An Assessment of the Impact of Non-Native Lake Trout Salvelinus namaycush and Mysis diluviana on the Growth and Survival of Pelagic Planktivores in Lake Tahoe

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Abstract

An Assessment of the Impact of Non-Native Lake Trout *Salvelinus namaycush* and *Mysis diluviana* on the Growth and Survival of Pelagic Planktivores in Lake Tahoe

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Due to introductions of non-native species and the extirpation of native species, the food web of Lake Tahoe has undergone many changes over the past century. This study quantified temporal and ontogenetic trophic interactions in Lake Tahoe to determine if pelagic planktivore growth was limited by food supply or by predation. Field data on growth, diet composition, abundance, distribution, survival, and thermal experience were used in bioenergetics models to quantify the seasonal consumption demand by Kokanee *Oncorhynchus nerka*, mysids *Mysis diluviana* and Lake Trout *Salvelinus namaycush*. Seasonal and depth-specific biomass was estimated for the key planktivore prey, adult *Diaptomus* and *Epischura*, and Lake Trout prey, mysids, Kokanee, and Lake Trout. Kokanee fed primarily on the copepods *Epischura* and *Diaptomus* and mysids. Mysids became increasingly important for Kokanee > 200 mm, but particularly so for adults > 300 mm. Stable isotope values of $\delta^{15}N$ indicated that mysids began to incorporate copepods into their diet between 8 - 12 mm TL, but mysids >12 mm TL still relied heavily on phytoplankton. When comparing the depth-stratified supply of zooplankton to the vertical distribution and consumption demand by mysids and Kokanee, the year round supply of zooplankton was sufficient for Kokanee and pelagic cyprinids, but still limited potential growth. The zooplankton supply was insufficient for mysids to consume the proportion of copepods modeled during spring, summer and winter. Vertical distribution and thermal segregation

allowed planktivorous fish access to zooplankton prey that was unavailable to mysids. Lake Trout undergo an ontogenetic dietary shift wherein fish feed predominantly on mysids when fork length (FL) ≤ 500 mm, become increasingly piscivorous over 501-625 mm, and are primarily piscivorous at FL >625 mm with fish prey representing 80% of the diet. Lake Trout targeted predation on pre-spawning adult Kokanee through the summer and fall with the Lake Trout > 625 mm consuming 24% of the adult Kokanee biomass. In Lake Tahoe, Lake Trout can potentially regulate the Kokanee population, while also self-regulating their own population via cannibalism. Although heavy, Lake Trout predation does not limit the mysid population; mysid production (growth) throughout the year is sufficient enough to absorb the mortality sustained from Lake Trout predation. Understanding the factors that allow the co-existence of Lake Trout, mysids and Kokanee will be beneficial to managing these species in other systems.

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INTRODUCTION

The introduction of a species into a new ecosystem can dramatically change the flow of energy and nutrients in food webs (Lodge 1993). Non-native species can affect pre-existing species at multiple trophic levels and even alter interactions between aquatic and terrestrial species (Ellis et al. 2011). Non-native species can negatively affect existing populations through competition, increased predation, or indirect effects that reverberate through the food web (Carpenter et al. 1985; Bowles et al. 1991). Invasions by non-native species are the second leading cause of native species decline, while the largest cause is attributed to habitat loss (Simberloff 2001). Many non-native species outcompete native species, putting native populations in decline or extirpating them entirely. In the United States, there are 163 fish species that are federally listed as endangered or threatened (USFWS 2013), and a number of these examples occur in large lakes throughout the Western United States where native salmonids were extirpated or are struggling to persist in sympatry with non-native species, particularly Lake Trout (*Salvelinus namaycush*) and mysids (*Mysis diluviana*).

The native range of Lake Trout in North America covers the majority of the continent between northern latitudes 50° - 70°, and south into the great lakes basin (Lindsey 1964). Throughout their native range, Lake Trout fill important ecological (Ryder et al. 1981) and societal niches. Lake trout are considered apex predators in many lake food webs. The long life span and trophic role enable Lake Trout to attain large sizes, making them the second largest of the North American salmonids (Donald and Alger 1986). They support valuable recreational, commercial and subsistence fisheries throughout their native range (Sellers et al. 1998). Their popularity as a trophy sized sport fish motivated people to introduce Lake Trout to lakes outside of their native range.

Within in the United States, Lake Trout have successfully established self-supporting populations in 10 of the 15 states they were introduced outside of their natural range (Crossman

1995). There are self-sustaining populations in Montana, Colorado, Utah, California, Nevada, Oregon, Washington, Idaho, Wyoming and New Mexico (Crossman 1995). Lake Trout typically assume the role of apex predator (Martinez et al. 2009; Ellis et al. 2011), and reduce the amount of prey available for the native predators (Donald and Alger 1993). They also prey on juvenile or smaller individuals of native predators (Ruzycki et al. 2001, 2003; Beauchamp et al. 2007; Ellis et al. 2011). In Yellowstone Lake, fish prey (mostly native Cutthroat Trout *Oncorhynchus clarkii*) represented 95% of the diet for Lake Trout aged ≥ 9 years (Ruzycki et al. 2003). Native Cutthroat Trout and Bull Trout *Salvelinus confluentus* populations have been particularly impacted by the rise of Lake Trout in western montane lakes.

Lake Trout were introduced into Lake Tahoe in 1889 and established a self-sustaining population (Miller & Alcorn 1945). The diets of Lake Trout in Lake Tahoe have changed over time as the availability of prey species changed. Lake Trout collected in Lake Tahoe between 1938 and 1964 exhibited reduced growth rates compared to other large oligotrophic lakes, and this reduced growth was hypothesized to be caused by a lack of transitional prey between zooplankton and fish for smaller Lake Trout (Hanson and Cordone 1967). Mysids were introduced to Lake Tahoe in 1963 to increase the prey supply for juvenile Lake Trout (Linn and Frantz 1965). In lakes where mysids have also been introduced, juvenile Lake Trout rely heavily on this prey until they grow large enough to become piscivorous (Beauchamp et al. 2007; Ellis et al. 2011). This alternative prey allows more Lake Trout to reach the piscivorous life stage (Donald and Alger 1986; Ellis et al. 2011).

Mysids have invaded numerous cold-water lakes and reservoirs across temperate regions of the northern hemisphere, especially the western region of North America. Mysids were originally introduced to Kootenay Lake in British Columbia as an experimental prey source to supplement diets of Rainbow Trout *O. mykiss* (Northcote 1991; Larkin 1948). Rainbow Trout growth did not increase; however, the introduction was initially considered a success because Kokanee *O. nerka* in the shallow, west arm of the lake fed heavily on the mysids and grew rapidly. Soon thereafter, mysids were introduced into hundreds of lakes across the western United States and British Columbia. Numerous reports of unintended consequences and alterations of the native food webs emerged within the decade following these introductions (Northcote 1991), including the disappearance of cladocerans in Lake Tahoe (Morgan et al 1978; Goldman et al. 1979; Richards et al. 1991). The success of the Kokanee in Kootenay Lake turned out to be an anomaly due to the unique hydrology that advected mysids from shallower depths of the deep main basin into the shallow west arm of the lake which prevented descent to deeper dark refuges from foraging fish (Martin and Northcote 1991). In deep basins, mysids perform diel vertical migration (DVM) where the ascended during late dusk to feed on zooplankton at night, then descend to deep depths before dawn where they are generally inaccessible to pelagic planktivores. Mysids in deep lakes often reduced macrozooplankton densities available to planktivorous fish, while DVM effectively minimized their vulnerability to predation by planktivorous fishes; consequently, mysid introductions in many lakes led to reductions in productivity of macrozooplankon (primarily *Daphnia*), Kokanee, and other planktivorous fish populations (Rieman and Falter 1981; Morgan et al. 1978; Beattie and Clancey 1991; Bowles et al. 1991; Richards et al. 1991; Ellis et al. 2011).

Mysids are omnivorous and compete with native planktivores for the available zooplankton in lakes. Because of their diel vertical migrations, mysids can redistribute pelagic nutrients to the hypolimnion and thus reduce the productivity of epi-pelagic phytoplankton, zooplankton and planktivores (Jassby et al 1992; Jassby 1998). In addition to competing with planktivores for food resources (resource competition), mysids can indirectly increase predation on native salmonids and Kokanee (apparent competition). Lake Trout use mysids as a key prey resource and consequently, more of these predators grow large enough to become piscivorous (Beauchamp et al. 2006, 2007; Ellis et al. 2011; Schoen et al. in press). The strength of resource competition and apparent competition between mysids and planktivorous fish can vary depending on the temperature and depth of the lake or reservoir (Schoen et al. in press).

The introduction of mysids to Lake Tahoe altered the food web (Morgan et al. 1978; Goldman et al. 1979; Vander Zanden et al. 2003); managers and researchers continue to study mysids' impact on trophic relationships 50 years later. After being introduced in 1963, the mysid population quickly increased. The introduced Kokanee population increased concurrently and by 1967 was able to support a recreational fishery (Cordone et al. 1971). *Daphnia* are the preferred prey for both mysids and Kokanee (Cooper and Goldman 1980; Cordone et al. 1971; Scheuerell et al. 2005). By 1971, the three native cladoceran species *D. pulicaria*, *D. rosea* and *Bosmina longirostris* disappeared (Richards et al. 1991). It is believed that predation from mysids during a population boom and predation from Kokanee caused the increased death rates of cladocerans in Lake Tahoe (Goldman et al 1979). Birth rates also slowed, and the population was not able to replace itself (Goldman et al 1979). After the cladoceran population decreased, copepod densities increased, while adult Kokanee abundance and mean body size decreased (Goldman et al 1979; Morgan et al. 1978; Beauchamp et al. 1994).

Mysids were also introduced to Lake Pend Oreille, Idaho during 1966-1970, and while the effects of this introduction were not as drastic as in Lake Tahoe, impacts on macrozooplankton were clearly measurable (Rieman and Falter 1981). The temporal distribution of the cladocerans was altered. *Daphnia* and *Bosmina* did not appear until mysids were thermally isolated from the surface strata (Rieman and Falter 1981). The species composition of *Daphnia* also changed after mysids were introduced as the pointed-helmet daphnid (*D. galeata mendotae*) became more dominant than the round-helmet species (*D. thorata*), a common response to increased threat from predatory invertebrates (Rieman and Falter 1981).

The physical properties and primary productivity of Lake Tahoe have a long, rich data set, whereas the upper trophic levels of pelagic food web are relatively understudied. With non-native species dominating multiple trophic levels, the food web processes in Lake Tahoe are heavily altered from their pre-introduction state. The focus of this thesis was to determine if Kokanee in Lake Tahoe are regulated by either competition for food resources with non-native mysids, or predation from non-native Lake Trout. The first chapter of this thesis investigates how the seasonal availability of zooplankton in Lake Tahoe affects the growth and production of planktivorous salmonids. We estimated seasonal consumption demands by Kokanee and mysids and compared these to the available biomass of zooplankton to determine if Kokanee growth was limited by prey availability or thermal constraints on prey access. The second chapter thesis examines the hypothesis that predation by non-native Lake Trout was capable of regulating key species in the pelagic community of Lake Tahoe. We estimated the size-structured consumption demand by Lake Trout on Kokanee, pelagic minnows, and bentho-pelagic mysids and determined if predation by Lake Trout represented a significant source of mortality for Kokanee and mysids.

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Chapter One:

Seasonal Prey Supply and Consumption Demand by *Mysis diluviana* and Planktivorous Fish in Lake Tahoe

ABSTRACT

Due to introductions of non-native species and the extirpation of native species, the food web of Lake Tahoe has undergone many changes over the past century. This study quantified temporal and ontogenetic trophic interactions in Lake Tahoe to determine if pelagic planktivore growth was limited by food supply. Field data on growth, diet composition, abundance, distribution, survival, and thermal experience were used in bioenergetics models to quantify the seasonal consumption demand by Kokanee *Oncorhynchus nerka* and mysids *Mysis diluviana*. Seasonal and depth-specific biomass was estimated for the key prey, adult *Diaptomus* and *Epischura*. Kokanee fed primarily on the copepods *Epischura* and *Diaptomus* and mysids. Mysids became increasingly important for Kokanee > 200 mm, but particularly so for adults > 300 mm. Pelagic Tui Chubs (*Gila bicolor pectinifer*) and hybrid cyprinids all ate exclusively copepods, whereas the Lahontan Redsides (*Richardsonius egregious*) ate primarily copepods, followed by mysids and *Bosmina*. Stable isotope values of $\delta^{15}N$ indicated that mysids began to incorporate copepods into their diet between 8 - 12 mm TL, but mysids >12 mm TL still relied heavily on phytoplankton. We expanded the per capita consumption estimates to the population level and estimated that the Kokanee population consumed 413 MT of copepods and 263 MT of mysids throughout the simulation year, while mysids consumed 1,841 MT of copepods. When comparing the depth-stratified supply of zooplankton to the vertical distribution and consumption demand by mysids and Kokanee, the year round supply of zooplankton was sufficient to satisfy the current consumption demand by Kokanee and pelagic cyprinids. The zooplankton supply was insufficient for mysids to consume the proportion of copepods modeled during spring,

summer and winter. For Kokanee, the ratio of consumption demand to biomass of adult copepods was highest in the spring at 88% of the available biomass. However, the copepod biomass in spring and summer would not allow increased consumption demand on adult copepods within or above the thermocline. Intensified thermal stratification partially segregated Kokanee from mysids and reduced competition for copepods during the summer, but also potentially reduced access by Kokanee to exploit mysids as a prey resource.

INTRODUCTION

The introduction of a species to a new ecosystem can dramatically change the flow of energy and nutrients in freshwater food webs (Lodge 1993). The introduced species can affect pre-existing species at multiple trophic levels and even alter interactions between aquatic and terrestrial species (Ellis et al. 2011). An introduced species can negatively affect existing populations through competition, increased predation, or indirect effects that reverberate through the food web (Carpenter et al. 1985; Bowles et al. 1991).

The opossum shrimp, *Mysis diluviana*, was introduced or has invaded numerous cold-water lakes and reservoirs across temperate regions of the northern hemisphere, especially the western region of North America. Mysids were originally introduced to Kootenay Lake in British Columbia as an experimental prey source to supplement diets of Rainbow Trout *Oncorhynchus mykiss* (Northcote 1991; Larkin 1948). Rainbow Trout growth did not increase; however, the introduction was initially considered a success because Kokanee *O. nerka* in the shallow, west arm of the lake fed heavily on the mysids and grew rapidly. Soon thereafter, mysids were introduced into hundreds of lakes across the western United States and in British Columbia. Numerous reports of unintended consequences and alterations of the native food webs emerged within the decade following these introductions, including the disappearance of cladocerans in Lake Tahoe (Morgan et al 1978; Goldman et al. 1979; Richards et al. 1991) and significant declines or shifts in species composition, timing, and depth distribution of cladocerans in other western lakes (Rieman and Falter 1981; Northcote 1991; Beattie and Clancey 1991).

Mysids are omnivorous and compete with native planktivores for the available zooplankton biomass in lakes. Mysids avoid many visual predators by performing diel vertical migrations (DVM): ascending from darker, deep daytime habitats to shallower depths at night to feed on zooplankton, then descending before dawn to depths where they are generally inaccessible to pelagic planktivores. Because of DVM, mysids can redistribute pelagic nutrients to the hypolimnion and thus reduce the productivity of epi-pelagic phytoplankton, zooplankton and planktivores (Jassby et al 1992; Jassby 1998). In addition to competing with planktivores, apparent competition by mysids can indirectly increase predation on native salmonids and Kokanee; Lake Trout (*Salvelinus namaycush*) use mysids as a key prey resource and consequently, more of these predators recruit to piscivorous size (Beauchamp et al. 2006, 2007; Ellis et al. 2011; Schoen et al. in press).

The introduction of mysids to Lake Tahoe in 1963-1964 (Linn and Frantz 1965) altered the food web (Morgan et al. 1978; Goldman et al. 1979; Richards et al. 1991; Vander Zanden et al. 2003); managers and researchers continue to study mysids' impact on trophic relationships 50 years later. Lake Tahoe supports a popular sport fishery for Kokanee and Lake Trout, and is co-managed by California, and Nevada. In other lakes within the basin, managers are attempting to reintroduce the native Lahontan Cutthroat Trout *O. clarkii henshawi* (Al-Chokhachy et al. 2009). Quantifying mysid predation on zooplankton and total zooplankton demand and supply in the system can help identify trophic bottlenecks, whether they be seasonal prey shortages or inability to access prey due to thermal constraints. Managers can use this information to determine if sufficient prey are available throughout the year to support increases in planktivore populations.

Our objective was to investigate how seasonal availability of zooplankton in Lake Tahoe affects the growth and production of planktivorous salmonids. We estimated seasonal consumption demands by Kokanee and mysids and compared these to the available biomass of zooplankton to determine if Kokanee growth was limited by prey availability or thermal constraints on prey access.

STUDY AREA

Lake Tahoe is a large ultra-oligotrophic subalpine lake located in the Sierra Nevada Mountains of California and Nevada. The lake's mean depth is 313 m and it has a surface area of 500 km^2. The water column normally becomes isothermal by December and remains so through May. The thermocline is well established by July, with peak stratification occurring at the end of August (UC Davis Tahoe Environmental Center 2014). The top of the thermocline initially starts at 6 m deep, but deepens to 15 m by September. Temperatures $\geq 18^oC$, which inhibit growth or become stressful to most western salmonids in waters with low- or moderately-productive food supplies (Beauchamp 2009), are encountered from the surface down to 10-15 m during August-September; temperatures declined rapidly from the top of the thermocline to approximately 10^oC at about 30 m deep during summer (**Figure 1**).

Like many western lakes, the species composition has changed over time including the extirpation of the Lahontan Cutthroat Trout. In 1889, the first recorded introduction of Lake Trout occurred in Lake Tahoe (Miller & Alcorn 1945). In 1938, biologists recorded the last spawning run of Lake Tahoe's Lahontan Cutthroat Trout in the Truckee River; the primary causes of this local extinction were presumably overharvest and degradation of stream spawning and nursery habitat from logging (Gerstung 1988). Lake Trout assumed the top trophic position in the lake at some point before or after the demise of Lahontan Cutthroat Trout and now support an economically valuable recreational fishery (Vander Zanden et al. 2003). Whether Lake Trout played a role in the collapse of the Lahontan Cutthroat Trout population is unknown. In 1963 mysids were introduced to increase the forage base for Lake Trout (Linn & Frantz 1965; Frantz & Cordone 1970). Kokanee were originally stocked in Lake Tahoe starting in 1949, but did not support a recreational fishery until 1967 (Cordone et al. 1971). By 1971, the three native cladoceran species *Daphnia pulicaria*, *Daphnia roses* and *Bosmina longirostris* disappeared (Richards et al. 1991). The disappearance of the cladocerans coincided with a peak in mysid and Kokanee populations. With non-native species dominating multiple trophic levels, the food web processes in Lake Tahoe are heavily altered from their pre-introduction state. The current bentho-pelagic food web is composed primarily of: calanoid copepods *Diaptomus tyrelli* and *Epischura nevadensis*, mysids, Kokanee, and Lake Trout. Lahontan Redsides *Richardsonius egregious*, and Tui Chub-pelagic *Gila bicolor pectinifer* also utilize the pelagic zone but are rare compared to Kokanee.

METHODS

We estimated seasonal consumption demand for pelagic planktivores and mysids and compared demand to the seasonal and depth-specific biomass of adult copepods (prey supply) using a combination of field data, literature values, and bioenergetics modeling. Field data on distribution, diet, and size structure of pelagic planktivores and mysids were collected in the summer, fall and winter of 2012, and the spring and summer of 2013. Abundance estimates for kokanee were generated from hydroacoustic and midwater trawl surveys during summer, whereas mysid abundance was estimated by synoptic vertical net tow surveys conducted each season. These data were used as biological inputs into bioenergetics models to calculate seasonal, size-structured population-level consumption demand by mysids and Kokanee, the main pelagic planktivores in the lake. The available biomass of adult copepods was calculated by expanding the data from seasonal, depth-stratified zooplankton samples to lakewide estimates of depth-specific biomass. We compared the seasonal consumption demand by Kokanee and mysids to the available biomass of zooplankton to identify potential periods when consumption demand exceeded the available biomass.

Kokanee & Other Pelagic Fishes

Hydroacoustic sampling was performed during the day-dusk-night transition period, followed by synoptic night surveys to estimate the abundance of Kokanee and to record the diel vertical migration patterns of pelagic fish and mysids. We surveyed 10 parallel transects spanning the width of the main body of the lake and two transects spanning the width of Emerald Bay (**Figure 2**). Surveys were conducted seasonally (April, July, August September, and November), to record distribution patterns of fish and mysids during representative periods in the thermal regime of the lake. All 12 transects were surveyed during thermally-stratified periods, whereas a smaller representative subset of transects were surveyed during destratified seasons (November and April).

A BioSonics DT-X Digital Scientific Echosounder with a split-beam 200 kHz transducer was used to collect the hydroacoustic data on pelagic fish abundance and distribution. Kokanee abundance was estimated from the August 2012 survey and used to expand estimates of age-specific consumption for individual Kokanee to population-level consumption rates. The mid-summer nocturnal sampling provided the best opportunity to assess Kokanee abundance estimates because the spatial distribution of all age classes were most conducive to assessment during stratified lake conditions (Beauchamp et al. 2009).

Depth-stratified mid-water trawls were conducted by a chartered commercial fishing vessel (approximately 10m) during the same periods as the hydroacoustic sampling (no trawling in August 2012) to provide data on depth-specific species composition of the acoustic estimates and to collect fish samples for diet, growth and stable isotope analysis. The net was 8 m high by 15 m wide, with a cod-end mesh size of 9.5 mm to retain juvenile fish and native minnows (Lahontan Redsides and Tui Chubs) while allowing most mysids to pass through the mesh. Mid-water trawl samples were supplemented with adult Kokanee caught by trolling from commercial charter boats during August 2012. Fish were measured while fresh and then frozen onboard for further processing for diet analysis, aging and stable isotope analysis in the lab. All vertebrate handling was conducted under the auspices of the University of Washington IACUC protocol 3286-21.

Diet analysis was performed on 5-10 fish of each age class (when available) from each species caught by mid-water trawling and supplemental trolling each season, totaling 131 fish. Prey items were identified to species; blotted wet weights were measured for each group of prey. The proportional contribution of each prey type by blotted wet weight was calculated for each stomach sampled, then averaged over all non-empty samples from the same species and size class combination for each sampling period. Diets were preserved in 98% ethanol. The average diet proportions for each size class were used as inputs in bioenergetics modeling for calculating consumption demand.

Annual growth increments and size-at-age for Kokanee were estimated using scale back-calculation. These data were used as growth inputs for bioenergetics simulations to estimate Kokanee consumption demand. Kokanee scales were removed from the preferred region between the posterior edge of the dorsal fin and lateral line and pressed into acetate slides for viewing with a dissecting microscope. The radius of the scale (focus to outer margin) and the radius from the focus to each annulus were measured to the nearest 0.01 mm. We regressed scale radius (SR) versus fork length (FL) of 55 Kokanee ranging 75 – 375 mm (**Figure 3**). The FL at each annulus was back-calculated using the Fraser-Lee method (Fraser 1916; Lee 1920). We then computed the mean back-calculated FL at each age for the 55 Kokanee. Lastly, the Log_{10}(FL, mm) was regressed against Log_{10}(weight W, g) for Kokanee captured during August 2012 through November 2012 ($r^2 = 0.99$, N = 165, $P < 0.0001$, 48-382 mm FL):

$$\mathbf{W(g) = 0.000003 \cdot FL(mm)^{3.2304}}.$$

The regression was used to calculate the initial and final body masses used for each age class in bioenergetics simulations. It assumed that annulus formation was completed by 1 April each year, which approximates the emergence and lakeward migration date for Kokanee fry at the end of winter.

Mysids

Mysid samples were collected at night at 10 representative long-term sites throughout the lake (**Figure 2**). We used a 1-m diameter 1-mm mesh conical mysid net lowered to a depth of 100 m (or 3 m above the bottom where bottom depths were < 100 m) and raised vertically at a rate of 0.4 m/s. This depth was well below the nocturnal scattering layer (average = 60 m) and was checked prior to sampling using the echosounder. The deck lights and navigation lights were turned off while retrieving samples to avoid affecting the distribution of the mysids with additional light. All of the mysid stations were sampled each season concurrently with the hydroacoustic surveys. Mysid samples were preserved in 80% ethanol.

Each mysid sample was enumerated and at least 60 individuals were measured to produce seasonal length frequency histograms. The difference in the seasonal modal size distribution of each age class of mysids was used to infer growth. Because the bodies of mysids in preserved or frozen samples were often bent between the carapace and abdomen, we initially measured lengths to the nearest 0.1 mm for both the total length (from the anterior tip of the rostrum to posterior tip of the telson) and the "carapace length" (from the anterior tip of the rostrum to posterior end of the carapace) using an image analysis system. Total length (TL) was highly correlated with carapace length ($r^2 = 0.92$, $N = 60$, $p < 0.0001$):

$$\mathbf{TL\ (mm) = -0.4 + 3.05 \cdot Carapace\ Length\ (mm)}$$

Since carapace lengths were measured efficiently with the image analysis system, we measured carapace lengths for all samples and used the regression equation to estimate TL. Mean TL was converted to mean wet weight using a length-weight regression developed for mysids in Lake Pend Oreille (Chipps 1997; ($r^2 = 0.91$, $N = 110$, range 5-19 mm TL):

$$\mathbf{W(g) = 0.000001112 \cdot TL(mm)^{3.676}}$$

The regression was used to calculate the initial and final body masses used for each age class in bioenergetics simulations.

Zooplankton

Zooplankton samples were collected at 3-4 sites along three nearshore-offshore transects (**Figure 2**) during daylight with a 0.31 m closing 150 µ mesh zooplankton net, towed at a rate of 0.4 m/s. Three depth-stratified samples were taken (0-10, 10-25, and 25-100 m) at each site. When the bottom depths were shallower than the deepest stratum, we lowered the net within 3 m of the bottom and adjusted the recorded sampling volume accordingly. At least two replicate samples were taken for each depth. Zooplankton sampling periods coincided with the hydroacoustics surveys. Zooplankton samples were preserved in 80% ethanol.

Zooplankton samples were processed in the lab to determine volumetric density (adults/L) and size distribution for the adult stage of each species. We focused on the adult stage, because Kokanee and mysids feed selectively on cladocerans when available, or adult copepods (Cooper and Goldman 1980; Beauchamp et al. 2004; Scheuerell et al. 2005). Copepods reach the adult life stage once the fifth leg starts to develop; smaller individuals with four leg pairs or fewer were considered copepodids and were not included in density or size distribution calculations. We scanned each sample for large rare organisms, and then diluted it to a varying volume depending on the density of adults estimated from the visual scan. The sample was then stirred and a 1-5 ml aliquot (depending on density of adults) was removed with a VWR high performance volumetric pipettor while the sample was still suspended homogenously. The subsample was placed in a counting chamber, and zooplankton were identified to species and enumerated under 60X magnification. For each zooplankton sample, two subsamples were enumerated and 15-20 lengths per species (when available) were measured to the nearest 0.01 mm. Adult copepods were measured from the top of the head to the base of the caudal rami. Cladocerans were measured from top of the helmet to the base of the tail spine. The subsample counts were averaged together and expanded to the sample volume to estimate volumetric density (organisms/L). To measure the length of the mysids and zooplankton, ImagePro Plus image analysis software was used in conjunction with an image capturing CCD camera linked to a dissecting microscope.

Stable Isotope Analysis

Stable isotope analysis for $\delta^{13}C$ and $\delta^{15}N$ was performed to update and refine the pelagic food web structure reported by Vander Zanden et al. (2003) in terms of seasonal and size-specific trophic positions of key bentho-pelagic species. The samples were collected with the mid-water trawl, zooplankton tows or mysid hauls as described above. Frozen fish samples were thawed in the lab, and a plug of dorsal muscle tissue (fin clips were used for a few fish instead of muscle tissue) was removed for stable isotope analysis. Zooplankton and mysid samples were preserved in 80% ethanol after capture. Previous work by Vander Zanden et al. (2003) found a negligible preservation effect of EtOH on fish and invertebrates. The mean preservation effect on all taxa enriched the signal by 0.32 for $\delta^{13}C$ and by 0.01 for $\delta^{15}N$, and these slight shifts did not change the interpretation of the data. All samples were dried in a 60° oven for 48 hours and then ground into powder using a mortar and pestle. Approximately 0.5 grams of the ground sample was placed into an aluminum capsule. All samples were processed by the IsoLab at the University of Washington using a mass spectrometer (ThermoFinnigan MAT 253; Thermo Fisher Scientific, US). PeeDee Belemnite was used as reference material for $\delta^{13}C$ and atmospheric N_2 was used for $\delta^{15}N$.

To evaluate the trophic relations between planktivores and zooplankton, we plotted the mean $\delta^{13}C$ and $\delta^{15}N$ values for each major species. We also plotted the $\delta^{15}N$ for mysids and Kokanee against body length to identify ontogenetic changes in trophic status. We fit a representative set of linear models to test if the mysid $\delta^{15}N$ signal varied among months or habitat zones, while accounting for mysid total length as a covariate.

Bioenergetics Modeling

Consumption demand and feeding rates for mysids and Kokanee were calculated via bioenergetics modeling. We used the Wisconsin Bioenergetics 3.0 modeling software (Hansen et al. 1997) to estimate the feeding rate and consumption demand by Kokanee and mysids. The model is based on a basic energy balance equation where the energy consumed (C) must equal the combined energy demands for metabolism (M), waste (W) and growth (G):

$$C = M + W + G$$

The model uses mass- and temperature-dependent functions for maximum consumption (Cmax), and metabolism, and consumption-dependent functions for egestion, excretion, and specific dynamic action. The initial and final weight of each growth cohort is used in model simulations to fit the consumption required to satisfy the observed growth over a specific simulation period while accounting for temporal variability in thermal experience and diet. Growth cohorts can either span entire annual growth increments for individual age classes, or when data permit, can be divided into shorter growth stanzas that treat low versus high feeding or growth periods separately. For each day in a simulation, the model followed the change in temperature, diet composition, and energy density (J/g) of the prey and consumer to calculate the consumer's change in body mass and daily consumption (g/d) of each prey item. Each simulation estimates the average feeding rate for the consumer as a percentage of the theoretical maximum consumption rate over the simulation interval (%Cmax) that accounts for the body size and thermal experience of the consumer. The feeding rate is particularly useful for determining if growth is constrained by food supply, prey energy density, or temperature (Beauchamp 2009). This seasonal and size specific per capita information on growth and consumption was scaled to the population level by using size-structured abundance data (Beauchamp et al. 2007).

We used the physiological parameters for Kokanee from Beauchamp et al. (1989) and mysids from Rudstam (1989; Chipps and Bennett 2002) in the model simulations. For Kokanee we used input data for age and growth derived from scales, seasonal diet composition data collected from the field, literature values for energy content of predators and prey, and the thermal experience estimated from hydroacoustic data on vertical distribution combined with corresponding vertical temperature profiles for model simulations to estimate feeding rate and seasonal consumption demand for key prey (Beauchamp et al. 2007). To estimate mysid consumption, we used size-specific stable isotope data to construct seasonal and size-specific diet inputs for the model. Shifts in the seasonal modal size distribution of mysids were used to determine growth, and the thermal experience was derived from the hydroacoustic data on mysid vertical distribution, combined with vertical temperature profiles. The remainder of the methods to calculate mysid consumption were similar to the approach for Kokanee.

For both species, the simulation year began on 1 April and continued for 365 days until 31 March. Field data were collected during August 2012 – August 2013; we re-ordered the data to represent the biologically relevant sequence starting in April when the smallest mysids and Kokanee were encountered. The oldest age classes of mysids and Kokanee were not available for the full 365-day simulation. Age-1 mysids disappeared between the November and April sampling dates and virtually all age-3 Kokanee spawned and died during or after the October-November sampling periods.

Size & Growth Inputs

We tracked mysid growth by determining the modal length of each age class among seasons using length frequency distributions (**Figure A1**). This approach yielded initial and final weights for four seasonal growth cohorts for age-0 mysids and three for age-1 mysids in bioenergetics simulations (**Table 1**).

Most Kokanee in Lake Tahoe spawn and die around their fourth birthday; therefore, simulations tracked age-0 through age-3 Kokanee. The simulation year was separated into fast growth periods (1 April to mid-October) and slow growth periods (mid-October to 31 March). We assumed age-0 fry entered the lake on 1 April with an initial weight of 0.2 grams (Gemperle 1998). To estimate the initial weight on 1 April for ages 1-3, the average fork length at age was converted to weight using the length-weight regression. The final weights after the summer growing season were calculated as the mean weight for the modal size associated with each age recorded during the October-November sampling period (**Table 2**). These weights were also used as the initial weights for the slow growth season.

Thermal Experience

The monthly average thermal experiences for mysids and Kokanee were calculated using vertical distribution data from hydroacoustic surveys matched with the corresponding vertical temperature profiles. The position of mysids in the water column depends on light attenuation and temperature (Beeton and Bowers 1982; Boscarino et al. 2009). During peak thermal stratification, echograms showed mysids concentrated within a layer at depths of 40-85 m at night, descending below 200 m during the day. We estimated the thermal experience of the mysids by averaging the temperatures between 40-85 m (**Table 3**). Temperatures varied minimally below 40 m for any given month, except during the final stages of mixing in October-November.

During peak thermal stratification in August, Kokanee were concentrated within and below the thermocline (15 – 30 m). By October, the lake began to mix, and warmer water mixed to lower depths, pushing the modal depth of Kokanee to 30-40 m. During the mixed season (December – June), Kokanee used the top 50 m of the water column. The thermal experience for Kokanee was separated into three seasons, each representing a different state of the thermocline (**Table 3**). For peak stratification (July – September) we used the mean temperature for the 15 – 30 m depth strata. During destratification (October – November) we used the mean temperature for the 30 – 40 m depth strata. During the isothermal season (December – June) we used the mean temperature for the 0 – 50 m depth strata.

Diet

The seasonal diet composition for mysids was inferred from literature and stable isotope data. Mysids in Lake Tahoe and other systems are omnivorous (Rybock 1978; Grossnickle 1982; Lasenby et al. 1986), but we lacked current data to inform the seasonal composition and ontogeny of the mysid diets. Instead we used the relative trophic positions of mysids and their prey to determine their reliance on zooplankton. Stable isotope data collected in 2000 (Vander

Zanden et al. 2003) and during 2012 and 2013 for this study showed the trophic position of larger mysids was only slightly elevated above *Epischura* (mean = 19% of a trophic level) and *Diaptomus* (mean = 10%) (**Figure 4**). From these results, we inferred that adult mysids continue to rely on algae or detritus to some degree even after zooplankton are added to the diet.

Mysids in Lake Tahoe start preying on zooplankton at a TL of 7 – 8 mm (Rybock 1978). Stable isotope data from copepod and mysid samples from 2000 and 2012 indicated that mysids were not as predatory as previously suggested (Rybock 1978; Vander Zanden et al. 2003). Between April and August, mysids < 14 mm TL showed very low $\delta^{15}N$ signals, indicating little to no reliance on copepods (**Figure 4**). Mysids of the same length sampled in November and April exhibited higher $\delta^{15}N$ signals, indicating more reliance on copepods. During all seasons mysids >14 mm TL had $\delta^{15}N$ signals higher than copepods, suggesting increasing reliance on copepods as they grow. Using the above data, we constructed a diet that was composed of 100% algae for mysids less than 8 mm TL (age-0, 1 April – 8 August); then increased the proportion of copepods in their diet to 30% over the next 30 days and remained at that level for the remainder of the simulation year. For age-1 mysids, the diets started on 1 April with 30% copepods and 70% algae, then increased to 80% copepods from mid-May (day 45) through mid-July (day 105), and decreased back to 30% copepods by the end of the simulation year (**Table 4**).

Kokanee diet inputs were based on seasonal size-specific stomach contents obtained through angler and trawl caught fish (**Table 5**). Major prey categories included *Epischura*, *Diaptomus*, and mysids, followed by adult and immature insects and unidentified food. For Kokanee and mysids, the energy density of each prey type was obtained from literature values (**Table 6**).

Population Abundance

Seasonal mysid densities were averaged across 10 sites sampled by night-time vertical tows each season. Annual survival rates were calculated by dividing the proportion of age-1 mysids by the proportion of age-0 mysids in a season. The daily instantaneous mortality rate Z was calculated using the mean annual survival rate and the equation for daily instantaneous mortality (t = 365):

$$Z = \frac{-\ln\left(\frac{N_t}{N_0}\right)}{t}$$

Using the equation $N_t = N_0 \cdot e^{-zt}$ we estimated the daily abundance of mysids for both age classes.

For Kokanee, we assumed constant survival across all age classes and seasons, and approximated annual survival by iteratively fitting the survival rate to the observed abundance of each size class from the August 2012 hydroacoustic survey. The annual survival rate was converted to a daily instantaneous survival rate Z. The hydroacoustic estimate of age-0 Kokanee in August was back-calculated to the abundance of Kokanee fry entering the lake on 1 April, and the daily abundance of each age class of Kokanee was estimated using the following equation:

$$N_t = N_0 \cdot e^{-zt}$$

Consumption

For both Kokanee and mysids, population level daily consumption for each age class was calculated by scaling the individual daily consumption of each prey category for each age class by the corresponding daily abundance. These consumption estimates were summarized into season- and age-specific estimates for the biomass (in metric tons MT) of each prey category.

Prey Availability

To determine the temporal supply of zooplankton available to meet the consumption needs of both mysids and Kokanee, we calculated depth specific seasonal biomass estimates for edible-sized (adult) copepods. Biomass calculations incorporated average depth-specific seasonal densities, length frequency distributions, and literature based species- and genus-specific length-dry weight regressions.

Seasonal depth-stratified zooplankton densities were averaged across all sampling locations in the lake. The average zooplankton density for each depth strata was expanded using the volume of each stratum to estimate the lake wide abundance. The proportional length frequency (**Figure A2**) for each season was used to calculate the number of individuals in each length bin. Preliminary analysis using Kolmogorov-Smirnov tests indicated minimal variability in length frequency distributions among depth strata. All depths for each site were compared for the month of September 2012. We assumed that size distributions were similar among depths during other seasons and years as well. For the abundance calculations, the seasonal length frequency distributions for adults of each zooplankton species were constant across depth strata.

To estimate the depth-specific biomass of copepods available to planktivores each season, we used data on abundance and length. We used length to weight regressions to estimate the dry weight of individuals within each length bin. For *Epischura nevadensis* parameters were pooled for Calanoida in Bottrell et al. (1976). For *Diaptomus tyrelli*, we pooled the parameters for *D. pallidus*, *D. siciloides*, and *D. gracilis* from McCauley (1984) based on (Rosen 1981; Pace and Orcutt 1981; and Botrell et al. 1976). Both equations convert length (mm) to dry weight (µg).

Epischura: $W = 7.049805 \cdot L^{2.40}$

Diaptomus: $W = 3.5552 \cdot L^{2.151}$

Total dry biomass for each depth-season combination was calculated by multiplying the number of individuals in each length bin by the individual dry weight for that length bin. Dry weight was converted to wet weight using a ratio of 9.6% for copepods. Biomass estimates for May, June, July and October were calculated by linearly interpolating the abundance and length frequency data from the field sampled zooplankton data.

To determine the spatial-temporal overlap of copepods available to Kokanee and mysids, we combined the seasonal thermal profile of the lake (**Figure 1**), vertical distribution data from hydroacoustics and thermal tolerances for each species. Throughout all seasons mysids were never observed above 20 m; therefore, we assumed that mysids only foraged on copepods within the 25-100 m depth stratum. We assumed that Kokanee had access to all three depth strata (0-10 m, 10-25 m and 25-100 m) throughout the year. Warmer epilimnetic temperatures in the summer would require Kokanee to consume slightly more food to maintain the observed growth rates while in the epilimnion, but would not cause any weight loss.

RESULTS

Pelagic Fish

The August 2012 hydroacoustic survey produced Kokanee abundance estimates of 531,000 age-0 (TL < 100 mm) plus 730,000 age-1 through age-3 Kokanee (100-400 TL), and 176,000 larger fish assumed to be Lake Trout (**Table 7**). During peak stratification in August, most of the fish targets were within the thermocline (15-30 m) (**Figure 5**). The hydroacoustic target strengths, converted to a length frequency distribution were used to estimate a 65% annual survival rate, which was then converted to a daily instantaneous survival rate ($Z = 0.00118$). We used the hydroacoustic estimate of 531,536 age-0 Kokanee in August and the instantaneous mortality rate to estimate that 614,355 Kokanee fry entered the lake on 1 April.

Although mid-water trawling did not coincide with the hydroacoustic survey in August 2012, the species composition from trawling in October 2012 and August 2013 suggested that most of the smaller fish targets (35-100 mm) in the thermocline were a mix of small Kokanee and minnows (Lahontan Redsides and Tui Chubs), 101-400 mm targets were Kokanee, and targets larger than 400 mm were presumed to be Lake Trout (**Figure 6**). Using mid-water trawl catch proportions and depth-specific densities of the 35-100 mm acoustic targets, we estimated 159,000 minnows (Tui Chubs and Lahontan Redsides) in the 0-10 m depths of the lake. Due to the low spatial overlap between pelagic minnows and Kokanee, we assumed that the minnows did not bias the Kokanee abundance estimate.

In October and early November of 2012, the majority of fish caught by the mid-water trawl in the 0-10 m depths were Lahontan Redsides (24-86 mm), Tui Chub (62-106 mm), and unidentified cyprinids (these two species or hybrids), whereas a mix of cyprinids, Kokanee (53-382 mm), and Lake Trout (415-668 mm) were captured in 10-30 m; primarily Kokanee plus some Lake Trout were captured at 30-40 m (**Figure 6**). The deeper modal distribution in fall aligned with the erosion of the thermocline and warmer water mixing deeper. During April 2013 the trawls targeted the 10-30 m depths where the modal density of targets were observed on the echograms; however only three Kokanee (84-284 mm) and one juvenile Lake Trout (83 mm) were captured in the five trawls performed. Trawling during August 2013 was focused within the thermocline (10-30 m) and caught predominantly Kokanee (48-362 mm), followed by Lake Trout (400-785 mm). One Tahoe sucker was also caught in August 2013.

Kokanee fed primarily on the copepods *Epischura* and *Diaptomus* and mysids during summer (**Figure 7**). Mysids became increasingly important for Kokanee larger than 200 mm, but particularly so for adults > 300 mm. Only two non-empty Kokanee stomachs were sampled in April, but both contained predominantly mysids. The diets of pelagic Tui Chubs and hybrid minnows (Evans 1969) only contained copepods, whereas the Lahontan Redsides contained mostly copepods (84% by weight) followed by mysids (14%) and *Bosmina* (2%).

Because mysid feeding by Kokanee in deep lakes is rare, we examined the possibility that the apparent importance of mysids in the diet was an artifact of Kokanee feeding on mysids concentrated in the midwater trawl instead of in the lake. First, only 17% of the mysids in Kokanee stomachs were fresh, indicating that most or all mysids were consumed before Kokanee entered the net. Second, diets from angler-caught Kokanee (no possible net-feeding) consisted of 25% mysids by weight, further supporting the conclusion that mysids found in the Kokanee diets were naturally occurring and not an artifact of “net feeding”.

We used stable isotope analyses to describe the trophic positions and energy pathways associated with Kokanee, cyprinids, mysids and key invertebrates in the Lake Tahoe pelagic food web, based on $\delta^{15}N$ and $\delta^{13}C$ signatures (**Figure 4**). Kokanee, Lahontan Redsides and Tui Chub were highly planktivorous and exhibited strong overlap in isotopic signatures among species. The mysid contribution to Kokanee diets observed in the field was consistent with the stable isotope results. The mean $\delta^{15}N$ for Kokanee was 2-3‰ higher than mysids with $\delta^{13}C$ within 1‰, indicating potentially heavy reliance on a mix of small and large mysids as a prey source in addition to zooplankton.

The bioenergetics simulations indicated that all age classes of Kokanee fed at higher rates during the spring-summer growing season (41-78% Cmax during April through mid-October) than during fall-winter (20-29% Cmax; **Table 2**). Despite feeding at 20% Cmax and consuming an estimated 310 g, the average age-2 Kokanee incurred 6% weight loss during fall-winter. The annual population-level consumption by Kokanee was composed primarily of Calanoid copepods (413 MT) and secondarily mysids (357 MT). Consumption was highest during spring-summer on copepods (162-164 MT) and mysids (118-143 MT) and lowest during fall and winter on copepods (43-45 MT) and mysids (34-62 MT) (**Table 9**).

Mysids

The lake-wide average areal density from August 2012 through August 2013 was 215 mysids/m^2 with coefficients of variation ranging from 29% to 88% of the mean density (**Figure 8**). In August 2013 the mean lake-wide mysid density decreased to 143 mysids/m^2, but was not significantly different than the densities on the other sampling dates (Kruskall-Wallis test; p = 0.09). The surface area of Lake Tahoe where bottom depths exceeded 40 m is 480 km^2. We estimated the lake-wide abundance at the beginning of the simulation year to be 103.2 billion mysids by expanding the mean areal density (215 mysids/m^2, CV = 60%) to represent the lake-wide areal density over depths exceeding 40 m. The seasonal length frequency distributions indicated that age-0 mysids represented an average 85% (80-91%) of the population, resulting in 87.7 billion age-0 mysids on April 1st. The resulting annual survival rate was 17.7% and the daily instantaneous mortality rate was Z = 0.00475.

Mysids performed extensive DVM throughout the year, but the depth of the nocturnal distribution varied among seasons. During daylight in August, mysids were distributed below the 125 m maximum observable depth of our hydroacoustic system. The mysids ascended at dusk, forming a dense band between 40-80 m at night, with the modal depth generally around 60 m (**Figure 9**). In April and August 2013, the nocturnal mysid layer was less consistent than in

2012. The top end of the mysid layer was as shallow as 20 m, and the modal density ranged between 40-60 m.

The higher abundance of age-0 mysids in August 2012 through November 2012 followed the expected relative abundance between the two age classes (**Figure A1**). The appearance of a new smaller size mode in April 2013 indicated the recent release of a new brood. In April and August 2013, the relative abundance between the two age classes was opposite of what was expected with a higher ratio of age-1 mysids than age-0 mysids.

Stable isotope analysis indicated that mysids exhibited an ontogenetic shift from herbivory to omnivory and that the degree of carnivory varied by season (**Figure 10**). The partially elevated $\delta^{15}N$ of larger mysids suggested that they acted as both primary and secondary consumers, whereas the calanoid copepods *Epischura* and *Diaptomus* were predominantly primary consumers. In August 2012, the smaller mysids (≤ 12 mm) exhibited much lower $\delta^{15}N$ than mysids of equivalent lengths during other months. The model that best described the $\delta^{15}N$ signal for mysids was a function of length and month, with an interaction between the two factors (**Table 8**). The $\delta^{15}N$ signal increased with length but the rate of increase depended on the month. Smaller mysids were primarily herbivorous between April and August, the increased $\delta^{15}N$ signal in November indicates an increasing reliance on copepods after the August sampling.

Both age classes of mysids fed at relatively low rates (16-25% Cmax) during all seasons (**Table 1**). Annual population-level consumption was estimated as 3,002 MT of algae and 1,841 MT of copepods (**Table 10**). Age-0 mysids consumed approximately 5x more algal biomass, but only about 60% of the copepod biomass consumed by age-1 mysids. For both ages combined, mysids consumed 497 MT of copepods in spring, 684 MT in summer, 237 MT in fall, and 423 MT in winter. Overall, the estimated predation on adult copepods was 4.5-times higher by mysids than by Kokanee.

Prey Availability

The calanoid copepods *Epischura,* followed by the less abundant *Diaptomus*, were the predominant crustacean zooplankton available in the lake during all seasons (**Figure 11**). Densities were consistently low (< 0.5 adult copepods/L) across all depths and seasons. In all seasons except November, densities were highest in the 10-25 m depth stratum. Throughout all seasons, the combined density above and within the thermocline (0-10 m and 10-25 m) was 2-11 times greater than the density below the thermocline (25-100 m). *Bosmina* were encountered infrequently and at extremely low densities. The estimated biomass of adult copepods in the 0-100 m depth layer was highest during summer (698 MT) and fall (702 MT) (**Table 11**). Copepod density (by biomass) was highest in the 10-25 depth strata during all seasons, except for in winter when then 0-10 m strata was highest.

When the consumption demand for copepods by Kokanee and mysids was compared to prey availability across all depth strata, deficits in the supply of adult copepods were apparent in spring and summer for mysids but not Kokanee (**Table 12**). When comparing the prey availability to the predator depth distribution, the depth stratified prey supply was insufficient to support the estimated consumption demand by mysids during spring (-139 MT) and summer (-254 MT), and an additional deficit for mysids emerged in the winter (-187 MT) (**Table 11**). Kokanee consumed less biomass and maintained access to higher densities of copepods within the thermocline during stratified periods, and thus a larger pool of zooplankton were available to satisfy consumption demand in depth strata that were thermally inaccessible to mysids. The consumption of mysids by Kokanee is also important to consider. Kokanee consumed 39% of the mysid biomass in the spring, 25% in the summer, 8% in the fall and 26% in the winter. Most consumption of mysids by Kokanee likely occurred during dawn and dusk as mysids were completing their DVM.

DISCUSSION

Mysids imposed much greater consumption demand on the supply of zooplankton than did planktivorous fishes in Lake Tahoe, and although the availability of zooplankton was limited, thermal stratification conserved a sufficient supply of adult copepods for Kokanee and pelagic cyprinids in and above the thermocline during the growing season, because they were inaccessible to mysids. Low biomass and seasonal inaccessibility of zooplankton could explain the high level of herbivory/omnivory exhibited by mysids. Similar to other systems where mysids have been introduced, the mysids in Lake Tahoe appear to be limiting Kokanee growth and survival through direct competition for prey resources (Morgan et al. 1978; Rieman and Falter 1981; Ellis et al. 2011; Johnson and Martinez 2012; Schoen et al. in press). Kokanee are particularly limited by the low zooplankton surplus in the spring and summer, where the depth stratified ratio between consumption and biomass is below 50%.

The carrying capacity estimate in this study was conservative in one sense, because it did not include the additional biomass from copepod production. Production of edible-sized adult copepods is much lower than cladoceran production in freshwater systems. Kokanee and adult mysids prey on larger, adult size classes of copepods (Cooper and Goldman 1980). Only a small fraction of production would exist in the form of edible-sized adult copepods, rendering most of the copepod production unavailable to Kokanee. We initially calculated copepod production using a temperature dependent production:biomass model (Shutter & Ing 1997), but did not include this estimate because it was unclear what portion of the biomass from production would result in edible-sized adult copepods. The additional biomass from the edible-sized adult proportion of the production estimate could increase the zooplankton biomass available to Kokanee, allowing some additional carrying capacity for pelagic planktivores. It would also add to the biomass available to mysids, potentially removing the consumption deficit for mysids in the spring and summer.

The zooplankton community in Lake Tahoe changed dramatically after mysids were introduced in 1963. Predation by the expanding mysid population and introduced Kokanee increased the death rates of cladocerans in Lake Tahoe (Goldman et al 1979). *Daphnia* are the preferred prey for both mysids and Kokanee (Cooper and Goldman 1980; Cordone et al. 1971). After the cladoceran population decreased, copepod densities dramatically increased, while adult Kokanee abundance and mean body size decreased (Goldman et al 1979; Morgan et al. 1978; Beauchamp et al. 1994).

In response to the changing zooplankton community, the diet and abundance of the Kokanee population has also changed. Kokanee have adapted to feeding primarily on copepods and mysids, which supports modest feeding and growth rates. Kokanee met their copepod consumption demand primarily in the depth strata that did not overlap with mysids during the growing season. Even if Kokanee spent a majority of the time foraging in the 25-100 m depths where they would experience competition for copepods with mysids, they were also able to exploit mysids as prey in the dusk and dawn hours, which partially compensated for the reduced zooplankton availability compared to the pre-mysid era. During spring, when the lowest surplus of zooplankton was available to Kokanee, their diets included large proportions of mysids (66-83%). Significant predation on mysids by Kokanee is rare in most lakes, but is common in Lake Tahoe. The underlying mechanisms enabling kokanee predation on mysids are currently not understood and warrant further investigation.

Resource competition between mysids and pelagic planktivores like Kokanee can be accentuated in large, deep lakes generally due to lower productivity and weaker thermal stratification (Schoen et al. in press; Johnson and Martinez 2012). In Lake Tahoe, prey deficits for mysids were more likely caused by intraspecific competition rather than interspecific competition with Kokanee, which was exacerbated by spatial segregation throughout the year and thermal segregation during the growing season. The spatial distribution of copepods generally created a segregated food supply with higher densities available to planktivorous fishes, but less accessible to mysids. Mysids were never observed higher in the water column than 20 m, and the modal depth was generally 60 m. During all seasons, zooplankton density was highest in 0-25 m depths. This allowed Kokanee to forage on higher densities of copepods than were available to mysids.

The relatively low proportion of zooplankton in the diets of mysids has important implications for potential responses to either mysid reductions or increased zooplankton productivity. Either of these cases would increase the availability of zooplankton to mysids and would increase the per capita zooplankton consumption by mysids. These shifts in the predation response by mysids could significantly dampen any beneficial increases in zooplankton availability for planktivorous fishes.

Collecting more data regarding mysid diets would add more certainty to the mysid consumption estimates and better inform our estimate of the carrying capacity of Lake Tahoe. The most recent data regarding mysid gut analysis was performed in the 1970s, when cladocerans were still commonly encountered but beginning to decline (Rybock 1978). Contemporary data on mysid gut contents would add more certainty to the diet proportions used in the bioenergetics simulations. To identify any potential increase in copepod consumption, stable isotope analysis could be performed on a routine basis and compared with historical values. If future data showed that copepods represented a smaller proportion the diet for mysids, the prey deficits suggested by our simulations would be reduced. Depending on extent of the reduction of the proportion of copepods in mysid diets, it could potentially increase the copepod surplus available to Kokanee.

The health of Kokanee and native minnow populations is of upmost importance to many of the native trout species in western lakes. Piscivorous native Cutthroat Trout and Bull Trout rely on Kokanee and minnows as important prey. Lake Tahoe lost the native Lahontan Cutthroat Trout in the mid-1900s, while native Cutthroat Trout and Bull Trout are struggling to persist in other lakes. The introduction of mysids into western lakes has changed food webs by decreasing or eliminating preferred zooplankton species (Cooper and Goldman 1980; Morgan et al. 1978; Lasenby et al. 1986; Ellis et al. 2011). In rare cases, Kokanee and native fishes eat mysids, while in most other lakes mysids are often inaccessible. Each food web responds differently to the introduction of non-native species (Whall and Lasenby 2009), making it important to understand the interactions in each system.

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TABLES AND FIGURES

Table 1. An outline of the bioenergetics simulations performed for mysids. Inputs to the model include initial and final weights for each age class and season. Model outputs include the proportion of theoretical maximum consumption (% Cmax), total individual consumption over the entire simulation (C), and the growth efficiency (GE). April 1st represents day 1 of the simulations.

Age	Sim Days	Months	TL (mm)	Initial Weight (g)	Final Weight (g)	%Cmax	C	GE
age-0	1-134	Apr-Aug	5.6	0.0006	0.0029	0.21	0.016	14%
age-0	135-164	Aug-Sep	8.5	0.0029	0.0044	0.22	0.007	23%
age-0	165-224	Sep-Nov	9.5	0.0044	0.0044	0.16	0.011	0%
age-0	225-365	Nov-Apr	9.5	0.0044	0.0160	0.25	0.064	18%
age-1	1-134	Apr-Aug	13.5	0.0160	0.0374	0.22	0.096	22%
age-1	135-165	Aug-Sep	17	0.0374	0.0416	0.22	0.029	14%
age-1	165-224	Sep-Nov	17.5	0.0416	0.0416	0.20	0.056	0%

Table 2. An outline of the bioenergetics simulations performed for Kokanee. Inputs to the model include initial and final weights for each age class and season. Model outputs include the proportion of theoretical maximum consumption (%Cmax), total individual consumption over the entire simulation (C), and the growth efficiency (GE). April 1st represents day 1 of the simulations.

Age	Simulation Days	Months	Initial Weight (g)	Final Weight (g)	Growth (g)	%Cmax	C	GE
age-0	1-195	Apr-Oct	0.2	2.6	2.4	0.41	22.6	11%
age-0	195-365	Oct-Mar	2.6	6.2	3.6	0.29	30.8	12%
age-1	1-195	Apr-Oct	6.2	60.1	53.9	0.78	437.1	12%
age-1	195-365	Oct-Mar	60.1	73.0	13.0	0.29	234.7	6%
age-2	1-195	Apr-Oct	73.0	175.5	102.5	0.61	1019.3	10%
age-2	195-365	Oct-Mar	175.5	156.1	-19.4	0.20	310.1	-6%
age-3	1-195	Apr-Oct	156.1	349.4	193.3	0.63	1740.5	11%

Table 3. The average thermal experience for mysids and Kokanee used in the bioenergetics simulations. April 1st represents day 1 of the simulations.

Day of Year	Simulation Day	Mysid Temp °C	Kokanee Temp °C
April 1, 2012	1	5.3	5.3
April 24, 2012	24	5.4	5.9
June 13, 2012	74	5.9	8.6
July 27, 2012	118	7.0	11.7
August 9, 2012	131	6.3	11.1
August 15, 2012	137	6.4	11.7
September 7, 2012	160	6.6	14.3
September 27, 2012	180	7.1	11.9
October 10, 2012	193	7.4	10.4
November 6, 2012	220	8.5	12.2
November 26, 2012	240	7.9	10.0
December 20, 2012	264	7.1	7.3
January 19, 2013	294	5.3	5.3
March 31, 2013	365	5.3	5.3

Table 4. Seasonal age specific mysid diets used as bioenergetics model inputs. Indicates the proportion of the diet that each of three major prey categories represent. April 1st represents day 1 of the simulations.

Simulation Day	Month	Proportion of Diet	
		Algae	Copepods
Age-0			
1	April	1	0
110	July	1	0
130	August	0.7	0.3
365	March	0.7	0.3
Age-1			
1	April	0.7	0.3
45	May	0.2	0.8
105	July	0.2	0.8
365	March	0.7	0.3

Table 5. Seasonal age specific Kokanee diets used as bioenergetics model inputs. Indicates the proportion of the diet that each of the prey categories represent. Diets were obtained through the stomach analysis of angler and trawl caught Kokanee. April 1st represents day 1 of the simulations.

Sim			**Proportion of Diet**						
Day	**Month**	**N**	**Diap.**	**Epi.**	**Clad.**	**Mysid**	**Im. In.**	**Ad. Ins.**	**Unid**
25-100 mm									
1	April	2	0.17	0.17	0	0.66	0	0	0
135	August	3	0.1	0.9	0	0	0	0	0
195	October	7	0.1	0.53	0	0.32	0	0.05	0
365	March	0	0.17	0.17	0	0.66	0	0	0
100-200 mm									
1	April	0	0.12	0.13	0	0.75	0	0	0
135	August	4	0.02	0.98	0	0	0	0	0
195	October	16	0.17	0.5	0	0.27	0	0.06	0
225	November	4	0.1	0.66	0	0.22	0	0.02	0
365	March	0	0.08	0.09	0	0.83	0	0	0
200-300 mm									
1	April	1	0.08	0.09	0	0.83	0	0	0
135	August	29	0.28	0.54	0	0.15	0	0	0.03
195	October	12	0.44	0.07	0	0.49	0	0	0
365	March	0	0.08	0.09	0	0.83	0	0	0
300-400 mm									
1	April	0	0.08	0.09	0	0.83	0	0	0
135	August	20	0.3	0.2	0	0.49	0	0	0.01
195	October	6	0.15	0.07	0	0.49	0.17	0	0.12
365	March	0	0.08	0.09	0	0.83	0	0	0

Table 6. Energy density values for Kokanee (a) and mysid (b) prey obtained from literature values. April 1st represents day 1 of the simulations.

(a) *Mysid Prey*

Simulation Day	Algae	Copepods	Detritus
1	1870	2721	1000
365	1870	2721	1000

(b) *Kokanee Prey*

Simulation Day	Diaptomus	Epischura	Cladoceran	Mysid	Immature Insect	Adult Insect	Unid
1	2260	2260	1900	3474	3400	5000	3000
365	2260	2260	1900	3474	3400	5000	3000

Copepods – Luecke and Brandt (1993)
Cladoceran - Luecke and Brandt (1993)
Mysids - Cummins and Wuycheck (1971), Rudstam (1989)
Immature Insect - Hansen (1997)
Adult Insect – Cummins & Wuycheck (1971)

Table 7. (a) Size specific abundance estimates for different regions and bathymetry zones in the lake from the August 2012 hydroacoustic survey. (b) Kokanee survival rate estimated by through iteratively fitting the value to the age structure in table 7a.

(a) Abundance estimates

	Slope zone			**Pelagic zone**		
Region	**35-100 mm**	**101-400 mm**	**>400 mm**	**35-100 mm**	**101-400 mm**	**>400 mm**
South	28,870	52,001	7,203	109,183	229,639	75,708
Central	13,809	98,572	13,174	127,556	170,882	55,780
North	25,089	35,790	3,566	226,850	142,918	20,511
Total	67,768	186,363	23,943	463,588	543,439	151,999
Kokanee-0	531,356					
Kokanee 1-3	729,802					
Lake trout	175,942					

(b) Iteratively fit survival rate and estimates of the abundance of each age class in August when the hydroacoustic survey was performed (day 123) and back calculated to April 1st (day 1).

	Day 123	**Day 1**
Age	**N(age)**	**N(age)**
0	531,356	614,355
1	345,382	399,331
2	224,498	259,565
3	145,924	168,718
N1-3 =	715,803	827,614
S =	0.65	

Table 8. Results from fitting representative set of linear models to test whether mysid $\delta^{15}N$ levels differed between months and habitat zones after accounting for the effect of mysid total length. The values in bold italics (ΔAIC_c = difference in Aakike's information criterion corrected for small sample size; w_i = Akaike weight) represent the best fitting model (i.e. ΔAIC_c values ≤ 2).

Linear Model	AICc	ΔAICc	wi
δ15N ~ Length + Month + Zone+ (Length x Month) + (Length x Zone) + ε	34.6	7.6	0.02
δ15N ~ Length+ Month+ Zone+ (Length x Zone) + ε	38.9	11.9	0.00
δ15N ~ Length+ Month+ Zone+ (Length x Month) + ε	30.5	3.5	0.14
δ15N ~ Length+ Month+ Zone + ε	35.5	8.5	0.01
δ15N ~ Length+ Zone+ (Length x Zone) + ε	46.2	19.2	0.00
δ15N ~ Length+ Month+ (Length x Month) + ε	**27.0**	**0.0**	**0.78**
δ15N ~ Length+ Zone + ε	43.5	16.5	0.00
δ15N ~ Length+ Month + ε	32.5	5.5	0.05
δ15N ~ Length + ε	41.0	13.9	0.00

Table 9. Season- and age-specific estimates for the biomass (MT) of each Kokanee prey category and Kokanee abundance.

Season	Average Abundance	Simulation Days	Diaptomus Cons. (MT)	Epischura Cons. (MT)	Mysids Cons. (MT)	Insects Cons. (MT)	Total Cons. (MT)
Age-0							
Spring	582,184	1-91	0.5	1.5	1.3	0.0	3.2
Summer	522,598	92-183	0.8	5.8	0.9	0.1	7.6
Autumn	481,557	184-229	0.4	2.0	1.3	0.2	3.9
Winter	432,938	230-365	1.6	3.4	5.7	0.2	10.9
		Year Total	3.2	12.7	9.2	0.5	25.6
Age-1							
Spring	378,420	1-91	3.4	20.1	19.4	0.0	42.9
Summer	339,690	92-183	5.9	75.4	10.6	1.4	93.3
Autumn	313,013	184-229	4.5	17.6	7.6	1.4	31.1
Winter	281,410	230-365	4.6	19.3	26.9	0.5	51.4
		Year Total	18.4	132.5	64.5	3.3	218.7
Age-2							
Spring	245,973	1-91	13.6	22.6	51.8	0.0	89.0
Summer	220,798	92-183	38.1	51.0	34.8	0.0	126.6
Autumn	203,458	184-229	13.3	3.0	15.6	0.0	32.0
Winter	182,916	230-365	10.1	3.5	29.5	0.0	43.1
		Year Total	75.1	80.2	131.7	0.0	290.7
Age-3							
Spring	159,883	1-91	15.9	13.0	70.6	0.0	99.9
Summer	143,519	92-183	35.0	22.8	71.8	5.3	139.6
Autumn	132,248	184-195	3.0	1.5	9.1	2.9	18.6
		Year Total	54.0	37.3	151.5	8.1	258.0
All Ages							
Spring	1,366,459	1-91	33.5	57.2	143.0	0.0	235.0
Summer	1,226,605	92-183	79.8	155.0	118.1	6.7	367.1
Autumn	1,130,276	184-229	21.2	24.1	33.6	4.5	85.5
Winter	897,265	230-365	16.3	26.2	62.1	0.7	105.4
		Year Total	150.7	262.6	356.9	11.9	792.9

Table 10. Season- and age-specific estimates for the biomass (MT) of each mysid prey category and mysid abundance and biomass.

Season	Average Abundance	Average Biom. (MT)	Simulation Days	Algae Cons. (MT)	Copepod Cons. (MT)	Total Cons. (MT)
Age-0						
Spring	7.2E+10	94	1-91	669.4	0.0	669.4
Summer	4.8E+10	154	92-183	617.1	164.6	781.6
Autumn	3.5E+10	156	184-229	212.7	91.2	303.9
Winter	2.4E+10	240	230-365	987.3	423.1	1410.4
			Year Total	2486.5	678.8	3165.4
Age-1						
Spring	1.3E+10	276	1-91	236.9	497.1	734.1
Summer	8.4E+09	315	92-183	184.4	519.4	703.8
Autumn	6.1E+09	259	184-229	93.6	145.4	239.0
			Year Total	515.0	1162.0	1676.9
All Ages						
Spring	8.5E+10	370	1-91	906.3	497.1	1403.5
Summer	5.6E+10	469	92-183	801.5	684.0	1485.5
Autumn	4.1E+10	418	184-229	306.3	236.6	542.9
Winter	2.4E+10	240	230-365	987.3	423.1	1410.4
			Year Total	3001.5	1840.8	4842.3

Table 11. Seasonal comparisons of total copepod supply (MT) and demand (MT) by mysids and Kokanee at each depth stratum. The Kokanee Surplus is the surplus biomass of copepods (MT) at depths accessible to Kokanee after both mysid and Kokanee demand have been removed from the available biomass. The Mysid Surplus is the biomass of copepods (MT) at depths accessible to mysids after mysid demand has been removed from the copepod biomass available to the mysids.

Season	Depth Strata (m)	Copepod Supply	Accessible to Kokanee	Accessible to Mysids	Kokanee Demand	Mysid Demand	Kokanee Surplus	Mysid Surplus
Days 1-91								
Spring	0-10	34	34	-				
Spring	10-25	150	150	-				
Spring	25-100	358	358	358				
		Total	543	358	162	497	22	-139
Days 92-183								
Summer	0-10	42	42	-				
Summer	10-25	226	226	-				
Summer	25-100	430	430	430				
		Total	698	430	164	684	104	-254
Days 184-229								
Fall	0-10	141	155	-				
Fall	10-25	249	313	-				
Fall	25-100	312	352	352				
		Total	821	352	45	237	539	70
Days 230-365								
Winter	0-10	186	186	-				
Winter	10-25	232	232	-				
Winter	25-100	236	236	236				
		Total	654	236	43	423	375	-187

Table 12. Seasonal comparisons of total copepod availability (MT) across all depths (0-100 m) and total demand (MT) by mysids and Kokanee. The Copepod Surplus column shows Copepod Total – Total Demand.

Season	Simulation Days	Copepod Biomass	Mysid Demand	Kokanee Demand	Total Demand	Copepod Surplus
All Ages						
Spring	1-122	543	497	162	659	- 116
Summer	123-183	698	684	164	848	- 150
Autumn	184-229	702	237	45	282	420
Winter	230-365	654	423	43	466	189
	Year Total	2,596	1,841	413	2,254	342

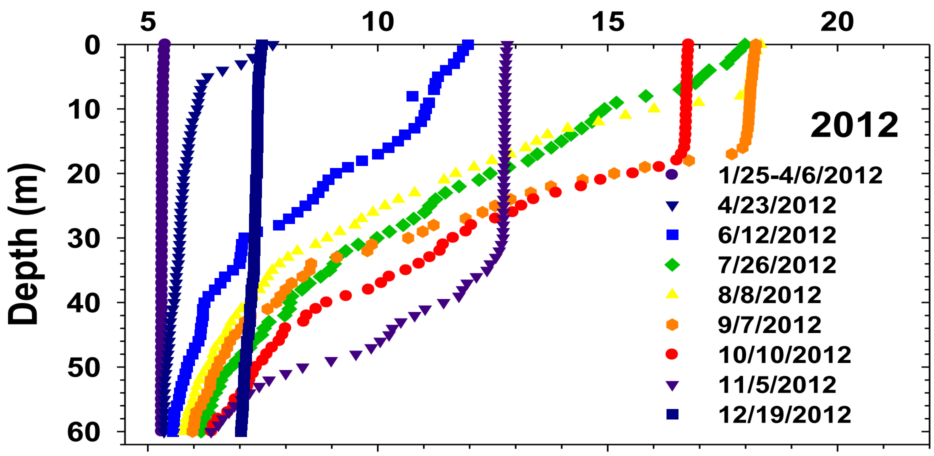

Figure 1. Monthly vertical temperature profiles from the UC Davis limnological long term profile site off Tahoe City for 2004, 2005, and 2012.

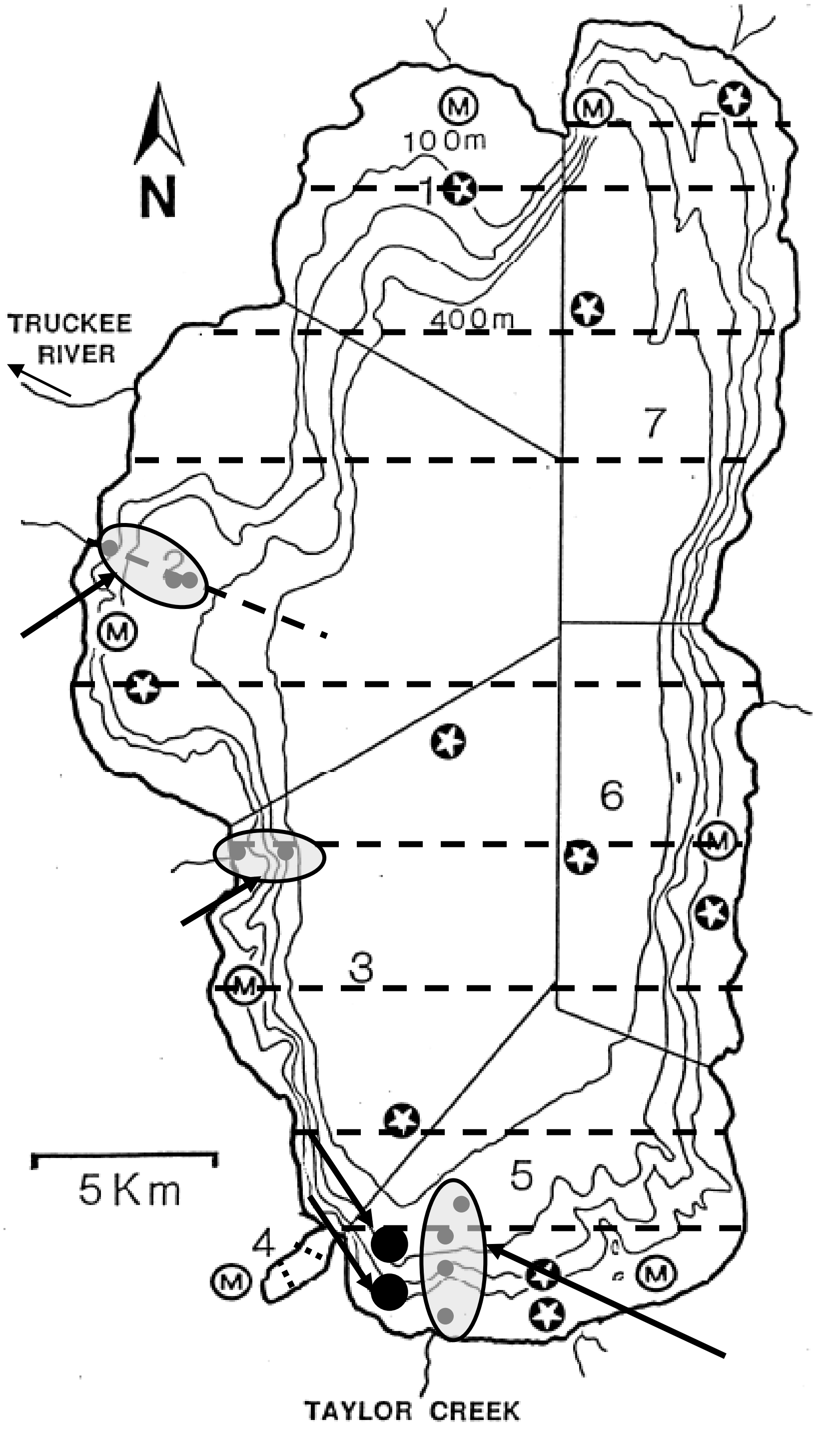

Figure 2. Sampling locations used in Lake Tahoe during 2012-2013. Nearshore, mid-shelf and offshore zooplankton sites and associated offshore limnology stations were located in the vicinity of the mouths for Taylor, Meeks, and Blackwood Creeks. Black filled circles (with or without stars) indicate sites for night vertical mysid tows. Dashed red lines represent hydroacoustic transects.

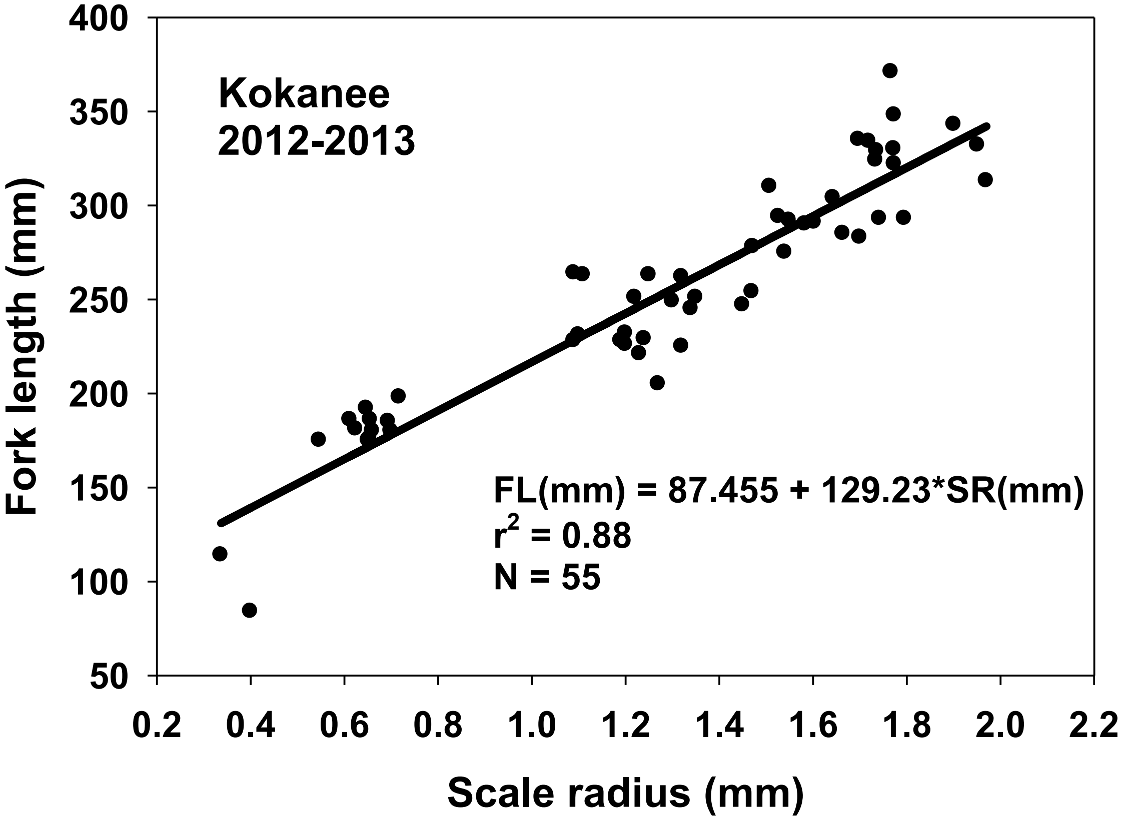

Figure 3. The regression relationship between scale radius and fork length for Kokanee sampled in Lake Tahoe during 2012-2013. Fish undergoing pre-spawning morphological changes were excluded from this analysis.

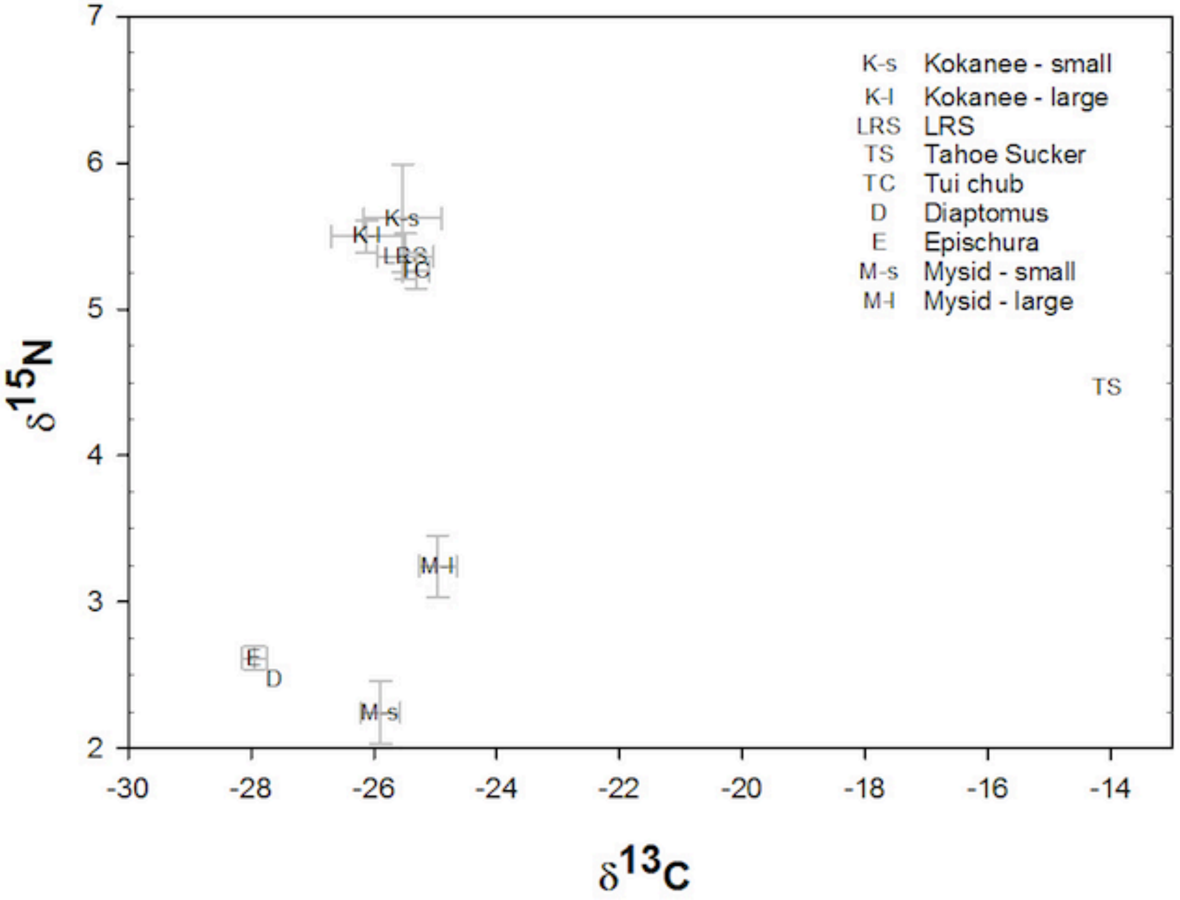

Figure 4. Average isotopic signatures of the Lake Tahoe pelagic food web. Error bars represent 2 SE in each direction. The δ^{15}N values represent the trophic level of the species. The δ^{13}C values represent the reliance on pelagic (smaller values) and benthic (larger values) energy pathways. Small Kokanee ≤ 100 mm, large Kokanee > 100mm. Small mysids ≤ 12mm, and large mysids > 12 mm.

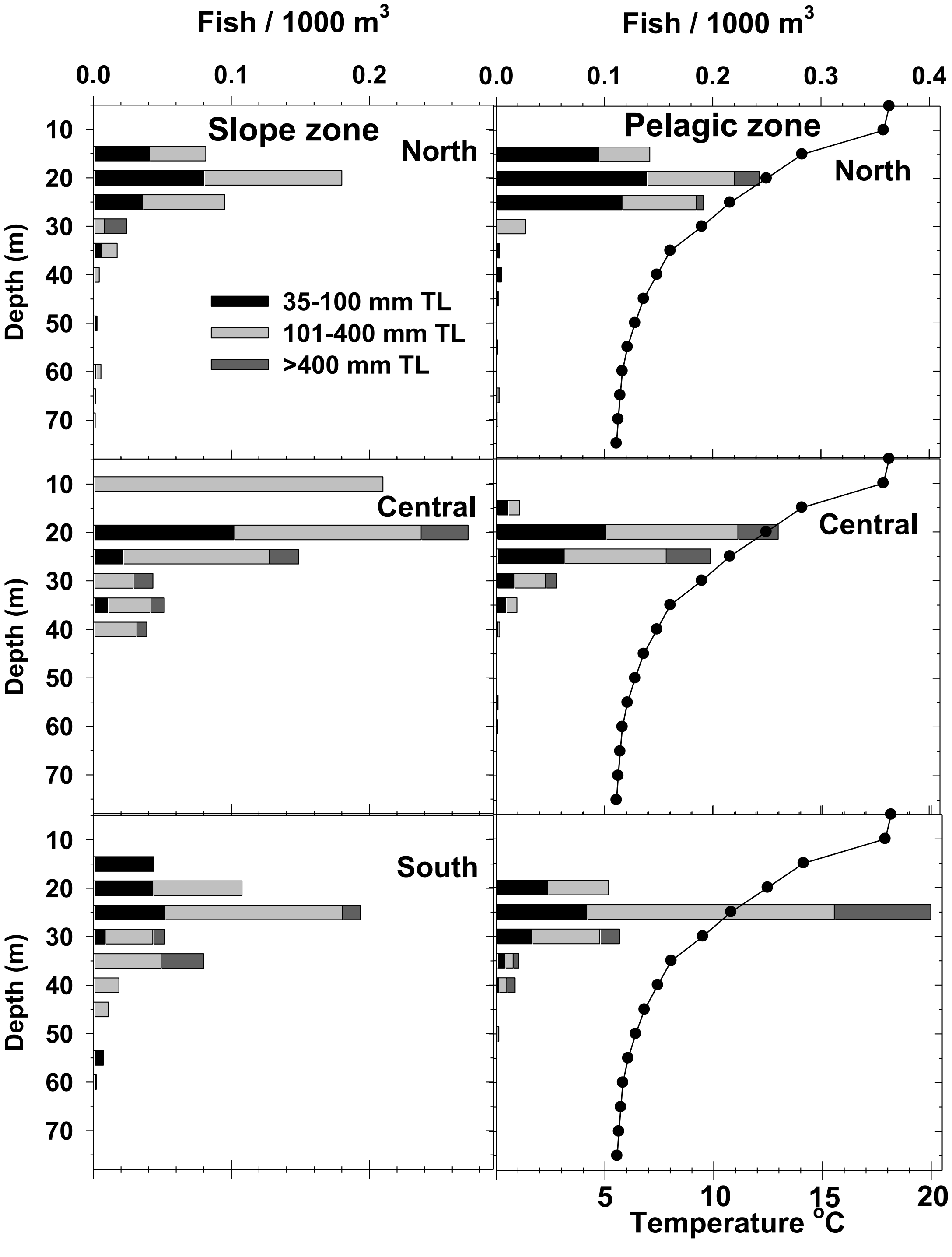

Figure 5. Density of different size classes of fish by depth in slope (left panels) and pelagic (right panels) habitats during night hydroacoustic surveys in Lake Tahoe August 2012.

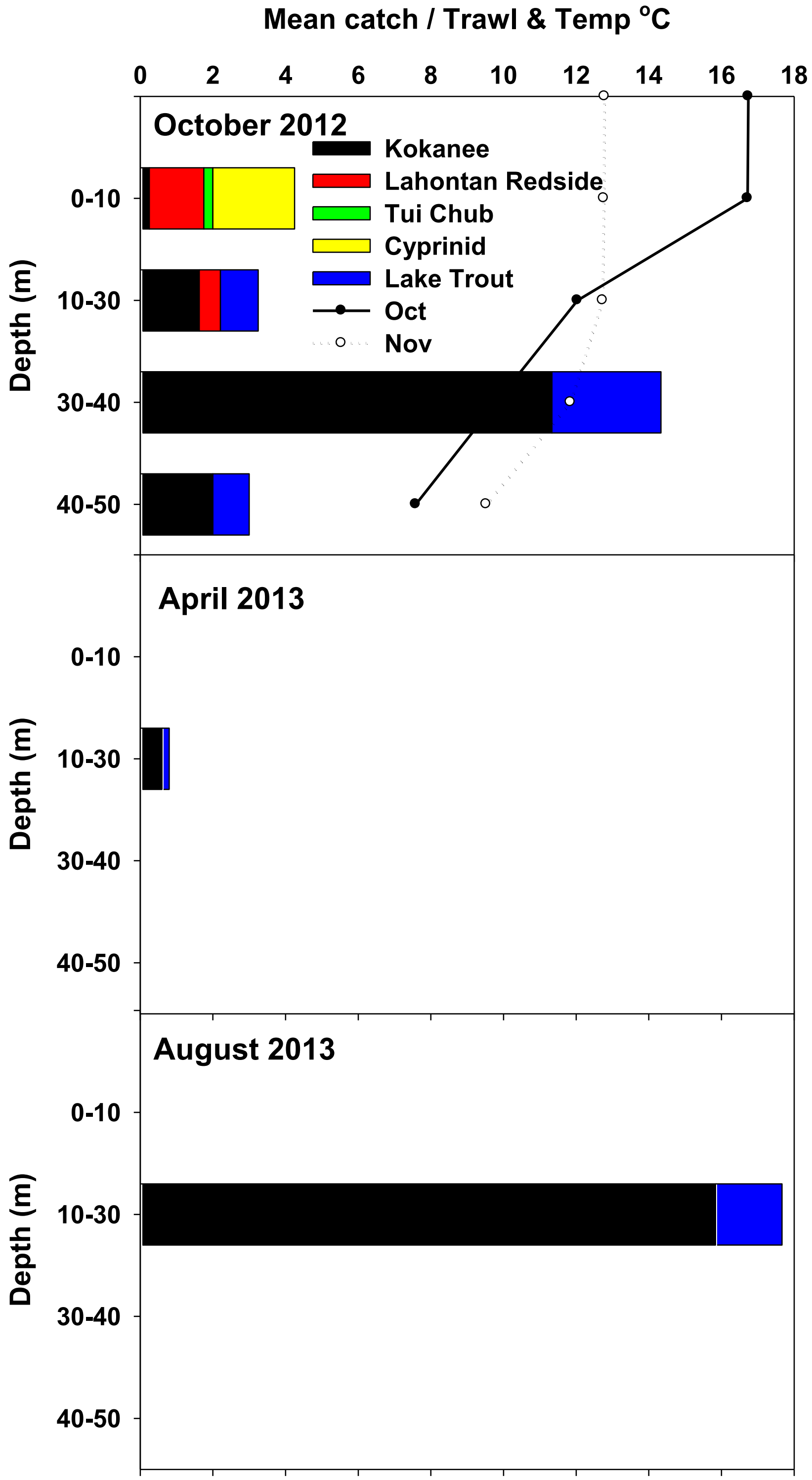

Figure 6. Mean catch per tow by nocturnal midwater trawling in Lake Tahoe during October 2012, April and August 2013. The vertical temperature profiles for mid-October and early November span the period when midwater trawling was conducted.

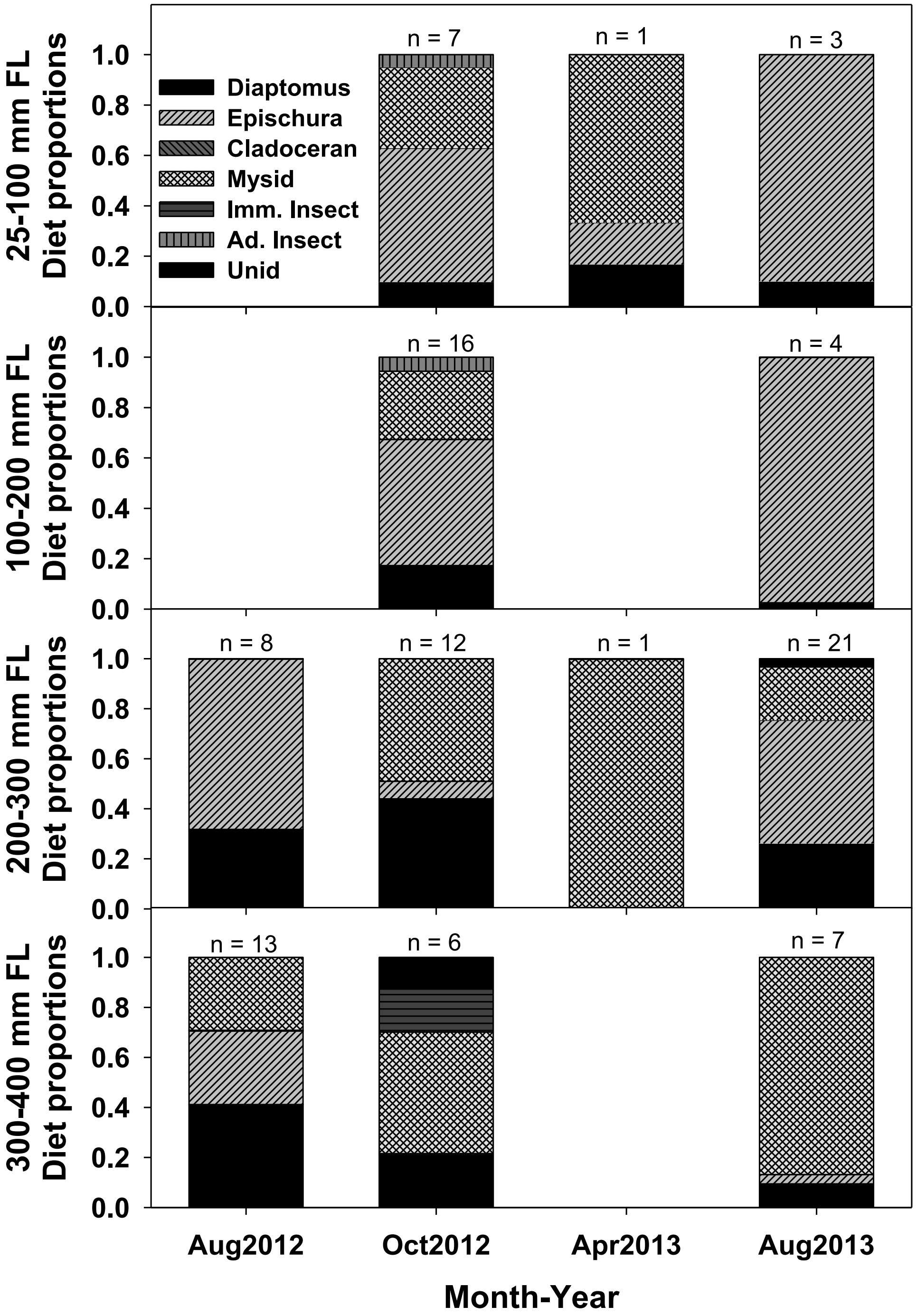

Figure 7. Proportional diet contribution of major prey categories by wet weight for different size classes of Kokanee by sampling period in Lake Tahoe during 2012-2013.

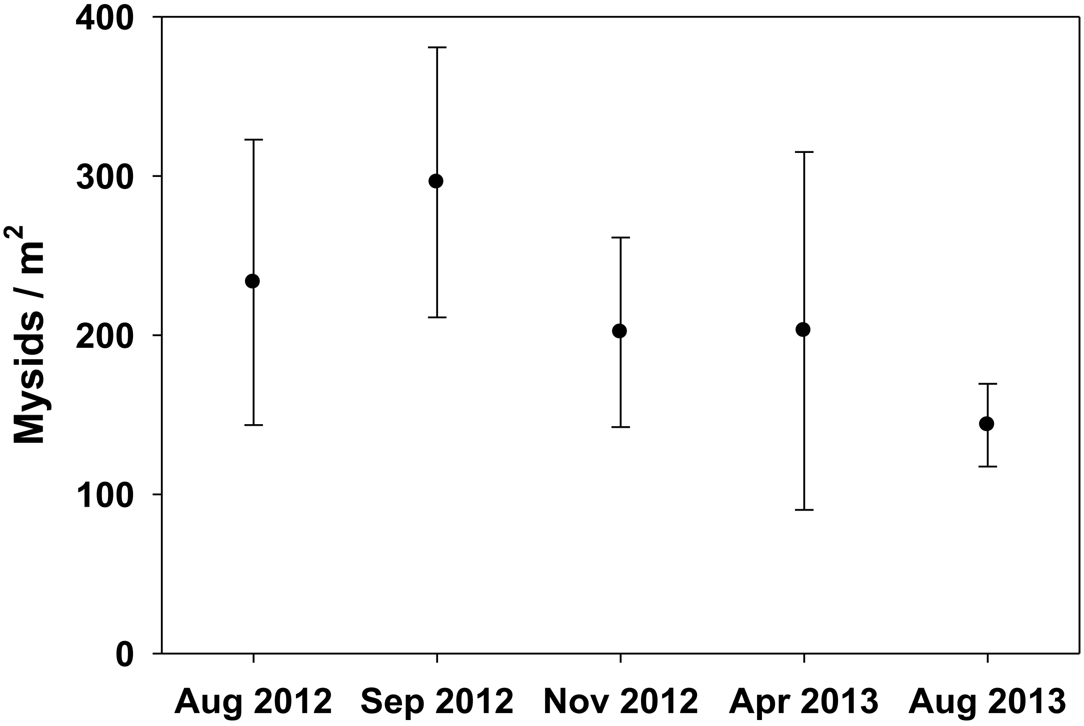

Figure 8. The average density of mysids, pooled across all bottom depth strata among sampling months, based on nocturnal vertical tows with a 1-m diameter mysid net. Error bars represent ±2SE.

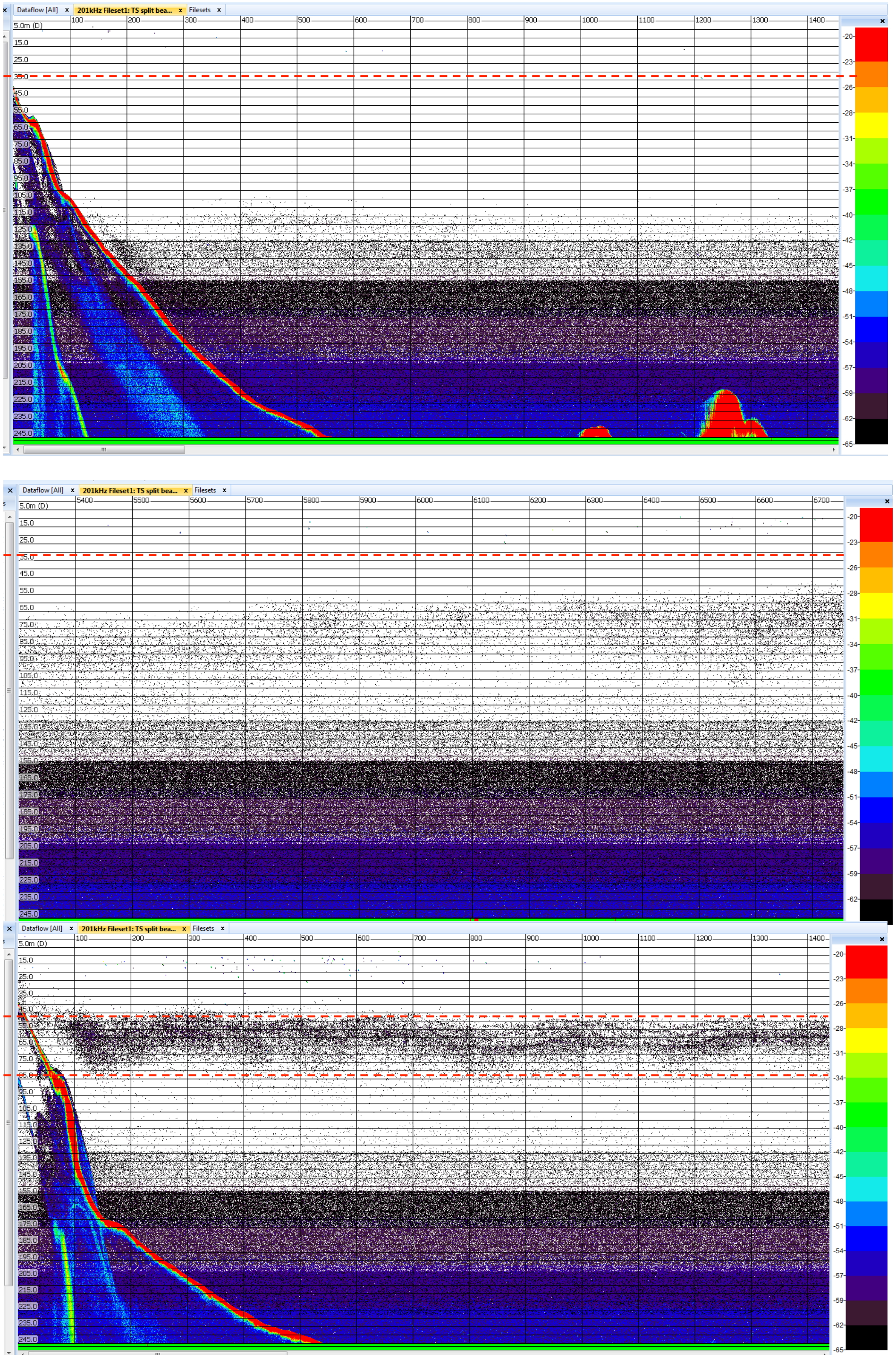

Figure 9. Echograms of a day-dusk-night sequence of mysid distribution through the water column in Lake Tahoe during August 2012. During daylight, mysids are deeper than the 125-m detection depth of the 200-kHz echosounder during this survey. Targets ascend in a diffuse cloud during dusk, then concentrate in a high-density band in 40-85 m at night.

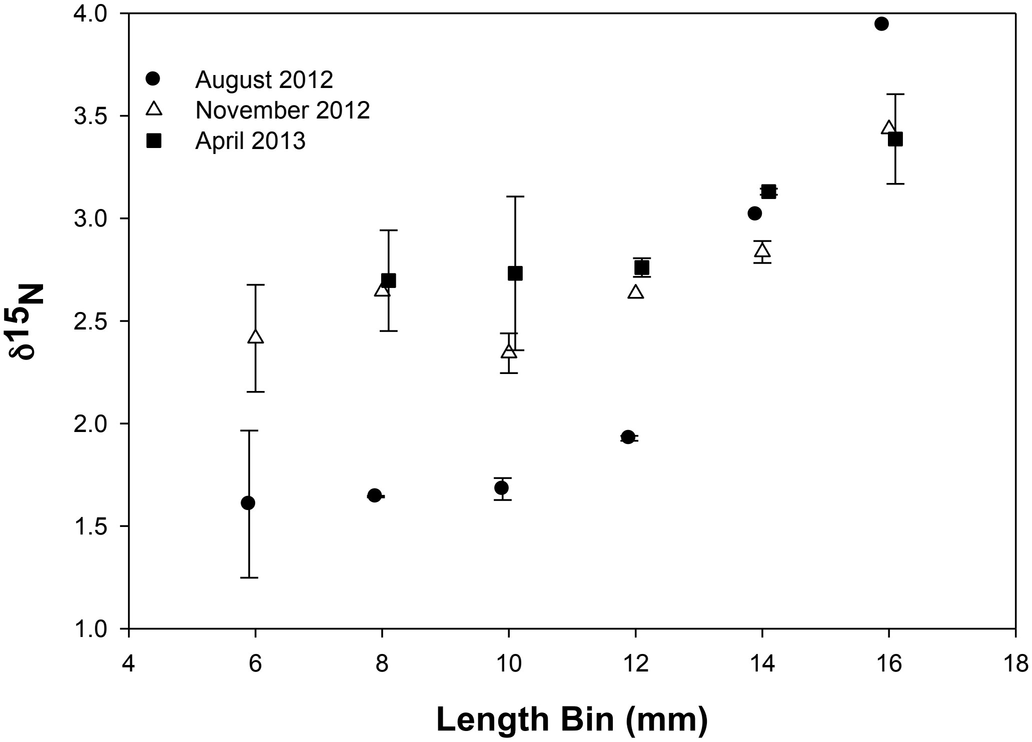

Figure 10. Seasonal $\delta^{15}N$ values for varying mysid total lengths. Error bars represent ±2 SE.

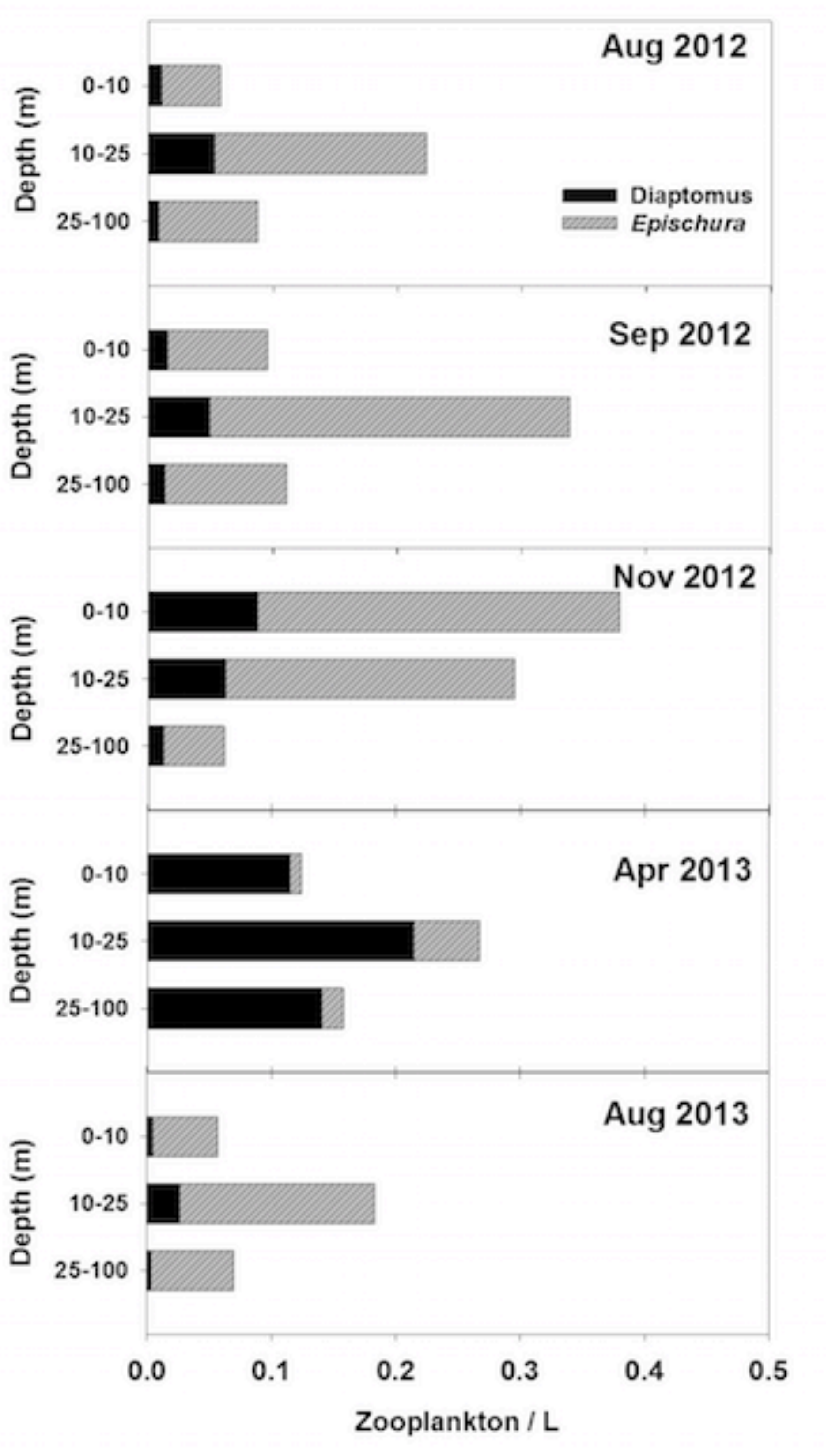

Figure 11. Monthly depth-stratified densities of the major crustacean zooplankton taxa in Lake Tahoe during seasonal sampling in 2012-2013.

APPENDIX

Table A1. Seasonal, depth-stratified, lake-wide estimates for copepod biomass and production. Monthly production estimates are shown for months during growing season.

Season	Depth (m)	Biomass (MT)	Prod. (MT)	Total (MT)
Days 1-91				
Spring	**0-10**	**33.9**	**22.2**	**56.2**
Spring	**10-25**	**150.2**	**88.3**	**238.5**
Spring	**25-100**	**358.4**	**148.6**	**507.1**
	Total	**542.6**	**259.2**	**801.8**
May	0-10	32.9	9.7	42.7
May	10-25	147.3	37.7	185.0
May	25-100	348.5	72.3	420.8
June	0-10	32.1	12.5	44.6
June	10-25	158.4	50.6	209.0
June	25-100	350.8	76.4	427.2
Days 92-183				
Summer	**0-10**	**41.7**	**100.8**	**142.5**
Summer	**10-25**	**225.7**	**377.2**	**602.9**
Summer	**25-100**	**430.1**	**329.3**	**759.4**
	Total	**697.5**	**807.3**	**1504.8**
July	0-10	34.3	25.1	59.4
July	10-25	178.2	84.8	263.0
July	25-100	382.8	102.0	484.8
August	0-10	40.3	33.1	73.4
August	10-25	215.3	98.9	314.2
August	25-100	444.3	106.0	550.3
September	0-10	50.5	42.6	93.1
September	10-25	283.6	193.5	477.1
September	25-100	463.2	121.2	584.5
Days 184-229				
Fall	**0-10**	**141.1**	**14.2**	**155.3**
Fall	**10-25**	**249.0**	**64.5**	**313.4**
Fall	**25-100**	**311.9**	**40.4**	**352.4**
	Total	**702.0**	**119.1**	**821.1**
October	0-10	141.1	14.2	155.3
October	10-25	249.0	64.5	313.4
October	25-100	311.9	40.4	352.4
Days 230-365				
Winter	**0-10**	**186.4**	**0.0**	**186.4**
Winter	**10-25**	**231.6**	**0.0**	**231.6**
Winter	**25-100**	**236.3**	**0.0**	**236.3**
	Total	**654.3**	**0.0**	**654.3**

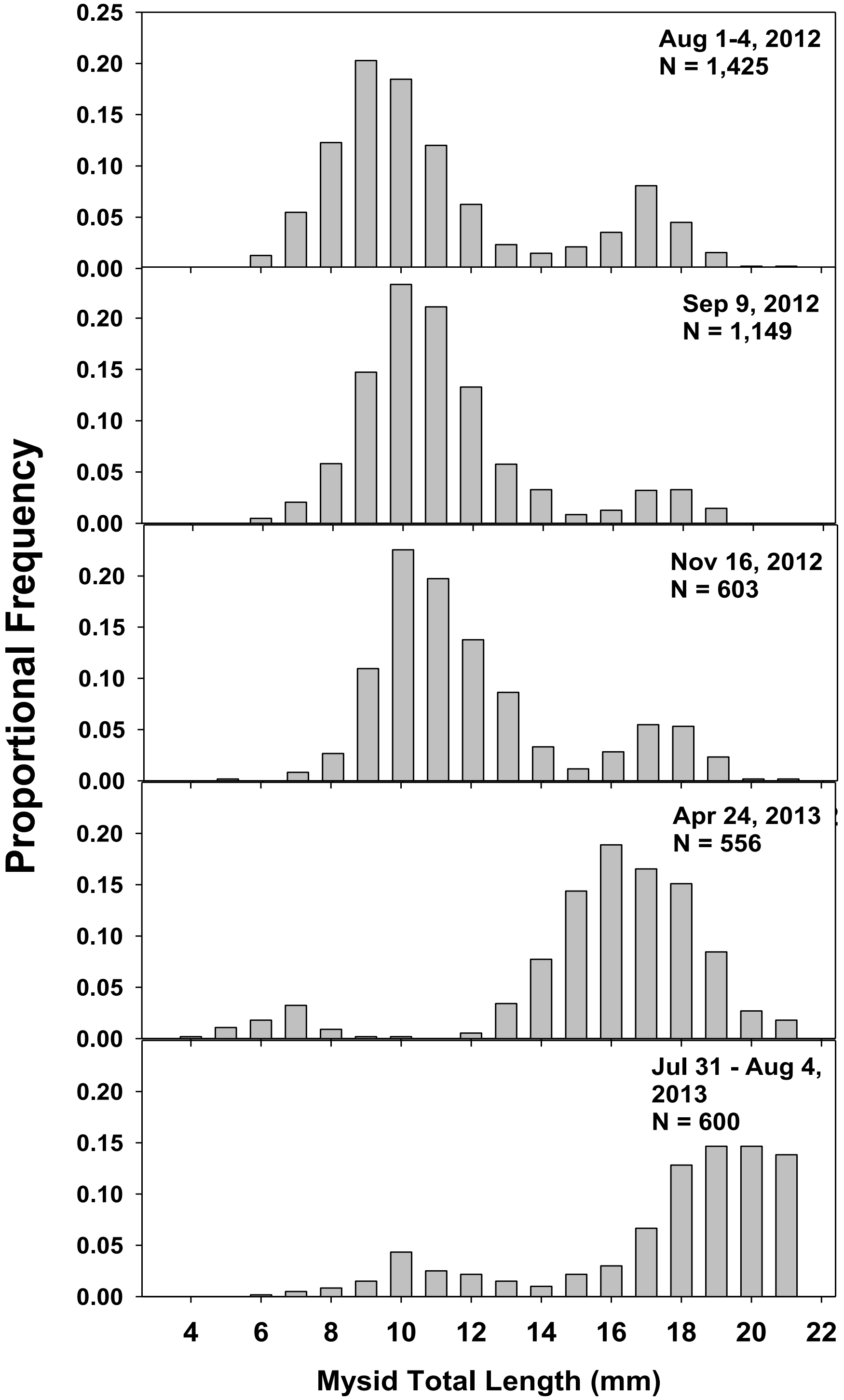

Figure A1. Seasonal length frequencies of mysids in Lake Tahoe sampled during 2012-2013.

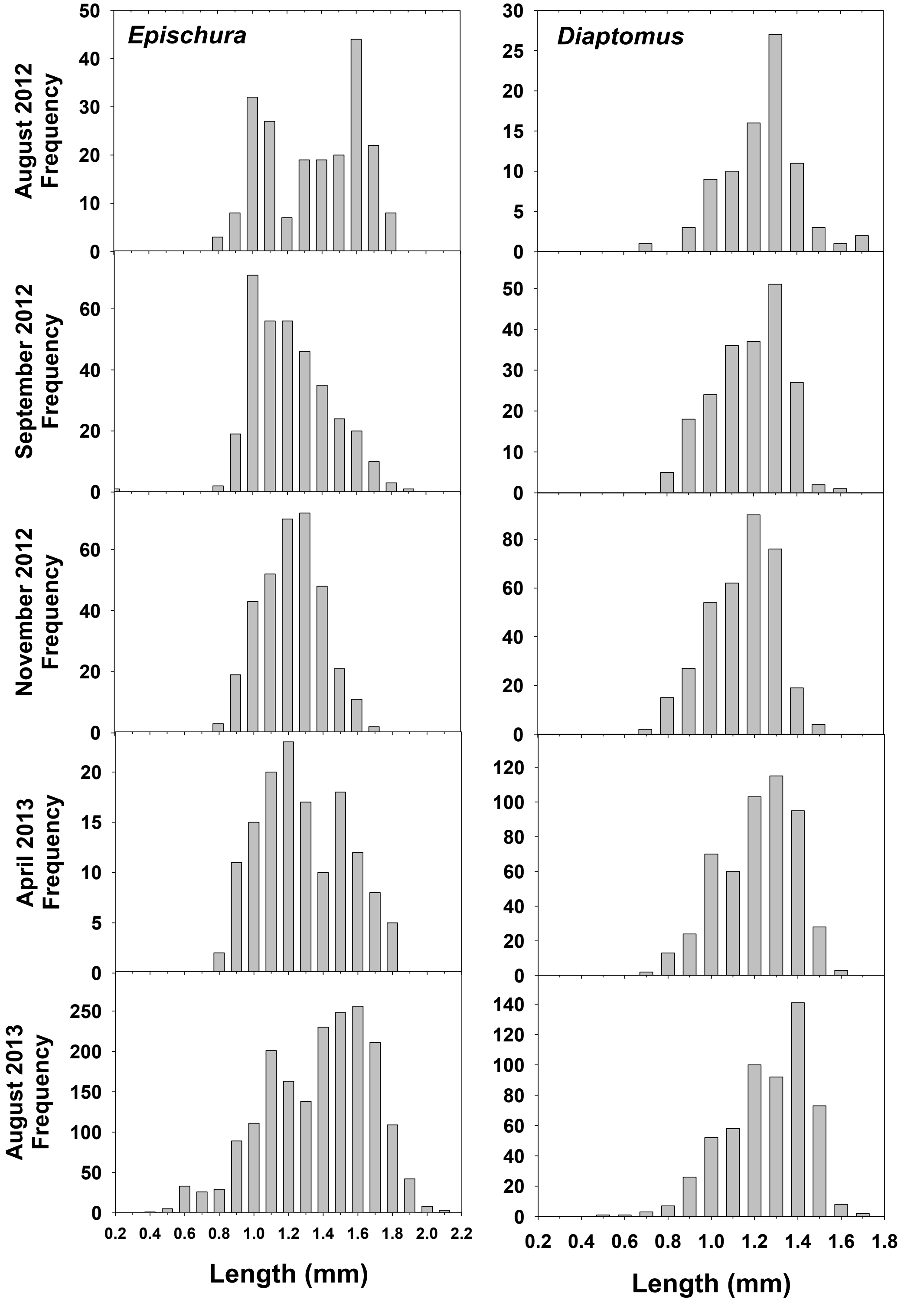

Figure A2. Seasonal length frequencies for adult *Epischura* (Left) and *Diaptomus* (Right).

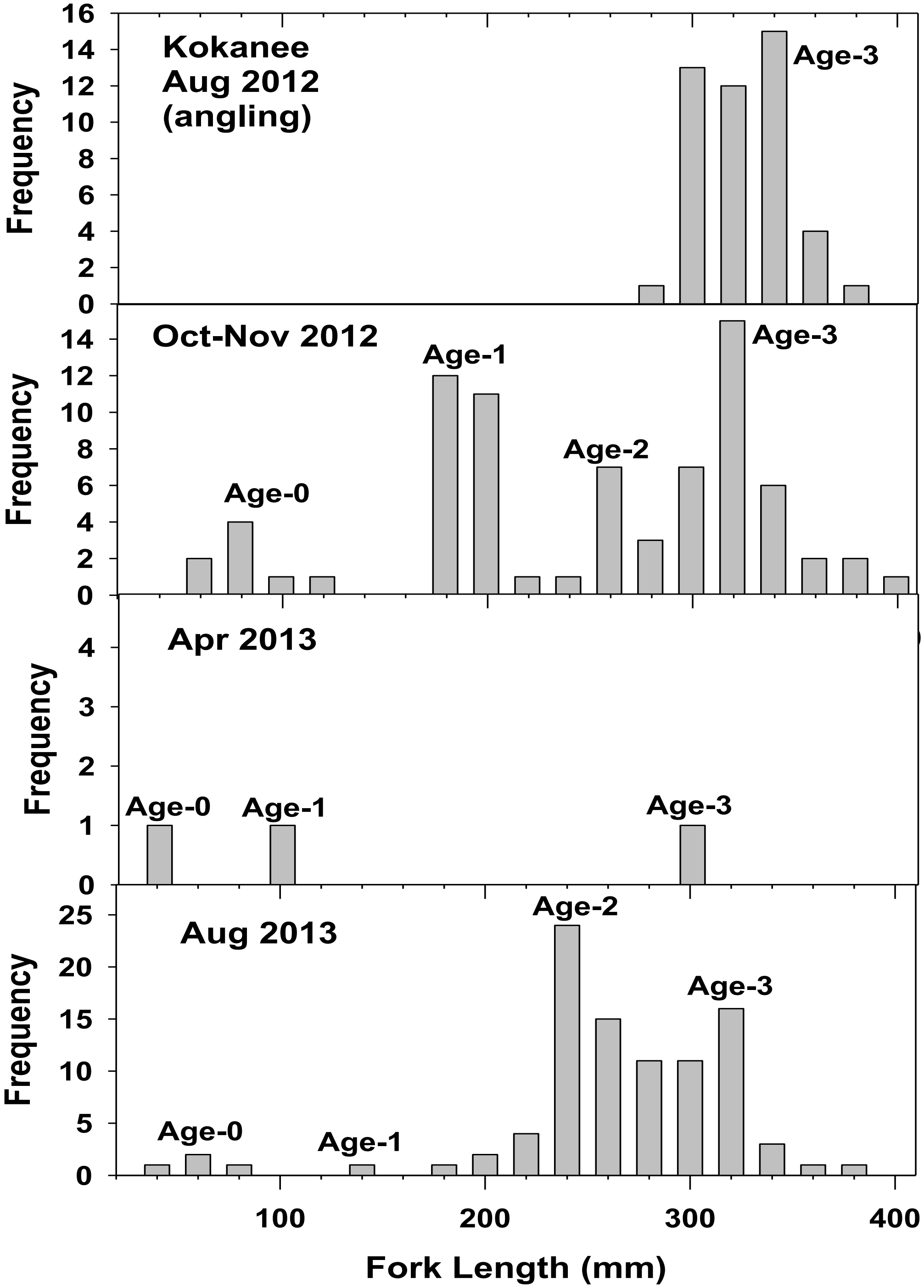

Figure A3. Length frequency histograms indicating the relative size differences among age classes of Kokanee sampled by angling (only adults vulnerable) in August 2012 compared to midwater trawls (all ages vulnerable during October-November 2012 and April and August 2013). Note that the bars are centered over the maximum value for each 20-mm size bin.

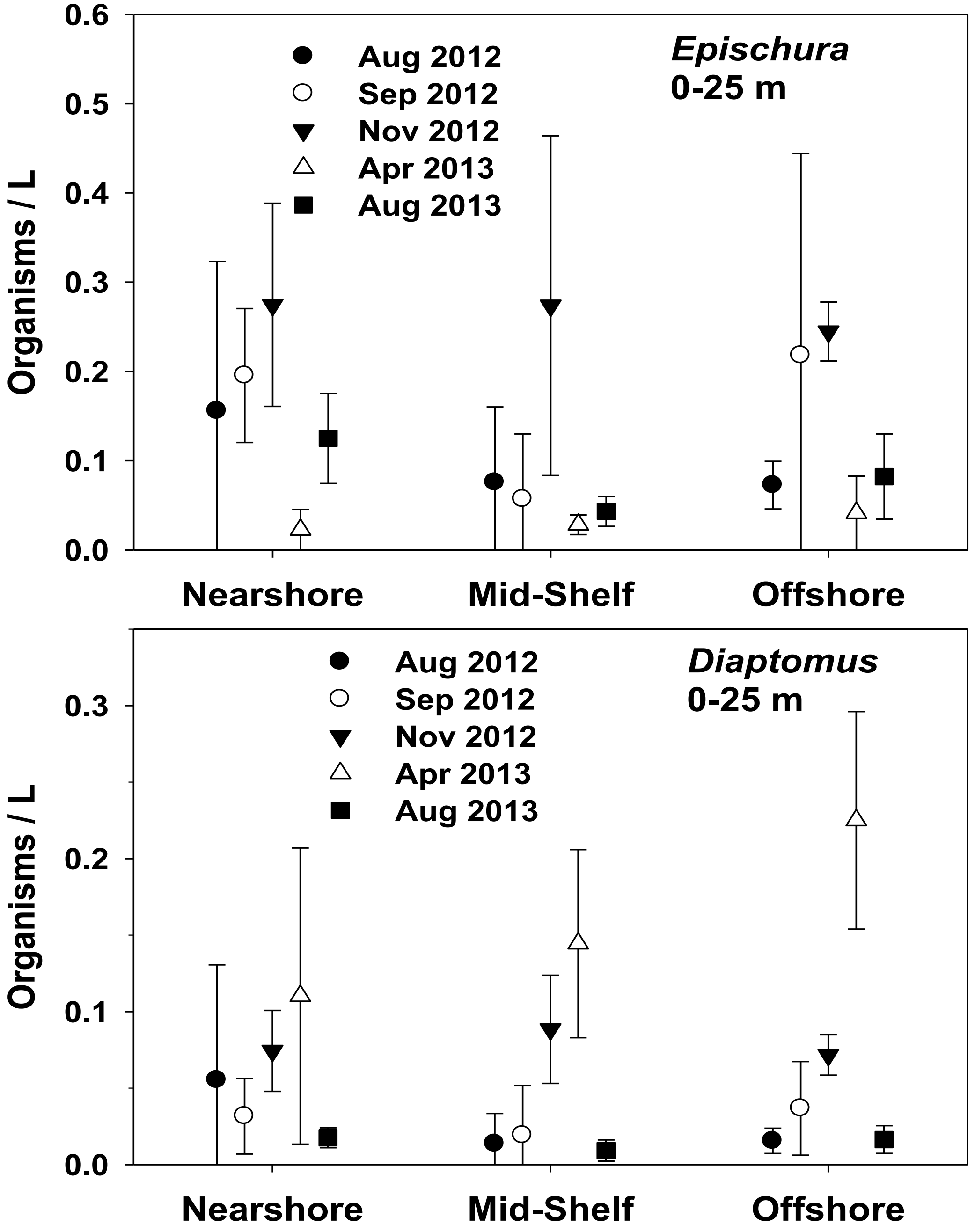

Figure A4. Seasonal densities of the major zooplankton species *Epischura* (Top panel) and *Diaptomus* (Bottom panel) pooled over 0-25 m (Within and above thermocline) in relation to nearshore, mid-shelf, and offshore habitats. The error bars represent 2 SE.

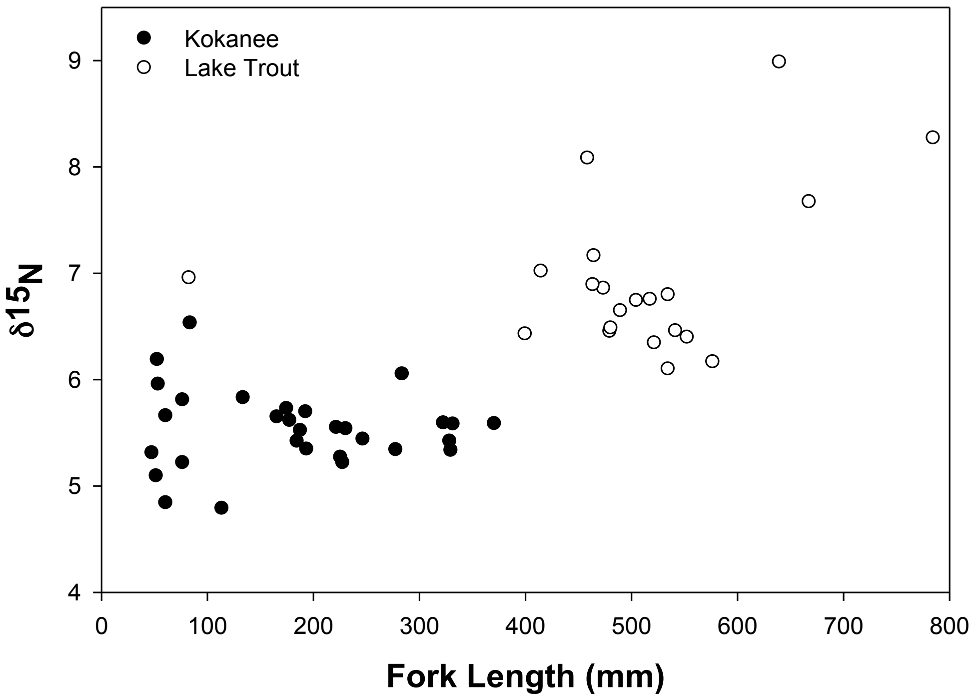

Figure A5. $\delta^{15}N$ values for different sizes of Kokanee and Lake Trout pooled across all seasons. Increasing $\delta^{15}N$ values represent an increase in trophic status.

Chapter Two:

Predator and Prey Interactions Between Lake Trout *Salvelinus namaycush* and Kokanee *Oncorhynchus nerka* and *Mysis diluviana* in Lake Tahoe

ABSTRACT

The non-native Lake Trout *Salvelinus namaycush* was introduced in Lake Tahoe in 1889 and became the top bentho-pelagic predator in the system. Field data on abundance, seasonal distribution, diet, and age/size structure of Lake Trout from a previous study during 1992-1995 were combined with contemporary data to simulate the current predation demand on Kokanee *Oncorhynchus nerka, Mysis diluviana* and other pelagic prey fishes. Stable isotope analysis of representative species in the contemporary bentho-pelagic food web supported the assumption that trophic positions and diet of Lake Trout were similar between the 1990s and present. Using bioenergetics simulations, we compared consumption demand by Lake Trout to the estimated age-structured biomass of Kokanee to evaluate the potential for piscivory to regulate the Kokanee population. Lake Trout undergo an ontogenetic dietary shift wherein fish feed predominantly on mysids when fork length (FL) ≤ 500 mm, become increasingly piscivorous over 501-625 mm, and are primarily piscivorous at FL >625 mm with fish prey representing 80% of the diet. Kokanee represented 2%-7% of the annual prey biomass consumed by Lake Trout >501 mm FL. For Lake Trout ≥ 250 mm FL, Kokanee represented only 2% (13 MT) of the total annual biomass consumed, whereas mysids represented 58% (351 MT). Assuming a similar abundance and size structure as in the 1990s, bioenergetics simulations indicated that the Lake Trout population would have consumed an estimated 15% (range 8-22%) of the biomass of the Kokanee population in 2012. More importantly, Lake Trout targeted predation on pre-spawning adult Kokanee through the summer and fall with the Lake Trout > 625 mm consuming 24% of the adult Kokanee biomass. In Lake Tahoe, Lake Trout can potentially regulate the Kokanee

population, while also self-regulating their own population via cannibalism. Predation on Kokanee by Lake Trout in Lake Tahoe is relatively low compared to other western lakes. Although heavy, Lake Trout predation does not limit the mysid population; mysid production (growth) throughout the year is sufficient enough to absorb the mortality sustained from Lake Trout predation. Understanding the factors that allow the co-existence of these two species in Lake Tahoe, particularly in conjunction with mysids, will be beneficial to managing these species in other systems.

INTRODUCTION

Lake Trout *Salvelinus namaycush* are large-bodied apex predators in coldwater lake food webs of North America, providing valuable recreational, commercial and subsistence fisheries throughout their native range (Sellers et al. 1998). Their popularity as a trophy-sized sport fish motivated their introduction into lakes outside of their native range. In the United States, introduced Lake Trout have successfully established self-supporting populations in 10 states outside of their natural range (Crossman 1995). When Lake Trout are established in a lake, they typically assume the role of apex predator (Martinez et al. 2009; Ellis et al. 2011), and reduce the amount of prey available for the native predators (Donald and Alger 1993). They also prey on juvenile or smaller individuals of native predators (Ruzycki et al. 2001, 2003; Ellis et al. 2011). In Yellowstone Lake, fish prey (mostly native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*) represented 95% of the diet of larger Lake Trout aged ≥ 9 years (Ruzycki et al. 2003). Native adfluvial Cutthroat Trout and Bull Trout *Salvelinus confluentus* have been particularly impacted by introductions and expansions of Lake Trout populations in western lakes.

Lake Trout predation on the native species can vary within and across lakes depending on biological and physical factors. In lakes where mysids *Mysis diluviana* have also been introduced, juvenile Lake Trout are heavily subsidized by this non-native bentho-pelagic prey while growing to piscivorous size (Beauchamp et al. 2007; Ellis et al. 2011). Lake depth and thermal regime play a role in structuring spatial overlap between Lake Trout and prey species. In Lake Chelan, apparent competition between mysids and Kokanee *O. nerka* was stronger in shallower lake basins where Lake Trout could feed more effectively on mysids along the bottom (Schoen et al. in press). In Flathead Lake, predation by Lake Trout caused the Kokanee population to collapse (Ellis et al. 2011). Subsequent efforts to restore a hatchery-supported Kokanee population were abandoned after managers discovered that Lake Trout consumed an estimated 87% of the stocked yearling Kokanee within the first year after release (Beauchamp et al. 1996). It is important to understand how predation by non-native Lake Trout influences the dynamics of prey populations in each system, as the impacts can vary depending on unique factors within each lake.

Lake Trout were introduced into Lake Tahoe in 1889 and established a self-sustaining population (Miller & Alcorn 1945). Like many western lakes, the species composition of Lake Tahoe has changed over time including the extirpation of the Lahontan Cutthroat Trout *O.c. henshawi*. In 1938, biologists recorded the last spawning run of Lake Tahoe's Lahontan Cutthroat Trout in the Truckee River; the primary causes of this local extinction were presumably overharvest and degradation of stream spawning and nursery habitat from logging (Gerstung 1988). Lake Trout assumed the top trophic position in the lake at some point before or after the demise of Lahontan Cutthroat Trout (Vander Zanden et al. 2003), and now support an economically valuable recreational fishery. Whether Lake Trout played a role in the collapse of the Lahontan Cutthroat Trout population is unknown. Kokanee were originally stocked in Lake Tahoe in 1949 (Cordone et al. 1971), and mysids were introduced in 1963 (Linn & Frantz 1965, Frantz & Cordone 1970). With non-native species dominating multiple trophic levels, the food web processes in Lake Tahoe have been heavily altered (Vander Zanden et al. 2003). Despite extensive attention to the physical limnology and lower trophic levels in Lake Tahoe, much less is known about interactions at higher trophic levels of the pelagic food web.

The goal of this study was to examine the hypothesis that predation by non-native Lake Trout was capable of regulating key pelagic species in the pelagic community of Lake Tahoe. Our objectives were to: 1) estimate size-structured consumption demand by Lake Trout on Kokanee, bentho-pelagic mysids, and other major prey species; and 2) determine if predation by Lake Trout represented a significant source of mortality for Kokanee and mysids. The results of this study can be used to inform decisions to maintain the delicate balance between the bentho-pelagic predator and prey populations in Lake Tahoe.

STUDY AREA

Lake Tahoe is a large (mean depth: 313 m, area: 500 km^2) ultra-oligotrophic subalpine lake in the Sierra Nevada Mountains of California and Nevada. The water column is normally isothermal December through May; the thermocline becomes established by July with peak stratification by the end of August (UC Davis Tahoe Environmental Center 2014). The top of the thermocline initially starts at 6 m deep, but deepens to 15 m by September. Temperatures ≥ 18^{o}C, considered stressful to some salmonids in waters with low- or moderately-productive food supplies (Beauchamp 2009), were encountered from the surface down to 10-15 m during August-September; temperatures declined rapidly from the top of the thermocline to approximately 10^{o}C at about 30 m deep during summer (**Figure 1**).

The current pelagic food web is composed primarily of: calanoid copepods *Diaptomus tyrelli* and *Epischura nevadensis*, mysids, Kokanee, and Lake Trout. Lahontan Redside *Richardsonius egregious*, and the pelagic form of Tui Chub *Gila bicolor pectinifer* also utilize the pelagic zone but are relatively rare in comparison to Kokanee.

METHODS

We combined past and contemporary field data with bioenergetics model simulations to estimate the seasonal and size-structured consumption demand by Lake Trout for Kokanee, native minnows, mysids, and other prey. We compared the annual consumption demand by Lake Trout to the contemporary biomass of Kokanee and mysids to determine the potential extent of annual predation mortality imposed by Lake Trout on the populations of these key species in the pelagic food web.

Field Data Collection

Because directed sampling for Lake Trout was prohibited, we used field data for abundance, age/size structure, and seasonal distribution and diet of Lake Trout reported from a previous study in Lake Tahoe during 1992-1995 (Beauchamp et al. 1995; Thiede 1997). We assumed that the current diet proportions, abundance, and thermal experience for Lake Trout were similar to historical conditions, but tested the assumptions related to diet (i.e., using stable isotope and minimal diet data from contemporary samples) and thermal experience (using depth distribution and thermal profiles). We acknowledge that large differences between historical and current conditions could alter the results of this study; however, no changes in the key factors used in this analysis were evident between study periods.

Lake Trout were collected seasonally from July 1992 through March 1995 using sinking horizontal gill nets with eight panels of 38, 50, 63, 75, 90, 100, 115, and 130 mm stretched-mesh, stratified by depth and region. These data were compared to and supplemented with contemporary diet and stable isotope data from 14 Lake Trout sampled incidentally during 2012-2013 to determine suitability for representing current conditions, then used as inputs for a bioenergetics model to calculate seasonal, size-specific consumption demand by Lake Trout. The size-structured biomass of the Kokanee population was calculated from survey data collected in 2012 and 2013.

We surveyed 10 parallel transects spanning the width of the main body of the lake and two transects spanning the width of Emerald Bay (**Figure 2**) using a BioSonics DT-X Digital Scientific Echosounder with a split-beam 200kHz transducer to collect hydroacoustic data on abundance and distribution. The mid-summer nocturnal sampling provides the best opportunity to estimate Kokanee abundance, because the vertical distribution of all age classes are conducive to assessment during stratified conditions before adults form prespawning aggregations in late summer or early fall (Beauchamp et al. 2009). Additional hydroacoustic surveys were performed during September and November of 2012, and April and August of 2013 to characterize the vertical and horizontal distribution of pelagic fishes and mysids.

Mid-water trawling provided the seasonal, depth-specific composition of pelagic fish species for the hydroacoustic abundance estimates and provided biological samples for diet, growth and stable isotope analysis for pelagic fishes and mysids. Depth-stratified mid-water trawls were conducted by a chartered commercial fishing vessel (hull length approximately 10 m) during October and November of 2012, and April and August of 2013 concurrent with hydroacoustic surveys. The midwater trawl was 8 m high by 15 m wide, with a cod-end mesh size of 9.5 mm to retain juvenile fish and native minnows while allowing most mysids to pass through the mesh. Mid-water trawl samples were supplemented with adult Kokanee caught by trolling from commercial charter boats during August 2012. Fish were measured while fresh and then frozen onboard for further processing for diet analysis, aging and stable isotope analysis in the lab. All vertebrate handling was conducted under the auspices of the University of Washington IACUC protocol 3286-21.

Lake Trout Bioenergetics Simulations

Consumption demand and feeding rates for Lake Trout were calculated through bioenergetics modeling using the Wisconsin Bioenergetics 3.0 modeling software (Hansen et al.

1997). The model is an energy balance equation where the energy consumed (C) must equal the combined costs of metabolism (M), waste (W) and growth (G):

$$C = M + W + G$$

The model used the species-specific equations and parameters of Stewart et al. (1983) for mass- and temperature-dependent functions for maximum consumption (Cmax), and metabolism, and consumption-dependent functions for egestion, excretion, and specific dynamic action. The bioenergetics model estimates the amount of consumption required to fit the growth observed over a specific simulation period. Annual growth, represented by the initial and final body mass for each age class was used to solve for consumption and feeding rate (% Cmax) while accounting for variability in diet composition and thermal experience of the predators. This seasonal and size-specific per capita growth and consumption was scaled to the population level by using size-structured abundance data (Beauchamp et al. 2007). The simulation year for each age class began on April 1st and continued for 365 days until March 31st.

Size & Growth

For the bioenergetics simulations in this study, we used size-at-age estimates for Lake Trout from Thiede (1997) from ages based on scales and opercles (**Table 1**). Lengths were recorded to analyze seasonal length frequency and growth. The age of the Lake Trout was determined through opercle analysis, but could not be estimated with confidence beyond age-9 due to increased variability; however, Lake Trout > age-9 represented only 8% of population (Beauchamp et al. 1995). For Lake Trout ≥ 501 mm FL, the simulations included an 8.3% loss of body weight on 15 October to account for spawning.

Diet Composition, Stable Isotope Analysis, and Energy Density

The diet proportions used as inputs into the bioenergetics simulations were seasonal, size-specific prey proportions averaged across all years of Thiede's (1997) study (**Table 2**). The focal prey categories for this study were mysids, Kokanee and Lake Trout. Other prey species included Paiute Sculpin *Cottus beldingi*, Tahoe Sucker *Catastomus tahoensis*, Mountain Whitefish *Prosopium williamsoni*, Rainbow Trout *O. mykiss gairdneri*, Lahontan Redsides, Speckled Dace *Rhinichthys osculus robustus*, and Tui Chub. Stable isotope data from the Lake Trout collected in 2012 and 2013 allowed an interpretation of contemporary diets, which were compared with historical data.

The historical diet data was compared to the contemporary stable isotope data to determine whether it was representative of contemporary diets. The stable isotope data indicated that the ontogenetic shift towards maximum piscivory remained around 625 mm FL and that Lake Trout ≤ 625 mm FL still relied heavily on mysids (**Figure 3**). The low number of diet samples for Lake Trout from 2012-2013 were qualitatively similar to the historical diet data in terms of the high reliance on mysids by smaller and intermediate sizes of Lake Trout, and increasing piscivory by larger Lake Trout (**Table 2b**). The reliance on mysids by smaller Lake Trout and the ontogenetic shift to piscivory in the historical diets was maintained in both the contemporary diets and stable isotope analysis, and supported the use of historical data to represent contemporary diets. However, unlike the historical data, the contemporary data for Lake Trout ≥ 625 mm FL during summer 2013 indicated consumption of Kokanee. For this size class and season only, the historical data and the contemporary data were averaged, weighted by the sample sizes of each period, and these new averaged diet proportions were used in the simulations (**Table 2b**). When the historical diet data were collected in 1992-1995, Kokanee spawning populations ranged from 17,000-75,000 (Beauchamp et al. 1994; Gemperle 1998), whereas our hydroacoustic survey in August 2012 estimated 146,000 pre-spawning adult

Kokanee. Lake Trout would likely have eaten more Kokanee in 2012 when pre-spawners were 2-8 times more abundant than in 1992-1995.

The contemporary stable isotope data was also compared to stable isotope data collected for the same species between 1998-2000 (**Figure A2**) (Vander Zanden et al. 2003). The comparison shows that both the $\delta^{15}N$ and $\delta^{13}C$ values for large Lake Trout (>580 mm) collected in 1998-2000 and 2012/2013 were not significantly different. For small Lake Trout (≤ 580 mm) the $\delta^{15}N$ values were not significantly different, whereas the $\delta^{13}C$ values were significantly different by less than 2 $\delta^{13}C$ units. This comparison also suggested that the 1992-1995 diet composition of Lake Trout was a reasonable surrogate for the contemporary diet composition.

The energy density of each prey type was obtained from literature values (**Table 3**). The energy density of Lake Trout was based on a weight dependent calculation (Stewart et al. 1983), daily values were linearly interpolated from initial and final energy densities used as inputs for each simulation.

Thermal Experience

The Lake Trout thermal experience was the average of the three years in the historical study (Thiede 1997) (**Table 4**). Depth-weighted monthly average thermal experience was computed by combining depth-specific catch per unit effort (CPUE) with the concurrent vertical temperature profile of the lake (Beauchamp et al. 2007). Using the August 2013 hydroacoustic depth distribution of targets > 401 mm and the thermal profile from 2012, we estimated Lake Trout thermal experience for the month of August during 2012-2013 was 9.9 °C, which compares well to the 1992-1995 average of 9.7 °C for the month of August.

Abundance

Using the population abundance and survival rates estimated by Beauchamp et al. (1995) based on the Petersen mark-recapture method and the Chapman (1951) small sample bias correction (**Table 5**), there were estimated to be 145,380 +/- 64,925 Lake Trout during 1992-1995. Recapture data for tagged Lake Trout was obtained from Lake Trout captured in gill nets and from the logbooks of trusted charter fishery operators. Lake Trout did not fully recruit to the gill nets or charter fishery until they reached 475 mm in length. However, the smaller size classes were incorporated into the abundance estimate through the use of length frequency distributions and size at age relationships developed from scale- and opercle-based aging of the Lake Trout.

Abundance, Size Structure and Seasonal Biomass of Prey Populations

Abundance estimates for Kokanee were calculated from nocturnal hydroacoustic surveys in August 2012. Echo-counting procedures were used to estimate depth- and size-specific density of targets, which was then expanded by the volume of water within each depth interval (Beauchamp et al. 1997, 2009). The age-structured abundance for the Kokanee population was estimated as described in Chapter 1 of this thesis.

The biomass of an individual Kokanee from each age-class was estimated using mean fork lengths at each age obtained from seasonal length frequencies and scale back-calculations (Chapter 1), and then converted to body mass with a length-weight regression (Chapter 1). The Kokanee population biomass was estimated using the average biomass of an individual of each age-class, multiplied by the abundance of the corresponding age-class, then summed across all ages. The biomass of Kokanee in August was used to represent the entire year. The seasonal average biomass of mysids was calculated using the average lake-wide mysid density, the length frequency distribution, and the average weight at each age for mysids collected in 2012-2013 (Chapter 1). The impacts of Lake Trout predation on the Kokanee and mysid populations were calculated in terms of the biomass of each species consumed by Lake Trout as a proportion of the biomass of each species in the lake.

RESULTS

Lake Trout Consumption Demand and Prey Supply

Assuming the abundance of Lake Trout FL > 250 mm was 145,380, bioenergetics estimate of total annual consumption was 13 MT (95% confidence interval: 7–19 MT) of Kokanee and 387 MT +/- 173 MT of mysids. Lake Trout fed between 46-82% (mean of 62%) of their maximum feeding rate (**Table 1**). For all size classes < 625 mm, mysids represented the largest portion of Lake Trout consumption, followed by fish (**Figure 4**). For Lake Trout ≥ 625 mm, fish represented the largest portion of consumption; mysids were second but only represented 8%. Kokanee biomass represented 1% of the annual consumption of 501-625 mm Lake Trout, while all prey fish combined represented 25% of annual consumption. For Lake Trout ≥ 625 mm, Kokanee represented 7% of annual consumption, while all fish contributed 80%. Lake Trout ≥ 501 mm FL were cannibalistic, with smaller Lake Trout contributing 2% of total annual consumption for Lake Trout 501-625 mm FL and 35% for Lake Trout > 625 mm FL. Given the mean size of conspecifics found in Lake Trout diets during the 1992-1995 study (158 g.; Thiede 1998), the Lake Trout population >250 mm could have consumed 360,000 juvenile Lake Trout < 350 mm. Benthic prey sources (Paiute Sculpin, Tahoe Sucker and crayfish) were consumed by all size classes, except that Paiute Sculpin were not eaten by Lake Trout > 625 mm.

Predation by Lake Trout represented significant levels of mortality for Kokanee, Mysids, and smaller Lake Trout. Lake Trout consumed an average 15% (8-22% based on error bounds around predator abundance) of the estimated annual mean biomass of 86 MT for the Kokanee population in 2012. However, most of this predation was directed at adult Kokanee during summer and fall, and likely focused on pre-spawning aggregations that formed below the thermocline in the vicinity of Taylor Creek (Beauchamp et al. 1994). The weight of age-3 (spawning age) Kokanee, averaged across the summer and fall when most were consumed, was 301 g; therefore, Lake Trout ≥ 625 mm could have removed 36,545 prespawning adults

(301 g), which represented 24% of the estimated age-3 Kokanee population in 2012. Lake Trout > 250 mm FL consumed 351 MT of mysids annually, representing 70% of the estimated 510 MT of annual lakewide production of mysids during 2012-2013.

DISCUSSION

As top predators in Lake Tahoe, non-native Lake Trout impose significant mortality on Kokanee and mysids, the major planktivores in the pelagic food web, but also potentially regulate their own population through cannibalism. Based on the biomass of Kokanee consumed versus the average annual biomass of Kokanee in the lake, Lake Trout appeared to exert a moderate amount of mortality. However, because most of this predation appeared to target prespawning adult Kokanee Lake Trout could have removed a quarter of the spawning population in late summer and fall before they could reproduce.

The highly variable abundance of Kokanee spawners over time could impact the proportion of Kokanee in Lake Trout diets as well as the extent of the predation mortality exerted on Kokanee by Lake Trout. During 1991-1995, the annual abundance of spawning Kokanee in Taylor Creek was highly variable: 3,237 in 1991, 16,733 in 1992, 73,968 in 1993, 57,548 in 1994, and 33,868 in 1995 (Beauchamp 1995, Gemperle 1998). In the summer of 2012 we estimated 146,000 age-3 adult Kokanee, which would presumably spawn that fall. The 2012 adult Kokanee estimate is two-times higher than the highest spawner count during the historical study (1992-995). With higher adult Kokanee densities, Lake Trout could have incorporated more Kokanee into their diets in 2012 than in 1992-1995. The abundance of the adult spawning population is also important to determine the extent of the predation mortality exerted on the Kokanee population by Lake Trout. Predation on Kokanee was highest in the summer and fall, and the Kokanee found in Lake Trout stomachs were mostly adults. The summer season lasts through September, so it is possible that heavy predation could have occurred in late summer as spawners were aggregating (e.g., at the mouth of Taylor Creek). Lake Trout in Lake Tahoe exhibit high fidelity within the seven specific regions of the lake across all seasons (Beauchamp et al. 1995); therefore, Lake Trout from northern or central regions of the lake were unlikely to interact with prespawning aggregations of Kokanee near Taylor Creek in the southwest corner of the basin. This would imply that not all of the biomass consumed in the summer and fall could have been pre-spawning adult Kokanee. Historically, 1,600-2,000 beach spawning Kokanee were reported in other areas of Lake Tahoe during the 1960s (Cordone et al. 1971), but the primary spawning grounds are in Taylor Creek. So predators from central and northern regions conceivably exploited some of the smaller prespawning aggregations or simply ate adult Kokanee prior to forming these aggregations in late summer. Targeted predation on adult Kokanee exerted moderate mortality on Kokanee, but could vary in other years depending on the abundance of Kokanee spawners.

Lake Trout consumed a large proportion of the annual average biomass of mysids (65%); despite heavy predation mysid densities remained high. The additional biomass from the production of the existing population was more than enough to absorb the mysids consumed by Lake Trout > 250 mm. This does not include any additional biomass from the production of new broods each year, which if included, would reduce the effects of Lake Trout predation. The large amount of predation exerted on mysids by Lake Trout did not impose a significant impact on the mysid population likely because the robust production balanced out the predation loss.

Mysids were introduced to Lake Tahoe with the intent of supplementing Lake Trout diets to improve growth (Frantz and Cordone 1970). An analysis of Lake Trout otoliths from Flathead Lake (Montana) did not show increased growth rate after mysid invasion (Stafford et al. 2002), but the rapid increase in the Lake Trout population within the following 10 years suggested a significant increase in survival for juvenile Lake Trout (Ellis et al. 2011). In Lake Tahoe, trophy sized (> 640 mm) Lake Trout declined after mysids became established in 1973, while the abundance of Lake Trout remained high (Richards et al. 1991). A similar pattern of increased catch rates of smaller Lake Trout after the introduction of mysids has also been documented in Priest Lake, Idaho (Bowles et al. 1991). The mysids in Lake Tahoe provide a large energy subsidy for young Lake Trout, potentially helping them avoid a prey bottleneck as the juveniles grow larger and consume more (Ellis et al. 2011). Mysids represent the largest prey category for all Lake Trout < 625 mm. Lake Trout with slower growth rates require more consumption over time to attain the same lengths as Lake Trout with higher growth rates, leading to the loss of more prey fish through predation. Mysids indirectly compete with Kokanee and other prey fish by providing the Lake Trout population an abundant prey resource that increases Lake Trout survival and consumption of prey fish, also known as apparent competition (Ellis et al. 2011, Schoen et al in press).

Survival of juvenile Lake Trout was likely increased due to mysid subsidies but there was a considerable amount of cannibalism on juvenile Lake Trout by conspecifics ≥ 625 mm. We did not assess the balance between these two sources of survival and mortality, but our modeling indicated that cannibalism accounted for 35% of the annual consumption by Lake Trout ≥ 625 mm. Lake Trout cannibalized four times more biomass of smaller conspecifics than of Kokanee. This high proportion of cannibalism could be due to lack of overlap with other prey fishes and the high density of juvenile Lake Trout. It is possible that cannibalism could be mediating the potential predation impacts on Kokanee and other prey fishes.

The conclusions drawn from model simulations are potentially vulnerable to errors in input variables. There is an obvious temporal discrepancy between when the Lake Trout diet, thermal experience and abundance data was collected and the time period that consumption and the impacts on the prey population were simulated; however several analyses validated the use of the historical data to represent contemporary conditions. We justified this use of historical data based on reasonable similarities between stable isotope and limited diet data from contemporary Lake Trout samples compared to the historic diet data and earlier stable isotope analyses. We acknowledge that significant discrepancies in such variables could alter the amount of prey that Lake Trout consumed and therefore the impact on the prey populations, but such discrepancies were not indicated by our analyses. Because targeted capture of Lake Trout was not permitted during the 2012-2013 study, we used detailed diet and growth data from a Lake Trout study performed in 1992-1995 to determine Lake Trout consumption then compared these consumption estimates to contemporary estimates of Kokanee and mysid prey during

2012 and 2013. Support for the critical assumptions used in the simulations and analysis could be evaluated by comparisons of additional data. A qualitative report on the changes in average size, catch depths and catch rates of Lake Trout since 1992 from charter operators that participated in the 1992-1995 study would give updated information on size, distribution and abundance. Using the small sample size of Lake Trout we were able to obtain in 2012/2013, scale analysis could be performed to compare contemporary growth and size at age to the historical data we used. The complete historical Lake Trout thermal experience could be compared to the contemporary thermal experience using the depth distribution of large fish targets from the 2012-2013 hydroacoustic surveys, the depth distribution from 2012-2013 mid-water trawl catches and the 2012 thermal profile. This information could add more certainty to our assumption or guide us in potentially altering any of the historical variables.

Data from this study can be used as a baseline to predict how interactions among Lake Trout, Kokanee and mysids would change in response to significant changes in abundance, distribution, or behavior of any of the three species. The Lake Trout population could respond to increases in Kokanee or other pelagic planktivores in different ways. Increased Kokanee abundance would increase per capita consumption of Kokanee by large Lake Trout. High levels of cannibalism could indicate low density of other prey fishes, and could decline if Kokanee abundance increased. We do not know if the high rates of cannibalism are linked directly to low prey densities or possibly a lack of overlap with other prey fishes. If availability of prey fishes increased, Lake Trout could become more piscivorous and potentially reach their historical trophy-sized lengths.

The interactions in Lake Tahoe’s pelagic food web have changed considerably since Lake Trout were first introduced in 1889. As other species were introduced, extirpated or reduced, the food web continued to change. This study provides a look at the impact of Lake Trout predation on the key species in the pelagic food web, Kokanee and mysids. This data can be used to support and inform management decisions and used to evaluate how the pelagic food web interactions may change if the abundance of any of the key species changes.

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TABLES AND FIGURES

Table 1. Inputs to the bioenergetics model simulations for Lake Trout include initial and final weights for each age class and season. Model outputs include the proportion of theoretical maximum consumption (% Cmax), total individual consumption over the entire simulation (C), and the growth efficiency (GE). April 1st represents day 1 of the simulations.

Age	Simulation Days	Size-class (mm)	Months	Initial Wt. (g)	Final Wt. (g)	Initial ED (j/g)	Growth (g)	%Cmax	C	GE
2	1-90	250-375	Apr-June	209	285	6,345	76	0.82	438	17%
2	91-365	250-375	July-March	285	486	6,579	201	0.60	1616	12%
3	1-365	250-375	Apr-March	486	888	7,198	402	0.66	3334	12%
4	1-365	376-500	Apr-March	888	1304	8,437	416	0.64	4439	9%
5	1-365	376-500	Apr-March	1304	1460	9,718	156	0.51	4205	4%
6	1-183	376-500	Apr-Sep	1460	1518	10,199	58	0.46	2130	3%
6	184-365	376-500	Oct-March	1518	1726	10,378	208	0.69	2845	7%
7	1-365	501-625	Apr-March	1726	2585	10,436	859	0.71	7893	11%
8	1-365	501-625	Apr-March	2585	2767	11,105	182	0.52	6751	3%
9+	1-365	>625	Apr-March	2767	3950	11,246	1183	0.58	8832	13%

Table 2. (a) Seasonal age-specific Lake Trout diets used as bioenergetics model inputs. The sample sizes and diet proportions of each prey category averaged across all three years of Thiede's study (1997), except for the ≥ 625 mm size class for summer which was averaged with contemporary data, are indicated. April 1st represents day 1 of the simulations. (b) Seasonal and size-specific contemporary diet data (2013) compared to the historical (mid-1990s) diet data.

(a) Seasonal age specific Lake Trout diets

			Proportion of Diet									
Sim Day	Season	N	Mysid	Kok	Paiute Sculpin	Tahoe Sucker	Other Forage	Lake Trout	Mount. Wht. Fsh.	Rainbow Trout	Crayfish	Other
250-375 mm												
1-91	Spring	54	0.86	0	0.03	0.07	0.01	0	0	0	0	0.03
92-183	Summer	61	0.78	0	0.14	0	0.06	0	0.01	0	0	0.01
184-229	Fall	25	0.67	0	0.04	0.09	0.18	0	0	0	0.02	0
230-365	Winter	20	0.9	0	0.03	0	0.06	0	0	0	0	0.01
376-500 mm												
1-91	Spring	136	0.86	0	0.03	0.04	0.04	0.01	0	0	0.01	0.01
92-183	Summer	114	0.68	0	0.01	0.11	0.05	0.01	0	0.01	0.1	0.03
184-229	Fall	77	0.71	0	0.04	0.04	0.02	0	0	0	0.09	0.1
230-365	Winter	95	0.73	0	0.15	0.03	0.03	0	0	0	0.04	0.02
501-625 mm												
1-91	Spring	64	0.73	0	0.03	0.07	0.03	0	0.02	0	0.09	0.03
92-183	Summer	64	0.51	0.01	0.08	0.14	0.07	0.01	0	0	0.18	0
184-229	Fall	50	0.53	0	0.02	0.12	0.11	0	0	0.06	0.14	0.02
230-365	Winter	73	0.67	0.04	0.05	0.06	0.03	0.05	0	0.01	0.06	0.03
> 625 mm												
1-91	Spring	4	0	0	0	0.24	0	0.14	0.03	0.26	0.09	0.24
92-183	Summer	13	0.12	0.15	0	0.31	0.12	0.24	0	0	0.06	0
184-229	Fall	5	0	0.17	0	0.08	0.22	0.33	0	0.03	0.17	0
230-365	Winter	5	0.13	0	0	0.27	0	0.6	0	0	0	0

(b) Historical Lake Trout diet composition compared to contemporary (2013).

			Proportion of Diet									
Season	Year	N	Mysid	Kok	Paiute Sculpin	Tahoe Sucker	Other Forage	Lake Trout	Mount. Wht. Fsh.	Rainbow Trout	Crayfish	Other
376-500 mm												
Summer	Mid-1990s	114	0.68	0	0.01	0.11	0.05	0.01	0	0.01	0.1	0.03
	2013	5	0.80	0	0	0.06	0.14	0	0	0	0.01	0
Fall	Mid-1990s	77	0.71	0	0.04	0.04	0.02	0	0	0	0.09	0.1
	2013	1	0	0	0	0	1	0	0	0	0	0
501-625 mm												
Summer	Mid-1990s	64	0.51	0.01	0.08	0.14	0.07	0.01	0	0	0.18	0
	2013	1	1	0	0	0	0	0	0	0	0	0
Fall	Mid-1990s	50	0.53	0	0.02	0.12	0.11	0	0	0.06	0.14	0.02
	2013	5	0.815	0	0	0	0.185	0	0	0	0	0
> 625 mm												
Summer	Mid-1990s	11	0.14	0	0	0.37	0.14	0.28	0	0	0.07	0
	2013	2	0	1	0	0	0	0	0	0	0	0

Table 3. Energy density values (J/g) and the proportion of indigestible material for each Lake Trout prey type.

Diet Item	Energy Density	Proportion Indigestible	Reference
Mysid	3474	0.1	ED - Rudstam 1989, PI - Stewart et al. 1983
Kokanee	6803	0.033	ED - Beauchamp et al. 1989
Paiute sculpin	5410	0.033	ED - Cummins and Wuycheck 1971
Tahoe sucker	5004	0.033	ED - Hewett and Johnson 1992
Minnows	5004	0.033	ED - Hewett and Johnson 1992
Lake trout	6011	0.033	ED - Assumed 100g, e=5701 + 3.1g
M. whitefish	8489	0.033	ED - Hewett and Johnson 1992
Rainbow trout	6067	0.033	ED - Rand et al. 1993
Crayfish	6159	0.25	ED & PI - Stein and Murphy 1976
Other	3711	0.1	ED - Inverts/Mysid, PI - Stewart et al. 1983

Table 4. The average thermal experience for Lake Trout used in the bioenergetics simulations. April 1st represents day 1 of the simulations.

Month	Sim Day	LT Temp °C	Season
April	1	5.4	spring
May	31	5.8	spring
June	62	6.6	spring
July	92	9.1	summer
August	123	9.7	summer
September	154	10	summer
October	184	9.8	fall
November	215	9	fall
December	245	6.9	winter
January	276	5.8	winter
February	307	5.5	winter
March	335	5.5	winter
March 31st	365	5.4	winter

Table 5. Age-specific Peterson mark-recapture abundance estimate for Lake Trout with the Chapman correction.

Age Class	Percentage Of Population	Abundance Estimate	+/- 2 SE
2	22%	32,350	14,447
3	18%	25,880	11,558
4	14%	20,704	9,246
5	11%	16,563	7,397
6	9%	13,250	5,917
7	7%	10,600	4,734
8	6%	8,480	3,787
+9	12%	17,553	7,839
sum	100%	145,380	64,925

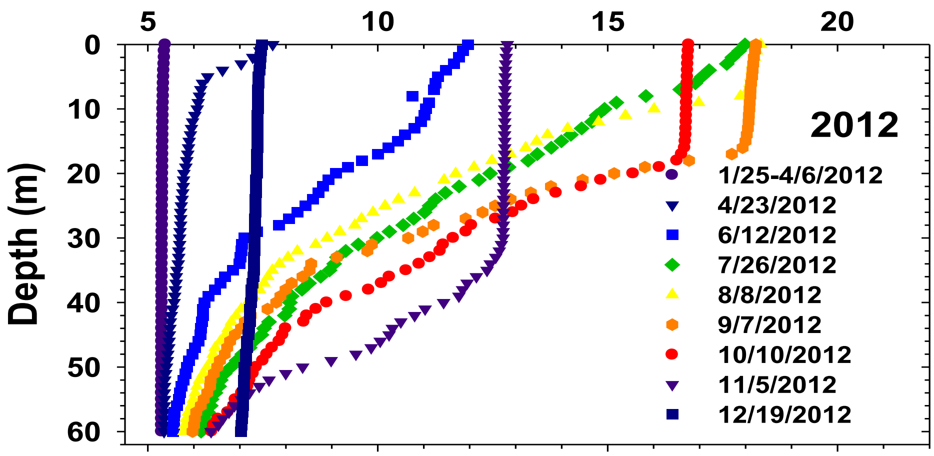

Figure 1. Monthly vertical temperature profiles from the UC Davis limnological long term profile site off Tahoe City for 2004, 2005, and 2012.

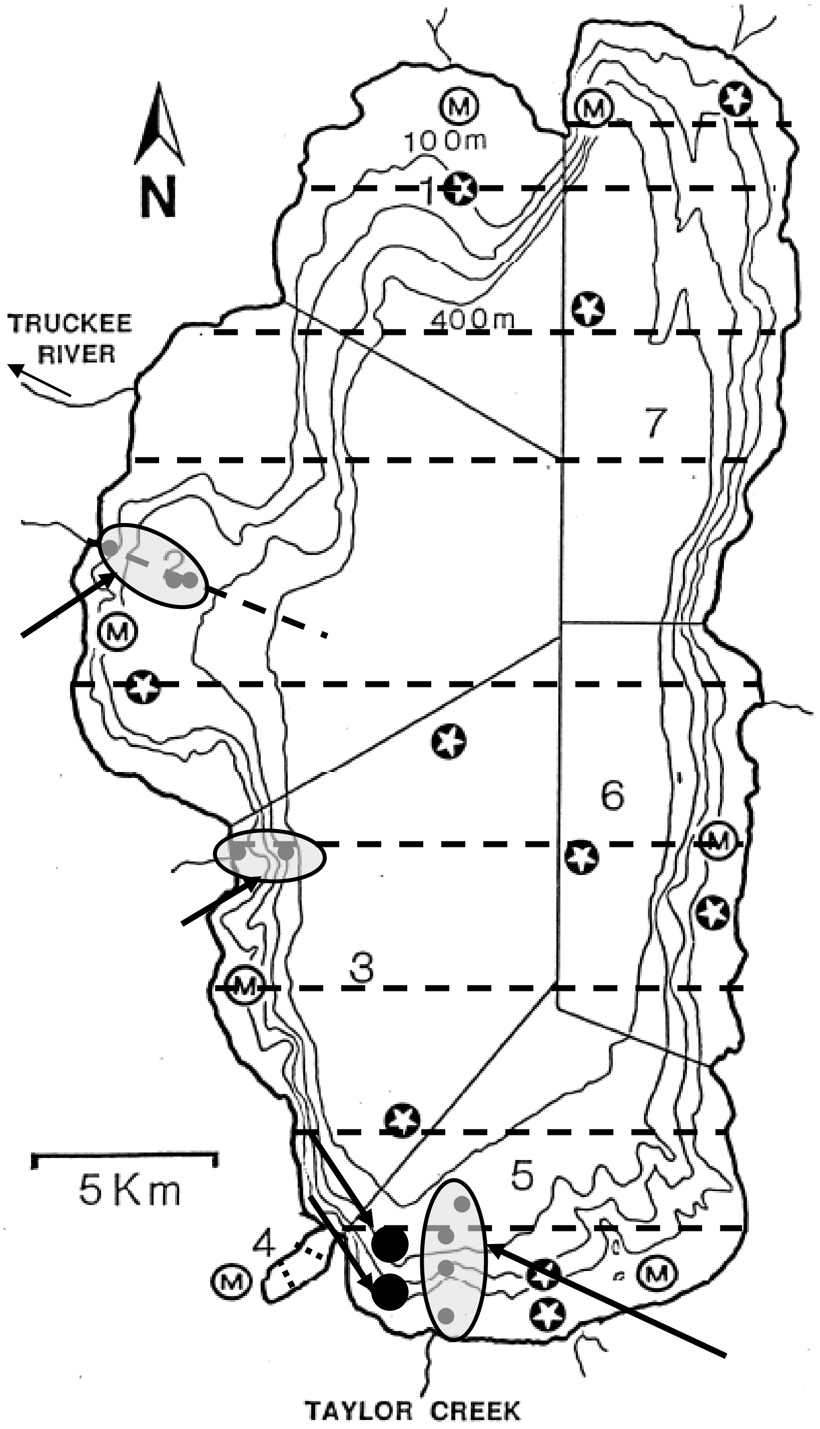

Figure 2. Sampling locations used in Lake Tahoe during 2012-2013. Dashed lines represent hydroacoustic transects.

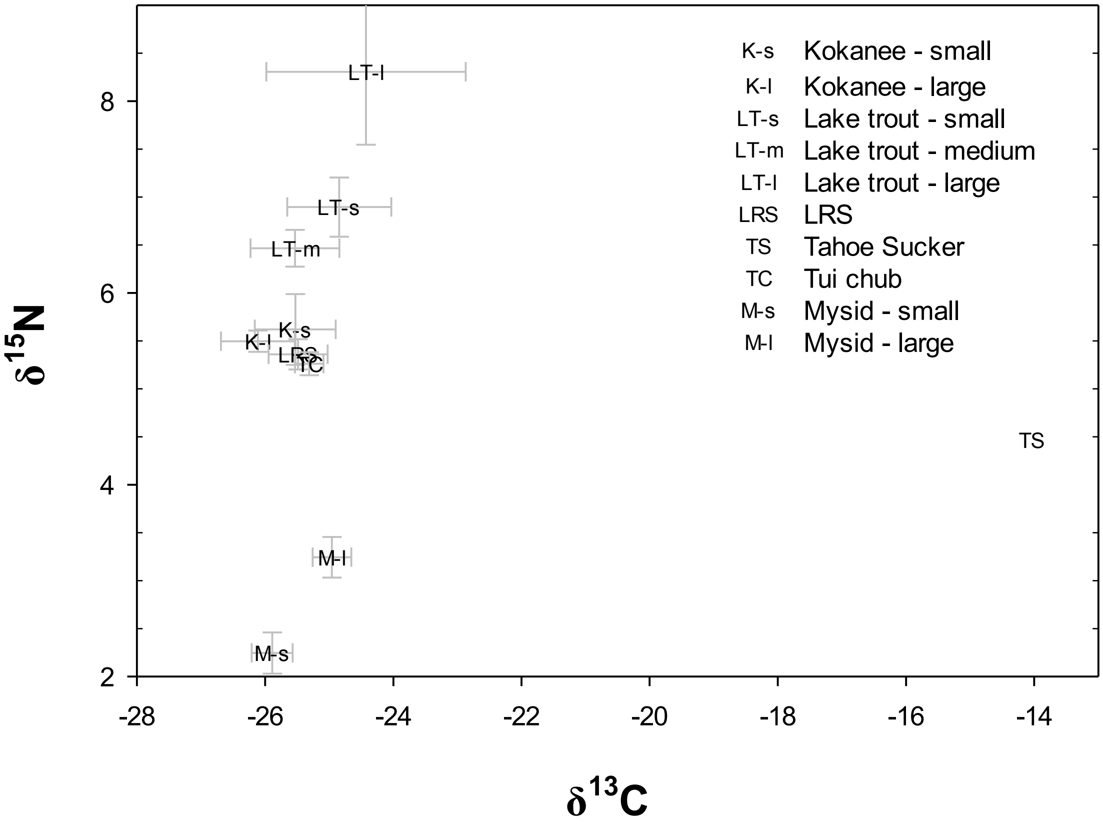

Figure 3. Average isotopic signatures of the Lake Tahoe pelagic food web. Error bars represent 2 SE in each direction. The δ^{15}N values represent the trophic level of the species. The δ^{13}C values represent the reliance on pelagic (smaller values) and benthic (larger values) energy pathways. Small Kokanee ≤ 100 mm, large Kokanee > 100mm. Small Lake Trout ≤ 500 mm, 500 mm < medium Lake Trout ≤ 625 mm, and large Lake Trout > 625mm. Small mysids ≤ 12mm, and large mysids > 12 mm.

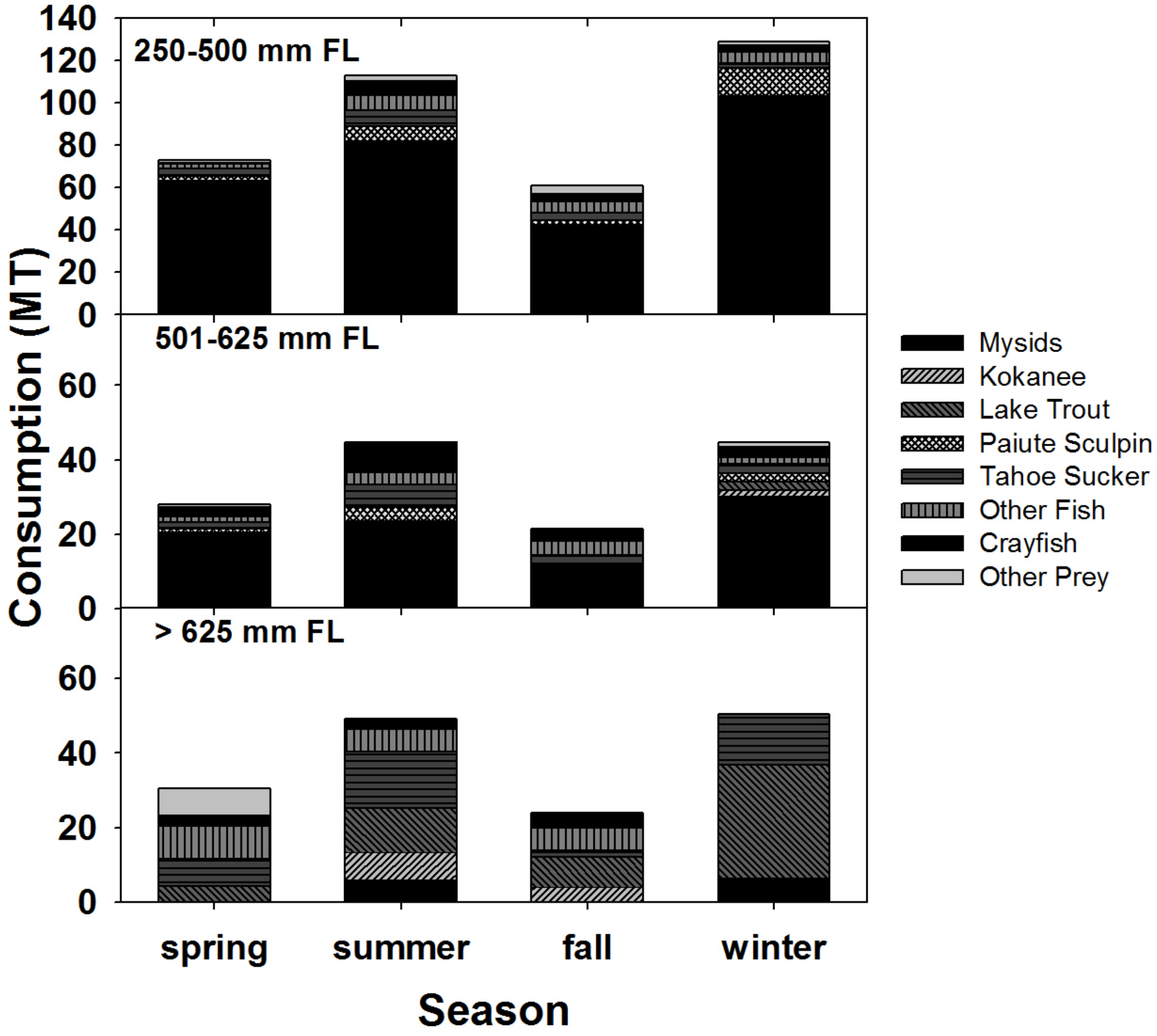

Figure 4. Season- and size-specific estimates for the biomass (MT) consumed of each Lake Trout prey category.

APPENDIX

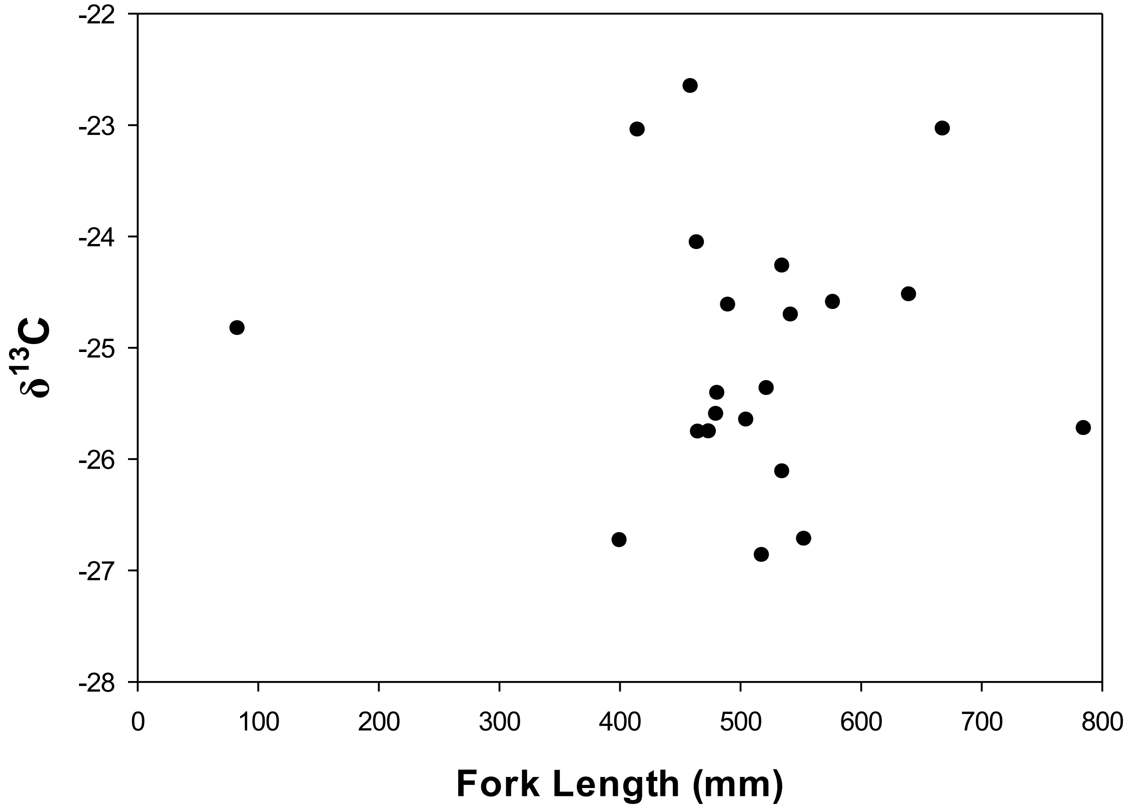

Figure A1. $\delta^{13}N$ values for different sizes of Lake Trout pooled across all seasons. The $\delta^{13}C$ values represent the reliance on pelagic (smaller values) and benthic (larger values) energy pathways.

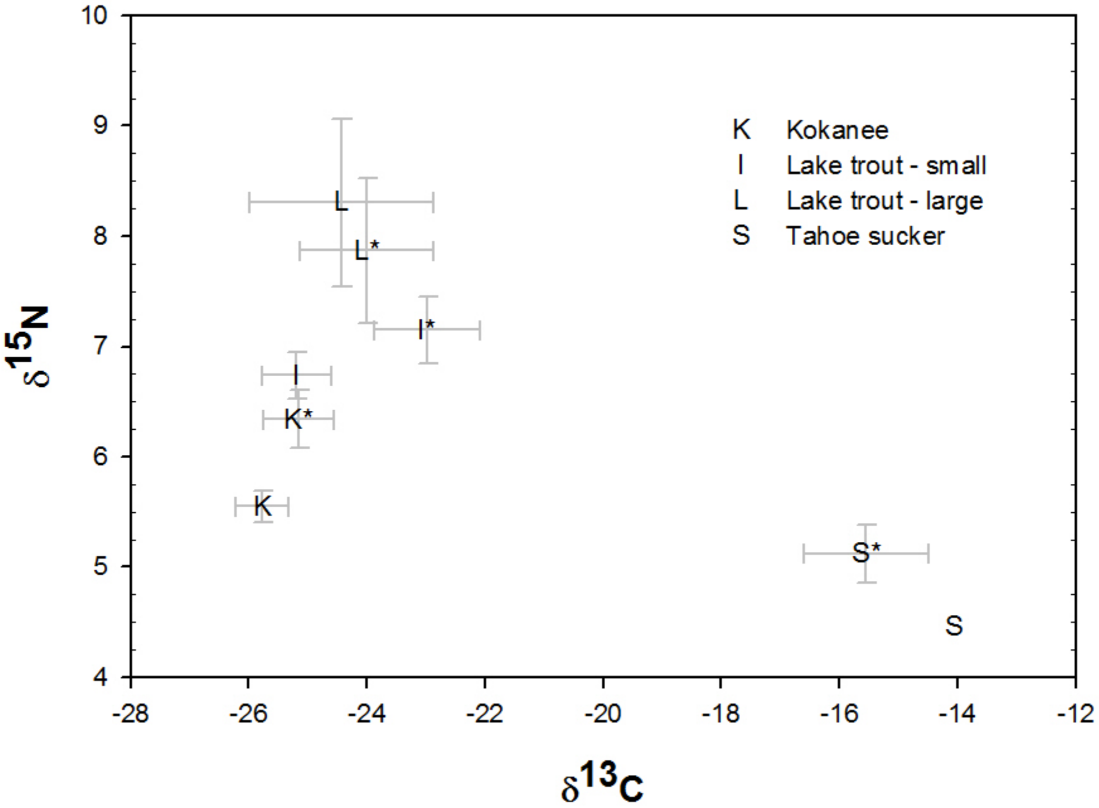

Figure A2. Average isotopic signatures for fish in the Lake Tahoe pelagic food web. Values without an asterisk are from data collected in 2012/2013, values with an asterisk (*) are from data collected in 1998-2000 summarized from Appendix in Vander Zanden et al. (2003). Error bars represent 2 SE in each direction. The δ^{15}N values represent the trophic level of the species. The δ^{13}C values represent the reliance on pelagic (smaller values) and benthic (larger values) energy pathways. Small Lake Trout ≤ 580 mm, and large Lake Trout > 580mm.

SUMMARY

- Contemporary Kokanee growth in Lake Tahoe is limited by seasonal prey availability. However, the supply of zooplankton during the summer growing season is protected from additional predation by mysids because of thermal segregation between mysids below the thermocline versus Kokanee within the thermocline, and a modest pool of adult copepods within or above the thermocline.
- Mysid growth in Lake Tahoe is limited by prey availability. Mysids in Lake Tahoe take two years to reach reproductive maturity while in Flathead Lake it only takes mysids one year to reach reproductive age (Chess and Stanford 1998).
- Mysids in Lake Tahoe are omnivorous, but zooplankton only contribute to a fraction of their diet. Increases in zooplankton or decreases in mysids would likely increase the per capita consumption rate of zooplankton, allowing the mysids to attain higher growth rates as observed in other lakes and dampening any potential benefit to the zooplankton population.
- Lake Trout impose significant mortality on the Kokanee population in Lake Tahoe, primarily by targeting pre-spawning aggregations of adults in the summer and fall.
- Cannibalism by Lake Trout is an important factor to consider in terms of its role in self-regulation of the top predator and implications for the pelagic food web in Lake Tahoe.
- Lake Trout consume a large proportion of the mysids in Lake Tahoe, but the production (510 MT) from the standing stock throughout the year is sufficient to absorb the full predation mortality (351 MT) exerted by Lake Trout. However, the 357 MT of mysid consumption by Kokanee also needs to be considered when analyzing the predation impacts on mysids.
- Mysids contribute a substantial amount to the annual energy budget of young Lake Trout (61-82%).

- The abundant mysid supply could be boosting the number of Lake Trout that survive to the largest size class (>625 mm); which is also the size class that consumes the most Kokanee and other prey fishes.