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 Hesslein 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 km^2 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
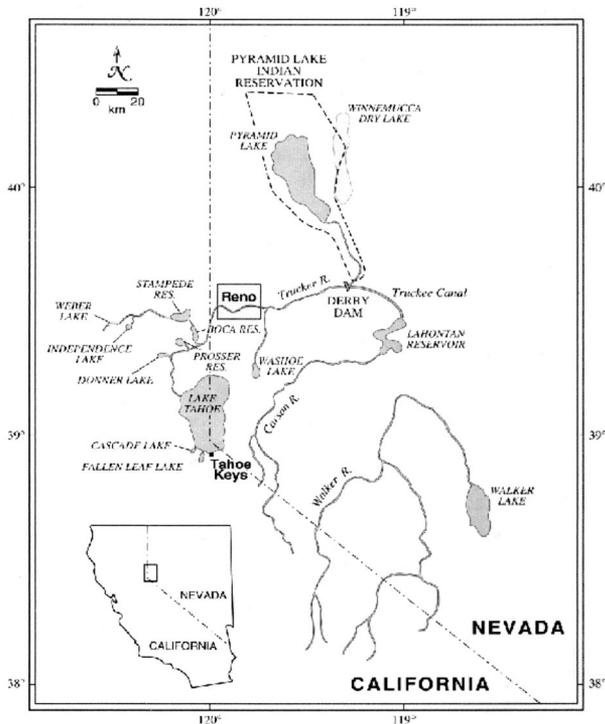
Figure 1. The Lake Tahoe–Pyramid Lake drainage system. The inset shows the system's location in the Sierra Nevada mountains of California–Nevada, USA.

stocks of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*; hereafter referred to as LCT) (Juday 1906; Snyder 1912, 1940).

LCT evolved in Lake Lahontan, a large late Pleistocene lake that covered roughly 22,000 km² (Nielsen and Sage 2002). This species was adapted to foraging on the vast schools of pelagic fishes that inhabited the lake (Ono and others 1983; Nielsen and Sage 2002). As Lake Lahontan receded during the Holocene period, LCT populations persisted in remnant lake and stream habitats. Until the early 20th century, the Truckee River system supported a highly valued LCT fishery comprised of fish occasionally exceeding 25 kg (Snyder 1940; Ono and others 1983; Gerstung 1988). The last recorded spawning run of LCT in the Truckee River was in 1938 (Ono and others 1983; Gerstung 1988). Their ultimate demise is attributed to the combined impacts of nonnative species introductions (lake trout in particular), overexploitation, dam construction on the Truckee River, and the destruction of their spawning habitat (Ono and others 1983; Gerstung 1988; Coffin and Cowan 1995). With only remnant LCT populations in the Lahontan basin, the species was listed as endangered in 1970; it was then reclassified as threatened in 1975 to allow angling on

the remaining populations (Coffin and Cowan 1995). Presently, LCT are among the most endangered of the western salmonids, and it is debatable whether the Truckee River strain of LCT persists at all in a genetically pure form (but see Hickman and Behnke 1979; Nielsen and Sage 2002). At present, the US Fish and Wildlife Service is committed to the restoration of self-sustaining LCT in the Truckee River watershed (Coffin and Cowan 1995); introductions are planned at numerous sites throughout the basin. For this reason, efforts to characterize the restoration potential of lake and stream sites, based on an analysis of present-day and historical food webs and energy flow pathways, would be a valuable contribution to ongoing fishery restoration efforts in the Tahoe basin.

A number of nonnative species have established populations in Lake Tahoe (Table 1), although two species in particular—lake trout (*Salvelinus namaycush*) and the pelagic crustacean *Mysis relicta*—have dramatically restructured the Lake Tahoe pelagic food web (Richards and others 1991). Lake trout were first introduced in 1888, established by the early 20th century, and there is presently a large, self-sustaining population that supports an important recreational fishery (Snyder 1940; Frantz and Cordone 1970). *Mysis*, a freshwater shrimp native to eastern North America, was introduced into Lake Tahoe between 1963 and 1965 to increase the forage base for trout (Linn and Frantz 1965). By the early 1970s, a tremendous *Mysis* population had become established (more than 300/m²). Their establishment corresponded with the virtual disappearance of two cladoceran zooplankton genera, *Daphnia* and *Bosmina*. A number of studies have since concluded that *Mysis* predation was the primary factor responsible for their disappearance (Richards and others 1975; Goldman and others 1979; Threlkeld and others 1980; Morgan and others 1981). Prior to the establishment of *Mysis*, forage fishes and crayfish were the main prey of lake trout in Lake Tahoe (Miller 1951; Frantz and Cordone 1970). After *Mysis* establishment, only lake trout larger than 58 cm in length relied significantly on forage fishes, while the diet of lake trout smaller than 58 cm consisted almost exclusively of *Mysis* (Thiede and others unpublished).

Cascade Lake is a much smaller (0.86 km²), oligotrophic lake directly upstream of Lake Tahoe. In contrast to Lake Tahoe, Cascade Lake is unusual in that it has remained relatively free of species introductions over the past century due to the restricted public access allowed by private landowners. Lake trout and *Mysis*, the two species that so dramatically restructured the pelagic food web of Lake Tahoe,

Table 1. Native and Introduced Fishes for Lake Tahoe and Cascade Lake

Species	Latin Name	Code	Lake Tahoe	Cascade Lake
Native fishes				
Tahoe sucker	*Catostomus tahoensis*	suc	X	X
Lahontan speckled dace	*Rhinichthys osculus robustus*	dac	X	X
Lahontan redside	*Richardsonius egregius*	red	X	X
Lahontan cutthroat trout	*Oncorhynchus clarki henshawi*	lct	X	X
Mountain whitefish	*Prosopium williamsoni*	whi	X	X
Tui chub—benthic	*Gila bicolor obesa*	tui-b	X	X
Tui chub—pelagic	*Gila bicolor pectinifer*	tui-p	X	
Paiute sculpin	*Cottus beldingii*	scu	X	
Established nonnative salmonids[a]				
Rainbow trout	*Oncorhynchus mykiss*	rbt	X	X
Brown trout	*Salmo trutta*	bt	X	X
Kokanee salmon	*Oncorhynchus nerka*	kok	X	
Lake trout	*Salvelinus namaycush*	lt	X	
Nonnative fishes with restricted distribution				
Golden trout	*Salmo aquabonita*	—	X	
Brook trout	*Salvelinus fontinalis*	—	X	
Goldfish[b]	*Carassius auratus*	—	X	
Bluegill[b]	*Lepomis macrochirus*	—	X	
Golden shiner[b]	*Notemigonus crysoleucus*	—	X	
White crappie[b]	*Pomixis annularis*	—	X	
Black crappie[b]	*Pomoxis nigromaculatus*	—	X	
Brown bullhead[b]	*Ictalarus nebulosus*	—	X	
Carp[b]	*Cyprinus carpio*	—	X	
Mosquitofish[b]	*Gambusia affinis*	—	X	
Largemouth bass[b]	*Micropterus salmoides*	—	X	
Smallmouth bass[b]	*Micropterus dolomieu*	—	X	

"Code" is the species abbreviation in Figures 3 and 4.
[a]*A number of other species (lake whitefish, Chinook salmon, Atlantic salmon, Arctic grayling) have been introduced into Lake Tahoe but have not established self-sustaining populations.*
[b]*These species are limited to the Tahoe Keys Marina, other isolated marinas, and a few river mouths in Lake Tahoe.*

were never introduced into Cascade Lake. Thus, it is not surprising that during our field studies we discovered a previously unrecorded, relict population of LCT in Cascade Lake. Preliminary genetic analysis using microsatellite and MtDNA markers suggests that the LCT population of Cascade Lake is partially hybridized with rainbow trout (*Oncorhynchus mykiss*) (M. Campbell personal communication; M. Peacock personal communication). Fish hatchery records indicate that both rainbow trout and brown trout (*Salmo trutta*) were stocked into Cascade Lake in the early decades of the 20th century. Despite some obvious differences between Cascade Lake and Lake Tahoe, present-day Cascade Lake contains a native species assemblage that is remarkably similar to that of Lake Tahoe prior to the onslaught of exotic species over the past 100 years (Table 1). Because of these similarities, analysis of the present-day food web of Cascade Lake may provide insights into the historical food web of Lake Tahoe.

Analysis of Samples

Carbon and nitrogen stable isotope ratios (δ^{13}C and δ^{15}N) are well-documented tracers of energy flow in aquatic food webs (Peterson and Fry 1987; Fry 1988; Pinnegar and Polunin 2000). There is typically a 3‰–4‰ increase in δ^{15}N from prey to predator, such that δ^{15}N can be used to estimate consumer trophic position (Minagawa and Wada 1984; Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 2001). The δ^{13}C of phytoplankton is isotopically depleted relative to benthic algae due to boundary layer–driven differences in isotopic discrimination for dissolved inorganic carbon (DIC) (Hecky and Hesslein 1995). These carbon isotope differences between benthic and pelagic habitats are conserved up the food chain (that is, they re-

main relatively constant from prey to predator), and can thus be used to estimate the contributions of littoral and pelagic resources to higher trophic levels (Hecky and Hesslein 1995; Vander Zanden and others 1999a).

Fish, benthic invertebrates, *Mysis*, and zooplankton samples from pelagic, littoral, and profundal habitats were collected for stable isotope analysis between 1999 and 2001 from Lake Tahoe and during 2000 and 2001 from Cascade Lake. Isotopic signatures did not differ significantly among years, so that species-specific mean values from several years were used to represent present-day Lake Tahoe and Cascade Lake food webs. Fish were collected using gill nets, minnow traps, trap nets, and rod and reel. Approximately 1 g of dorsal muscle tissue was removed from each fish and frozen for isotope analysis. Zooplankton was collected from vertical tows with an 80-μm mesh zooplankton net. Individual zooplankton species were hand-separated and frozen for isotope analysis. Benthic invertebrates were collected along depth gradients using dip nets, an Ekman grab sampler, and a benthic trawl. Fresh specimens were sorted, identified, and frozen.

Our historical food web reconstructions of Lake Tahoe (all but the 1998–2000 food web) are based on stable isotope analysis of muscle tissue of formalin-preserved archived fish and aquatic invertebrates. For each preserved fish specimen from museum collections (California Academy of Sciences, the Smithsonian Institute, and the University of Michigan), approximately 0.5 g of dorsal muscle tissue was removed and frozen for stable isotope analysis. Preserved aquatic invertebrates collected from Lake Tahoe in 1963 were also analyzed for stable isotope ratios. The food web of Lake Tahoe was reconstructed for 4 historical time periods. The first 3 periods had a predominantly native species assemblage, including LCT as the native top predator, although this species was extirpated during the 3rd period. The 4th period (1959–66) includes lake trout as the top predator. The present-day food web (2000) includes lake trout, kokanee salmon, and the freshwater shrimp, *Mysis relicta*.

Fish and invertebrate specimens for our historical reconstructions were preserved in formalin or initially preserved in formalin and transferred to ethanol (EtOH). Because chemical preservation of tissues has the potential to alter isotopic signatures, we develop correction factors based on the published experimental studies examining the effects of tissue preservation on isotopic signatures (Table 2 and Figure 2). This correction factor is comparable to that of Sarakinos and others (2002), but it has

been updated with the most recent experimental values. The published estimates of tissue preservation effects (difference between preserved and unpreserved sample of the same tissue) for fish, insects, and crustaceans are shown in Figure 2. For formalin and formalin/ethanol preservation experiments, fish muscle tissue and invertebrates both show a decrease in $\delta^{13}C$ resulting from preservation (mean ± SE; –1.12‰ ± 0.23 and –1.77‰ ± 0.52, respectively). This difference was not statistically significant (t-test, $t = 1.295$, df = 10, $P = 0.224$). Thus, the mean effect for all taxa (fish and invertebrates; –1.28‰ ± 0.22) was used as the $\delta^{13}C$ correction factor. The mean preservation effect for $\delta^{15}N$ was +0.53‰ ± 0.15 for fish and –0.18‰ ± 0.29 for invertebrates. This difference was statistically significant (t-test, $t = 2.347$, df = 13, $P = 0.035$), and a separate correction factor was used for fish and invertebrates. To correct for tissue preservation effects, the appropriate correction factor was subtracted from the measured isotopic values of the preserved specimens. The SE associated with the mean preservation effect contributes an equivalent amount of error to the isotopic signature of the preservative-corrected specimens.

Samples were dried at 60–75°C for 24–48 h, ground into a fine powder with mortar and pestle, and packed into acid-washed 5 × 8 mm tin capsules for C and N isotope analysis (Vander Zanden and others 1999a; Vander Zanden and Rasmussen 1999). Stable isotope analysis was performed on a continuous flow isotope ratio mass spectrometer (dual-inlet Europa 20/20; PDZ Europa, Crewe, England, UK) at the University of California–Davis. Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}]-1) \cdot 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. Approximately 20% of the samples were analyzed in duplicate. The mean standard error for sample duplicates of these samples was 0.09‰ for $\delta^{13}C$ and 0.15‰ for $\delta^{15}N$.

$\delta^{15}N$ values were converted to a continuous measure of trophic position (TP) to standardize for within- and among-system variation in $\delta^{15}N$ at the base of the food web (Vander Zanden and Rasmussen 1999):

$$TP_{consumer} = ((\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4) + 2$$

$$(1)$$

where 3.4 is the assumed per trophic level enrichment in $\delta^{15}N$. Primary producers are trophic level 1, primary consumers are trophic level 2, and so on. To estimate $\delta^{15}N_{baseline}$, a primary consumer $\delta^{13}C$–

Table 2. The Effects of Chemical Preservation (EtOH and formalin) on Fish Muscle Tissue Stable Isotope (δ^{13}C and δ^{15}N) Signatures

Latin Name	Common Name	EtOH δ^{13}C	EtOH δ^{15}N	Formalin δ^{13}C	Formalin δ^{15}N	Study
Fish						
Argyrosomus hololpidotus	Cob	0.7	0.1	−0.5	0.30	Kaehler and Pakhomov 2001
Four separate fish species[a,b]	—			−1.12	0.62	Arrington and Winemiller 2002
Catostomus occidentalis	Sacramento sucker	0.21	0.37	−1.33	0.16	Sarakinos and others 2002
Pleuronectes americanus	Winter flounder			−0.74	1.21	Bosley and Wainright 1999
Pleuronectes americanus[a]	Winter flounder			−2.17	1.41	Bosley and Wainright 1999
Hemibarbus barbus	—				−0.17	Ogawa and others 2001
Lepomis macrochirus	Bluegill		−0.07			Ogawa and others 2001
Micropterus salmoides	Largemouth bass		−0.13			Ogawa and others 2001
Zacco platyput	—				0.41	Ogawa and others 2001
Percina caprodes	Logperch			−1.70	0.81	Edwards and others forthcoming
Rhinichthys cataractae	Longnose dace			−1.84	0.41	Edwards and others forthcoming
Percina roanoka	Roanoke darter			−0.03	−0.10	Edwards and others forthcoming
Etheostoma tippecanoe	Tippecanoe darter			−0.67	0.72	Edwards and others forthcoming
	Mean—fish	0.45	0.07	−1.12	0.53[d]	
	SE	0.20	0.10	0.23	0.15	
Invertebrates						
Hydropsyche sp.	Caddisfly	0.04	−0.21	−0.75	−0.12	Sarakinos and others 2002
Crangon septemspinosa	Mud shrimp			−2.05	0.35	Bosley and Wainright 1999
	Marine zooplankton			−2.50	−1.00	Mullen and others 1984
Neomysis intermedia	Freshwater shrimp				0.04	Toda and Wada 1990
	Mean—invertebrates			−1.77	−0.18[d]	
	SE			0.52	0.29	
	Mean—all taxa	0.32	0.01	−1.28[c]	0.34	
	SE	0.20	0.10	0.22	0.15	

[a]*Samples preserved in formalin and transferred to EtOH.*
[b]*Arius felis, Cynoscion nebulosus, Dorosoma cepedianum, Mugil cephalus*
[c]*Mean for all taxa is used because there is no significant preservation difference between invertebrates and fish.*
[d]*Taxa-specific preservation corrections are used because there is a significant difference between invertebrates and fish.*

δ^{15}N relationship was established using linear regression, which provided an adequate fit for these data. This approach differs slightly from that of Vander Zanden and Rasmussen (1999), which used a sigmoid-shaped curve fit. For Lake Tahoe, baseline relationships for samples collected in 2000 and 1963 were not significantly different using analysis of covariance (ANCOVA). Therefore, a common baseline curve using data from both periods was developed (δ^{15}N $= -0.094 \cdot \delta^{13}$C $+ 0.898$) and used for all 5 time periods. A separate primary consumer baseline relationship was developed for Cascade Lake (δ^{15}N $= -0.123 \cdot \delta^{13}$C -0.860). The baseline δ^{15}N value was calculated separately for each consumer by solving for δ^{15}N using the consumer δ^{13}C

value and the lake-specific baseline equation. TP was estimated for each individual fish using Eq. 1. Population-specific TP estimates represent the mean trophic position of all adults sampled from a population.

δ^{13}C values of pelagic primary producers are isotopically enriched relative to benthic producers due to differences in fractionation relative to their inorganic carbon sources. Consequently, consumer δ^{13}C values are indicative of reliance on benthic versus pelagic prey. To facilitate comparisons among lakes, a two end-member δ^{13}C mixing model was used to estimate the fractional reliance of each fish population on benthic prey using the following equation:
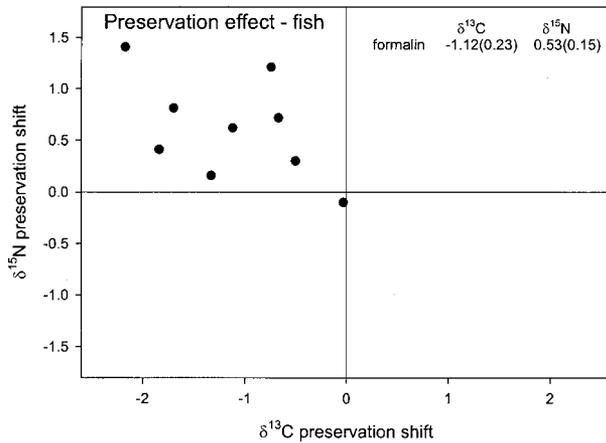
Figure 2. Effect of chemical preservation (formalin) on $\delta^{13}C$ and $\delta^{15}N$ of fish muscle tissue. Individual values are shown in Table 2. Values are mean preservation effect ($\pm$ 1 SE).

Percent benthic

$$= (\delta^{13}C_{fish} - \delta^{13}C_{pelagic})/(\delta^{13}C_{benthic} - \delta^{13}C_{pelagic}) \cdot 100$$

(2)

For Lake Tahoe, the pelagic end-member ($\delta^{13}C_{pelagic}$) was the mean of all zooplankton and *Mysis* specimens, and the benthic end-member was the mean of amphipod, crayfish, mayfly, snail, and fingernail clam $\delta^{13}C$ values. For Cascade Lake, only two zooplankton samples were collected, so the pelagic end-member also included profundal benthic invertebrates (specimens from depths greater than 50 ft). These consumers had $\delta^{13}C$ values similar to that of zooplankton in this lake and provided a more representative and time-integrated pelagic end-member for the mixing model. The benthic end-member for Cascade Lake was the mean value for snails and amphipods. Our model assumes no trophic fractionation for $\delta^{13}C$, which is a reasonable assumption based on a recent synthesis (Vander Zanden and Rasmussen 2001). Note that "trophic position" and "percent benthic" are secondary variables that are calculated directly from stable isotope values. Use of these secondary variables allows comparison of food web parameters across ecosystems. The food web reconstructions are based on an isotopic analysis of 317 fish specimens (270 fish from Lake Tahoe spanning 5 time periods and 47 from Cascade Lake) and 308 invertebrate specimens (40 from Cascade Lake and 268 from Lake Tahoe from 2 time periods).

RESULTS

Mean $\delta^{15}N$, $\delta^{13}C$, trophic position, and percent benthic values are presented for each fish species from the 5 time periods for Lake Tahoe and for Cascade Lake (Appendix 1). Isotopic values for invertebrates are shown in Appendix 2. Food web diagrams of trophic position versus percent benthic reliance were plotted separately for the 5 Lake Tahoe time periods (Figure 3). In the first 3 time periods, forage fishes relied predominantly (more than 80%) on benthic-derived production. Tui chub (the pelagic morph, *Gila bicolor pectinifer*) were an exception in that they were only 40% reliant on benthic production, corresponding with their previously described pelagic habits (Miller 1951). LCT was the least reliant of any fish species on benthic production (20%–40%), indicating that this species was primarily an open-water, pelagic consumer. The elevated trophic position (3.4–3.5) of LCT indicates a trophic niche that included piscivory. This result is supported by the historical accounts of LCT from Lake Tahoe, which indicate that LCT fed on large zooplankters such as *Daphnia*, as well as pelagic fishes (Juday 1906).

By the 4th period (1959–66), LCT had been extirpated from Lake Tahoe and lake trout dominated as the top predator of the pelagic zone. Comparison with the first 3 periods indicates that lake trout and LCT both had piscivorous diets. The primary difference between LCT and lake trout (1959–66) was that lake trout had a higher trophic position and exhibited greater reliance on benthic-derived energy, probably due to feeding on a greater proportion of benthivorous fishes.

The present-day (1998–2000) pelagic community of Lake Tahoe differs from that of 1959–66 in that Lake Tahoe now contains *Mysis*. Lake trout from the present have a reduced trophic position relative to the 1959–66 period. Large lake trout (those more than 58 cm in total length) from 1998–2000 had a higher trophic position than small lake trout (those less than 58 cm; 3.4 versus 3.2). Lake trout gut content studies reveal a distinct diet shift from *Mysis* to fishes when trout reach approximately 58 cm in size (S. Chandra and others unpublished). Lake trout in 2000 exhibited roughly 32% benthic reliance, which is low relative to lake trout from the period 1959–66. Also note that a number of other fish species shifted toward increased pelagic reliance between these two time periods (Figure 3).

The species assemblage of Cascade Lake in 2000 is similar to that of historical Lake Tahoe (Table 1). Specifically, *Mysis* and lake trout have not been
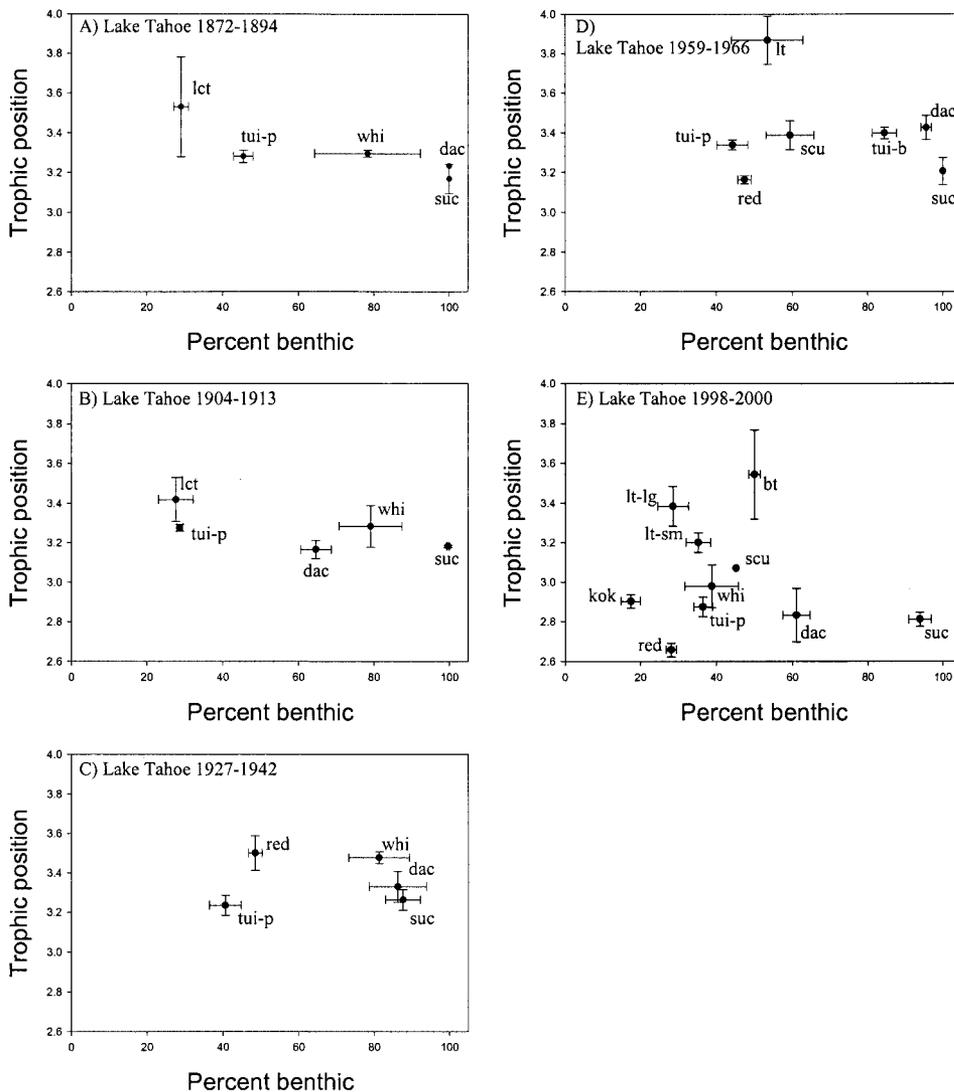
Figure 3. Stable isotope food web diagrams for Lake Tahoe, representing five distinct time periods: (**A**) 1872–94—preexotic conditions with Lahontan cutthroat trout (LCT) as the native pelagic top predator, (**B**) 1904–19—similar to A, (**C**) 1927–42—Lahontan cutthroat trout extirpated during this period, (**D**) 1959–66—lake trout are the top predator and are supported by a mix of benthic and pelagic carbon sources, (**E**) 1998–2000—*Mysis* have established in the pelagic zone, and the trophic position of lake trout is suppressed. The food web has shifted toward pelagic-based production. Species codes are shown in Table 1.

introduced, and the lake contains a remnant LCT population (although preliminary genetic analysis indicates that the LCT population is partially hybridized with nonnative rainbow trout). The Cascade Lake stable isotope food web diagram (Figure 4) indicates that LCT are largely pelagic in their energy provenience, exhibiting 25% benthic reliance. In Cascade Lake, LCT trophic position is slightly lower than the trophic position of LCT in historical Lake Tahoe; it is, in fact, similar to that of forage fishes in Cascade Lake such as redside shiner, tahoe sucker, speckled dace, and tui chub, indicating a primarily plankton-based diet for LCT. Brown trout were the top predator in Cascade lake and the only apparent piscivore, with a trophic position of 3.8 and primary reliance on benthic-derived energy sources (benthic-feeding fishes).

Discussion

Although the population's genetic structure is of central importance in efforts to restore native salmonid populations (Nielsen and Sage 2002), this study emphasizes the less well-studied ecological interactions and their implications for aquatic community restoration. Our stable isotope-based food web reconstructions, which span a 130-year period, indicate that dramatic changes have occurred in the Lake Tahoe food web over the last century. Historically, many of the forage fishes of Lake Tahoe were supported by benthic-derived production, whereas LCT were the top predator in the pelagic zone, relying on zooplankton and tui chub (pelagic morph). Today, Lake Tahoe no longer supports an LCT population, but rather is dominated by large
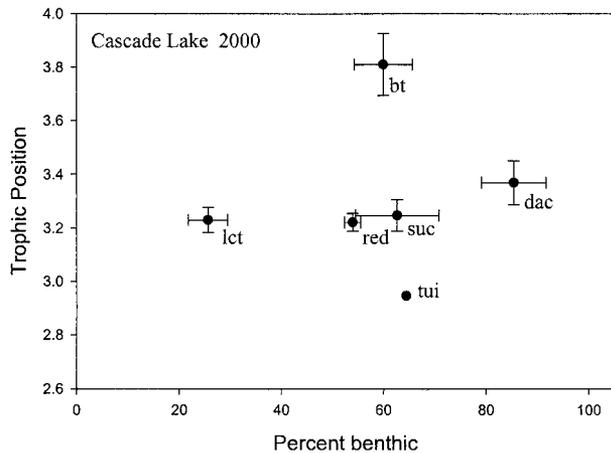
Figure 4. Food web diagram of Cascade Lake 2000. Cascade Lake has a fish community composition and food web structure similar to that of historical Lake Tahoe because nonnative species such as lake trout and *Mysis* were never introduced into Cascade Lake. Species codes are shown in Table 1.

lake trout, which occupies a similar trophic niche to that of historical LCT. In addition, the establishment of *Mysis* in the late 1960s eliminated large zooplankters such as *Daphnia*, leaving a *Mysis*/copepod–dominated zooplankton community. Long-term declines in forage fish populations have also been noted (Thiede and others unpublished), which may be the result of indirect food web effects related to lake trout and *Mysis* introductions (S. Chandra and others unpublished).

Methodological Issues

Although many studies have used stable isotope techniques to characterize energy flow in food webs, this study is among the first to attempt to reconstruct long-term food web changes using archived specimens. A somewhat similar approach was taken by Wainright and others (1993), who examined carbon and nitrogen stable isotope ratios in fish scales from a variety of Grand Banks fishes, with collections dating as far back as 1929. One concern in that study was that the isotopic signatures of fish scales were not referenced to that of a tissue of known isotopic fractionation, although one might assume that there is a relatively constant fractionation for fish scales.

The present study relies on stable isotope analysis of chemically preserved fishes and invertebrates. Preservation in formalin or EtOH could alter the tissue isotopic signature through either uptake of the preservative or selective leaching of compounds from the tissue (Sarakinos and others 2002). To correct for

preservation effects, we characterized the preservation-associated bias using the available experimental studies that have examined tissue preservation effects (Table 2 and Figure 2). Although the effect of tissue preservation on isotope signatures tended to be modest (less than 1.5‰), there was evidence of directional effects. Thus, we corrected all preserved samples according to the mean preservation bias. Of concern is the error associated with the use of the correction factor, which is equal to the standard error of the mean preservation effects (SEδs: ^{13}C = 0.22‰, δ^{13}N$_{fish}$ = 0.15‰δ, ^{15}N$_{inverts}$ = 0.29‰). Based on this SE for carbon, preservation effects represent an additional 2% error in our percent benthic estimates. For nitrogen, it represents error equivalent to 0.05 trophic level for fish and 0.1 trophic level for invertebrates. Overall, the correction for preservation bias is not a major source of error, and it is less than the error associated with trophic fractionation (Vander Zanden and Rasmussen 2001).

The experimental studies summarized in Table 2 that examined preservation effects were all conducted at relatively short time scales (weeks to months). Estimates of preservation bias derived from these short-term studies were applied to samples that have been preserved for much longer time periods, as long as 130 years. We make the assumption that tissue preservation effects are not strongly time-dependent over the potentially long time periods that the samples were preserved. Sarakinos and others (2002) found that preservation effects were stable over a 6-month period, and there is no obvious reason why preservation effects should change dramatically over time, since the preservation/fixation process generally occurs within a matter of weeks.

Another external factor that may affect the long-term interpretation is the possibility that δ^{13}C values may be biased by Seuss effects (Schelske and Hodell 1995). There has been a 1.4‰ depletion in the δ^{13}C of atmospheric carbon dioxide (CO_2) during historical times due to the burning of fossil fuels. The Seuss effect was not apparent in δ^{13}C values from a Lake Tahoe bulk sediment core (A. Heyvaert unpublished), which averaged –26.4‰ ± 0.1‰ over the last 100 years, and failed to show the predicted depletion trend. This suggests that the Lake Tahoe DIC pool is not in equilibrium with atmospheric CO_2, and that any changes in DIC δ^{13}C may have been swamped by other factors, such as variation in fractionation at the DIC-phytoplankton level.

A final issue to consider is that aquatic invertebrates, which comprise the baseline values for trophic position and benthivory calculations, were available from Lake Tahoe from only 2 years, 1963 and 2000. Fortunately, sampling during these two

periods was extensive, providing robust sample sizes for stable isotope analysis (Appendix 2; Tahoe 1963, 98 invertebrate samples; Tahoe 2000, 168 invertebrate samples; Cascade 2000, 40 invertebrate samples). $\delta^{13}C$ and ^{15}N values of Lake Tahoe primary consumers from 1960 and 2000 were not significantly different. Thus, we pooled primary consumers from the 2 time periods and used the combined $\delta^{13}C$–$\delta^{15}N$ baseline curve for all 5 periods. Based on the similarity between 1960 and 2000 (a period of relatively rapid cultural eutrophication) and the stability in $\delta^{13}C$ and $\delta^{15}N$ values over the last 150 years from the sediment record (A. Heyvaert unpublished), we assumed the general $\delta^{13}C$–$\delta^{15}N$ baseline relationship to be appropriate for earlier time periods as well.

Food Webs and Restoration Potential

Analysis of the historical (1872–94, 1904–13) Lake Tahoe food web indicates that the native top predator, LCT, was supported predominantly by pelagic production, consisting of a mix of pelagic fishes, particularly tui chub (*Gila bicolor pectinifer*) and zooplankton. Although few dietary records exist for the historical Lake Tahoe LCT, the available qualitative diet descriptions corroborate our findings (Juday 1906). Our discovery of an undocumented population of LCT (although possibly hybridized with rainbow trout) in nearby Cascade Lake provided a unique opportunity to compare the trophic niches of LCT populations of adjacent historical and contemporary ecosystems. Analysis of Cascade Lake indicates that LCT rely primarily on pelagic resources (Figure 4). One important difference between LCT from Lake Tahoe (1900) and LCT from Cascade Lake (2000) is their respective trophic positions. LCT from Cascade Lake had a lower trophic position than LCT from Lake Tahoe (3.2 versus 3.4–3.5). In fact, the trophic position of Cascade Lake LCT is similar to that of forage fishes from that system. This low trophic position from Cascade Lake LCT corroborates the limited gut content data (10 stomachs) indicating a diet of zooplankton.

Because Lake Tahoe and Cascade Lake are adjacent to each other, these two lakes share a common biogeographical history, historical species composition, climate, and geology. A major difference between these two lakes is that Cascade Lake has not been stocked with pelagic nonnative species such as lake trout and *Mysis*. For this reason, Cascade Lake provides additional insights into the historical, preintroduction food web of Lake Tahoe. Yet there are substantial differences between Lake Tahoe and Cascade Lake, given that Lake Tahoe is more than 500 times larger in surface area and substantially deeper than

Cascade Lake. The difference in LCT trophic position could be attributed to differences in lake size or habitat area between these systems, as recent studies have found that lake size and correlates such as species richness are important predictors of food chain length (Vander Zanden and others 1999b).

The last recorded spawning run of LCT in the Lake Tahoe–Pyramid Lake system was in 1938, after which LCT were extirpated, leaving lake trout as the predominant pelagic top predator in Tahoe (Frantz and Cordone 1970; Ono and others 1983). The 1959–66 food web indicated that lake trout occupied a trophic niche similar to that of the historical LCT population of Lake Tahoe, although lake trout had a higher trophic position and were more reliant on benthic-based production. This difference is most likely due to increased consumption of benthivorous fishes by lake trout, which might be expected because lake trout are adapted for foraging near the lake bottom (Scott and Crossman 1973).

Although lake trout had already replaced LCT as the top predator, the establishment of *Mysis* in the late 1960s probably had a more profound impact on the pelagic food web. Their introduction has been linked to the virtual elimination of *Daphnia* and *Bosmina* in Lake Tahoe (Richards and others 1975; Goldman and others 1979; Threlkeld and others 1980; Morgan and others 1981), which historically comprised an important prey of LCT (Juday 1906). Lake trout, which were largely piscivorous in the 1960s, now feed primarily on *Mysis*, as evidenced by dietary data and stable isotopes; only the very large lake trout (more than 58 cm) are piscivorous (Frantz and Cordone 1970; Thiede and others unpublished). This shift in lake trout diet from 1960 to the present may reflect a series of indirect food web changes in Lake Tahoe initiated by the introduction of *Mysis* (S. Chandra and others unpublished). A possible scenario is that *Mysis* introduction led to an overall increase in lake trout populations by providing a new and superabundant prey resource. The resultant increase in the size of the lake trout population may have augmented predation rates on forage fishes (tui chub, mountain whitefish, tahoe sucker), even though *Mysis* remained the primary prey of smaller lake trout. This hypothesis is similar to apparent competition and the hyperpredation process, which has been examined elsewhere (Holt 1977; Holt and Lawton 1994; Courchamp and others 2000), and provides one potential explanation for the roughly 10-fold reduction in forage fish populations in Lake Tahoe over this same period (Thiede and others). Alternatively, declines in pelagic forage fishes may be associated with decreases in non-*Mysis* zooplankton populations. This idea

presumes that *Mysis* are a less available or preferred prey item relative to zooplankters such as *Daphnia* and *Bosmina*. Although this situation has been found for kokanee salmon in Lake Tahoe and elsewhere (Richards and others 1991; Spencer and others 1991), the forage fishes of Lake Tahoe were predominantly reliant on benthic-derived production and would not be expected to be greatly impacted by changes in the zooplankton community alone.

Another important factor when considering the fisheries restoration potential of Lake Tahoe is its history of cultural eutrophication. The hallmark of lake eutrophication is an increase in phytoplankton-based primary production rates. This increase often occurs at the expense of benthic primary producers due to shading by phytoplankton. The result is an overall shift in the distribution of whole-ecosystem primary production from benthic to pelagic habitats (Vadeboncoeur and others 2001, 2002). Although the pelagic zone clearly dominates whole-ecosystem primary production in Lake Tahoe (Loeb and others 1983), our stable isotope evidence indicates an important role for benthic production in supporting fish production. Furthermore, there is evidence for a shift in the trophic basis for fish production from benthic to pelagic over the last 100 years (Figure 3), consistent with cultural eutrophication trends in recent decades. How these changes impact the restoration potential of LCT is unknown, although enriching the productivity of the pelagic food chain should augment the production capacity of pelagic-dependent species such as LCT.

The US Fish and Wildlife Service and other resource agencies have been working toward broad-scale restoration of native fish communities in the Lake Tahoe basin, with primary emphasis on the reintroduction of LCT populations (Coffin and Cowan 1995). Success in these restoration efforts would clearly benefit from a deeper understanding of the restoration potential of the lakes and streams in the region. To what extent is the presence of *Mysis* and lake trout in lakes a significant barrier to native community restoration? To what extent have these nonnative species altered the food web structure of potential restoration sites? Will successful restoration require additional management actions to shift the pelagic food web toward something more closely resembling the historical state? If the introduction of nonnative species (or other impacts) has not substantially changed energy flow pathways and reduced prey availability, restoration efforts might succeed, provided that the appropriate habitat and environmental conditions remain.

In the case of Lake Tahoe, all evidence indicates that the introduction of *Mysis* and lake trout has greatly restructured the food web, and in ways that will act as barriers to the restoration of LCT. Based on our understanding of these food web changes, the restoration of a native fish community would require concerted management efforts—in particular, the reduction of lake trout and *Mysis* populations through removal efforts and increased rates of lake trout harvest. Substantially reducing both their populations would be a tremendous undertaking. But since lake trout now support a valuable recreational fishery in Lake Tahoe, these restoration-oriented management actions would no doubt be viewed by a subset of the human population as a threat to the status quo. Any discussion of the restoration of a native fish community would almost certainly spark controversy over whether Lake Tahoe and its fishery should be managed for human exploitation or for biodiversity and ecological function (Lange and Smith 1995). Restoration efforts could more effectively be directed toward alternative sites such as Cascade Lake. Another promising restoration site is nearby Fallen Leaf Lake (Figure 1), which supports both lake trout and *Mysis* yet still retains large cladocerans and abundant forage fishes, perhaps due to its higher productivity relative to Lake Tahoe. In fact, Fallen Leaf Lake was chosen as an LCT reintroduction site during the summer of 2002. Analysis of trophic interactions in a broader range of Sierra Nevada lakes would allow lake managers to identify and target lakes with the greatest potential for LCT restoration success.

Our findings augment the limited understanding of the changes in the Lake Tahoe food web over the last 100+ years, since few records exist that might provide insights into historical food web interactions and energy flow pathways. In addition, food web information from present-day Cascade Lake can serve as an analogue for historical Lake Tahoe, providing further evidence for the historical food web and, in particular, the trophic niche of LCT in alpine lake ecosystems. With the restoration of native fish communities of increasing importance to fisheries managers (Horns and others 2002), approaches are needed that consider species as embedded within their broader food web context. Indeed, there is a vast ecological literature showing that individual species cannot be viewed apart from their broader food web context (Evans and others 1987; Pimm 1991; Polis and Winemiller 1996; Kitchell and others 2000).

This study shows how stable isotope techniques can be used to characterize the historical or baseline food web structure of aquatic ecosystems. Comparing the historical food web structure with the present-day structure enables us to detect food web

changes at long time scales (decades to centuries) that are otherwise difficult to identify. There will be growing demand on fisheries managers to balance economically important fisheries for nonnative species (that is, lake trout in Lake Tahoe, Pacific salmonids in the Laurentian Great Lakes) with the restoration of native species and fish communities. Thus, efforts to characterize the restoration potential of native fish communities, by considering long-term food web changes, can provide a basis for establishing restoration targets and developing management actions that will favor restoration success.

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Appendix 1. Stable Isotope Values ($\delta^{15}N$ and $\delta^{13}C$), Trophic Position, and Percent Benthic Reliance (mean ± 1 SE) for Fishes from 5 Time Periods in Lake Tahoe and Cascade Lake (2000)

Year	Species	n	Preserved	$\delta^{15}N$	SE	$\delta^{13}C$	SE	Trophic Position	SE	Percent Benthic	SE
Lake Tahoe											
1872–94	Tui chub—pelagic	6	P	7.32	0.10	−21.92	0.29	3.28	0.03	45.5	2.56
	Lahontan cutthroat trout	5	P	8.35	0.87	−23.82	0.22	3.53	0.25	29.0	1.94
	Speckled dace	1	P	6.18		−11.56		3.23		100.0	
	Tahoe sucker	2	P	6.14	0.21	−13.41	0.41	3.17	0.07	100.0	0.00
	Mountain whitefish	2	P	7.01	0.21	−18.14	1.62	3.29	0.02	78.3	14.02
1904–13	Tui chub—pelagic	4	P	7.49	0.05	−23.86	0.09	3.28	0.02	28.7	0.79
	Lahontan cutthroat trout	6	P	7.98	0.35	−23.98	0.53	3.42	0.11	27.6	4.59
	Speckled dace	6	P	6.72	0.18	−19.72	0.46	3.17	0.05	64.6	4.03
	Tahoe sucker	2	P	6.21	0.21	−13.65	2.06	3.18	0.01	99.7	0.30
	Mountain whitefish	10	P	6.91	0.46	−17.46	1.16	3.28	0.11	79.1	8.39
1927–42	Tui chub—pelagic	10	P	7.22	0.22	−22.48	0.48	3.24	0.05	40.6	4.20
	Redside shiner	20	P	8.03	0.29	−21.57	0.21	3.50	0.09	48.5	1.80
	Speckled dace	15	P	6.91	0.34	−15.75	1.18	3.33	0.08	86.3	7.59
	Tahoe sucker	9	P	6.77	0.19	−16.68	0.70	3.26	0.05	87.7	4.64
	Mountain whitefish	5	P	7.55	0.16	−17.27	1.24	3.48	0.03	81.4	8.04
1959–66	Tui chub—benthic	14	P	7.28	0.10	−17.32	0.42	3.40	0.03	84.4	3.24
	Tui chub—pelagic	8	P	7.53	0.10	−22.06	0.47	3.34	0.03	44.3	4.05
	Redside shiner	36	P	6.90	0.07	−21.70	0.20	3.16	0.02	47.4	1.73
	Paiute sculpin	11	P	7.53	0.28	−20.32	0.73	3.39	0.07	59.4	6.34
	Speckled dace	12	P	7.22	0.21	−15.63	0.36	3.43	0.06	95.5	1.42
	Tahoe sucker	3	P	6.13	0.29	−11.96	0.67	3.21	0.07	100.0	0.00
	Lake trout	5	P	9.23	0.41	−21.00	1.08	3.87	0.12	53.4	9.39
1998–2000	Tui chub—pelagic	3	F	6.37	0.35	−22.69	0.81	2.98	0.11	38.8	7.05
	Kokanee salmon	9	F	6.34	0.13	−25.15	0.30	2.90	0.03	17.4	2.57
	Redside shiner	2	F	5.39	0.13	−23.93	0.16	2.66	0.03	28.1	1.35
	Paiute sculpin	1	F	6.61	0.00	−21.96	0.00	3.07	0.00	45.1	0.00
	Speckled dace	5	F	5.63	0.47	−20.13	0.42	2.83	0.14	61.0	3.61
	Tahoe sucker	16	F	5.12	0.13	−15.54	0.53	2.81	0.04	93.8	2.99
	Mountain whitefish	3	F	6.04	0.20	−22.96	0.28	2.87	0.05	36.5	2.43
	Brown trout	2	F	8.17	0.78	−21.40	0.17	3.54	0.22	50.0	1.48
	Lake trout—small	25	F	7.15	0.15	−22.97	0.45	3.20	0.05	35.2	3.27
	Lake trout—large	12	F	7.87	0.33	−24.00	0.56	3.38	0.10	28.5	4.09
Cascade Lake											
2000	Tui chub	1	F	5.56	—	−26.13	—	2.95	—	64.4	—
	Lahontan cutthroat trout	10	F	7.16	0.17	−31.29	0.51	3.23	0.05	25.6	3.84
	Redside shiner	10	F	6.67	0.1	−27.53	0.21	3.22	0.03	53.9	1.58
	Speckled dace	6	F	6.49	0.41	−22.01	1.84	3.37	0.08	85.4	6.27
	Tahoe sucker	16	F	6.52	0.21	−25.59	1.36	3.25	0.06	62.6	8.18
	Brown trout	4	F	8.57	0.32	−26.73	0.75	3.81	0.12	59.9	5.66

P, preserved samples; F, fresh samples.
Values for preserved samples are corrected for tissue preservation effects.
Samples size (n) represents the number of individual fish from each time period.

Appendix 2. ^{15}N and $\delta^{13}C$ Values (mean $\pm$ 1 SE) for Invertebrates from Lake Tahoe and Cascade Lake

Taxa	Habitat	n	$\delta^{15}N$	SE	$\delta^{13}C$	SE
Cascade Lake 2000						
Trichoptera	Littoral	2	2.89	0.64	−26.81	0.67
Hemiptera	Littoral	2	3.26	0.48	−26.10	1.27
Odonata	Littoral	1	2.80	—	−22.26	—
Dytiscidae	Littoral	2	3.35	0.74	−26.37	0.57
Decapoda	Littoral	10	5.32	0.21	−25.35	0.59
Hyalella	Littoral	1	−1.46	—	−21.90	—
Ephemeroptera	Littoral	1	−1.31	—	−20.90	—
Chironomidae	Depth gradient	12	2.58	0.52	−27.48	2.21
Oligochaeta	Depth gradient	4	3.08	0.87	−31.50	1.93
Zooplankton	Zooplankton	2	3.71	0.51	−36.48	0.50
Terrestrial insects	Terrestrial	3	2.39	0.67	−25.47	0.22
Lake Tahoe 1963						
Gastropoda	Depth gradient	5	1.48	0.46	−21.66	1.14
Oligochaeta	Depth gradient	41	3.24	0.36	−21.23	0.59
Chironomidae	Depth gradient	30	3.63	0.28	−19.76	0.62
Hirudinea	Depth gradient	1	4.35	—	−21.64	—
Turbellaria	Depth gradient	4	6.20	0.57	−25.47	1.25
Ostracoda	Depth gradient	4	6.37	0.56	−20.04	2.08
Gammarus	Depth gradient	13	7.22	0.12	−26.41	0.28
Lake Tahoe 2000						
Gastropoda	Littoral	4	1.60	0.60	−16.31	0.95
Hyalella	Littoral	3	−0.58	0.04	−12.87	0.27
Bivalvia	Littoral	1	0.00	—	−16.31	—
Decapoda	Littoral	20	4.23	0.13	−15.67	0.49
Ephemeroptera	Littoral	3	0.52	0.73	−17.26	0.35
Hirudinea	Littoral	1	4.65	—	−17.42	—
Oligochaeta	Depth gradient	32	3.80	0.38	−21.11	0.58
Chironomidae	Depth gradient	18	3.47	0.43	−19.17	0.92
Gammarus	Depth gradient	2	7.44	0.04	−24.79	0.02
Diaptomus	Zooplankton	29	2.67	0.08	−27.66	0.14
Epishura	Zooplankton	30	2.33	0.12	−26.76	0.14
Mysis relicta	Zooplankton	27	3.03	0.11	−27.07	0.23

Isotopic values became more depleted in $\delta^{13}C$ and more enriched in $\delta^{15}N$ as a function of depth, such that the mean values may not be representative of depth-specific values.
Values for preserved samples (Lake Tahoe 1963) were corrected for tissue preservation effects.
Samples size (n) represents the number of samples from each time period.