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Aquatic Food-web of the Grand Canyon: Historical Dynamics and Contemporary Disturbances

Freshwater aquatic ecosystems are one of the most threatened types of ecosystems on the planet (Dudgeon *et al.*, 2006; Geist, 2011). Threats to these systems manifest in different forms but many stem from anthropogenic proximity and alteration to freshwater systems (Dudgeon *et al.*, 2006). The southwest of the United States is a prime example of these conditions and the primary water source for the region, the Colorado River, is highly impacted and managed. Perhaps no region is more visible in this regard than the Grand Canyon. The natural aquatic ecosystem of the Grand Canyon is highly modified and native organisms are either endangered or have been extirpated from this world famous natural wonder (Minckley, 1991; Stevens *et al.*, 1997; Cross *et al.*, 2013). Consequently, understanding the drivers of these ecological changes and attempting to manage and conserve the native ecosystem is a focus of regional management.

The Colorado River is 2,330 kilometers long, draining almost 640,000 square kilometers and includes high altitude tributaries in the Rocky Mountains, warmer water reaches though the deserts and canyonlands of Arizona and ultimately empties into the Gulf of California via the historically large Colorado River delta. Along its length the Colorado River presents multiple environmental challenges to the aquatic ecosystem. Historical water temperatures of the Colorado River were just above 0 °C during the winter months and reaching 30 °C in the late summer. Furthermore, seasonal flooding caused by spring and summer snowmelt could yield flows in excess of 100,000 cfs (Howard & Dolan, 1981). This dynamic and isolated aquatic ecosystem developed a uniquely evolved assemblage of organisms (Johnson, 1991; Minckley, 1991; Coggins *et al.*, 2006). The native and historical fish community of the Grand Canyon consisted of eight species of *Cypriniformes*, six of which are endemic to the Colorado River system (Minckley, 1991).

Westward expansion has led to a series of environmental changes to the aquatic Grand Canyon ecosystem. In 1935 the construction of the Hoover Dam, followed by the completion of the Glen Canyon dam in 1963 as well as smaller dams on several of the Colorado River's tributaries have led to a complete alteration of the hydrologic processes native to the system (Tecle, 2017). Furthermore, introduction of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in 1920s as well as additional non-native warm water species have drastically altered the aquatic community. Understanding these impacts, and the impacts of future climatic or anthropogenic disturbance are necessary for properly managing the Colorado River for the needs of both humans and the ecosystem.

One framework for modeling and interpreting the impacts of environmental change on an ecosystem is through food webs. Food webs are a representational network of trophic interactions between organisms within an ecosystem and track fluxes of energy and nutrients among community members (Polis & Strong, 1996). Understanding an ecosystem's food web can allow for predictive insights into ecosystem bottlenecks, resiliency, and the effects of anthropogenic or environmental change. For instance, food web analysis of the invasion of bass into North American lakes demonstrated trophic shift from the native lake trout to lower trophic levels as the abundance of small prey fish declined (Vander Zanden *et al.*, 1999). This review will assess the aquatic ecosystem of the Grand Canyon through the lens of food webs. Starting with a review of the historical, unperturbed, state of the Grand Canyon aquatic ecosystem, it will then describe the influences of river damming and species introduction upon the Grand Canyon food web. Finally, it will examine modern management and conservation of the Grand Canyon from within this food web lens to evaluate the effectiveness of modern and proposed management actions.

Historical Food Web of the Grand Canyon

Food webs map the flux of energy through an ecosystem (Polis & Strong, 1996). For most natural systems on earth the primary source of energy is solar radiation. Energized photos carry with them minute amounts of kinetic force, which is captured via photosynthesis and converted into chemical energy for use throughout the food web. Nutrients are originally sourced as inorganic chemicals and enter the food web through either biotic (i.e. nitrification) or abiotic (i.e. curst erosion, dust deposition) processes. Both energy and nutrients are commonly recycled via decomposition of organic material. Isotopic analysis of the Grand Canyon food-web reveals three general trophic levels (Angradi, 1994), these are summarize below.

The Grand Canyon aquatic food web starts with the photosynthesis of algae. This algae exist in two basic forms; as suspended phytoplankton or affixed periphyton (e.g. diatoms and *cladophora glomerata*) (Angradi, 1994). Biomass production at this trophic level is controlled primarily by three factors, sunlight availability, nutrient availability, and temperature (Hall *et al.*, 2015). Direct relationships between biomass production and these factors exists in all but extreme circumstances. Primary production by algae influences the food web in multiple ways, most intuitively as a food source for herbivores, but also as a substrate (e.g. attachment of filter feeders) and microhabitat producer (e.g. flow modification, oxygen production). These secondary effects can have important influences upon higher trophic levels (Shannon *et al.*, 1994). Research by Wellard Kelly et al. (2013) demonstrated that terrestrial produced vegetation that gets deposited into the river is also an important input to the Grand Canyon system, this especially true in turbid waters (Haden *et al.*, 2003).

Consumption of primary producers by primary consumers constitutes the first trophic interaction (Wellard Kelly *et al.*, 2013). These participants include macroinvertebrates (e.g. chironomids, oligochaetes and amphipods) and the bluehead sucker (*Catostomus discobolus*) which grazes upon the periphyton (Minckley, 1991; Angradi, 1994). Biomass production at this level is again determined by temperature-dependent growth rates and food availability. Historically, high sediment loads would have reduced algal primary production and allochthonous terrestrial derived organic material would support a diverse array of macroinvertebrates (Haden *et al.*, 2003).

The next trophic level is occupied by the native fish of the Grand Canyon. The native assemblage are all cypriniformes and are broadly generalists and omnivorous (Figure 1). These fish eat varied diets containing both autotrophs as well as macroinvertebrates (Minckley, 1991; Childs *et al.*, 1998; Behn & Baxter, 2019). Childs et al. (1998) documented resource partitioning among larval and juvenile native fish species of the Grand Canyon. As an example, Minckley (1991) highlights that the three species of sucker (bluehead, flannelmouth [*Catostomus latipinnis*] and razorback [*Xyrauchen texanus*]) were adapted to feed upon different prey assemblages. This prey generalization and partitioning is credited with the capacity for the native fish community to tolerate such a wide variety of conditions (Behn & Baxter, 2019).

Historically, the top trophic level of the Grand Canyon ecosystem was occupied by a single fish, the Colorado pikeminnow (*Ptychocheilus lucius)*. This predator was the only piscivorous fish in the Colorado River. Furthermore, the Colorado pikeminnow is only piscivorous as an adult (Minckley, 1991). Historically this meant that juvenile fish of the Colorado river were likely free of predation pressure. The pikeminnow's predation pressure would have been temporal as adults engaged in long migrations from the Colorado River delta to high elevation reaches to spawn. Therefore, native fish could avoid predation pressure entirely through maintaining allopatry with the pikeminnow.

The final stage in the Grand Canyon food web is decomposers. This trophic level is occupied by detritivorous fish, alongside macroinvertebrates, fungi and bacteria. This suite of consumer's breakdown complex organic molecules originating from dead matter or waste. Fish species such as the razorback sucker as well as benthic macroinvertebrates operate as detritivores and recycle energy and nutrients back into the food web.

Perturbations to the Aquatic Food Web

Anthropogenic usage of the Colorado River for multiple purposes have drastically altered the aquatic food web of the Grand Canyon. The Glen Canyon dam is the primary water impoundment modulating water flow through the Grand Canyon. This dam has altered several environmental characteristics of the Colorado River including altered flow regime, reduced and homogenized river temperature and disruption of animal movement (Stevens *et al.*, 1997). Capitalizing upon these disturbances are an assemblage of invasive species which impact the food-web at multiple trophic levels.

Faux Flows

River flow regime has been shown across multiple systems to have varied and pronounced effects upon an aquatic community (Poff *et al.*, 1997; Bunn & Arthington, 2002; Wenger *et al.*, 2011; He & Marcinkevage, 2017). For example, the daily hydropeaking of the Colorado River below Glen Canyon has induced a daily 'tidal' cycle to the rivers flow pattern. This unnatural flow regime has been shown to prevent successfully reproduction of macroinvertebrates. Emergent invertebrates often cement their eggs to rocks along the river's edge (Kennedy *et al.*, 2016). However, with hydropeaking induced fluctuations in the rivers depth, these margins are continually inundated and then exposed. Kennedy et al. (2016) found that species of insects that cemented eggs to river banks experienced poor egg viability as opposed to species which laid their eggs in open, surface waters. This poor viability is due to desiccation of the eggs as river margins are dewatered during hydropeaking cycles. Impacted groups such as mayflies, a cornerstone of aquatic food webs (Cross *et al.*, 2013), declined in abundance and therefore a reduction in prey biomass for higher trophic levels.

Cold Creeks

Temperature is another environmental variable influenced by river damming. Water exiting the Glen Canyon dam is sourced from the cold deep waters of Lake Powell. Opposed to historical river temperatures which ranged from 0-30 °C, this deep water is cold and thermally stable (4-13°C) throughout the year (U.S. Fish and Wildlife Service, 2002). Subsequently the main stem of the Colorado River as it flows through the Grand Canyon are colder than historical conditions. Reduction in water temperature has multiple effects upon food web dynamics of the Grand Canyon. For instance, Ward and Morton-Starner (2015) demonstrated that predation upon juvenile chubs by non-native trout species is exacerbated by colder water temperatures. Reduced growth rate of native chub and sucker species (Robinson & Childs, 2001; Walters *et al.*, 2012) as well as reduced swim performance at cold temperatures may explain this temperature effect on predation.

Cooler water temperatures also reduce the spawning potential of native fish species which require temperatures above 16°C for successful reproduction (Minckley, 1991). While this temperature effect may not directly modulate trophic interactions, a reduction in native fish abundance due to poor spawning success reduces resource competition on non-native species who are better suited to colder water temperatures (i.e. trout).

Dammed Drifters

Dams create an impassible barrier which disrupts the flow of nutrients and organisms through the river corridor. This effect can be seen at multiple trophic levels. It is thought that adult Colorado pikeminnow historically migrated upwards of 300 km to spawn at specific locations throughout the Colorado River and its tributaries. The progeny would then drift down stream to suitable rearing reaches (Minckley, 1991). Construction of the Hoover and Glen Canyon dams placed an impassible barrier to this migration. This migratory disruption led to the extirpation of the Colorado pikeminnow from the of the Colorado River below Glen Canyon dam in the 1970s (Osmundson & Burnham, 1998). Remaining Colorado pikeminnow within the Colorado River exist in warm-water reaches of the upper Colorado Basin. Removal of the ecosystems top predator created an opening for other non-native fish species to take hold.

Fish are not the only organisms whose movement across the landscape was disrupted by the construction of the dams and corresponding reservoirs. The movement of aquatic macroinvertebrates and coarse and fine organic matter downstream is interrupted by the dam and yields modified macroinvertebrate community assemblage (Angradi, 1994). Reduced macroinvertebrate biomass or diversity can undermine the native higher trophic levels (Kennedy *et al.*, 2016), offering opportunities for non-native species.

Truculent Trout

Alongside the physical alteration of a river through damming, non-native species can lead to alterations in the food-web dynamics of an aquatic ecosystem (Vander Zanden *et al.*, 1999). Non-native rainbow and brown trout are two iconic examples of non-native fish of the Colorado River and Grand Canyon. First introduced in 1920s, trout species were a novel predator on the landscape. Prior to the construction of the Glen Canyon dam, non-native trout were constrained to cold water tributaries and did not have direct interactions with the warm-water native fish assemblage of the Grand Canyon (Minckley, 1991). However, the reduction in river temperature associated with the construction of Glen Canyon dam led to an expansion of suitable trout habitat and sympatry between native fish species and trout predators. Small trout of both species are initially insectivores, competing with juvenile native fish species for macroinvertebrate prey (Whiting *et al.*, 2014). However, as trout grow they become increasingly piscivorous. In cold water, these trout species are especially lethal upon native chub species (Figure 2: Ward & Morton-Starner, 2015). Yard et al. (2011) determined that trout species preferentially consume native fish (85% of their piscivorous diet) indicating that trout apply a strong top-down trophic pressure on native fish species. Paukert and Petersen (2007) determined that rainbow trout consumed 5-7 times more prey biomass than humpback chub. There results indicate that per-capita rainbow trout are dominant food-web competitor to the native humpback chub.

Additional Aliens

Since the construction of the dams and the associated reservoirs of lake Mead and Lake Powell there has been an increase of non-native warm-water fish. These reservoirs serve as a source habitat for non-native predators such as largemouth bass (*Micropterus salmoides*), channel catfish (*Ictalurus punctatus*) and common carp (*Cyprinus carpio*) (Minckley, 1991; Minckley *et al.*, 2003). Alongside the trout species, these non-native warm-water fish apply a strong predation pressure upon native fish of the Grand Canyon (Minckley, 1991; Marsh & Douglas, 1997). Bestgen et al. (2006) studied the small-bodied redside shiner (*Richardsonius balteatus*) and determined that it was an effective predator of larval native fish species including the Colorado Pikeminnow. Their results demonstrate that predation upon native fish can act across all life-stages. Non-native species also compete for food with native species. A comparison of the diets of native bluehead sucker, flannelmouth sucker, speckled dace (*Rhinichthys osculus*), and non-native fathead minnows (*Pimephales promelas*) demonstrated a high dietary overlap (Seegert *et al.*, 2014). This was most pronounced between the two sucker species and fathead minnows, indicating that these three species likely compete for food resources (Seegert *et al.*, 2014).

Greedy Gastropods

Finally, non-native invertebrates have invaded the Grand Canyon. The most pronounced of these are New Zealand mud snails (*Potamopyrgus antipodarum*). Mud snails are exceptionally good at consuming algae and in Yellowstone rivers were document to account for 65-92% of total invertebrate productivity (Hall *et al.*, 2006). This productivity is not being carried upward to higher trophic levels. Vinson and Baker (2008) found that rainbow trout fed unlimited mud snails lost mass and that over 50% of the snails survived consumption by trout (Figure 3). These results indicate that resources absorbed by mud snails does not readily make it into higher trophic levels. Despite their dominance on the riverscape and poor food-web connectivity, Cross et al. (2010) found that mud snails abundance did not seem correlated to decline in other aquatic species. The authors hypothesized that the lack of influence of mud snails may be due to the already highly impacted natures of the Colorado River ecosystem.

Managing a Food-web

Management actions have tried multiple strategies to adjust the food-web dynamics of the Grand Canyon to benefit both endangered native species as well as economically important recreational trout fishery. As per the recommendation of Kennedy et al. (2016) dam release strategies have been developed to increase the proportion of viable macroinvertebrate eggs by minimizing hydropeaking and subsequent river flow changes during weekends in the summer. The hope is that by increasing macroinvertebrate biomass, the prey resource for fish (both native and non-native) would increase, reducing interspecific competition and increasing growth potential.

There have also been more direct methods of food-web augmentation. Trout are both a strong predator (Ward & Morton-Starner, 2015) and competitor (Paukert & Petersen, 2007) to native fish species. Therefore, management actors conducted an intensive non-native fish removal which succeeded in shifting the fish community towards natives. However, the timing of the removals were confounded with a regional drought and subsequent increase in water temperatures which may also favored native species over non-native trout (Coggins *et al.*, 2011).

The Grand Canyon is a highly altered aquatic ecosystem. The native food-web has lost multiple fish species including top predator, the Colorado pikeminnow. It is also highly invaded with strong competitors (e.g. fathead minnows) and predators (e.g. trout, bass) of the native fish community. While removal of non-native species may serve to support local populations of native fishes, widespread restoration of the natural food-web will require restoration of historical flow and temperature regimes.

Figures:

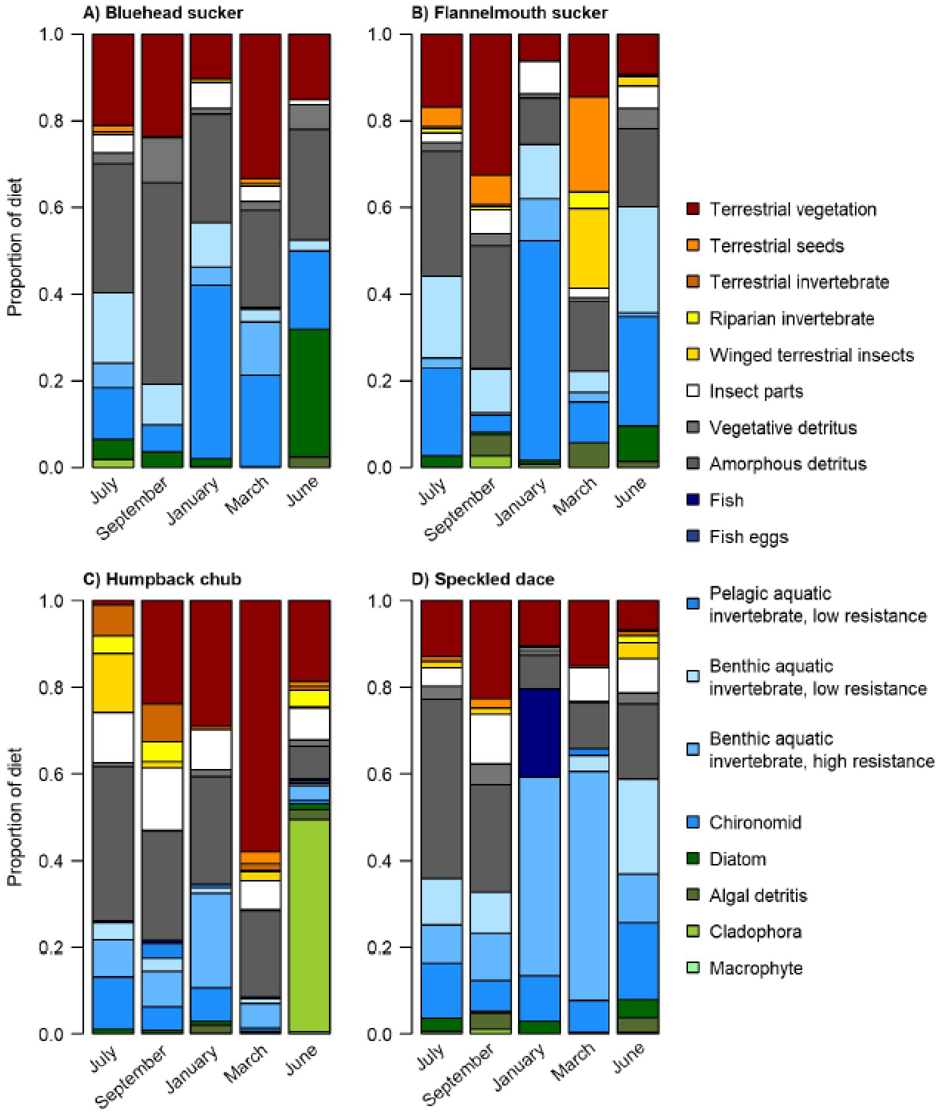

Figure 1: Dietary items for four species of native Colorado River fish across time. From Behn & Baxter (2019), colors represent different dietary components. Items are ordered according to origin terrestrial items are listed at the top, then items of ambiguous origin with items of aquatic origin near the bottom.

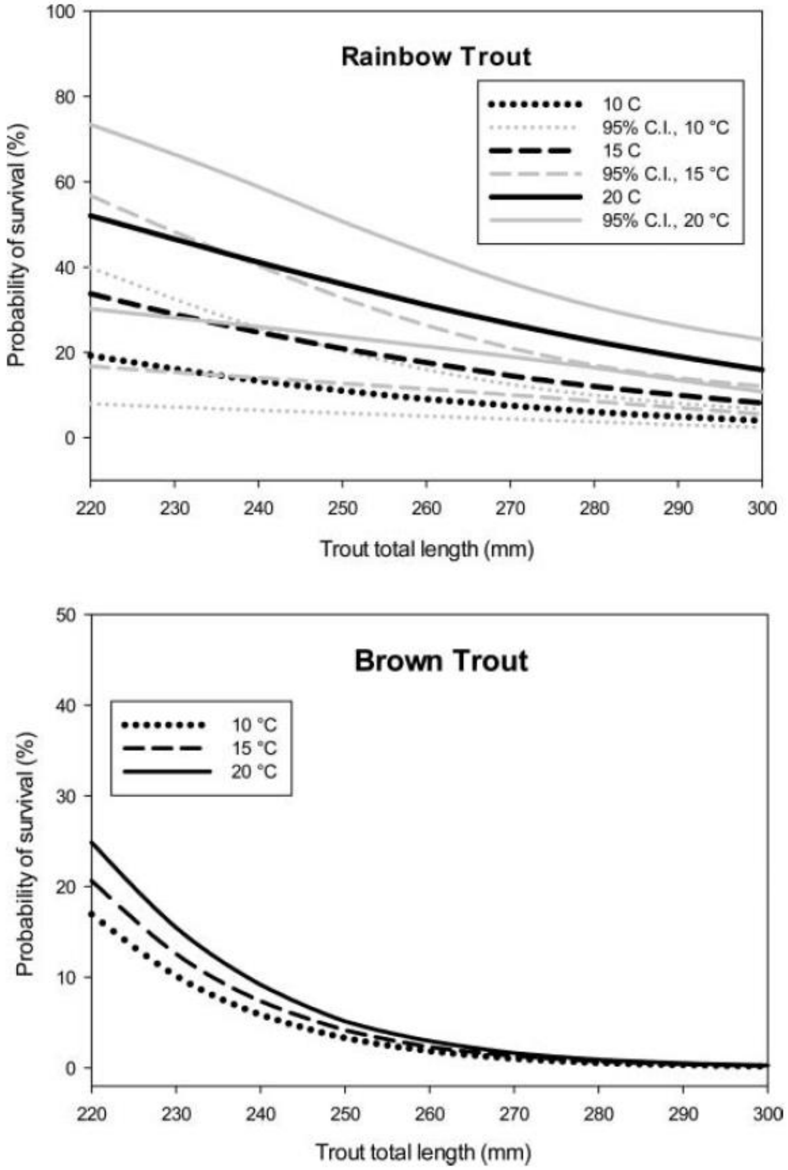

Figure 2: The role of temperature on predatory interactions between trout and native chubs across trout length. From Ward & Morton-Starner, (2015), data presented is for chubs 55 mm in length. Rainbow trout predation appears more temperature sensitive than brown trout predation. Grey lines indicate 95% C.I. bounds, they were not distinguishable for Brown trout and therefore not shown. Note that the y-axis for brown trout is half that of the rainbow trout.

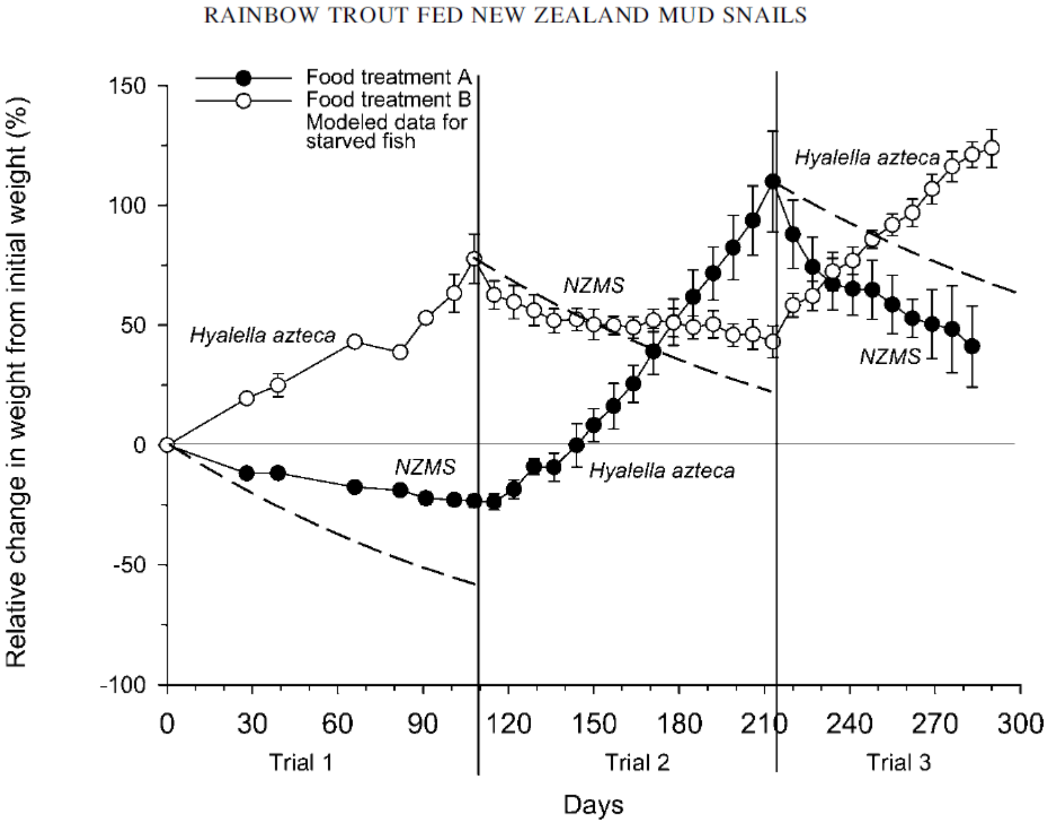

Figure 3: **Weight change of juvenile rainbow trout fed either New Zealand mud snails (NZMS) or amphipods (*Hyallell azteca*).** From Vinson & Baker (2008), fish were fed alternating food items. Treatment A was NZMS then amphipods then NZMS, while treatment B was the opposite. The dashed line is modeled weight data for starved fish.

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