Ecological Changes in Lake Tahoe: The Influence of Introduced Species

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Prior to large changes in community structure and water column nutrient concentrations, Lake Tahoe's community assemblage was relatively simple with 12 orders of zoobenthic taxa, 6 zooplankton species, and 8 fish taxa (Juday 1906, Miller 1951, Frantz and Cordone 1996, Chandra 2003, and Vander Zanden et al. 2003). The benthic invertebrate community consisted of one endemic, a wingless form of stonefly, while the fish community was comprised of 7 species and 2 subspecies. A series of species introductions combined with landscape disturbances (i.e., deforestation) in the mid to late 1800's, initiated the alteration of the lake's biology, and many of these changes exist today. The purpose of this article is to describe the ecology of the lake prior to the introduction and establishment of the nonnative species, and provide insights into the changes that have occurred as a result of the introduction of particular nonnative species in the last 140 years (Figure 1).

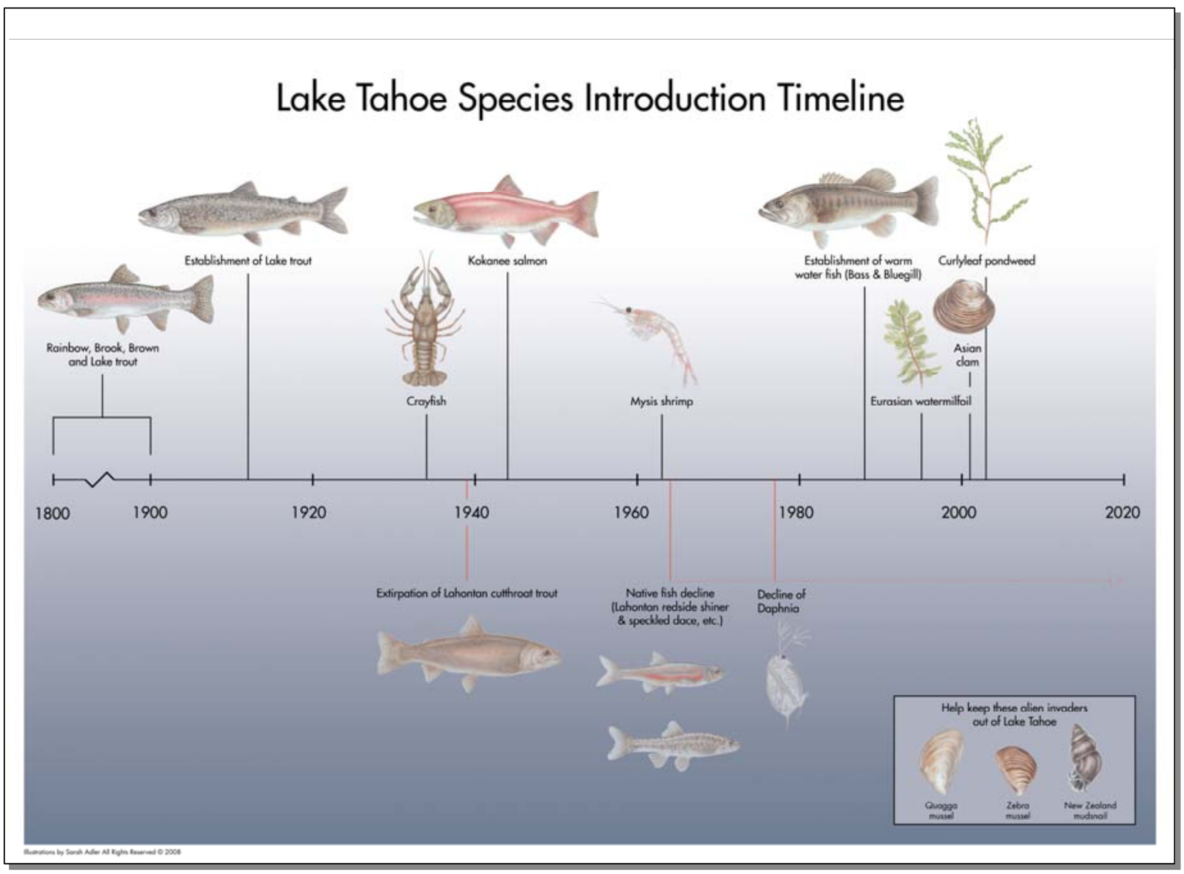


Figure 1 A historical timeline of species introductions and confirmed years of establishment in Lake Tahoe. Of recent concern is the establishment of invasive species in the nearshore area of the lake since the 1990's. The nearshore environment is a critical habitat for maintaining the lake's biodiversity and fish production.

Ecology of Lake Tahoe Prior to Nonnative Species Disruptions

The pre-invasion food web (1872) in Lake Tahoe was dominated by a single predator, Lahontan cutthroat trout (*Oncorhynchus mykiss*), which fed primarily on the native pelagic tui chub (*Siphateles bicolor pectinifer*) and zooplankton (Chandra 2003, Vander Zanden et al. 2003, Juday 1906). Forage fishes obtained energy from a mix of benthic and pelagic primary production sources. By 1939, cutthroat trout were extirpated from Lake Tahoe, and a large lake trout (*Salvelinus namaycush*) population replaced them as the top predator (Cordone and Frantz 1966). Three primary reasons for the demise of cutthroat trout were predation from introduced lake trout, the degradation of spawning stream habitat from increased siltation due to watershed deforestation (Moyle 2002), and the hybridization of trout with rainbow trout due to hatchery propagation (AJ Cordone, personal communication). While no direct observations of lake trout predation on cutthroat trout are available from this ecosystem, other studies showed that introduced lake trout prey heavily on native cutthroat trout (Ruzycki et al. 2001; Stapp and Hayward 2002).

Introduced Species and Their Impacts

<u>Crayfish</u>

Crayfish that dominate freshwater ecosystems can regulate the flow of energy and nutrients throughout the system, often having positive and negative impacts on algal production and benthic invertebrate production and diversity. A variety of subspecies (*Pacifastacus* spp.) were introduced into the Lake Tahoe watershed with at least 4 introductions of the signal crayfish (*Pacifastacus leniusculus*) and establishment by 1936 (Figure 2a). Found in large numbers (55 million) in the late 1960's (Abrahamsson and Goldman 1970), there are now up to 230 million adult crayfish (Chandra and Allen 2001, unpublished data) inhabiting the littoral zone (1-60 meters). Studies from Lake Tahoe suggest that under low densities (0.16 adult/ sq m) the crayfish stimulate periphyton productivity by removing old senescent cells (Flint 1975). Higher densities (1.07 adults/sq m), however, result in a decrease in periphyton production. At either density, crayfish have been found to excrete nitrogen and phosphorus, which are important stimulators of primary production. Crayfish and tui chub also contributed to the diet of nonnative lake trout. After the 1960's introduction of Mysid shrimp (see below), the food web structure in the lake shifted to one of pelagic dominance (Vander Zanden et al. 2003; Chandra 2003). As a result, crayfish no longer contribute to the energetics of nonnative lake trout except for the largest size classes (> 50 cm). It is hypothesized that the release from predation due to a shift of lake trout to a mysid diet has partially contributed to the increase of crayfish densities since measurements were first collected in the 1960's (Figure 2b, Umek and Chandra unpublished data 2009). Other hypotheses suggest that increased algal production in the nearshore is due to eutrophication and slight increases in temperature. Consequently, climate warming may also be driving crayfish production. Today, crayfish are a major food resource for invasive warmwater fish species such as largemouth bass and bluegill species that are restricted to the nearshore environment.

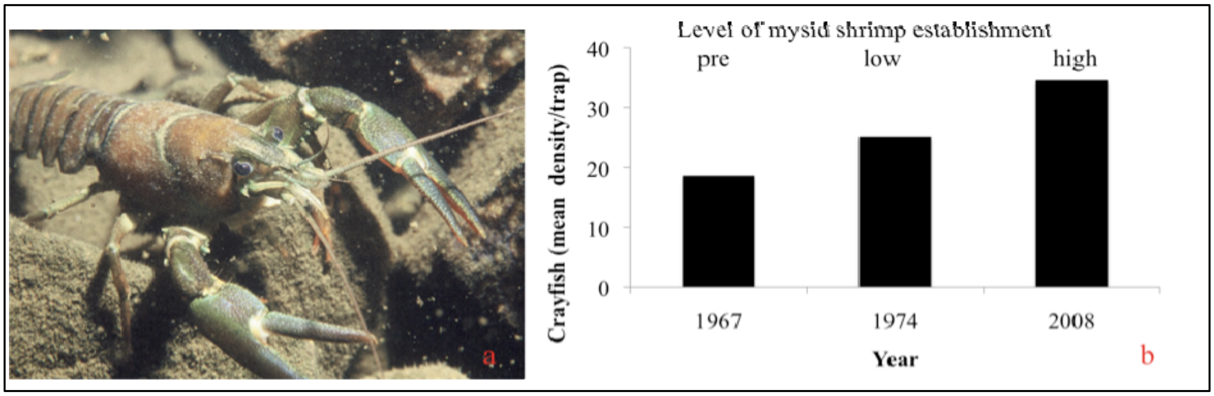
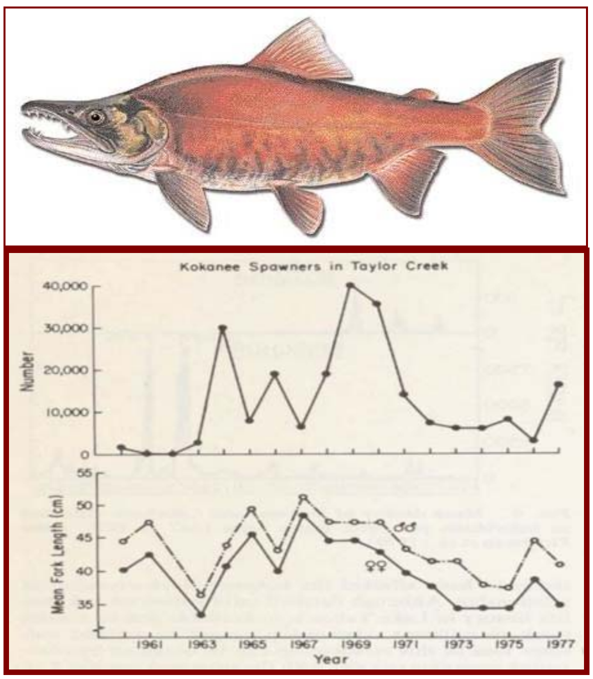


Figure 2 a) Photo of a signal crayfish introduced at least 4 times into Lake Tahoe and established by 1936. b) Crayfish densities have nearly doubled since first measurements were obtained by Dr. Charles Goldman's laboratory at UC Davis in 1967. We hypothesize that the introduction of mysid shrimp, an open water, offshore invertebrate, shifted the feeding behavior of lake trout--the dominant consumer of crayfish resulting in an increase in crayfish densities. An alternative hypothesis suggests that increased food availability due to increased algal production resulting from eutrophication of the nearshore may also explain the increase in crayfish densities.

Mysid shrimp

Mysid shrimp (*Mysis relicta*) were introduced into Lake Tahoe in the 1960's by the state departments of fish and game of Nevada and California. The shrimp were introduced to increase forage for game fish, namely kokanee which were thought to provide food for lake trout. The introduction of mysid shrimp was common in the 1950's to 1970's in reservoirs and lakes in the Western Unites States to increase fish production. The establishment of mysids corresponded with shifts in the trophic niches of forage fishes (chubs) and the top predator lake trout. Benthic and pelagic forage fishes showed decreases in trophic position. Both chub species decreased in trophic position as a result of feeding shifts to mysids, which was further supported by their increased utilization of pelagic energy. Prior to mysid establishment, gut content studies of these fish species showed that pelagic chub fed primarily on a mixed diet dominated by zooplankton with some selection for fish, while benthic chub fed on a mix of zoobenthos and fish. After mysid establishment, qualitative, observational data suggested a shift to mysids (S. Chandra, unpublished data). Mysid introduction corresponded with a feeding shift of Lake Tahoe's dominant predator, lake trout, to pelagic energy sources. Large lake trout did not reduce their trophic position after mysid invasion; they shifted to more pelagic resources, which indicated a mix of mysid and pelagic forage fish. Smaller lake trout size classes (12.7 cm and smaller) shifted to mysids (Thiede 1997). After mysid establishment, a 10-fold decrease in the abundance of forage fishes was documented (Thiede 1997) which indicated a potentially strong role of this nonnative invertebrate in restructuring food web interactions and energetics in the lake. While direct predation probably played a role in the regulation of forage fishes (Thiede 1997), one alternative hypothesis was that lake trout became donor controlled (Polis and Strong 1996). This hypothesis suggests mysid augment lake trout populations compared to pre-*Mysis* periods by providing an increased food source. The resultant increase in lake trout population size may have increased predation rates on native forage fishes and decreased their abundance (Vander Zanden et al 2003). Growth rates of lake trout before and after Mysid introduction do not appear to have changed except for smaller size classes of fish.

Post mysid invasion studies in Lake Tahoe showed impacts on other biological components of the lake. A strong restructuring of the zooplankton community as a result of mysid predation on native cladocerans occurred, shifting the lake to a mysid-copepod dominated system (Richards et al. 1975, Goldman et al. 1979, Threlkeld et al. 1980, Morgan et al. 1981) with an occasional appearance of cladocerans when pelagic primary production could support them (Byron et al. 1984). Furthermore, the restructuring of the zooplankton community impacted the energetics for kokanee salmon, who prior to mysid introduction, fed primarily on cladocerans (Figure 3, Cordone et al. 1971). After mysid establishment, the annual length and weight of returning spawners decreased, probably due to exploitative competition with mysid for cladocerans (Morgan et al. 1978). Thus, insertions of mysid into the middle of the food web played a strong role in restructuring upper trophic level energetics and in disrupting community dynamics at other middle-lower parts of the food web.



<u>Figure 3</u> a) Sketch of a kokanee salmon, introduced to Lake Tahoe in 1944 and maintained in the lake through a program by the US Forest Service and project Kokanee. b) A reduction in the number of kokanee entering Taylor creek, the primary spawning area for these salmon in Lake Tahoe, after mysid shrimp began to establish in the early 1970's (top panel) and the resulting reduction in kokanee fish length after shrimp establishment (bottom panel). Mysid shrimp feed heavily on a native zooplankton (*Daphnia* spp.) that is the preferred food source of kokanee. This competition for food resulted in a decrease of kokanee size. Data is from Morgan et al. 1978.

<u>Warmwater fishes</u>

Finally, in the mid to late 1970's and again in the late 1980's, a variety of nonnative species were found in the nearshore environment (Reuter and Miller 2000). The warmwater fish introductions were illegal and thought to be the result of anglers eager to catch these fish. At this time, warmwater fish species were rarely found in Lake Tahoe while native minnows remained abundant. Through support from many agencies (California Fish and Game, US Forest Service, Nevada Division of State Lands, Tahoe Regional Planning Agency, Nevada Department of Wildlife, Tahoe Resource Conservation District, and the US Fish and Wildlife Service), the universities of Nevada- Reno and California- Davis, have been examining the expansion and impact of warmwater fishes in the nearshore environment. In recent years, warmwater fishes occur at 58% of the 16 locations monitored in Lake Tahoe. Their establishment in the south (e.g. Tahoe Keys) has led to the continued decline of native fishes since 1999; when nonnatives are present, often no native fish are caught during the surveys. An establishment likelihood model was developed for largemouth bass based on limnological and satellite data at ~2 km resolution. Temperatures observed in this study revealed the entire nearshore is thermally suitable for warm water fish spawning, and that future establishment is currently limited by the distribution of aquatic macrophytes (see below). A bioenergetics model determined the potential impact of largemouth bass on native fishes indicates these predators could eliminate 100% of fish biomass at 37 to 80% of sites examined. Fortunately the movement and establishment of warmwater fishes is still in its early stages and fish exhibit generally slower growth rates, allowing for the potential control of these populations.

Aquatic macrophytes

Until 1994, no surveys for rooted aquatic macrophytes had been conducted in Lake Tahoe. Early reports (1975) of aquatic macrophyte species near Taylor Creek did not identify the species of *Myriophyllum*, nor were vouchers or photographic records made. However, severe impacts from aquatic plants were observed in the Tahoe Keys by the end of the 1970's and early 1980's, during which time mechanical harvesting had begun. Beginning in 1995, US Department of Agriculture/Agricultural Research Service conducted surveys periodically until 2006 (Anderson and Spencer 1995; Anderson and Spencer 1996; Anderson 1997). Specimen vouchers were made and all locations are georeferenced. The ten year trend is clear: expansion of populations of non-native Eurasian watermilfoil (*Myriophyllum spicatum*), coupled with the recent spread of the non-native curly leaf pondweed *Potamogeton crispus*. *M. spicatum* is now present at various levels of abundance in most of the Tahoe Keys and in over 30 locations in the rest of the lake, including new infestations (compared to 2003) along the western shore, at the mouth of the Lower Truckee River, and in the Truckee River. *P. crispus* is prevalent and spreading along the southern shoreline from the western Keys channel east to Lakeside Marina. It is exhibiting typical range-expansion into both unvegetated areas as well as those currently vegetated by *M. spicatum* and native aquatic plant species. The largest populations of *P. crispus* are at Ski Run and in the channels at the Tahoe Keys. However, based on the fall 2006 survey, it appears that new colonies are rapidly becoming established in other locations. It is likely that densities along the entire south shore will increase with each growing season unless management actions are taken. In 2005, California State Lands Commission began removal of an infestation of Eurasian watermilfoil (EWM) in Lake Tahoe's Emerald Bay (Figure 4). This effort has brought together public and private stakeholders interested in the removal/control of EWM and other invasive aquatic weeds. Collaboration by stakeholders has led to a grant funded project to continue EWM removal at Emerald Bay and Ski Run marina and the initial development of a feasibility plan of management options for invasive aquatic weeds in Lake Tahoe.

Figure 4 Eurasian water milfoil (*Myriophyllum spicatum*) in Emerald Bay.

Asian clam

The invasive bivalve Asian clam (*Corbicula fluminea***)** is established in the littoral zone of Lake Tahoe. High densities (up to 6000/m^2) have been observed in the southeast region of the lake, where the clam has negative impacts on benthic diversity and is associated with filamentous algal blooms of *Zygnema sp.* and *Cladophora glomerata* (Figure 5). Widely distributed (2-70 m water depth) along Lake Tahoe's well-oxygenated littoral zone, Asian clam maximum size and life expectancy are reduced in this subalpine, oligotrophic ecosystem, but growth rates and population densities are similar and can exceed those in warmer, more nutrient-rich ecosystems. Asian clam range expansion continues to locations out of its continuous range along the southeast portion of the lake to Emerald Bay and Glenbrook Bay, and experimental efforts to manage new populations using bottom barriers are currently underway. One half acre plots of rubber pond liner material will be installed on top of Asian clam beds during the summer of 2010 to reduce population densities and associated algal blooms. The areas will be monitored until 2011 for Asian clam and other native macroinvertebrate recolonization rates.

Figure 5 Two photos demonstrating the impact of invasive Asian clam on Lake Tahoe's clarity. Algal bloom due to the excretion of nutrients by Asian clam (left) and the clear conditions and natural sand bottom in an adjacent location without clams (right).

The idea of invasion facilitation: a reality for Lake Tahoe

In the last 140 years, Lake Tahoe has experienced a series of intentional and unintentional (illegal) nonnative species introductions. Of recent concern are the establishments of invasive species in the nearshore environment, which is a location important for rearing of native fishes and maintenance of the lake's biodiversity and function. The nearshore is also the Lake habitat that most humans experience. The idea of invasion facilitation postulates that the establishment of a small number of nonnative species may lead to the establishment of even more invasive species by altering the ecology of the ecosystem in favor of conditions that facilitate new invasions. There are many examples in the scientific literature regarding this idea, and scientists studying the invasion processes and impacts in Lake Tahoe have a strong interest in testing this idea. We believe we are already seeing invasion facilitation in the nearshore of Lake Tahoe. For example, we hypothesize the warmer water temperatures observed in the nearshore due to climate change combined with increased availability of food resources from introduced crayfish and habitat availability from invasive plants (see above) are facilitating the expansion of warmwater fishes (e.g. largemouth bass) around the lake (Figure 6). This in turn is leading to the decline of native fish, increased excretion of nutrients in the nearshore and the stimulation of algal blooms. Also of concern is the establishment of Asian clam in the lake which creates hard substrate and locally elevated calcium levels. Substrate and calcium are common limiting factors for the invasive bivalve, the quagga mussel (*Dreissena rostriformis bugensis*), a tiny but prolific and highly detrimental invasive invertebrate that has become established in the Midwestern United States, and more recently in Southern Nevada, California, and Colorado.

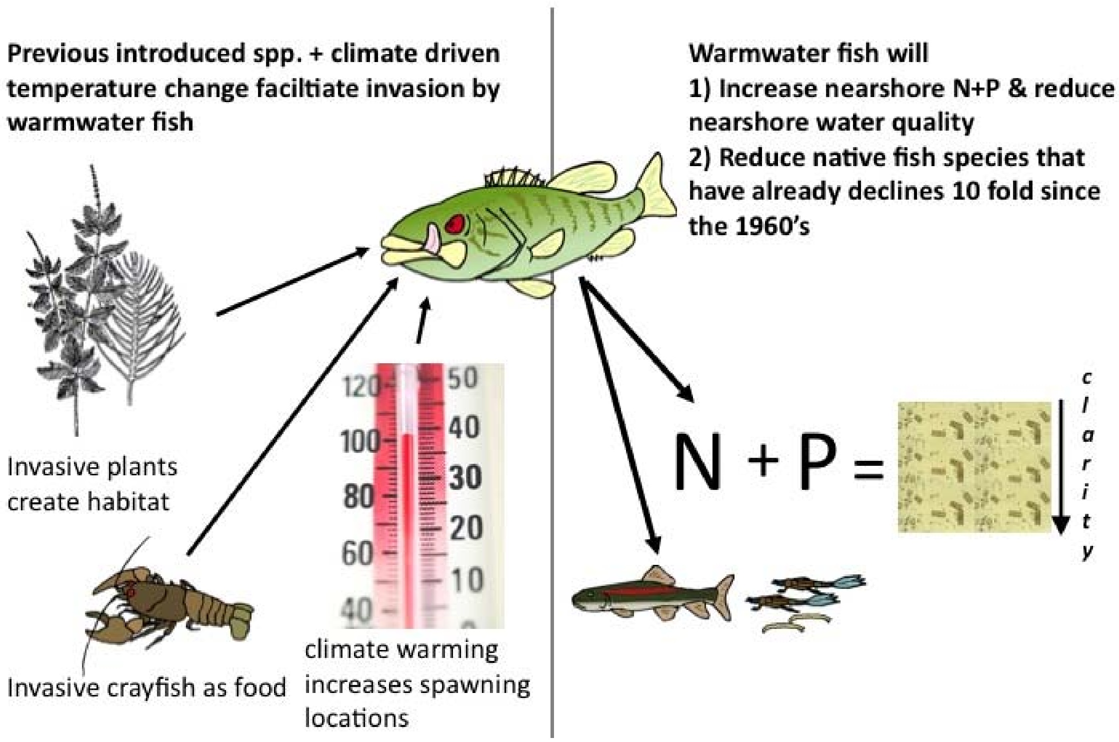


Figure 6 A schematic showing how two invasive species and changes in nearshore temperatures due to climate change facilitate the invasion of largemouth bass around nearshore areas of Lake Tahoe. Invasive plant (water milfoil and curly leaf pond weed) expansion provided habitat for fish in a normally plant free Lake, while crayfish provide an abundant food source. As a result of establishment in the nearshore, largemouth bass impact native fishes and excrete nutrients that stimulate algae and reduce nearshore clarity.

References

Available upon request.