Historical Food Web Structure and Restoration of Native Aquatic Communities in the Lake Tahoe (California–Nevada) Basin

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ABSTRACT

Plans for the restoration of aquatic ecosystems are increasingly focusing on the restoration and rehabilitation of self-sustaining native fish communities. Such efforts have not traditionally adopted an ecosystem-based perspective, which considers species as embedded within a broader food web context. In this study, we quantify food web changes in Lake Tahoe (California–Nevada) over the last century based on stable isotope analysis of museum-archived, preserved fish specimens collected during 4 historical periods and under present conditions. We also examine the contemporary food web of nearby Cascade Lake, which is free from most exotic species and contains a species assemblage resembling that of Lake Tahoe prior to historical species introductions. During the last century, the freshwater shrimp *Mysis relicta* and lake trout (*Salvelinus namaycush*) have been introduced and established in Lake Tahoe, and the native top predator, Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*; hereafter LCT), has been extirpated. Isotope analysis indicates that lake trout now occupy a trophic niche similar to that of historical LCT. Fish production has shifted from benthic to pelagic, corresponding with the eutrophication of Lake Tahoe during recent decades. The current Cascade Lake food web resembles that of the historical Lake Tahoe food web. Our isotope-based food web reconstructions reveal long-term food web changes in Lake Tahoe and can serve as the basis for setting historically relevant restoration targets. Unfortunately, the presence of nonnative species, particularly *Mysis* and lake trout, have dramatically altered the pelagic food web structure; as such, they are barriers to native fish community restoration. Fish community restoration efforts should focus on adjacent ecosystems, such as Cascade Lake, which have a high likelihood of success because they have not been heavily affected by nonnative introductions.

Key words: food webs; historical reconstruction; stable isotopes; carbon; nitrogen; Lake Tahoe; energy flow; benthic zone; pelagic zone; Lahontan cutthroat trout.

INTRODUCTION

The rehabilitation of native fish communities and fisheries is an emerging approach to fisheries management that is now embraced by numerous resource management agencies and authorities in North America (Burkett and others 1995; Fluharty 2000; Horns and others 2002). At the same time, studies of food webs over the last decades have...
revealed that individual species often play a central role in structuring aquatic ecosystems, either through trophic cascades or through the strong per capita influences of keystone species (Paine 1992; Power and others 1996). Furthermore, external drivers such as species invasions, fishery exploitation, and other perturbations can also play an important role in structuring aquatic food webs (Vanni and others 1990; Jennings and Polunin 1996; Kitchell and others 2000; Pinnegar and others 2000). Based on these realizations, a paradigm shift is underway. Fish community restoration is now adopting an ecosystem perspective, in which individual species are viewed within the context of their broader food webs (Pimm 1991; Kitchell and others 1994; Jones and others 1995; Lichatowich and others 1995; Walters and others 2000).

Ecosystem-based restoration efforts typically involve the establishment of restoration targets. Ideally, these targets should be reflective of historical conditions (Lichatowich and others 1995; Shuter and Mason 2001), although in reality, the relevant information on historical food web interactions and species’ trophic niches is rarely available or obtainable, leaving managers to speculate as to the historical state of ecosystems. The lack of baseline information on food web interactions is a major obstacle to efforts to characterize the ecological changes that result from species introductions. Such information may be a critical element in the evaluation of the restoration potential of native communities. New approaches based on the reconstruction of historical ecosystems and food webs could thus make a substantial contribution to ecosystem-based restoration efforts.

Ecosystem-based restoration can be limited by a number of constraints. Of central importance is the growing onslaught of exotic species, both vertebrate and invertebrate, in aquatic systems (Coblentz 1990; Lodge 1993; Mills and others 1994; Ricciardi and MacIsaac 2000). In many cases, aquatic ecosystems have lost much of their native species assemblage; instead they now host a variety of introduced and invasive species, many of which dramatically alter the structure and function of these systems (Ludyanskiy and others 1993; Mills and others 1994; MacIsaac 1996). How does the presence of these nonnative species affect our ability to reestablish or rehabilitate the native populations? The restoration of a native species assemblage may be thwarted by food web alterations and changes in species abundance resulting from species introductions. Similarly, might there have been historical prey resources, habitats, and energy flow pathways that were critical for supporting native species or species assemblages but are now no longer available? Addressing the implications of these questions can provide us with a basis for understanding the restoration potential of native aquatic communities.

In this study, we introduce a novel approach for examining the potential for aquatic ecosystem restoration based on a comparison of historical and present-day food web structure. We focus on two lakes, Lake Tahoe (California–Nevada) and Cascade Lake (California), which are located in the same drainage basin but differ dramatically in their history of species introductions. Many museums have substantial historical archives of preserved fish and invertebrate specimens. In the case of Lake Tahoe, fish specimens were collected at various times during the 20th century. Given the ability of stable isotope techniques to elucidate food web structure in aquatic systems (Minagawa and Wada 1984; Peterson and Fry 1987; Hecky and Hesselink 1995; Fry and others 1999), stable isotope analysis of museum-archived fish specimens could enable the reconstruction of historical food webs, provided that the effects of tissue preservation on isotope signatures are characterized and can be corrected for (Arrington and Winemiller 2002; Sarakinos and others 2002; Edwards and others 2002).

Herein we use this retrospective approach to describe historical food webs and energy flow pathways. By comparing the historical data with the present-day food web structure, we were able to elucidate long-term changes in food webs and energy flow pathways resulting from species invasions and other perturbations. We argue that knowledge of food web alterations is needed to characterize the restoration potential of any aquatic community, an issue of central importance in lakes of the Tahoe basin and elsewhere.

**METHODS**

**Study Systems**

Lake Tahoe is a deep (mean depth, 313 m), large (500 km² in surface area), oligotrophic (mean annual Secchi depth, approximately 20 m), subalpine (elevation, 1998 m) lake located in the Sierra Nevada mountains on the border of California and Nevada (Figure 1). Lake Tahoe has a well-documented history of cultural eutrophication (Goldman 2000), as well as a variety of successful and unsuccessful nonnative species introductions (Snyder 1940; Cordone and Frantz 1968; Jassby and others 2001). Historically, the Lake Tahoe–Truckee River–Pyramid Lake system (Truckee River watershed) supported one, and perhaps two, distinct...