

Evaluating the Reintroduction Potential of Lahontan Cutthroat Trout in Fallen Leaf Lake, California

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Abstract.—We evaluated the potential for reintroducing Lahontan cutthroat trout *Oncorhynchus clarkii henshawi*, a species listed under the Endangered Species Act, into a lacustrine system where the biotic community has changed dramatically since the species' extirpation there. Since 2002, 76,547 Lahontan cutthroat trout have been reintroduced into Fallen Leaf Lake, California; we used creel surveys, diet data, mark–recapture methods, bioenergetics modeling, and netting data across seasons to evaluate the habitat use, growth, and relative abundance of Lahontan cutthroat trout and the abundance, diet, habitat use, and predation by nonnative species. Sampling totals ($n = 2$) and survey observations ($n = 3$) indicate low survival and abundance of reintroduced fish and together with creel data indicate the importance of epilimnetic habitats across size-classes. Despite substantial growth, Lahontan cutthroat trout exhibited low condition factor values (average = 0.69). We found substantial predation pressure from a large population of lake trout *Salvelinus namaycush* ($\hat{N} = 8,799$ fish; 95% confidence interval [CI] = 4,990–16,530 fish); analysis of lake trout diets showed an increase in piscivory and in the percentage of stomachs containing Lahontan cutthroat trout anchor tags with increasing predator size. Overall, we estimated that lake trout consumed over 38% of reintroduced Lahontan cutthroat trout (mean number consumed = 7,736 fish; 95% CI = 4,388–14,534 fish). With bioenergetics modeling, however, we estimated that lake trout consumed considerable amounts of salmonid biomass during this period (mean biomass = 3,137 kg; 95% CI = 1,779–5,893 kg), which greatly exceeded the biomass of Lahontan cutthroat trout reintroduced in 2006. During the stratification period, there was little overlap in habitat use between lake trout and Lahontan cutthroat trout, but overlap was high during the spring and autumn. We found moderate-sized populations of nonnative brown trout *Salmo trutta*, kokanee *O. nerka* (lacustrine sockeye salmon), and rainbow trout *O. mykiss*. Together, our results suggest that Lahontan cutthroat trout have few refugia from direct and indirect negative interactions with nonnative species and that alternative approaches are needed.

Native subspecies of cutthroat trout *Oncorhynchus clarkii* have experienced significant declines across the western USA and Canada (Williams et al. 1989). In particular, habitat loss and degradation have resulted in substantial declines in cutthroat trout distribution and abundance and have isolated many cutthroat trout populations (Dunham et al. 1997; Horan et al. 2000; Kruse et al. 2000). Additionally, the introductions of nonnative species have negatively affected native cutthroat trout populations through hybridization (Allendorf and Leary 1988; Peacock and Kirchoff 2004; Muhlfeld et al., in press), competition (Kruse et al. 2000; McHugh and Budy 2005), and predation

(Kaeding et al. 1996; Vander Zanden et al. 2003). As management and recovery plans for cutthroat trout subspecies develop, it will be important to identify limiting factors and their magnitude and to determine methods for ameliorating their impacts on the viability of cutthroat trout populations.

The Lahontan cutthroat trout *O. clarkii henshawi*, which is native to the Lahontan Basin of northern Nevada, eastern California, and southern Oregon, has experienced significant declines in abundance and distribution as a result of habitat degradation (Dunham et al. 1997; Jones et al. 1998), overfishing (Coffin and Cowan 1995), and the introduction of nonnative species (Dunham et al. 1999); these factors ultimately led to the listing of Lahontan cutthroat trout as endangered in 1970 (USFWS 1970). The species' status was subsequently downgraded to threatened in

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1975 to allow for regulated angling (USFWS 1975). Most recent estimates of distribution indicate that Lahontan cutthroat trout occupy only 0.4% of their historic lacustrine habitat and 10.7% of their historic lotic habitat (Coffin and Cowan 1995).

In the 1995 U.S. Fish and Wildlife Service (USFWS) recovery plan for Lahontan cutthroat trout (Coffin and Cowan 1995), three distinct population segments (DPSs) were identified but not recognized formally as part of the recovery planning process. The northwestern (Quinn River, Summit Lake, and Coyote Lake basins) and eastern (Humboldt and Reese River basins) DPSs historically comprised large, interconnected fluvial systems that are now highly fragmented. The majority of extant Lahontan cutthroat trout populations are now isolated and, in general, are restricted to small headwater systems (Jones et al. 1998; Dunham et al. 2003). The only large lacustrine habitats for this subspecies are found in the western DPS, which encompasses the Truckee, Carson, and Walker River basins.

Prior to the collapse of the fishery in the 1940s, Lahontan cutthroat trout were widely distributed in the Lake Tahoe basin in both lacustrine and riverine habitat (Vander Zanden et al. 2003). The recovery plan identified the importance of maintaining diversity in life history forms across the species' native range as well as the need to reestablish lacustrine life history forms within the Lake Tahoe basin (Coffin and Cowan 1995). Similar to other imperiled species (Williams et al. 1988), reintroduction programs are an important component in the Lahontan cutthroat trout recovery plan (Coffin and Cowan 1995). However, the success of freshwater, nonanadromous fish reintroductions can hinge upon the quantity and quality of fish habitat (Williams et al. 1988; Harig et al. 2000), the frequency and magnitude of supplemental stocking (Hilderbrand 2002), and the presence of nonnative fishes (Marsh and Douglas 1997; Vander Zanden et al. 2003; Schooley and Marsh 2007). Ultimately, gauging the success or failure of a reintroduction may depend on the viability of a self-sustaining population (Hilderbrand 2002).

Within the Lake Tahoe basin, four lakes are known to have historically contained Lahontan cutthroat trout, including three relatively small lakes (Independence, Fallen Leaf, and Cascade lakes; size range = 96–567 ha) and the larger Lake Tahoe (49,469 ha). Of these lakes, only Independence Lake retains a native, naturally reproducing Lahontan cutthroat trout population, and research and monitoring efforts are currently evaluating Lahontan cutthroat trout population trends and removing nonnative species that are believed to negatively impact this population (Rissler et al. 2006). The small population within Independence Lake is

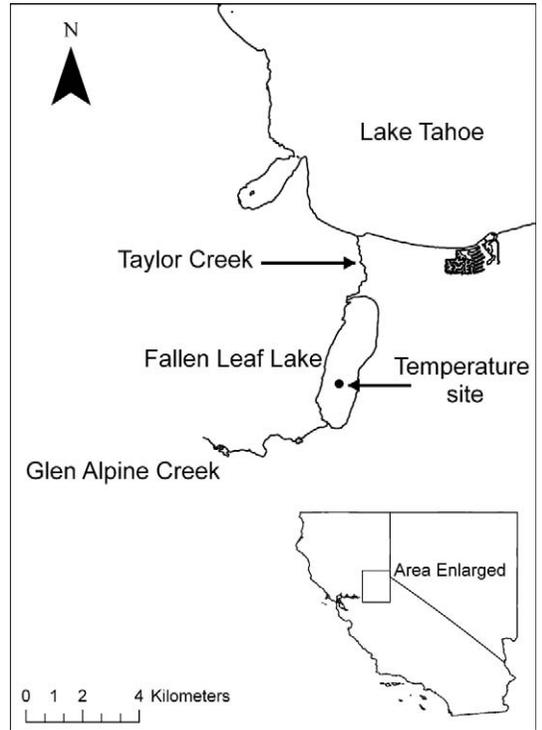


FIGURE 1.—Map of Fallen Leaf Lake, indicating the site of temperature profile data collection, Glen Alpine Creek, and Taylor Creek in the Lake Tahoe basin, California.

currently isolated from the network of streams and lakes within the Lake Tahoe basin, illustrating the importance of establishing other populations. Among the remaining lakes, the USFWS selected Fallen Leaf Lake as an area for Lahontan cutthroat trout reintroductions due to (1) the small size of the lake (relative to Lake Tahoe), which would allow for tractable sampling and monitoring efforts and robust evaluations of factors limiting Lahontan cutthroat trout; (2) a complement of nonnative species similar to that in Lake Tahoe, which would potentially help in identifying factors limiting future reintroductions into the larger, more ecologically and politically complex Lake Tahoe; (3) easy accessibility of Fallen Leaf Lake, as land surrounding Cascade Lake is largely private; and (4) support from regional state and federal biologists as well as local landowners.

As such, the USFWS began reintroductions in 2002 in Fallen Leaf Lake, which is connected to Lake Tahoe via a single stream, Taylor Creek (Figure 1). The goals of these reintroductions, which began in 2002 with a variety of different stocking scenarios (Table 1), were to establish a naturally reproducing population of Lahontan cutthroat trout and to identify the magnitude of factors limiting successful reintroductions. Monitor-

TABLE 1.—Recent history of the total number and average size (total length, TL) of Lahontan cutthroat trout reintroduced into Fallen Leaf Lake, California.

Year	Month(s)	Total number reintroduced	Average TL (mm)
2002	Jul	36,450	230
2003	Jun–Sep	7,468	280
2004	Sep, Nov	18,593	280
2006	Dec	14,036	140

ing efforts of the early reintroductions indicated that a large, resource-limited population of lake trout *Salvelinus namaycush* exhibited high consumption of stocked Lahontan cutthroat trout (Allen et al. 2006); the lake trout is an efficient piscivore of cutthroat trout (Ruzycski et al. 2001, 2003). Additionally, these efforts provided insight into the effectiveness of different stocking strategies, with suggestions of stocking large (>250 mm) Lahontan cutthroat trout that could escape predation by the majority of lake trout in Fallen Leaf Lake.

Despite previous research, significant gaps in our understanding of factors limiting Lahontan cutthroat trout in Fallen Leaf Lake still remain. In particular, there is little information regarding Lahontan cutthroat trout habitat use; such information could help to identify refugia and more effective stocking locations, the spatial and temporal extent of overlap with nonnative species, and ambient growth and condition factor (e.g., Fulton's *K*) of reintroduced Lahontan cutthroat trout, which may provide insight into the suitability of the system for hatchery-reared fish. Additionally, the seasonal habitat use and predation pressure exerted by lake trout, particularly large (i.e., >500 mm) lake trout, and other nonnative species that may negatively affect Lahontan cutthroat trout in Fallen Leaf Lake are largely unknown but are critical for identifying the extent of predation by lake trout, potential refugia for Lahontan cutthroat trout from predation, and the most effective seasons for reintroductions. Finally, aside from lake trout (Allen et al. 2006), there are no estimates of the abundance of other nonnative species in Fallen Leaf Lake, including rainbow trout *O. mykiss*, brown trout *Salmo trutta*, and kokanee *O. nerka* (lacustrine sockeye salmon). Therefore, the objectives of our current research were to estimate (1) Lahontan cutthroat trout relative abundance, habitat use, and growth after reintroduction; (2) habitat use by nonnative fishes prior to, during, and after the period of thermal stratification; (3) the relative abundance and dietary patterns of nonnative species (potential predators); and (4) the predation potential of lake trout. Finally, we summarize 3 years

of creel data (2005–2007) as a means to further evaluate Lahontan cutthroat trout habitat use, identify species targeted by anglers, and quantify angler pressure to better understand the potential effects of future nonnative species management options (i.e., active removal; Bigelow et al. 2003) on anglers visiting Fallen Leaf Lake. Ultimately, our results will provide critical insight into the factors limiting successful Lahontan cutthroat trout reintroductions in this and other lacustrine systems and will guide future management actions.

Methods

Study Site Description

Fallen Leaf Lake is a relatively high-elevation (1,953 m), meso-oligotrophic lake (567 ha) within the Lake Tahoe hydrographic basin in the northern Sierra Nevada Mountains of California (Figure 1). The lake is approximately 5.0 km at the longest point and 1.6 km wide (widest point). The average depth is estimated at 53 m, and the maximum depth is approximately 120 m (Allen et al. 2006). The benthic substrate within the lake is dominated by sand particles, but localized patches of large substrate do exist in the north, west, and southwest parts of the lake (authors' personal field observation). Across all depths, there is a substantial amount of large woody debris (LWD).

Fallen Leaf Lake is relatively isolated from other systems in the Lake Tahoe basin due to natural and man-made barriers. The main tributary into Fallen Leaf Lake, Glen Alpine Creek, is dominated by snowmelt; approximately 41 km² of the Desolation Wilderness drains into the southern end of the lake via this tributary. Glen Alpine Creek has an average width of 12.4 m during bank-full conditions (authors' unpublished data), with substantially lower flows and smaller widths during base flow conditions, and substrate is dominated by large sediment (i.e., cobbles) and bedrock. Approximately 500 m upstream of Fallen Leaf Lake, a series of natural waterfalls blocks the upstream movement of fishes in Glen Alpine Creek; above Glen Alpine Falls, the creek continues to a series of small lakes that primarily contain nonnative salmonids. The main outflow of Fallen Leaf Lake is Taylor Creek, which flows 2.7 km before connecting with Lake Tahoe. The flows of Taylor Creek are managed by the U.S. Forest Service through a small dam. Downstream movement of fishes is possible through the small dam, but no structures (i.e., fish ladder) exist to aid in upstream movement of fishes.

The reasons for extirpation of Lahontan cutthroat trout from Fallen Leaf Lake are largely unknown but likely include a combination of factors that have been attributed to the decline of this species throughout its

range (see above). Today, the fish community in Fallen Leaf Lake is mixture of both native and nonnative species. The native fish community includes the Lahontan redbreast *Richardsonius egregius*, speckled dace *Rhinichthys osculus*, Paiute sculpin *Cottus beldingii*, mountain sucker *Catostomus platyrhynchus*, Tahoe sucker *Catostomus tahoensis*, tui chub *Gila bicolor*, mountain whitefish *Prosopium williamsoni*, and recently reintroduced Lahontan cutthroat trout. While the initial introduction events of nonnative species into Fallen Leaf Lake have not been identified, there have been numerous supplemental stocking events since the 1950s to support recreational angling opportunities, including rainbow trout (1950–1980), kokanee (intermittently between 1962 and 2001), and brown trout (1966; Allen et al. 2006); each of these nonnative species is known to currently exist within the lake.

2006 Lahontan Cutthroat Trout Reintroduction

In December 2006, the USFWS reintroduced 14,036 Lahontan cutthroat trout from the Lahontan National Fish Hatchery (Gardnerville, Nevada) into Fallen Leaf Lake. The reintroduction occurred at one site on the southeast corner of the lake. Similar to the 2004 reintroduction, all individuals in 2006 were tagged with an external anchor tag containing a unique identification number prior to their release, and the average total length (TL) of fish was 140 mm (range = 100–226 mm).

Although earlier research had suggested that planting large fish (>250 mm) would reduce lake trout predation, financial, logistical, and bi-state disease policy constraints precluded the raising and stocking of such large fish in 2006.

Fish Sampling

During early June through mid-October 2007, we used a variety of sampling methods to evaluate the habitat use, distribution, and abundance of fishes in Fallen Leaf Lake. For each sampling method and location, we recorded the amount of effort, location (Universal Transverse Mercator coordinates), and depth (where applicable).

Benthic nets.—We set benthic gill nets perpendicular to the shoreline in the early morning prior to sunrise and in the late evening after sunset. We used a variety of gill nets and trammel nets across a wide range of depths and locations in the lake; additionally, we integrated temperature and depth information to identify the location of the thermocline, guide placement of nets above and below the thermocline, and help evaluate habitat use (i.e., depth) across seasons. Specifically, we used trammel nets (length =

45.7 m, height = 2.4 m, mesh bar length = 3.8 cm, walling = 10.2 cm); equal-sized, variable-mesh gill nets (length = 38.1 m, height = 2.4 m, mesh bar length = 1.27, 2.54, and 3.81 cm); and fixed-mesh gill nets (length = 53.3 m, height = 3.1 m, mesh bar length = 3.8 cm). All nets were typically set for 1–2 h to minimize mortalities.

Pelagic nets.—We deployed pelagic nets across a variety of locations and depths; however, similar to the benthic nets, the pelagic net depths were set with explicit consideration of the thermocline. Pelagic nets consisted of variable-mesh gill nets (see above) as well as large curtain gill nets (length = 24.4 m, height = 7.3 m, mesh = 2.5, 3.2, 3.8, and 5.1 cm). We originally set pelagic nets for short durations during early morning and late evening periods (similar to benthic nets; ~1 h), but we later increased the set duration to as much as 24 h.

Minnow traps.—Wire-mesh minnow traps (mesh = 0.64 cm, length = 44.5 cm, height = 22.9 cm) were used for sampling juveniles and smaller fishes in the lake. We set benthic minnow traps throughout the shallow locations of the lake (1.5–18.3 m) for a typical duration of 24 h.

Angling.—We used angling to sample the pelagic and nearshore areas of the lake. We typically angled during the morning and evening hours and used lightweight spinning gear with monofilament line. We used trolling methods (with 0.5–6.0 oz of weight) at depths ranging from 2 to 20 m, and we used shallow casting methods in the epibenthic zones throughout the lake.

Temperature

We measured the water temperature profile of Fallen Leaf Lake beginning in early June and subsequently every 3–4 weeks until the middle of October. We recorded the temperature at every meter of depth (beginning at the surface) until the temperature stabilized below the thermocline; thereafter, temperature was recorded every 2 m.

Marking and Capture

Upon capture, all unmarked lake trout were weighed, measured, marked with an individual-specific external anchor tag (T-bar), and released. All other fishes captured in nets were weighed, measured, and immediately released. We measured the lengths and weights of the first five fish of each species captured in minnow traps during June and July, and we enumerated all others by species; after July, we only enumerated fishes in minnow traps by species. We recorded the tag number of any fish that had been previously marked (both Lahontan cutthroat trout and

lake trout), and we measured and weighed each individual for estimates of growth and Fulton's K .

We used our capture–recapture data within a Schnabel closed-population mark–recapture model to estimate lake trout abundance in Fallen Leaf Lake (Krebs 1999). The Schnabel model estimates abundance as:

$$\hat{N} = \frac{\sum_t (C_t \times M_t)}{\sum_t R_t},$$

where \hat{N} is an estimate of population abundance, C_t is the number of fish captured in sample t , M_t is the number of marked individuals in the population just before sample t is taken, and R_t is the number of fish already marked when caught in sample t . To account for incidental mortalities in sampling occasions, we included both live and dead lake trout in our C_t totals. With the Schnabel model, we estimated the 95% confidence intervals (CIs) using a Poisson distribution (Krebs 1999).

Diet Analysis

We collected the stomachs from all incidental mortalities that resulted from sampling and the stomachs from a subset of captured target fishes (i.e., lake trout, brown trout) to evaluate dietary patterns across size-classes and time. All stomachs were removed and stored in 95% alcohol until processed in the laboratory. We identified aquatic macroinvertebrates to the genus level (when intact) and all prey fish to the species level when possible (otherwise, fish were identified as salmonid or nonsalmonid based on shape and structure of the vertebrae). Prey fish were measured to the nearest millimeter and weighed (blot-dry wet weights) to the nearest 0.001 g; macroinvertebrates were blot dried and weighed en masse. Diets were expressed as percent composition by wet weight.

Early diet data indicated that a substantial number of Lahontan cutthroat trout anchor tags were retained in lake trout stomachs. Because the time of lake trout consumption of Lahontan cutthroat trout was unknown, anchor tags were not included in the analysis of diet weights or species consumed. However, we performed a separate analysis for the anchor tags found in lake trout diets to first quantify the number of anchor tags consumed; we then expanded this to the lake trout population by using the following formula:

$$T = F_x \times \hat{N} \times S_x \times A_x,$$

where T is the total number of Lahontan cutthroat trout estimated to be consumed by lake trout, F_x is the

frequency of lake trout by size-class x , \hat{N} is the total lake trout population abundance estimated from mark–recapture methods (see above), S_x is the percent of sacrificed lake trout of size-class x that had anchor tags in the diet, and A_x is the average number of anchor tags observed in diets containing at least one anchor tag among lake trout of size-class x . With this, we used the 95% CIs of \hat{N} to calculate the CIs of lake trout consumption of Lahontan cutthroat trout. Finally, we evaluated any potential size preference in lake trout predation on Lahontan cutthroat trout. Here, we used a chi-square (χ^2) analysis to compare the length-frequency distribution of Lahontan cutthroat trout reintroduced into Fallen Leaf Lake in 2006 with the length-frequency distribution of Lahontan cutthroat trout consumed by lake trout (from anchor tag numbers).

Bioenergetics Estimates of Lake Trout Consumption

We combined field data on food habits, thermal history, and growth with a bioenergetics model (Hewett and Johnson 1991) to estimate predation by lake trout. We initially determined lake trout age and growth using the following equation from Allen et al. (2006):

$$TL = 12.66 \log_e(\text{age}) + 14.312.$$

We used this energetics-based model to estimate annual individual (size-specific) consumption for each lake trout age-class (age 3 to age 10 and older). Physiological parameters for lake trout were provided by Stewart et al. (1983). Simulations included an 8% loss of individual biomass to spawning on 15 October (day 288) for all age-5 and older lake trout.

We partitioned total individual daily consumption for an average individual in each lake trout age-class into prey-specific daily consumption. We assigned energy densities for different prey as follows: 6,069 J/g for salmonids (Rand et al. 1993); 5,005 J/g for nonsalmonids (primarily based on suckers and cyprinids; Hewett and Johnson 1991); 1,293 J/g for sculpins (Cummins and Wuycheck 1971); 2,029 J/g for mountain whitefish (Hewett and Johnson 1991); 3,766 J/g for crayfish (Stein and Murphy 1976); 3,361 J/g for mysid shrimp *Mysis relicta* in summer; 3,361 J/g for *M. relicta* in all other seasons (Johannsson 1995; Thiede 1997); and 2,742 J/g for other invertebrates (Cummins and Wuycheck 1971). Except for *M. relicta*, we assumed that energy densities remained constant throughout the year. We calculated the energy density of lake trout (predators) as an increasing function of weight (Stewart et al. 1983). We fixed the proportion of prey that was indigestible as follows: 3.3% for fish, 10% for invertebrates (Stewart

et al. 1983), and 25% for crayfish (Stein and Murphy 1976).

As a model input, we coupled seasonal depth distribution for each size-class with vertical temperature profiles to produce seasonal temperature patterns experienced by lake trout. We multiplied the percentage of the seasonal catch per unit effort (CPUE) in each depth stratum by the average seasonal temperature at that depth stratum, and we summed these products over all depths to produce a weighted monthly temperature.

For each age-class of lake trout, we modeled consumption for 365-d intervals beginning on 1 January (day 1) and calculated the daily individual consumption by lake trout for each prey type. The model linearly interpolated between daily values of growth, diet, energy densities, and temperature. To scale the average individual consumption by age-class up to population-level consumption, we multiplied individual (age-class) consumption by the estimated abundance of lake trout in each age-class.

In addition to consumption, we also calculated the proportion of maximum consumption, $p(C_{\max})$, for each age-class. The $p(C_{\max})$ is calculated for an average individual in each cohort over the run interval and can be an index of predatory intensity and an indication of prey availability (Rice et al. 1983). Age-class $p(C_{\max})$ values were fit iteratively from start weight to final weight. We held $p(C_{\max})$ constant in our simulations, although optimally the $p(C_{\max})$ values should be estimated seasonally by incorporating seasonal growth and diet information.

Snorkel and Dive Surveys

We conducted snorkel and dive surveys in Glen Alpine Creek and Fallen Leaf Lake for indices of salmonid abundance. First, we performed comprehensive weekly snorkel surveys beginning in June to quantify the abundance of spawning Lahontan cutthroat trout and other salmonids in Glen Alpine Creek during the spring spawning season. Similar to Thurow (1994), we proceeded upstream in a zigzag pattern within the stream channel while enumerating and estimating the sizes of all salmonids. Next, we performed extensive snorkel and dive surveys in Fallen Leaf Lake during June through September to estimate the relative abundance of salmonids in shallow depths (0–7 m; snorkel surveys) and shallow to moderate depths (6–18 m; dive surveys).

Creel Surveys

With the help of USFWS and U.S. Forest Service personnel, we conducted roving creel surveys from the end of May to the end of September (2005–2007). We only conducted weekday surveys in 2005 but expanded

to include weekdays, weekend days, and summer holidays in 2006 and 2007. During each survey, we used a motor boat to intercept and interview anglers (between 0800 and 1400 hours) regarding species in the catch, catch totals, maximum depth of capture, percentage of catch harvested, and amount of time spent angling. We used this information to estimate daily lakewide fishing effort (average number of anglers/d) and expanded these for estimates of annual angling pressure by the following formula:

$$A_i = (w_i \times m) + (x_i \times n),$$

where A_i is the estimated number of anglers in year i , w_i is the average number of anglers per holiday and weekend day, m is the total number of holiday and weekend days per year, x is the average number of anglers per weekday, and n is the total number of weekdays per year. Since no weekend days were collected in 2005, we used the difference in average number of anglers between weekdays and weekend days from 2006 to 2007 to estimate weekend angling effort for 2005. Finally, the expanded estimates of angler-hours were used to estimate the total annual harvest of each target species; this was done by dividing the actual harvest measured during creel surveys by the ratio of reported angler-hours to total estimated angler-hours.

Results

Nets and Traps

During early June through mid-October, total effort was 60.9 net-hours for benthic trammel nets, 158 net-hours for benthic gill nets (standardized to a net length of 100 m), 76.6 net-hours for pelagic curtain gill nets, 395.9 net-hours for pelagic gill nets (standardized to a net length of 100 m), and 10,364 trap-hours for minnow traps. The average depth for benthic gill nets was 38.2 m (upslope end), with minimum and maximum depths of 2.4 and 112.8 m, respectively (Table 2). We set a total of 350 benthic nets with an average set length of 1.4 h. We set pelagic gill nets at an average depth of 13.1 m (range = 6.1–21.3 m), and we set 77 total pelagic nets for an average set time of 14.8 h. We deployed 411 minnow traps at an average depth of 8.3 m (range = 1.2–19.2 m) for an average set time of 25.2 h.

Temperature

As expected, temperature profiles indicated that Fallen Leaf Lake developed a strong thermocline during the summer months. Our results indicated no thermal limitations at shallow depths for lake trout in early June (i.e., $>13^\circ\text{C}$; Martin and Oliver 1980; Figure 2a). Temperature profiles from late June

TABLE 2.—Number of net or trap sets, average set length, and average, minimum, and maximum set depths in Fallen Leaf Lake, California, 2007.

Gear type	Average depth (m)	Minimum depth (m)	Maximum depth (m)	Total number of sets	Average set length (h)
Benthic trammel or gill nets	38.2	2.4	112.8	350	1.4
Pelagic gill nets	13.1	6.1	21.3	77	14.8
Minnow traps	8.3	1.2	19.2	411	25.2

(Figure 2b) indicated substantial warming of the lake, where depths shallower than 14 m were above the thermal optima for lake trout. This trend continued until early August (Figure 2d), where the top of the thermocline was at approximately 14 m and depths shallower than 17.5 m were above 13°C. Despite the persistence of a thermocline until early October, water temperatures at all depths during this period were less

than 13°C (Figure 2). Based on this information, we defined the period of 6–18 June as spring, 19 June–15 September as summer, and the period after 15 September as autumn.

Capture Results

Lahontan cutthroat trout.—We captured two Lahontan cutthroat trout during 2007; both fish were

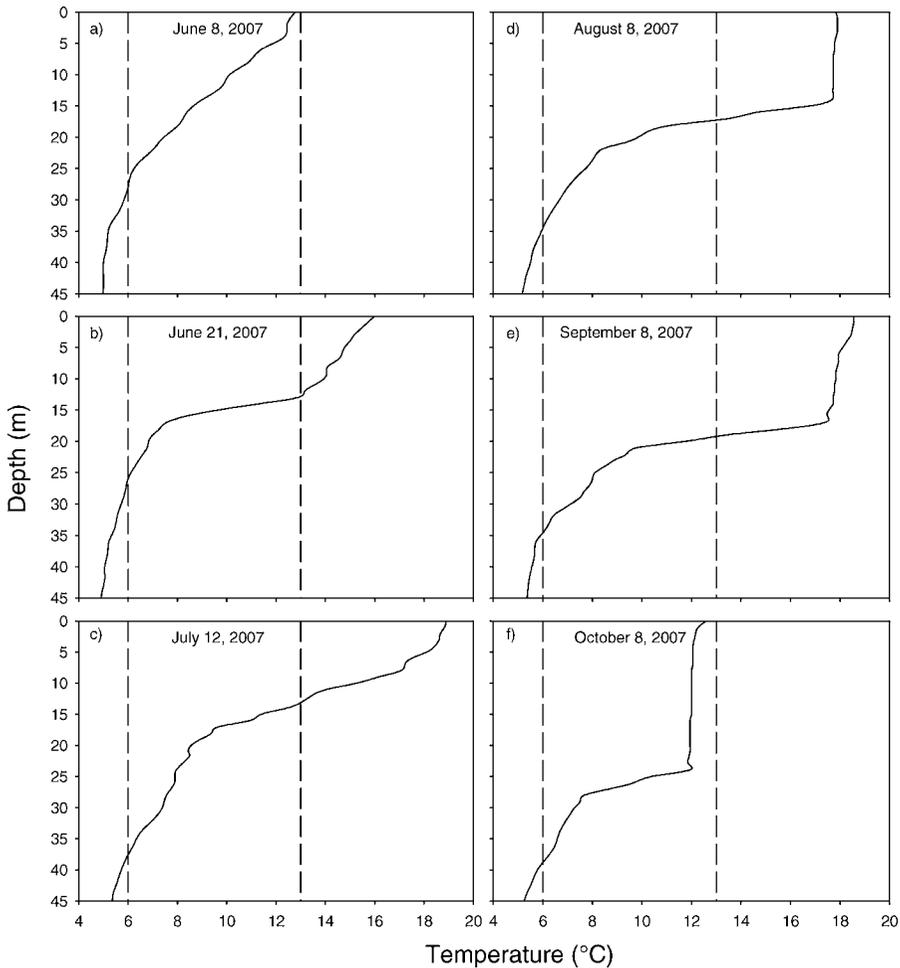


FIGURE 2.—Temperature profiles for Fallen Leaf Lake, California, in 2007: (a) 8 June, (b) 21 June, (c) 12 July, (d) 8 August, (e) 8 September, and (f) 8 October. Dashed vertical lines represent the lower and upper optimal temperatures for lake trout (Martin and Oliver 1980).

TABLE 3.—Total number (*n*) and average number (SD in parentheses) per sampling occasion of lake trout captured (C_t), marked (M_t), and recaptured (R_t) in Fallen Leaf Lake, California, 2007.

Statistic	C_t	M_t	R_t
<i>n</i>	515	346	10
Average	9.7 (6.8)	0.2 (0.6)	6.5 (4.6)

caught in shallow (<8.5 m) benthic areas that contained large, rocky substrate. One fish was captured on the southwest part of lake with a minnow trap in mid-June (TL = 473 mm, weight = 33 g). This fish grew 21 mm over the 173 d after its reintroduction (0.121 mm/d), and the *K*-value of this individual was 0.64. We captured the second fish with shallow angling methods on the west side of the lake in mid-September (TL = 205 mm, weight = 64 g). This fish grew 76 mm over 243 d (0.313 mm/d) and had a *K* of 0.74. We did not capture any adult Lahontan cutthroat trout from prior stocking occasions during 2007 sampling.

Lake trout.—During June through October, we marked and released a total of 346 lake trout and sacrificed a total of 169 lake trout for diet analyses (Table 3). The majority of fish (74%) were between 360 and 460 mm (Figure 3), and size ranged between 146 and 816 mm (average = 424 mm). We recaptured a total of 10 lake trout (average TL = 413 mm; range = 328–471 mm), and recaptures occurred over seven occasions. The average time between initial marking (capture) and recapture was 40.1 d (range = 1–61 d). With our mark–recapture data, we estimated the lake trout abundance to be 8,799 fish (95% CI = 4,990–16,530 fish).

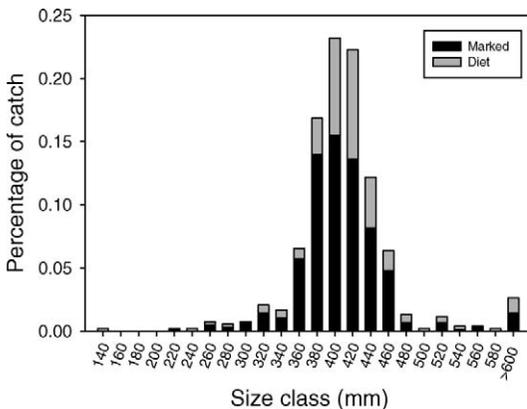


FIGURE 3.—Length-frequency distribution (mm total length; *n* = 515) of lake trout that were captured, marked, and released for capture–recapture estimates (marked) or captured and sacrificed for diet analysis (diet) in Fallen Leaf Lake, California, 2007.

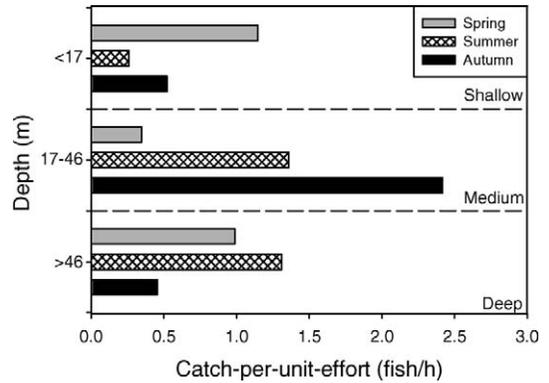


FIGURE 4.—Lake trout catch per unit effort (fish/net-hour) during spring (6–18 June), summer (19 June–15 September), and autumn (16 September and later) 2007 at shallow (<17 m), medium (17–46 m), and deep (>46 m) benthic gill-net sets in Fallen Leaf Lake, California. Depths indicate the depth at the deepest end of the gill net (set perpendicular to shore).

Lake trout CPUE varied considerably across set types (benthic versus pelagic), depths, and seasons (Figure 4). Average CPUE values for benthic nets (1.18 fish/net-hour) were considerably higher than those for pelagic nets (0.01 fish/net-hour), and 98% of our lake trout catch was in benthic nets (Table 4). In the spring, CPUE was highest at shallow (1.15 fish/net-hour; <17 m) and deep (0.99 fish/net-hour; >47 m) areas of the lake, and the CPUE was lowest at medium depths (0.35 fish/net-hour; 17–47 m). During the summer, CPUE was lowest at shallow depths (0.26 fish/net-hour) and was generally consistent across medium and deep sections of the lake (1.36 and 1.31 fish/net-hour, respectively). In the autumn, we observed an increase in CPUE at shallow depths (0.52 fish/net-hour), and the highest CPUE across all depths and seasons (2.42 fish/net-hour) was at medium depths (17–47 m).

We found large (>500 mm) lake trout to exhibit seasonal shifts in habitat use in Fallen Leaf Lake (Figure 5). The average depth of capture during the summer period for large lake trout was 36.6 m (downslope end of net; 95% CI = 29.3–43.8 m).

TABLE 4.—Average catch per unit effort (CPUE; fish/net-hour) values for lake trout, brown trout, rainbow trout, and kokanee in benthic (trammel and gill nets) and pelagic (gill nets) sampling gear in Fallen Leaf Lake, California, 2007.

Net type	Lake trout CPUE	Brown trout CPUE	Rainbow trout CPUE	Kokanee CPUE
Benthic	1.18	0.06	0.02	0.14 ^a
Pelagic	0.01	0.00	0.00	0.01

^a The CPUE estimate for kokanee in benthic nets includes sampling during the October spawning aggregation period. Prior to October, kokanee CPUE in benthic nets was 0.004 fish/net-hour.

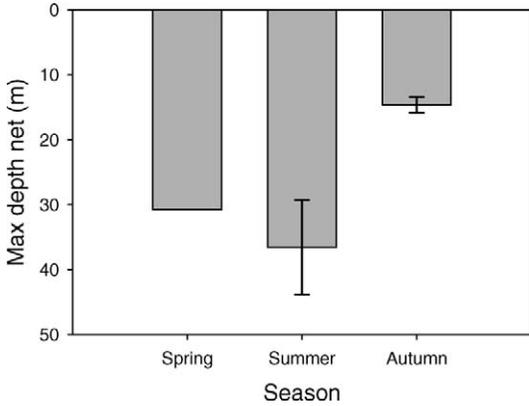


FIGURE 5.—Average habitat use (± 2 SEs; based on depth of capture) by large lake trout (>500 mm) during spring (6–18 June), summer (19 June–15 September), and autumn (16 September and later) 2007 in Fallen Leaf Lake, California.

During the autumn, however, when temperatures in the epibenthic and epipelagic areas were less than 14°C, the average depth at capture decreased considerably to 14.6 m (95% CI = 13.4–15.8 m). Only one large lake trout was captured in the spring, prior to the establishment of the thermocline, at a depth of 30.8 m.

Rainbow trout.—Across all sampling efforts, we captured seven rainbow trout in benthic nets in 2007. The average CPUE for rainbow trout across seasons (0.02 fish/net-hour; Table 4) was considerably lower than that of lake trout. Average rainbow trout TL was 379 mm (range = 209–510 mm), and average weight was 683 g (range = 93–1,310 g). All rainbow trout were captured at shallow depths (<31 m), and the majority of fish (71%) were captured at depths shallower than 17 m.

Brown trout.—We captured 32 brown trout in benthic nets, and no brown trout were captured in pelagic nets. The average CPUE for brown trout was 0.06 fish/net-hour, which is nearly three times higher than the rainbow trout CPUE but considerably lower than the lake trout CPUE (Table 4). The average TL of brown trout captured in 2007 was 504 mm (range = 230–735 mm), and brown trout weighed 1,568 g on average (range = 440–5,136 g); over 50% of brown trout captured in 2007 exceeded 500 mm. All brown trout were caught at depths less than 37 m, and most fish (72%) were caught at depths less than 19 m.

Kokanee.—We captured 72 kokanee, which averaged 287 mm TL (range = 172–381 mm) and 193 g in weight (range = 42–285 g). The majority of kokanee were over 280 mm (80%). We captured kokanee in both pelagic and benthic nets, and CPUE values were 0.14 and 0.01 fish/net-hour in benthic and pelagic nets, respectively. However, the high benthic CPUE was

largely driven by sampling during the autumn spawning season, and CPUE for benthic nets prior to October was 0.004 fish/net-hour. Across species, pelagic CPUE values were the highest for kokanee (Table 4). All kokanee were caught at depths less than 25 m in benthic nets and at depths between 7 and 24 m in pelagic nets.

Suckers.—We captured 233 suckers *Catostomus* spp. in benthic nets and minnow traps. Length-frequency distribution indicated that the majority of suckers were between 60 and 180 mm or over 300 mm (Figure 6). The average length of suckers was 246 mm (range = 45–377 mm), and the average weight was 193.8 g (range = 8–550 g). In benthic nets, all suckers

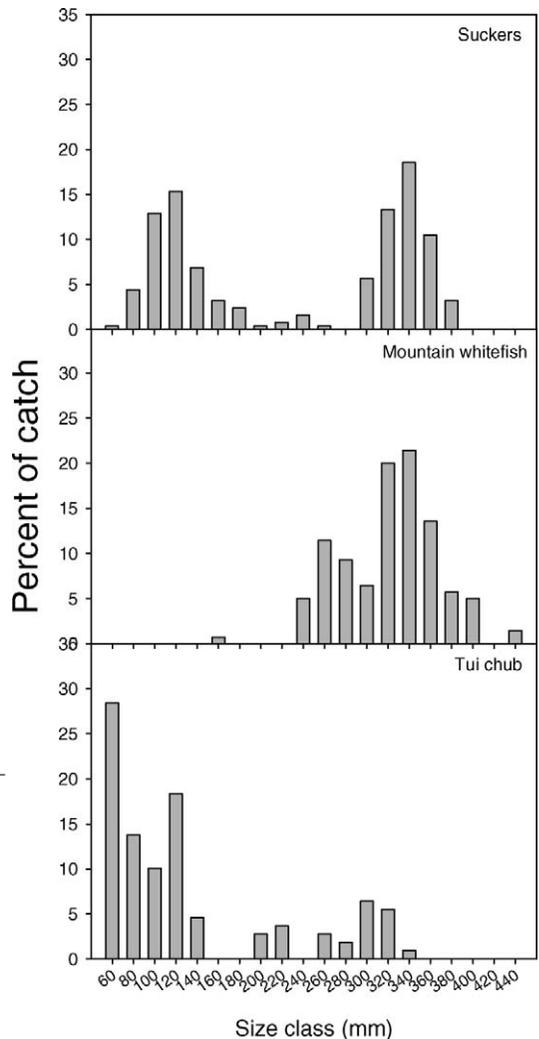


FIGURE 6.—Length-frequency distributions (mm total length) of suckers *Catostomus* spp., mountain whitefish, and tui chub in Fallen Leaf Lake, California, 2007.

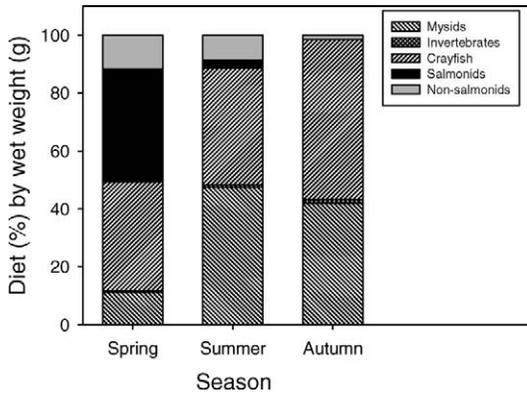


FIGURE 7.—Seasonal percentage (by wet weight) of mysid shrimp *Mysis relicta*, invertebrates (including terrestrial invertebrates), crayfish, salmonids, and nonsalmonids in lake trout diets ($n = 160$) during spring (1–15 June), summer (16 June–15 September), and autumn (16 September–14 October) 2007 in Fallen Leaf Lake, California.

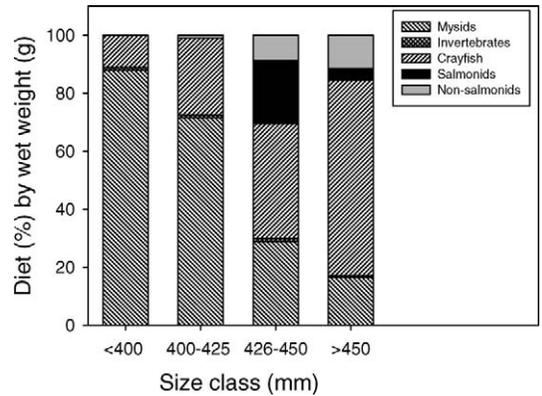


FIGURE 8.—Percentage of mysid shrimp *Mysis relicta*, macroinvertebrates (including terrestrial invertebrates), crayfish, salmonids, and nonsalmonids in the diets of different lake trout size-classes across all sample periods in Fallen Leaf Lake, California, 2007.

were captured at depths less than 33 m, and only 20% of the fish were captured at depths greater than 17 m. In minnow traps, 46% of suckers were captured at depths less than 8 m, and 54% of the catch was obtained at depths between 8 and 19 m. The CPUE of suckers was 0.01 fish/trap-hour in minnow traps and 0.17 fish/net-hour in benthic nets.

Mountain whitefish.—In 2007, we captured 140 mountain whitefish in benthic nets. The majority of mountain whitefish were larger than 300 mm (67%; Figure 6), and the average length and weight were 312 mm (range = 155–438 mm) and 331.4 g (range = 120–1,020 g), respectively. All mountain whitefish were captured at depths less than 36 m, and none were captured in minnow traps. Mountain whitefish CPUE in benthic nets was 0.27 fish/net-hour.

Tui chub.—We captured 109 tui chub in minnow traps and benthic nets. The majority of tui chub were smaller than 140 mm (76%), 11% were between 140 and 280 mm, and 13% were larger than 280 mm (Figure 6). The average length of all captured tui chub was 136 mm (range = 38–328 mm). Tui chub were captured in benthic nets at depths less than 33 m and in minnow traps at depths less than 16 m. Tui chub CPUE was 0.04 fish/net-hour in benthic nets and 0.007 fish/trap-hour in minnow traps.

Diet Analysis

We collected stomachs from 160 lake trout and 9 brown trout in Fallen Leaf Lake during 2007. Lake trout diets varied by season (based on thermal stratification of the lake), but *M. relicta* (range = 11.1–47.5%) and signal crayfish *Pacifastacus leniusculus* (range = 37.8–55.3%) were the dominant diet

items (in terms of percentage wet weight) across seasons (Figure 7). We did observe a substantial decrease in the amount of salmonids in lake trout diets from the early summer (prior to stratification), when 39% of lake trout diets consisted of salmonids, to midsummer (i.e., stratification; 2.8% of diets analyzed) and late summer, when no salmonids were found in lake trout stomachs. We found that nonsalmonids made up a considerably higher proportion of lake trout diets during the spring (11.7%) versus summer (8.7%) and autumn (1.5%). Over all periods, the percentages of macroinvertebrates (0.4–1.3%) and terrestrial invertebrates (0.00–0.04%) in lake trout diets were relatively low.

We found considerable differences in lake trout diets by size-class (Figure 8). The percent of *M. relicta* in lake trout diets (by wet weight) declined from 88% in small lake trout (<400 mm) to 16.6% in large lake trout (>450 mm). We also observed an increase in the amount of crayfish and fish (both salmonids and nonsalmonids) in the diets of larger (>425 mm) lake trout compared with the diets of smaller (≤425 mm) lake trout. There was little variability, however, in the percentages of terrestrial invertebrates and macroinvertebrates in diets across the different size-classes of lake trout.

We observed a substantial number of Lahontan cutthroat trout anchor tags in lake trout stomachs ($n = 108$). The percentage of sacrificed lake trout with anchor tags in their stomachs varied by size-class (Figure 9); only 4% of lake trout smaller than 400 mm had anchor tags in their stomachs, but 29% of sacrificed lake trout in the 426–500-mm size-class had anchor tags in their stomachs. Since few fish less

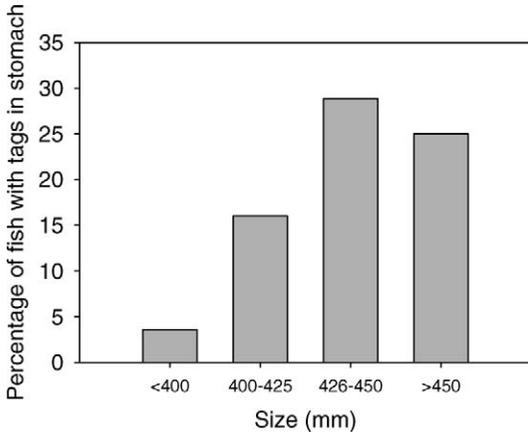


FIGURE 9.—Percentage of lake trout in different size-classes (mm total length) with stomachs containing Lahontan cutthroat trout anchor tags; fish were collected in Fallen Leaf Lake, California, during 2007.

than 400 mm contained anchor tags, we used the average number of anchor tags for all fish ≤ 425 mm in consumption estimates for this size class. The average number of anchor tags in lake trout stomachs that contained at least one anchor tag ranged from 2.78 (fish < 400 mm) to 4.29 (fish > 450 mm). We estimated consumption of anchor-tagged Lahontan cutthroat trout at the population level to be 5,377 fish (95% CI = 3,050–10,102 fish). Lake trout did not exhibit any size preference in consumption of this species, as we found no significant difference in length-frequency between Lahontan cutthroat trout (from anchor tag data) in lake trout stomachs and those reintroduced into Fallen Leaf Lake ($\chi^2 = 0.07$, $df = 5$, $P = 0.99$).

We collected stomachs from nine large (average TL = 505 mm) brown trout in Fallen Leaf Lake. There was considerably less variability in brown trout diets, which largely consisted of crayfish (32.4%), salmonids (33.6%), and nonsalmonids (33.4%) and a small amount (0.6%) of macroinvertebrates. We did not

observe any Lahontan cutthroat trout anchor tags in brown trout stomachs.

Bioenergetics Estimates of Lake Trout Consumption

The average $p(C_{max})$ for lake trout older than age 3 was 0.490, ranging from 0.471 for age-4 fish to 0.498 for age-5 fish (Table 5); these values indicate that lake trout fed at less than half the rate of maximum consumption. Based on a bioenergetics assessment, age-3 and older individual lake trout annually consume an average of 444.8 g of salmonids, 925.5 g of crayfish, 16.9 g of invertebrates, 693.4 g of *M. relicta*, and 165.5 g of nonsalmonids. At the population level, our results indicate that lake trout consumed 3,137 kg (95% CI = 1,779–5,893 kg) of salmonids during 2007, and age-7 (390 mm) and age-8 (406 mm) lake trout consumed nearly half of the salmonids consumed by the total lake trout population (Figure 10). Based on the average size of Lahontan cutthroat trout reintroduced in 2006 (28.4 g), our estimates of salmonid predation suggest that lake trout could have consumed 110,458 individual Lahontan cutthroat trout.

Snorkel and Dive Surveys

We conducted two comprehensive snorkel surveys of Glen Alpine Creek in June but were not able to continue additional surveys due to a wildfire. We found no reproductive Lahontan cutthroat trout in Glen Alpine Creek during the spring spawning season. Nonnative salmonids were present during each survey, including brown trout (average = 4 fish) and rainbow trout (average = 9 fish).

During extensive snorkel and dive surveys (24.4 h) in Fallen Leaf Lake at depths less than 20 m, we observed only three juvenile Lahontan cutthroat trout (<250 mm; 2006 stocking). All of these fish were observed in epibenthic areas (<7 m) and were associated with complex structure, including large rocky substrate and LWD. We also found nine Lahontan cutthroat trout anchor tags on the bottom of

TABLE 5.—Bioenergetics results, including proportion of maximum consumption ($p[C_{max}]$) and estimates of the average biomass (g) of salmonids, crayfish, invertebrates, mysids (*Mysis relicta*), and nonsalmonids consumed per year by lake trout (age 3 and older) in Fallen Leaf Lake, California, 2007.

Lake trout age-class	$p(C_{max})$	Salmonid biomass	Crayfish biomass	Invertebrate biomass	Mysid biomass	Nonsalmonid biomass
3	0.482	200.9	573.4	10.5	428.2	102.3
4	0.471	232.6	661.7	12.1	494.2	118.4
5	0.498	283.2	814.0	14.8	610.2	145.2
6	0.495	314.7	903.2	16.5	677.1	161.4
7	0.494	345.4	990.3	18.1	742.4	177.1
8	0.492	374.5	1,072.8	19.5	804.2	192.0
9	0.493	403.9	1,156.3	21.1	866.8	207.0
≥ 10	0.492	444.8	1,232.6	22.5	924.0	220.8

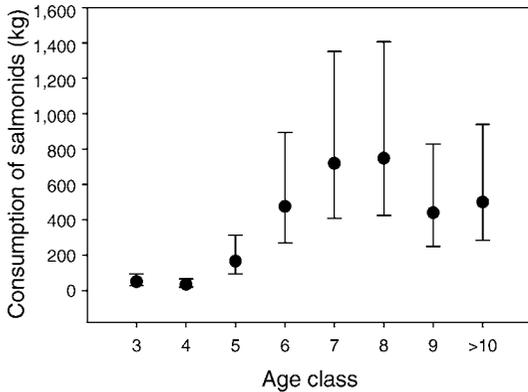


FIGURE 10.—Estimates of salmonid consumption (kg; from bioenergetics modeling) by individual lake trout age-classes in Fallen Leaf Lake, California, 2007.

the lake at depths ranging from 2 to 9 m. Large brown trout were the most abundant nonnative salmonid observed ($n = 10$ fish) during snorkel and dive surveys, and we also observed six rainbow trout; all brown trout and rainbow trout were found within epibenthic areas at depths less than 15 m.

Creel Surveys

On average, anglers spent 2.5 h fishing during weekdays and 3.3 h fishing on the weekends. The average number of anglers per weekday was 8.4 (SD = 5.5), and the average number per weekend day was 8.0 (SD = 5.2); we estimated the average number of angler visits per year as 1,091.1 (Table 6). During 2005, Lahontan cutthroat trout made up a relatively high percentage of catch (39%) and harvest (42.1%), and we estimated the total harvest in 2005 at 45 fish; no Lahontan cutthroat trout were captured in 2006 or 2007. Anglers reported catching Lahontan cutthroat trout at a median depth of 9.1 m (range = 3.7–18.3 m), kokanee at a median depth of 18.3 m (range = 42.2–76.2 m), and lake trout at a median depth of 48.8 m (range = 13.7–72.5 m). Only one rainbow trout (depth = 6.1 m) and one brown trout (no depth reported) were captured by anglers. Across all years, most captured fish were harvested, and we observed the highest

average percentages of catch and harvest for lake trout (59.7% and 62.2%, respectively) and kokanee (25.4% and 21.7%, respectively) and the lowest average catch and harvest for brown trout (1.1% and 0.0%, respectively) and rainbow trout (0.8% and 0.9%, respectively). As expected, estimates of total harvest were highest for lake trout (average = 125 fish, range = 48–220 fish) and kokanee (average = 66 fish, range = 11–144 fish) and lowest for brown trout (0 fish) and rainbow trout (3 fish; 2003 only).

Discussion

The presence of nonnative species can be a substantial impediment for successful reintroduction programs (Williams et al. 1988; Marsh and Douglas 1997; Mueller 2005). Despite substantial sampling efforts and creel surveys, we found relatively low survival of Lahontan cutthroat trout reintroduced into Fallen Leaf Lake. The current biotic community of nonnative species within Fallen Leaf Lake appears to result in little opportunity for Lahontan cutthroat trout to find refugia from negative interactions with nonnative species across seasons. However, the persistence of small native fishes (e.g., *Catostomus* spp.) in the presence of larger salmonid predators suggests that habitat segregation and at least the potential for spatial refugia may exist. Our results, combined with previous research in this system (i.e., Allen et al. 2006), highlight the need for continued reintroduction efforts, with explicit consideration of different temporal and spatial planting strategies and reductions of nonnative species.

Lahontan Cutthroat Trout

Creel surveys and sampling efforts suggested that both juvenile (fingerlings from the 2006 reintroduction) and adult (previous reintroductions) Lahontan cutthroat trout utilized epilimnetic habitats. The few Lahontan cutthroat trout we observed in this study were found in shallow (<9 m), benthic habitats. Although information on habitat use by similar-sized conspecifics is unavailable due to the limited distribution of Lahontan cutthroat trout in their native range, the use of shallow, benthic habitats is common for juvenile

TABLE 6.—Total number of anglers surveyed (n), total estimated annual angling effort, and percent of catch consisting of Lahontan cutthroat trout, lake trout, kokanee, rainbow trout, and brown trout in Fallen Leaf Lake, California, 2005–2007.

Year	n	Angler-days per season	Percent of catch				
			Lahontan cutthroat trout	Lake trout	Kokanee	Rainbow trout	Brown trout
2005	38	1,409.6	39.0	48.8	9.8	2.4	0
2006	29	916.8	0	79.3	17.2	0	0
2007	121	946.9	0	60	40	0	3.5

(<200 mm) cutthroat trout in lake systems (Nowak et al. 2004; Koel et al. 2006; McIntyre et al. 2006). The limited number of captures and observations of juvenile Lahontan cutthroat trout in this study occurred near complex habitats (i.e., LWD), which may suggest the importance of structure in providing refugia from predators (e.g., Beauchamp et al. 1994). This pattern warrants further research with additional observations across a range of habitat types. The use of epibenthic and epipelagic habitats by larger fish is consistent with historical data (Vander Zanden et al. 2003) and observations of other lacustrine cutthroat trout populations (Andrew et al. 1992; Beauchamp et al. 1992; Baldwin et al. 2002). Together, these results suggest the importance of epibenthic and epipelagic habitats for Lahontan cutthroat trout across size-classes, but further research is needed to identify possible ontogenetic shifts and specific differences in habitat use within these epilimnetic areas (e.g., Nowak et al. 2004).

Although based on very low catch numbers, the few Lahontan cutthroat trout recaptured in our sampling efforts exhibited low K -values relative to stocked cutthroat trout in other high-elevation lentic systems (Hepworth et al. 1999), a pattern that is consistent with previous results (Allen et al. 2006). A large proportion of the diets of lacustrine cutthroat trout juveniles can be contributed by zooplankton, primarily large cladocerans (e.g., *Daphnia* spp.; Nowak et al. 2004), and limited Lahontan cutthroat trout diet data show a similar preference for larger zooplankton (Chess et al. 1993). Clearly, there are limitations in extrapolating our assessments of Lahontan cutthroat trout condition from few individuals to the population level. However, our results in Fallen Leaf Lake are consistent with the current understanding of the impacts of mysids on the densities of large zooplankton species (Rieman and Falter 1981; Northcote 1991; Johnson et al. 2002) and the growth of juvenile salmonids (Clarke et al. 2004) and the limited availability of mysids as a forage base for fishes inhabiting the epilimnion (Spencer et al. 1991). Additionally, competition with kokanee, which have been found to compete with Lahontan cutthroat trout for forage resources in epilimnetic habitats within other systems (G. Scopettone, U.S. Geological Survey, personal communication), may also have been a factor in the reduced K . Finally, the low K may be indirectly affected by the spatial overlap with nonnative predators (He and Kitchell 1990; Johnson 1993; Haddix and Budy 2005), including (1) brown trout throughout the year and (2) lake trout in the absence of thermal constraints. Ultimately, the combination of these factors may have substantially reduced Lahontan cutthroat trout K and overall survival; however, further research with greater sample sizes are needed in the

future to better evaluate condition at the population level.

We did not observe any adult Lahontan cutthroat trout in Fallen Leaf Lake, indicating potentially low survival rates of the fish reintroduced in previous efforts. In addition to factors affecting K (see above), the low survival and low abundance of larger fish may indicate that predation pressure from nonnative species is greater than previously determined (i.e., Allen et al. 2006). In particular, we consider the predation risks presented by nonnative fish larger than 250 mm to be extensive. Here, we observed relatively few fish of 140–300 mm TL across native and nonnative fishes, indicating the loss of or few fish surviving in these size-classes. Thus, predation by large brown trout (25% of catch > 650 mm), which are capable of consuming prey that are 40% of predator TL (Hyvarinen and Huusko 2006), and large lake trout, which can consume prey up to 50% of predator TL (Yule and Luecke 1993), may be greater than expected. The retention of anchor tags indicated that the prey length : predator length ratio may exceed 50% for lake trout in Fallen Leaf Lake and may be a function of the low overall K of Lahontan cutthroat trout, a pattern that warrants further research. Overall, these results indicate that the Lahontan cutthroat trout reintroduced into Fallen Leaf Lake may need to be substantially larger than earlier indications (>250 mm; Allen et al. 2006), at least initially, in order to increase survivorship and establish an adult population. Survivorship of younger age-classes present in the lake either from planting or natural recruitment may be contingent on active management of the large, piscivorous nonnative fishes (e.g., Bigelow et al. 2003).

Limiting Factors

Lake trout.—We found a large population of lake trout, and the substantial predation pressure indicated in this study and elsewhere (Ruzycki et al. 2001, 2003; Koel et al. 2005) suggests that lake trout represent the greatest limiting factor for juvenile Lahontan cutthroat trout in Fallen Leaf Lake. At the population level, our bioenergetics results suggested that lake trout consumed a substantial amount of salmonid biomass during this study. The low lake trout $p(C_{\max})$ suggests that lake trout have the ability to consume considerably higher amounts of salmonid biomass if available. Although we were not able to delineate between salmonid species in our diet analyses, the relatively small number of rainbow trout and brown trout observed in Fallen Leaf Lake and the low consumption of kokanee in other studies (Thiede 1997) indicate that lake trout primarily consumed Lahontan cutthroat trout, mountain whitefish, and smaller lake trout. The large

discrepancy between the estimate of potential consumption of Lahontan cutthroat trout (110,458 fish) and the number of Lahontan cutthroat trout released in 2006 suggests that predation on other fishes, including larger Lahontan cutthroat trout from previous reintroductions, was substantial.

Consistent with other systems (Yule and Luecke 1993; Johnson and Martinez 2000; Ruzycki et al. 2001), we found an increase in lake trout piscivory with increasing predator size (>425 mm). Despite the higher piscivory rates observed in larger lake trout, however, our bioenergetics analyses indicated that smaller lake trout (<425 mm) represent the greatest predation threat in Fallen Leaf Lake. In particular, we found that the high overall abundance of these smaller lake trout resulted in greater rates of predation on salmonids at the population level (Thiede 1997).

Despite indications of epilimnetic refugia for Lahontan cutthroat trout from lake trout during periods of stratification, we observed seasonal shifts to increased use of epilimnetic habitats by lake trout during the spring and fall. In this study, these results suggest that the early winter period immediately after the Lahontan cutthroat trout reintroduction continuing up through the establishment of the thermocline was probably the period when the majority of predation occurred. The temperature regime, which allows for spatial overlap between lake trout and Lahontan cutthroat trout throughout much of year, and our estimates of salmonid predation potential together suggest that lake trout are a significant impediment to the establishment of a lacustrine Lahontan cutthroat trout population in Fallen Leaf Lake. Despite this predation, the presence of small populations of other salmonids, including the native mountain whitefish, suggests that spatial and temporal refugia from lake trout predation exist and illustrates the potential for reestablishing a naturally reproducing population of Lahontan cutthroat trout, albeit potentially small given predation and limited available spawning habitat.

Other nonnative species.—In addition to lake trout, we found an abundance of large brown trout and a relatively small population of rainbow trout in Fallen Leaf Lake. As nonnative predators, brown trout can significantly affect the abundance and structure of native fishes (Townsend 2003). In Fallen Leaf Lake, the large portion of fishes in brown trout diets (nearly 70% in this study) and the overlap in epilimnetic habitat use suggest that brown trout may consume large numbers of Lahontan cutthroat trout, although no direct evidence of predation by brown trout was observed in this study.

Despite indications of a relatively small population of rainbow trout, the similarities in life history

strategies (i.e., spawn timing) between rainbow trout and cutthroat trout could result in substantial negative effects through hybridization (Allendorf and Leary 1988; Kruse et al. 2000; Peacock and Kirchoff 2004). We found considerable spatial overlap in habitat use by rainbow trout and Lahontan cutthroat trout in the lake, and rainbow trout use of Glen Alpine Creek (the only spawning tributary) suggests a high potential for hybridization and potentially adverse implications for recovery (Allendorf et al. 2004; Campton and Kaeding 2005). Once a naturally reproducing population of Lahontan cutthroat trout is established within Fallen Leaf Lake, the limited rearing habitat in Glen Alpine Creek also suggests that rainbow trout could have negative effects on juvenile Lahontan cutthroat trout through competition (e.g., Kruse et al. 2000). Together, these potential direct and indirect effects on Lahontan cutthroat trout populations indicate that rainbow trout may represent a substantial impediment to Lahontan cutthroat trout recovery.

Future Research and Management

Understanding the factors limiting the successful reintroduction of Lahontan cutthroat trout into native lacustrine habitats is an important step in recovery efforts. Reestablishment of native species that have been extirpated from historical habitat represents a tremendous challenge because many of these habitats may be degraded or fragmented and may contain nonnative species (Denton et al. 1997; Allendorf and Lundquist 2003; Hayward 2009). This is especially true for inland salmonids (Dunham et al. 2002; Peterson et al. 2008). Despite apparently low numbers of Lahontan cutthroat trout from the 2006 and earlier stocking events, our evaluations clearly identified a number of factors that potentially limit Lahontan cutthroat trout. In particular, our findings suggest that the negative interactions with nonnative species, individually and synergistically, pose a substantial impediment to recovery; these interactions include the high predation rates by lake trout, the spatial overlap with and potential predation by brown trout, the potential for hybridization with rainbow trout, and potential competitive interactions with kokanee. Our estimates of predation from the bioenergetics analysis suggest that lake trout had the capacity to consume all of the recently reintroduced Lahontan cutthroat trout, but estimates of consumption from our anchor tag analysis indicate that actual consumption was substantially less. For Fallen Leaf Lake, this suggests that other potential factors causing reduced survival (i.e., condition; see above) also contributed to the low abundance of Lahontan cutthroat trout observed in this study. As such, our results indicate the need for

nonnative fish management as a means to increase survival rates and the recovery potential of Lahontan cutthroat trout within this system.

In lieu of these limiting factors, we acknowledge the need for additional research to improve the probability of successful Lahontan cutthroat trout reintroductions. First, robust evaluations of future stocking strategies are needed. Although Allen et al. (2006) suggested that the stocking of large fish (>250 mm) might improve Lahontan cutthroat trout survival, our results in combination with the high rearing costs and disease potential (i.e., bacterial kidney disease) suggest that this strategy may not be feasible. For Fallen Leaf Lake, these alternative reintroduction strategies may include (1) using hydroacoustic surveys to locate areas of high habitat complexity, (2) using the survey information to target multiple stocking sites, and (3) stocking during periods of thermal stratification, thus minimizing predator encounter rates (Beauchamp et al. 1999). Next, the use of remote-site incubators (RSIs) should be evaluated as a cost-effective means for reintroductions (e.g., Kaeding and Boltz 2004). There should be an explicit evaluation of the effectiveness of RSIs by quantifying young-of-year survival from Glen Alpine Creek to the lake. Ultimately, RSIs will allow for natal imprinting for fish returning to spawn, will permit acclimation to lake conditions, and will limit the influence of hatchery rearing conditions on individual resource use (e.g., Griffiths and Armstrong 2002). Finally, managers need to consider the use of temporary rearing pens to allow habituation of Lahontan cutthroat trout to the lake environment, which may increase fish condition, reduce predatory effects, or both (e.g., Schlechte and Buckmeier 2006).

Finally, there needs to be agreement among relevant state and federal agencies in developing management strategies that support and directly coincide with the Lahontan cutthroat trout recovery efforts. The reintroduction effort in 2006 highlights the need for coordinated efforts based upon empirically driven science. The timing, size, and number of reintroduced fish in 2006 were recognized at the time as suboptimal; however, because multiple agencies were involved, the December planting represented the only reintroduction opportunity for that year. In addition to a coordinated agency effort, the management framework for Fallen Leaf Lake must consider the most cost-effective and socially accepted means for managing nonnative species (Quist and Hubert 2004). The creel surveys indicated low numbers of anglers per day (1.9 angler-days/ha), with most anglers targeting lake trout, which suggests that (1) managing nonnative species, particularly rainbow trout and brown trout, may result in minimal adverse reactions from anglers (Quist and

Hubert 2004; Clarkson et al. 2005); and (2) angler incentive programs to increase harvest (e.g., Friesen and Ward 1999), even for lake trout, would not by themselves be effective at reducing nonnative fish abundance. As such, we recommend a progressive management plan that would include increasing the daily harvest limits for all nonnative species and initiating active removal programs. Albeit costly, active removal efforts have been found to be effective at reducing the impacts of lake trout in other systems (Ruzycski et al. 2003); in Fallen Leaf Lake, a similar reduction of population-level predation would probably facilitate the reintroduction efforts and the establishment of a naturally reproducing population of Lahontan cutthroat trout. Increased harvest limits and removal should also extend to brown trout and rainbow trout, both within the lake system and in Glen Alpine Creek, the only spawning tributary. These efforts will help to minimize the predatory effects of brown trout (Allen et al. 2006) and the potential for hybridization with rainbow trout. The relatively short length of this tributary (500 m) indicates that the mechanical removal of nonnative fish is possible. Ultimately, this suggests that barriers to the reentry of nonnative species from the lake would be needed to prevent further colonization of Glen Alpine Creek. However, this strategy would require a robust evaluation of downstream movements of nonnative fishes from the reaches of Glen Alpine Creek above Glen Alpine Falls, since these populations may act as a source of nonnative fish to the lower part of the system.

Lastly, this new management framework must consider appropriate harvest limits and future reintroduction strategies for Lahontan cutthroat trout. Our results indicated considerable harvest of reintroduced Lahontan cutthroat trout in 2005, and the current harvest limits are equal to those for nonnative salmonids within the basin. A suitable harvest strategy will eventually need to balance the goals of establishing a naturally reproducing population of Lahontan cutthroat trout while maintaining support from the local community through limited angling opportunities. Once this population is established, reintroduction strategies will also have to be altered to maximize viability by maintaining sufficient genetic diversity (i.e., Fraser et al. 2007). The current broodstock used by USFWS in this and future reintroductions is a lacustrine strain that is native to the Lake Tahoe basin (i.e., Pilot Peak strain; Peacock and Kirchoff 2007). The Pilot Peak hatchery strain was derived from a naturalized population of Lahontan cutthroat trout whose progenitors from Pyramid Lake had been outplanted into streams in the Pilot Peak Mountains, Utah, prior to Lahontan cutthroat trout extirpation from the Tahoe-Truckee River watershed

in the 1940s (Behnke and Zarn 1976; Peacock and Kirchoff 2007). These wild Pilot Peak populations have maintained relatively high levels of genetic diversity, and USFWS hatchery production has focused on maintaining this diversity through their breeding program (Peacock and Kirchoff 2007), a pattern that will be increasingly important for the long-term success of this reintroduction.

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