially out compete water column phytoplankton for nutrients, including cyanobacteria.

Snails (gastropods) were the preeminent grazers of benthic algae and epiphytes growing on aquatic vegetation in Utah Lake in historic times. See section: Gastropods, snails, *The Grazers* for more details.

Macrophytes, aquatic plants

Macrophytes (aquatic plants) play a central role in stabilizing substrate, provide shelter and nurseries for zooplankton and fishes, reducing turbidity, regulating nutrient cycling, and regulating cyanobacteria blooms. Macrophytes were a primary factor that maintained Utah Lake's integrity, stability, resistance, and resilience and combined with molluskan ecosystem engineers reinforced these functions.

Unfortunately, macrophytes were significantly more abundant in Utah Lake in the past; macrophyte habitats are now a very small portion of the lake habitat (Richards et al. 2019, Richards and Miller 2017). Ecosystem services provided by macrophytes in Utah Lake included:

- Habitat structure that reduced abiotic and biotic stress (Gagnon et al. 2021),
- maintenance and increased biodiversity (Nordlund et al. 2016; Hyman et al. 2019; Ysebaert et al. 2019, Gagnon et al. 2021),
- shoreline protection from wind, waves, and ice (Fonseca & Cahalan 1992; van der Zee et al. 2012, Richards papers),
- carbon sequestration (Fourqurean et al. 2012; Rohr et al. 2018, Richards 2018),
- as allogenic ecosystem engineers, reduced turbidity and increased light penetration though filtration (Walles 2015, Richards papers) and increased sediment nutrient availability through biodeposition via pseudo-feces (Worm & Reusch 2000; Vinther & Holmer 2008, Richards 2018, Ysebaert et al. 2019), and
- macrophytes facilitated bivalves via protection from physical disturbances (Reusch & Chapman 1995, Richards), promoted larval settlement (Reusch 1998), and increased food availability (Ruckelshaus et al. 1993).

It is uncertain if macrophytes are increasing in the lake since the reduction of carp abundances and biomass circa 2009, as macrophyte abundance and diversity is highly variable between years due to several other environmental factors (Landom and Walsworth 2021, Walsworth and Landom 2021). Macrophyte diversity and abundance and their much-needed contribution to Utah Lake's ecosystem functioning is delegated to small, localized patches. Even though macrophytes contribute disproportionately to ecosystem functioning and the food web, the small area they occupy in the lake appears to have little overall benefit to the large area of nonexistent macrophyte habitat within the lake.

Zooplankton

Zooplankton grazers are the number one water column regulator of phytoplankton, including cyanobacteria in Utah Lake (Iglesias et al. 2007, Scheffer 1998, Richards and Miller reports). Zooplankton frequently move between habitats including daily horizontal migration. Subsequently zooplankton are a vital linkage between the pelagic, benthic and littoral zones (Vander Zanden and Vadeboncoeur 2002, Jones and Waldron, 2003). Zooplankton are the main consumers of phytoplankton and are in turn consumed by small fish, including all juvenile fishes and all juvenile and adult June Suckers in Utah Lake (Richards et al. 2019). They are the chief intermediaries between primary production and higher trophic levels, and thus play a critical role in Utah Lake food web dynamics (Richards et al. 2019).

Zooplankton obviously have top-down (trophic cascade) grazing effects on phytoplankton and cyanobacteria and in turn are affected by these (bottom- up effects) (Iglesias et al. 2007). Zooplankton also have different modes of feeding including grazing and predation, some of which prey upon other zooplankton. Most zooplankton are selective feeders. All of these complex interactions directly and indirectly influence nutrient cycling in the water column. Zooplankton excretion and respiration of nitrogen, phosphorus, and ammonia is immediately available and consumed by phytoplankton, often within minutes. This phytoplankton-zooplankton component of water column nutrient cycling has been well documented and known by limnologists and ecologists for several decades and is likely an important driver of cyanobacteria blooms in Utah Lake (Iglesias et al. 2007, Scheffer 1998). Medium- and large-sized cladocerans, typically *Daphnia* spp. can markedly reduce phytoplankton biomass (Jeppesen et al. 1990, Scheffer 1998), even in communities dominated by cyanobacteria (Jeppesen et al. 2003, Lampert et al. 1986, Brooks and Dodson 1965, Gorokhova and Engstrom-Ost 2009, and Hogfors et al. 2014). *Daphnia* spp. can feed on bacteria, protozoa, phytoplankton and even some small zooplankton, highlighting their important role in freshwater food webs (Yin et al. 2010). It has been demonstrated that intensive zooplankton grazing can promote a clear-water state (Scheffer 1998). For example, grazing by *Daphnia* sp. has been reported to be responsible for spring clearing in temperate lakes (Meijer et al. 1999).

Phytoplankton assemblages can have a bottom-up control on zooplankton assemblages via several mechanisms, including relative abundance, digestibility, nutrient content, etc. Conversely, zooplankton assemblages can have a top-down control on phytoplankton assemblages via selective and non-selective grazing and contrary to past assumptions, it has become apparent that zooplankton routinely and selectively rely on cyanobacteria in their diets. Consequently, zooplankton assemblages can shift phytoplankton assemblages toward better adapted cyanobacteria consumer species (Motwani et al. 2017, Woodland et al. 2013, Koski et al. 2002, Gorokhova and Engstrom-Ost 2009, Hogfors et al. 2014, Ger et al. 2016).

Utah Lake supports a zooplankton assemblage that varies spatially and temporally (Richards and Miller 2017). There are approximately 20 zooplankton taxa occurring in Utah Lake including cladocerans, copepods, and rotifer taxa from several functional groups, each with different life history and feeding strategies (Richards and Miller 2017, Richards 2019, Marshall 2019, and unpublished data). The taxonomy of Utah Lake's zooplankton has never been fully documented and verified. Because of this gap, zooplankton taxonomy is under revision by OreoHelix Ecological and River Continuum Concepts, Manhattan, MT. It is of utmost importance to correctly identify zooplankton taxa in the lake.

Unfortunately, zooplankton assemblages in Utah Lake have also undergone bottlenecks and assemblage shifts, including those stressors discussed in the previous sections that have resulted in Utah Lake's zooplankton assemblages becoming analogs of past natural assemblages and that may no longer be able to regulate cyanobacteria. One of the most important factors not discussed so far has been and continues to be predation on zooplankton by planktivorous invasive fish and how this affects cyanoHABs.

Fish predation on zooplankton, planktivory has strong deleterious effects on zooplankton prey. Planktivory also negatively affects entire zooplankton assemblages and often initiates trophic cascades throughout the food web (Carpenter and Kitchell, 1996, Scheffer and Jeppesen, 1998; Jeppesen et al., 1998; Moss et al., 1998, Iglesias et al. 2007). This can be especially catastrophic if planktivorous fish are invasive and the native zooplankton assemblages haven't evolved with invaders.

Planktivory is thought to be the main factor controlling the spatial distribution, abundance and body size of zooplankton in shallow lakes (e.g. Scheffer, 1998; Burks et al., 2002, Iglesias et al. 2007) and often induces major shifts in the size distribution of zooplankton (Hrbáček et al., 1961; Brooks and Dodson, 1965) or behavioral shifts (Timms and Moss, 1984; Schriver et al., 1995; Lauridsen and Lodge, 1996; Burks et al., 2002; Romare and Hansson, 2003). For example, in Lake Blanca, Uruguay, the small size of the dominant cladocerans and the dominance by copepods and rotifers likely reflect the extremely high abundance of planktivorous fish predators (Iglesias et al. 2007). The effect of planktivory on decreasing zooplankton size can increase the likelihood of cyanobacteria blooms. This is because larger sized zooplankton are often better at feeding on larger strands of algal particularly cyanobacteria (Carpenter and Kitchell 1988, Caroni 2010, Jeppesen et al. 2011, Attayde and Bozelli 1998, Carpenter et al. 1985, Jeppeson et al 2000, Jeppesen et al 2003, Lamper et al 1986, Gannon and Stemberger 1978, others). Sarnelle (2007) also reported that high abundances of generalist grazers (i.e., *Daphnia*) may control blooms when released from planktivorous fish predation (Ger et al. 2016).

Our group conducted the most extensive zooplankton diversity, abundance, and spatial and temporal dynamics research in Utah Lake to date. We found that diversity (approximately 20 taxa) was quite low compared to other lakes in North America (Richards 2019) and that the effective number of taxa was only 3 to 4. We also found that overall body size was lower than expected suggesting selective pressure from planktivorous fishes in the lake (Richards and Miller 2019). All the fish species in Utah Lake are planktivorous at least during juvenile stages. USU researchers have suggested that zooplankton body lengths have increased after the carp removal project was initiated but time will tell if this trend continues due to apparently increasing carp densities post 2013 (Walsworth et al. 2020, Walsworth and Landom 2021, Landom and Walsworth 2021).

In addition, zooplankton now appear to have limited control of phytoplankton densities in Utah Lake. The zooplankton to phytoplankton biomass ratio, Z/P is often used as a metric evaluating trophic status of a water body and ecosystem functioning, and as a component of food web models. Z/P typically decreases with increased eutrophication (Gulati, 1983; Andronikova, 1996; Jeppesen et al., 1999, 2000, 2005; Haberman & Laugaste, 2003, Blank et al. 2010). We calculated that Utah Lake Z/P varied seasonally with higher values in winter vs. summer. The highest Z/P was in March = 0.18, lowest in September and order of magnitude lower at 0.018 (annual mean = 0.07). Z/P showed that zooplankton grazing was very inefficient from June through November when harder to digest phytoplankton were dominant and infers that much of the unconsumed phytoplankton (and dead zooplankton) falls as detrital 'snow' to the sediments. Large amounts of detrital snow alter the benthic portion of the food web from past benthic algae autotrophic to heterotrophic and signify a food web much out of balance. It also emphasizes that the microbial loop in Utah Lake likely contributes disproportionately more to the food web than typical although there have been no studies on this important component in the lakes function.

Mollusks, the Catastrophic Loss of Utah Lake's Penultimate Ecosystem Engineers

Mollusk (mussels, clams, and snails) diversity and abundances peak in the Utah Lake-Jordan River drainage and the surrounding areas in the depauperate western USA (Richards 2017, Richards 2014). Utah Lake's historic mollusk diversity and abundances were due to its Lake Bonneville heritage of abundant nutrients, relatively high pH and high $CaCO_3$ levels originating from the > mile thick limestone base rock within the watershed (Richards and Miller 2019).

Native mollusks were the dominant benthic ecosystem engineers in Utah Lake when early explorers and Americans of European descent first arrived in the 1800's. Native mollusks were also responsible for much of the water column functioning (Richards 2014, 2017, 2018b, and 2019a) and until recently likely governed almost all its ecosystem functions. Unfortunately, their role as keystone species and ecosystem engineers has been eliminated.

Bivalves, clams and mussels, '*Poster Species for Water Quality*'

Utah Lake's native bivalves likely dominated the benthic invertebrate community responsible for water column nutrient cycling in Utah Lake both numerically and in terms of biomass ≥150 years ago. They performed both the function of particle removers from the water column and regulated other biota involved in water purification, including algae, bacteria, and fungi in the sediments (Ostroumov 2005, Newell 1988, Newell and Ott 1998). They also controlled the key process of oxidation of organic matter particularly the major oxidizer, bacteria (Wetzel 2001, Sorokin et al. 1997, Ostroumov 2005). Native mussels likely directly reduced the amount of particulate organic matter (POM) available to be remineralized by pelagic consumers and bacterioplankton in the lake (Officer et al. 1982, Newell et al. 2005). Bivalves are world renowned for the ability to filter large volumes of water and Utah Lake's native bivalves were likely able to filter the entire lake's water column in just a few days or weeks (Richards 2014, 2017, 2018b, and 2019a).

Native freshwater mollusks likely constituted the largest portion of benthic invertebrate standing crop biomass in Utah Lake. Consequently, mollusks were the primary contributors to calcium and carbonate cycling in the lake, both critical for regulating phosphorus in the water column (Toner and Catling 2020) and other nutrients and trace metals (Malathi and Thippeswamy 2013; Mann, 1964; Negus, 1966; Cameron et al. 1979; Liu et al. 2010).

Mollusks in Utah Lake bio-actively removed large quantities of $CaCO_3$ in the water column to grow their shells. Their living and empty shells bound $CaCO_3$ for perhaps hundreds of years in Utah Lake and thousands of years prior as Lake Bonneville. By actively removing $CaCO_3$ from the water column, mollusks allowed phosphate to precipitate from the water column as apatite further chemically reducing phosphorus from the water column and subsequently reducing the amount of phosphorus available to phytoplankton (water column algae). This biochemical reaction by mollusks also reduced pH (Toner and Catling 2020). Thus, the loss of native mollusks was in a large part responsible for increased phosphorus in the water column and current algal blooms. This loss was exacerbated by Americans of European decent induced reduction in tributary flows to the lake that had much more Ca^{2+} than the resulting closed basin Utah Lake, which then began to concentrate phosphate even more (Toner and Catling 2020).

At least one species of native mussel dominated the lake, the 'imperiled' *Anodonta californiensis/nutalliana (*common name = Floater). Several species of fingernail clams (Family Sphaeriidae) also occurred at very large densities. Examination of relict snail samples from the shoreline of eastern Goshen Bay, Utah Lake resulted in identification of eleven highly abundant taxa. Many of these species required cool-cold, well oxygenated water with thick stands of aquatic vegetation and ample benthic algal primary production.

Unfortunately, due to human activities, Utah Lake's native mollusk assemblage has all but been annihilated. The native mussel, Anodonta *californiensis/nutalliana*, is extinct in the lake even though the lake was home to more mussels than any other water body in Utah (Richards 2014). Fingernail clams, primarily *Sphaerium* sp. are almost extinct in Utah Lake and may now be below viable population levels and extinction prone. One invasive clam, the Asian clam, *Corbicula* sp. exists in the lake but even this highly invasive and tolerant species only occurs at relatively low densities due to degraded conditions. Of the eleven native snail taxa that historically occurred in the lake, only two tolerant taxa, *Physella* sp. and *Stagnicola* sp. remain.

Gastropods, snails, *The Grazers*

It is well known that grazers (herbivores) are critical to the health and integrity of ecosystems worldwide (Joern and Raynor 2018). Zooplankton are the water column phytoplankton grazers in Utah Lake, whereas, snails are the dominant benthic algae, periphyton, and epiphyte grazers.

Lake primary production typically responds positively to grazing (McNaughton 1979, Frank et al. 1998). Snails facilitate primary production by preventing self-shading, facilitate nutrient flux to the algae (periphyton/epiphyton), and recycling limiting nutrients (Lamberti and Resh 1983). Snail grazing causes periphyton and epiphyton to increase production consequently taking up more nutrients from the water column than would occur in the absence of snail grazers. Snail diversity and abundance was perhaps greater in Utah Lake than any other aquatic ecosystem in the western USA. (Richards and Miller 2019). The loss of snail herbivory (grazing) in Utah Lake is thus linked to the transition from clear water state with high levels of submerged vegetation to a turbid state with little to no submerged vegetation and super abundant phytoplankton (Jeppesen et al. 1997).

Utah Lake's native snail populations likely consisted of more than a dozen species, all of which had a different ecological niche and provided vital ecosystem functions in the lake (Richards 2014, 2017, 2018b, and 2019a). Almost all these taxa are extinct in Utah Lake including several species of springsnails in the genus, *Pyrgulopsis*, the pebble snail, *Fluminicola coloradoensis*, two valvata species, *Valvata humeralis*, the glossy valvata, and *Valvata utahensis*, the Utah round mouth snail or desert snail, *Planorbella binney,* the Coarse Rams-Horn, and the iconic *Helisoma newberryi newberry,* the Great Basin Ramshorn. Utah Lake probably supported he largest population of *Planorbella binney* in Utah (Oliver and Bosworth 1999). Several other tolerant snail species still exist in the lake, including those in the families Lymnaeidae and Physidae. We continue to find thousands of the now extinct snail shells along Utah Lake's shorelines and in benthic sediments during routine benthic sampling.

This loss of native mollusks in Utah Lake has resulted in dramatic ecosystem shifts perhaps far greater than any other biological group, including the loss of native fishes. At present, Utah Lake's heavily degraded resistant ecosystem state will preclude any natural reestablishment of these lost heritage ecosystem engineers and the lake will continue to remain in its degraded condition.

Benthic invertebrates, midges dominate

After their inevitable demise of the keystone ecosystem engineering mollusks and associated ecological shift to a lower trophic state, remaining benthic invertebrate species had to replace and endeavor to fill their functional roles. Benthic substrate conditions shifted from a substrate stabilized by mussels and clams, macrophytes, and benthic algae to a mostly unconsolidated mud-clay-silt unstable substrate that occupies most of the top layers of the lake substrate today. The dominant benthic invertebrates in the lake presently consist of just a handful of taxa, predominantly pollution tolerant chironomid (midge) larvae and segmented (oligochaetes) and non-segmented (nematode) worms. However, some areas of the lake including areas in Provo Bay and the limited macrophyte habitats outside of the bay have a greater diversity, albeit lower overall abundance and biomass, of benthic invertebrates including corixids (bugs) and coleoptera (beetles) as well as odonates (dragonflies) and isopods and amphipods, etc. (Landom and Walsworth 2021). Out of approximately twenty macroinvertebrate taxa found in our 2016 research that included 93 benthic samples, only three taxa dominated the invertebrate biomass, *Chironomus* sp. (midge), *Tanypus* sp. (midge larvae), and oligochaete worms. These three pollution tolerant indicators comprised 99% of the biomass (Richards and Miller 2019) and continue to do so, although it appears that midge larvae densities in the lake fluctuate greatly from year to year and may be decreasing (Richards and Miller 2019, and unpublished data).

This extreme low effective number of benthic invertebrate taxa is of great concern because it reflects the degraded condition of Utah Lake's benthic environment. Dominance by only three pollution tolerant taxa is a red flag in all biological assessments of water quality throughout the world. However, these remaining three dominant taxa are now the default keystone ecosystem engineers that struggle to maintain the lake's present ecological state and are a crucial component of the lake's food web (Richards and Miller 2019). Their presence and role in Utah Lake's ecosystem should not be underestimated nor undervalued. Midge larvae are responsible for much of the lake's benthic/sediment function and interaction with the water column given their sheer volume, biomass, secondary production, and ecology (Richards and Miller 2019c, Holker et al. 2015); and has been reported by Randal et al. (2017) and Hogsett et al. (2019), the sediment water interface appears to be a major controlling factor of phosphorus recycling and subsequent algal blooms. Although midge larvae densities often exceed 10,000 m^{-2} in the lake, primary production estimates suggest that their numbers should be substantially greater (Richards 2022). For example, in Lake Myvatn (Midge Lake), Iceland, midge larval density often exceeds 500,000 m^{-2}. The reason for the relatively low density of midge larvae in Utah Lake can be attributed to heavy predation from fishes and to a lesser extent unsuitable conditions. Midge larvae are the most common prey item of all fish species in the lake, including those fishes that typically should focus their diets on other smaller fishes (Richard 2022). This conundrum of low biomass and preferred food item of large numbers of fish suggest that midge larvae secondary production is very high (i.e., the production to biomass ratio could be near 100 or more) and that Utah Lake's foodweb is severely out of balance.

Fishes

Utah Lake once supported 13 species of native fish. Ten of which have been extirpated or gone extinct. The lake currently only supports three of its native species including the threatened June Sucker (*Chasmistes liorus*), Utah Sucker (*Catastomus ardens*), and Utah Chub (*Gila artraria*) that account for less than 2% relative abundance. Twelve non-native and highly invasive species now account for 98% relative abundance. The introduction of non-native fishes has disrupted the lake's food web and in combination with the loss of its natives has severely impaired the lake's biological and ecological integrity.

Common carp (*Cyprinus carpio)* have played a major role in the reduction of aquatic vegetation and unmeasured but likely substantial impact throughout the food web from juveniles to adults. Carp ecosystem effects have been documented worldwide including their effects on turbidity, clear to turbid water state, and declines and other detrimental effects on aquatic vegetation. Carp biomass values where these effects have been estimated are in Table 1.

Table 1. CARP DENSITIES (TONS KM^{-2}) ECOSYSTEM EFFECTS OF CARP. DERIVED FROM KOEHN ET AL. 2016

Ecosystem Effect	Carp biomass (tons km^{-2})
Significant increase in turbidity[1]	5 to 7.5
Noticeable shift clear to turbid[2]	20 to 30
Decline and detrimental effects on aquatic vegetation[3]	6.8 to 45
Management threshold density[4]	10 to 17.4

[1] Zambrano and Hinojosa 1999, Vilizzi et al. 2014

[2] Williams et al. 2002, Parkos et al. 2003, Haas et al. 2007, Matsuzaki et al. 2009

[3] Hume et al. 1983, Fletcher et al. 1985, Osborne et al. 2005, Pinto et al. 2005, Bajer et al. 2009, Vilizzi et al. 2014

[4] Haas et al. 2007, Bajer et al. 2009, Matsuzaki et al. 2009

Walsworth et al. (2022) estimated carp biomass in Utah Lake in 2021 at approximately 91 tons km^{-2}. This is far greater biomass than the minimum ecosystem effects and management threshold densities shown in Table 1 and indicates that carp biomass needs to be drastically reduced from current levels to have any restorative effects on the Utah Lake ecosystem. Researchers have shown that carp populations have been increasing since 2013 despite an intense carp removal program initiated in 2009. Consequently, carp are likely to continue to be a prime factor in retaining the lake's degraded and resistant trophic state.

Although millions of dollars have been spent on improving June Sucker populations and habitat over the last decade and reducing its status from federally Endangered to Threatened, this species continues to struggle. It appears that insuring population viability is not forthcoming without regular hatchery supplementation and continued management intervention.

In addition, our preliminary food web models show that size/age classes of predatory fish diets that should be focused on preying on smaller fishes (piscivory) are focusing on benthic invertebrates. This further demonstrates an out of balance fishery and food web.

Aquatic and semi aquatic dependent birds

Migratory shorebirds, waterfowl, and birds of prey among other avian groups depend on Utah Lake's ecosystem for food, shelter, rearing, etc. One of Utah Division of Water Quality's designated beneficial uses is protection of aquatic birds. It has often been reported that Utah Lake supports millions of birds, however, this statement is somewhat misleading compared to the numbers it once supported before Americans of European decent settled along it shores. The vast majority of Utah Lake is turbid open water with average depth of about 3 meters. Most of the potential open water food resources consist of phytoplankton, zooplankton, irregular midge pupae and surface struggling adults, and fishes. Turbidity severely restricts visual bird predators and energy inefficient plankton and sporadic midge hatches do not support as many birds, either diversity or abundances. Puddle dabbling ducks are restricted to shoreline areas, diving ducks and waterbirds such as mergansers and grebes have difficulty finding prey in open water. Only limited shallow water areas with aquatic vegetation (e.g., Provo Bay) or vegetation free shoreline habitat that is not conducive to high benthic invertebrate densities due to wind and wave action and water level management not geared to protecting the lake's natural resources provides feeding habitat for migratory shorebirds. In addition, much of Provo Bay (and other area) substrate when it is available to wading shorebirds during low water years has a sticky clay content that makes safe wading near impossible. Many birds that wade these waters gets stuck in the mud and perish. Savvy birds avoid these areas.

There is very little available resting, brooding, nesting, and rearing habitat in Utah Lake. One of the only habitats available is Bird Island where all available habitat is occupied either by Caspian Terns, California Gulls, Cormorants, and sometimes White Pelicans. Now mostly California Gulls.

Although there is a small population of pelicans that utilize Utah Lake's abundant fishes, due to extremely limited nesting habitat, most adult breeding pelicans that use this food resource commute to islands on Great Salt Lake. Only non-breeding individuals or those few breeding pairs that find space on Bird Island avoid the commute. Utah Lake is a migratory spring and autumn stop over for millions of birds, even though there are limited food resources and habitat. For example, Bald Eagles are often observed in spring along its shores. Unfortunately, there are very few secure areas for these birds due to the careless destruction of mature riparian trees such as native cottonwoods and the burgeoning human encroachment along its shores. Most migratory birds only stop over at Utah Lake on their way to better habitat, the next closest being Farmington Bay of Great Salt Lake that when full is about the same size as Utah Lake but orders of magnitude more productive and conducive habitat (Richards et al. 2021). Utah Lake had many hundreds of hectares of aquatic vegetation habitat and a robust riparian community with mature cottonwoods prior to settlement. It will take a concerted long-term effort to replace these lost plant communities enough restore aquatic bird diversity and densities.

Abiotic Conditions

Nutrients

Nutrients are essential for primary production and contribute to Utah Lake eutrophication. Sources of nutrients include tributaries, surface water runoff, groundwater, wastewater treatment facilities, sediment flux-resuspension, and atmospheric deposition. Tributary and surface water phosphorus loads are estimated to be between 30 to 50 tons per year. Atmospheric deposition is estimated to be between 70 to 200 tons of phosphorus per year and it is expected to increase as the human population grows and as winds increase (Utah Lake Science Panel April 2022). Estimated phosphorus loads from wastewater treatments facilities are expected to be around 53 tons per year when they begin to operate at new standards (Wasatch Front Water Quality personal communication). The only export of phosphorus is downstream via the Jordan River at less than 20 tons per year (Utah Lake Science Panel 2021). The largest contributor to nutrients to the lake water column is sediment flux where it becomes immediately available to cyanobacteria and algae. Phosphorus loading from sediments to the water column is estimated to be about 1500 tons per year.

Nitrogen levels are also extremely high from all these sources. Subsequently, there is more than enough nutrients available and accumulating in Utah Lake to keep it eutrophic to hyper-eutrophic for many more centuries.

The catastrophic shift from benthic dominated primary production to water-column primary production was in part due to increasing nutrient loads. However, and potentially more important was the disruption of the food web, in particular the disruption and alteration of top-down control, trophic cascades (Carpenter and Kitchell 1996) and as discussed throughout this report. Nutrient addition was not solely responsible for algal blooms in Utah Lake hence, nutrient reduction alone cannot control algal blooms.

Disconnect from tributaries in its watershed

As briefly mentioned in the introduction, disconnect of Utah Lake from its tributaries within its watershed (watershed connectivity) is a major impediment to its health. Severing of connectivity via digging of irrigation canals was one of the first tasks initiated with the arrival of settlers to Utah Lake’s valley (Janetski 1990, Carter 2005). Today Utah Lake’s watershed is riddled with tributary disconnects including dams, diversions, and unnatural flow regimes that degrade it headwaters to lake continuum (see *River Continuum Concept*). This disconnect affects all physical and chemical processes and the aquatic biota within the watershed. Metapopulation dynamics (specifically included in the definition of biological integrity (Angermeier and Karr, 1994; Frey, 1975; Karr and Dudley, 1981; Karr et al., 1986)) are eliminated, increasing extinction risk for all aquatic species (Altermatt 2011, Oliver et al. 2013). Isolated populations and communities have very limited or no dispersal and connectivity to other populations or communities resulting in much higher extinction probabilities either through demographic or environmental stochasticity (Hanski 1999, MacArthur and Wilson 1967, Fagan et al. 2002, Strayer 2008). Habitat connectivity is key to ecosystem resistance and long-term resilience (Oliver et al. 2015).

Lake Retention Time

Lake retention time (also known as flush rate) is the time it takes water to enter and then exit Utah Lake It is estimated to be between six months to one year (Utah Lake Science Panel 2021). High flush rates reduce the probability of cyanobacteria blooms because of their relatively slow growth rates compared to the competitors, green algae (Scheffer et al. 1997). Alternatively, loss or reduction of flushing increases cyanobacteria dominance (Jónasson and Adalsteinsson 1979, Einarsson et al. 2004).

Unfortunately, Utah Lake rarely meets compromise level. Unless lake water is physically pumped out of the lake. It most often functions as a terminal lake and its flush rate is so slow that there is an extremely low likelihood of reducing cyanobacteria blooms given the large amounts of nutrients ever present and their superior competitiveness under these conditions.

Water clarity and turbidity

The photic zone (also known as euphotic zone) is the depth at which light penetration is sufficient for photosynthesis and the aphotic zone is the zone below the photic zone and insufficient for photosynthesis. The lower limit of the photic zone is almost universally considered as the depth at which < 1% light energy occurs (Kirk 2011). Utah Lake has a very shallow photic zone due to suspended solid (predominantly silt and calcium precipitates) and algal turbidity that varies spatially and temporally. Estimated photic zone depth using Secchi disk measurement has shown that it is often much less than 30 cm and often less than 10 cm. Except for the very shallowest locations on the lake (or sometimes under ice cover) photosynthetically available light does not penetrate to the benthos to allow for benthic primary production in which case, only heterotrophic bacterial production occurs in the benthos (Richards and Miller unpublished data).

Although Utah Lake is naturally prone to turbid conditions, likely it was much less turbid prior to settlement. This is because of the abundance of macrophytes, mollusks, the major contribution of benthic algae to filter and stabilize the substrate compared to present day water column phytoplankton, absence of bioturbation by invasive carp, and natural flow and water level regime.

Wind and wave action induced turbidity is a major impediment for all members of the food web. High turbidity makes it extremely difficult for visual predators (e.g., piscivorus fishes) to feed and in most of the lake when wave action is strong fish may not even attempt feeding. Turbidity acts as a cover for planktivorus fishes (e.g., all juvenile fishes in Utah Lake) allowing them to feed on zooplankton that would have helped control phytoplankton (Trochine et al 2022). Sediment resuspension from strong waves can last for many days after a storm event. Strong wave action also dislodges benthic invertebrates, including the most abundant taxon, midge larvae and is in part one of the reasons why midge larvae densities are not higher. Filter feeding invertebrate including remaining bivalve clams cease to feed when total suspended solids (TSS) reach concentrations of as little as 20 mg l^{-1} (Hornbach et al. 1984, Way et al. 1990). Even relatively pollution tolerant invasive Asian clams (*Corbicula* sp.) and less tolerant fingernail clams (Sphaerium) initiate pseudofeces[2] production at 17 to 20 mg l^{-1} TSS (Fuji

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[2] Pseudofeces are a specialized method of expulsion that filter-feeding bivalve mollusks (and filter-feeding gastropod mollusks) use to expel suspended particles that cannot be used as food, and which have been rejected by the animal. The rejected particles are wrapped in mucus and are then expelled without having passed

1979, Hornbach et al. 1984, Way et al. 1990). Increasing rates of suspended solids from sediment resuspension, calcium precipitate, and increasing algal concentrations may have been partly responsible for the demise of native mussels and severe reduction in native clam populations. The invasive Asian clam, *Corbicula* sp. occurs at very high densities in most tributaries and the Jordan River but at low densities in the lake. High levels of suspended solids may be partially responsible.

Climate Change, Mega Drought, and Desertification

Most of Utah remains in severe drought conditions and are expected to do so. Utah Lake's location in the semi-arid western U.S. predisposes itself to continued and increasing drought conditions during climate change, the mega drought, and desertification of its watershed, an impending unavoidable threat. Resistance and resilience to these perturbations is likely to diminish and a future even more degraded (un)stable state is possible.

Conclusion

From the discussion in this report, it is obvious that Utah Lake has been severely degraded since first settlement by Americans of European descent over 150 years ago. By all standards presented here, the lake has lost its ecological integrity and is in poor health. Utah Lake's resilience to future perturbation is low and its resistance to improvement (restoration) is great.

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through the digestive tract. Thus, although they may closely resemble the mollusk's real feces, they are not actually feces, hence the name pseudofeces, meaning false feces.

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