Introduced Lake Trout Produced a Four-Level Trophic Cascade in Yellowstone Lake

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Abstract.—Introduction of lake trout Salvelinus namaycush into a system can add a trophic level, potentially affecting organisms at lower trophic levels. Similar to many lakes and reservoirs in the western United States, lake trout were introduced into Yellowstone Lake, Wyoming. Previous studies showed that lake trout reduced the population and altered the size structure of native Yellowstone cutthroat trout Oncorhynchus clarkii bouvieri in Yellowstone Lake, but we sought to determine the degree to which lake trout predation changed lower trophic levels. We predicted that the structure of lower trophic levels would change in conformance with trophic cascade theory because Yellowstone cutthroat trout consume zooplankton. We compared zooplankton and phytoplankton assemblages between the period when Yellowstone cutthroat trout were abundant and the period after they declined. As predicted by trophic cascade theory, zooplankton biomass shifted from being dominated by copepods before lake trout introduction to being dominated by cladocerans after lake trout introduction, with zooplankton body lengths 17% longer after introduction. Vertical water clarity increased by 1.6 m because of a twofold decrease in chlorophyll a and a three- to sevenfold decrease in phytoplankton biovolume. Thus, the introduction of lake trout and subsequent decline of Yellowstone cutthroat trout likely altered lower trophic levels in Yellowstone Lake. Trophic cascades may be common in western U.S. lakes and reservoirs where native salmonids are present and where lake trout have been introduced.

Lake trout Salvelinus namaycush are introduced predators in many lakes and reservoirs in the western United States (Martinez et al. 2009). Lake trout are apex predators (Post et al. 2000) and can cause native and nonnative fishes to decline (Martinez et al. 2009). For example, lake trout reduced the populations of native Lahontan cutthroat trout Oncorhynchus clarkii henshawi in Lake Tahoe, California, and bull trout Salvelinus confluentus in Lake McDonald, Glacier National Park, Montana. However, the degree to which lower trophic levels are affected by the introduction of lake trout is largely unknown.

Introduction of lake trout into a system may add a trophic level to a food web, potentially producing a four-level trophic cascade (Fretwell 1987; Post and Takimoto 2007). Research has focused on the functional controls of the common two- and three-level trophic cascades (Borer et al. 2005; Halpern et al. 2005; Shurin and Seabloom 2005). Four-level trophic cascades have seldom been included in meta-analyses, probably because they are more difficult to observe in longer food chains as top-down effects from predators attenuate down the food chain (Shurin et al. 2002). Additionally, the cumulative probability of strong interactions among four trophic levels is lower than that for two or three trophic levels. Nonetheless, nonexperimental four-level trophic cascades have been observed. For example, overfishing and removal of Atlantic cod Gadus morhua, which served as the fourth trophic level of the Scotian Shelf food web, increased phytoplankton standing stocks (Frank et al. 2005).

Characteristics of the plankton assemblages depend on the number of trophic levels in the ecosystem (e.g., Carpenter et al. 1987, 2001). The addition of piscivores reduces planktivorous fish abundance, causing large-bodied zooplankton to dominate the herbivore assemblage. The biomass of zooplankton and large zooplankton species (length > 1 mm) is higher in piscivore-dominated lakes because of lower predation...
on zooplankton by planktivorous fish (Carpenter et al. 1987, 2001). Conversely, in lakes with three trophic levels, the zooplankton assemblage is dominated by small zooplankton species (length < 1 mm) because planktivorous fish consume large-bodied zooplankton (Brooks and Dodson 1965). These differences in the zooplankton assemblage alter the phytoplankton assemblage. In experimental lakes with four trophic levels, phytoplankton biomass and biovolume were lower than those in lakes with three trophic levels because of higher grazing by zooplankton (Carpenter et al. 2001).

Lake trout were introduced into Yellowstone Lake, where native Yellowstone cutthroat trout *O. clarkii bouvieri* were previously the top predator. The introduction of lake trout potentially increased food chain length from three to four trophic levels. Lake trout reduced the Yellowstone cutthroat trout population in Yellowstone Lake (Ruzycki et al. 2003; Koel et al. 2005); our goal was to evaluate the extent to which lake trout affected lower trophic levels via a trophic cascade. We tested 10 predictions based on trophic cascade theory to evaluate the degree to which lake trout induced a trophic cascade in Yellowstone Lake (Figure 1). We tested these predictions using data from before and after the lake trout introduction. Taken together, tests of these predictions represent an approach that uses multiple lines of evidence to assess the degree to which a trophic cascade occurred in Yellowstone Lake. Our specific questions were (1) “To what degree did a trophic cascade occur in Yellowstone Lake after the introduction of lake trout?”; (2) “How

**FIGURE 1.**—Predicted characteristics of the zooplankton and phytoplankton assemblages of Yellowstone Lake under three trophic levels (Yellowstone cutthroat trout dominated) and four trophic levels (lake trout dominated).
did the strength of interactions among trophic levels compare with trophic cascades in other ecosystems?"; and (3) "What other factors in the Yellowstone Lake ecosystem could potentially cause changes in the plankton of Yellowstone Lake?"

**Study Site**

Yellowstone Lake is on the Yellowstone Plateau, Wyoming, and is the largest high-elevation (2,357-m) lake in North America (Gresswell et al. 1997), with a surface area of 341 km² and average depth of 43 m (Kaplinksi 1991). Yellowstone Lake is mesotrophic (Kilham et al. 1996) and ice covered from December through May (Gresswell and Varley 1988). Surface water temperatures during the ice-free season vary between 9°C and 18°C (Koel et al. 2007).

The plankton assemblage in Yellowstone Lake is composed of relatively few species that are abundant. Phytoplankton are dominated by diatoms (Stephanodiscus spp., Cyclotella bodanica, Aulacoseira subarctica, and Asterionella formosa; Interlandi et al. 1999). The crustacean zooplankton in Yellowstone Lake consist of three species of copepods (Diacyclops bicuspitatus thomasi, Leptodiaptomus ashlandi, and Hesperodiaptomus shoshone) and two species of cladocerans (Daphnia schodleri and Daphnia pulicaria; U.S. Fish and Wildlife Service [USFWS], unpublished data).

The fish assemblage in Yellowstone Lake includes two native species: Yellowstone cutthroat trout and the less-abundant longnose dace Rhinichthys cataractae (Gresswell et al. 1997). Adult Yellowstone cutthroat trout (>325 mm total length [TL]) live in the littoral zone and consume both benthic macroinvertebrates and zooplankton (Benson 1961). Jones et al. (1990) demonstrated that Yellowstone cutthroat trout in Yellowstone Lake rely heavily on zooplankton. Gut contents collected in 1989 indicated that 20% of Yellowstone cutthroat trout ate copepods (1.6% by volume) and 89% ate cladocerans (78% by volume, n = 132; Jones et al. 1990).

Lake trout were introduced into Yellowstone Lake (Kaeding et al. 1996) in approximately 1985 (Munro et al. 2005). Based on bioenergetics modeling of consumption, lake trout predation is a serious threat to the native Yellowstone cutthroat trout population in Yellowstone Lake (Ruzyczki et al. 2003). The abundance of Yellowstone cutthroat trout has declined by 60% in Yellowstone Lake and by 99% in a spawning stream since 1990 (Koel et al. 2007). To conserve Yellowstone cutthroat trout, the National Park Service (NPS) actively removes lake trout by using gill nets and electrofishing and requires anglers to kill all captured lake trout (Koel et al. 2005). Between 1994 and 2006, the NPS removed more than 198,000 lake trout from the lake (Koel et al. 2007).

Other threats to Yellowstone cutthroat trout include whirling disease and drought. *Myxobolus cerebralis*, the parasite that causes whirling disease, was discovered in Yellowstone Lake in 1998 and primarily affects age-0 Yellowstone cutthroat trout only in some spawning streams (Koel et al. 2006). Additionally, recent drought affected age-0 Yellowstone cutthroat trout in small tributary streams by causing the stranding of individuals (Koel et al. 2005). The decline of Yellowstone cutthroat trout is widespread; thus, most Yellowstone cutthroat trout losses over the past decade have been attributed to predation by lake trout (Koel et al. 2008).

**Methods**

*Inter-gill-raker spaces of Yellowstone cutthroat trout and zooplankton width.*—We compared the spaces between gill rakers and zooplankton width to assess the size of zooplankton that could potentially be consumed by Yellowstone cutthroat trout in Yellowstone Lake. We measured five inter-gill-raker spaces (GRSs) on the first gill arch of 31 unpreserved Yellowstone cutthroat trout (200–500 mm TL) that accidentally perished in gill nets (Langeland and Nost 1995; Link and Hoff 1998; Budy et al. 2005). To estimate the size of zooplankton that could be filtered by Yellowstone cutthroat trout, we measured mean width (mm; the two narrowest body dimensions) on arbitrarily selected samples of over 10 individuals of each zooplankton species. We assumed that the GRS does not change during feeding and that gill rakers function similar to a sieve (i.e., we assumed that zooplankton function smaller than the GRS were not retained; O’Brien 1987).

To estimate the filtering potential of Yellowstone cutthroat trout populations before and after lake trout introduction, we calculated the number of Yellowstone cutthroat trout that could potentially consume each zooplankton species. First, the maximum size of Yellowstone cutthroat trout that could eat each zooplankton species was determined based on zooplankton width and Yellowstone cutthroat trout GRSs. Using estimates of the number of Yellowstone cutthroat trout in each 10-mm size-class before and after the introduction of lake trout (L. M. Tronstad, unpublished data), we calculated the number of Yellowstone cutthroat trout that could potentially consume each zooplankton species in Yellowstone Lake.

*Zooplankton sampling.*—To measure zooplankton density, biomass, size, and production, we collected two samples every 2–4 weeks during the ice-free season in 2004 at four locations of Yellowstone Lake.
(east of Stevenson Island, West Thumb, South Arm, and Southeast Arm). These are the same sites that were sampled by the USFWS prior to the invasion of lake trout. In 2004, we collected zooplankton with 20-m vertical hauls using the same procedures and nets (80-μm mesh size) as used by USFWS between 24 May and 3 October 1977–1980 (n = 20 pre-introduction zooplankton samples preserved in formalin). We collected zooplankton samples on nine dates between 21 May and 19 October 2004 (n = 72 postintroduction samples preserved in cold sugared formalin). We enumerated and measured both pre- and postintroduction zooplankton samples under a dissecting microscope. Because the density, biomass, and size of the zooplankton assemblage during 1977–1980 were similar among years (analysis of variance: P > 0.05), we combined data among years. We calculated zooplankton biomass (dry mass [DM]) using published length–mass regressions (Dumont et al. 1975; Downing and Rigler 1984). We divided zooplankton into length categories: (1) small species, which were less than 1 mm in length (Diacyclops, Leptodiaptomus, and nauplii), and (2) large species, which were greater than 1 mm in length (Hesperodiaptomus, Daphnia schodleri, and Daphnia pulicaria).

We calculated zooplankton production (μg DM·L⁻¹·d⁻¹) during the ice-free season in both time periods using the egg ratio method (Downing and Rigler 1984) for Daphnia and the size-frequency method for copepods (Guerrero and Rodriguez 1994). To calculate Daphnia secondary production (Downing and Rigler 1984), we estimated density (individuals/L), mean individual biomass (μg DM/individual), and instantaneous birth rate (b; d⁻¹) on each sampling date. We assumed that the finite birth rate (β) was equal to b (i.e., birth rate = death rate) and growth rate (g; d⁻¹), and we calculated b as

\[ b = g = \beta = \frac{N_{\text{eggs}}}{N_{\text{females}}D_{\text{eggs}}} \]

where \( N_{\text{eggs}} \) is the total number of Daphnia eggs (counted both inside and outside of individuals), \( N_{\text{females}} \) is the total number of female Daphnia, and \( D_{\text{eggs}} \) is the development time of eggs (d) calculated using the model of Bottrell (1975):

\[ \log_e D_{\text{eggs}} = 3.4 + 0.22 \log_e T - 0.34 \log_e T^2 \]

where \( T \) is surface water temperature (°C) measured in the past (1977–1980; Theriot et al. 1997) and present (2004). We calculated total biomass on each date \( i \) by multiplying density by mean individual mass. Secondary production \( (P) \) was estimated by

\[ P = \sum_{i=1}^{n} \Delta B_i b_i \Delta t_i \]

where \( \Delta B \) is the change in biomass (μg DM/L), and \( \Delta t \) is the number of days between sampling dates.

We calculated copepod secondary production using the size-frequency method (Guerrero and Rodriguez 1994), which is used when a species is constantly reproducing. To calculate copepod production, we divided individuals into six equal length-classes and a nauplius (immature copepod) size-class. Because we could not identify nauplii, we divided nauplii among the species based on the percent abundance of each copepod taxon. We calculated biomass by multiplying the density of individuals within each size-class across all sampling dates by individual biomass. We calculated production as

\[ P = \sum_{i=1}^{n} \Delta B_i S_i \]

where \( S \) is the number of size-classes. To calculate copepod production on a per-unit-time basis, the cohort production interval (total sampling interval/development time) was multiplied by \( P \). To derive the cohort production interval, we used an empirical model developed by Gillooly (2000) to estimate the postembryonic development time \( (D; d) \) of zooplankton:

\[ D = \frac{(138M^{0.3})}{T} \]

where \( M \) is adult copepod DM (μg) and \( T \) is between 5°C and 20°C.

Phytoplankton sampling.—To measure density and biomass of the postintroduction phytoplankton assemblage, we collected water from 5- and 15-m depths using an Alpha bottle (Wildco) every 2–4 weeks during the ice-free season of 2004 in the same four areas used for zooplankton sampling. We preserved 100 mL of water to a final concentration of approximately 0.5% glutaraldehyde, and we permanently mounted samples on 25-mm, white-gridded HAWG filters (0.45-μm pore size; Millipore Corporation, Billerica, Massachusetts). Using phase contrast on a compound microscope, we estimated phytoplankton abundance and biovolume by scanning at 160× for large species and at 400× for smaller species. Knight (1975) measured phytoplankton biovolume at five locations to 20-m depth in the West Thumb of Yellowstone Lake between 14 June and 24 September 1972. Interlandi et al. (1999) and Interlandi and Kilham (2001) measured phytoplankton density and biovolume in northern Yellowstone Lake down to 50-m depth during the open-water seasons of 1996 and 1997. From these data, we used only
chlorophyll
Sciences, Port Washington, New York). We extracted
through 25-mm, type-A/E glass-fiber filters (Pall Life
1,200 mL of water from 5, 10, and 15 m in 2005. To
lake water in the West Thumb from 5 m in 2004 and
chlorophyll
a
solution of ethanol buffered with MgCO and measured
a pheopigment correction (Nusch 1980) on a TD-700
fluorometer (Turner Designs, Sunnyvale, California).
We calibrated a secondary solid standard using a
primary chlorophyll-a commercial standard of Anacys-
tis nidulans (Sigma-Aldrich) before each field season.
Knight (1975) measured chlorophyll-a concentrations
to 20-m depth in the West Thumb during 1972 by
using acetone extraction and a spectrophotometer
(Strickland and Parsons 1972). We corrected Knight’s
(1975) chlorophyll-a concentrations using Nusch’s
(1980) comparisons of acetone and ethanol extractions.

Water clarity was measured by the NPS using a
Secchi disk during the ice-free seasons of 2003–2006
in three areas of Yellowstone Lake (east of Stevenson
Island, South Arm, and West Thumb), Historical water
clarity data for the ice-free seasons of 1976–1991 at the
same sites are from Theriot et al. (1997).

Statistical analysis.—To calculate the filtering
ability of Yellowstone cutthroat trout, we used ordinary
least-squares (OLS) regression to estimate the relation-
ship between Yellowstone cutthroat trout TL and GRS.
To quantify the filtering size of the zooplankton
assemble in Yellowstone Lake, we regressed mean
width against length for each zooplankton species by
using OLS linear regression.

We compared the size structure of Yellowstone
cutthroat trout and zooplankton in Yellowstone Lake
before and after the introduction of lake trout. To
quantify the size structure of Yellowstone cutthroat
trouth, we compared the number of Yellowstone
cutthroat trout per net (standardized index of Yellow-
stone cutthroat trout abundance in Yellowstone Lake) in
each size-class by using the Kolmogorov–Smirnov
goodness-of-fit test (Zar 1999). We binned individuals
into 100-mm TL classes, calculated the percentage of
fish in each length-class, and compared the percentages
of Yellowstone cutthroat trout in each bin between pre-
We tested for differences in the distribution of
zooplankton sizes between pre-introduction (1977–
1980) and postintroduction (2004) periods using a
Kolmogorov–Smirnov goodness-of-fit test. We binned
zooplankton individuals into 1-mm size-classes and
calculated the percentage of individuals in each size-
class.

To compare density and biomass of zooplankton
between 1977–1980 and 2004, we used a bootstrap
procedure. For each of the 36 sample pairs (two
samples per date and location), we randomly selected
two observations with replacement. For the 1977–1980
period, the data collected had only one observation at
some of the time points. Thus, we used a parametric
bootstrap, resampling each datum from a normal
distribution with a mean equal to the logarithm of the
observed datum (or the mean of values for dates with
multiple observations) and SDs. These values were
then back-transformed to become the bootstrap values
for each sampling event. Bootstrap means of 1977–
1980 and 2004 data were repeated 1,000 times, and we
calculated the difference in their means. The SD of
these difference values was used as our bootstrap
estimate of the SE of the mean difference.

Phytoplankton density and biovolume were sampled
at even intervals among time periods. To compare the
differences in mean phytoplankton density and biovol-
ume between pre- and postintroduction time periods,
we estimated the SE for each period using a sequential
differences formula designed to reduce the upward bias
in the variance estimator based on the usual sample
variance (Wolter 1984). For both zooplankton and
phytoplankton, we calculated the difference in the
means between the two time periods and a 95%
confidence interval (CI) for that difference (upper and
lower 2.5% of data were removed), assuming the two
samples to be independent. Confidence intervals that
did not include zero implied biologically significant
differences. Finally, we compared chlorophyll-a con-
centrations using a t-test. West Thumb concentrations
in 2004 and 2005 were not different (t-test: \( t = -0.40, \)
df = 17, \( P = 0.70 \)), so we combined these data and
compared the concentrations with those collected in
1972 (Knight 1975).

To evaluate whether Secchi depths changed through
time, and because this variable was the only one that
was measured continuously, we checked for first-order
autocorrelations using a Durbin–Watson (DW) test
test statistic values range from 0 to 2) and for higher-
order correlations using autocorrelation functions in the
Statistical Package for the Social Sciences (version
12.0.1; SPSS, Inc., Chicago, Illinois). We did not
detect temporal autocorrelation (i.e., DW test statistic
thus, we used multiple regression. To account for increases in water clarity throughout summer stratification, we used multiple regression with year and Julian day as independent variables and Secchi depth as the dependent variable.

To estimate the effect size for each variable before 1998 compared with after 2003, we used the log response ratio \( \log(\frac{X_{\text{present}}}{X_{\text{past}}}) \), where \( X_{\text{past}} \) is the mean of the variable before 1998 and \( X_{\text{present}} \) is the mean of the same variable after 2003 (Osenberg et al. 1997; Hedges et al. 1999; Shurin et al. 2002).

**Results**

**Effect of Yellowstone Cutthroat Trout on Zooplankton**

Yellowstone cutthroat trout in Yellowstone Lake were able to consume zooplankton throughout their lives, even when they reached sizes exceeding 400 mm TL. The GRS (mm) was positively related to TL (mm) of Yellowstone cutthroat trout:
The number of Yellowstone cutthroat trout that could potentially consume zooplankton was lower in 2004 than in 1977–1980 due to decreased abundance and increased size of Yellowstone cutthroat trout (Figure 2B). Yellowstone cutthroat trout abundance declined after the introduction of lake trout, and the size structure of adult Yellowstone cutthroat trout shifted to longer individuals, changing the ability of these fish to consume zooplankton. Larger Yellowstone cutthroat trout have larger GRSs and can consume only the largest zooplankton species (Figure 2A). After the introduction of lake trout, fewer Yellowstone cutthroat trout had the potential to consume zooplankton of all species present in Yellowstone Lake (Figure 2C).

Zooplankton in Yellowstone Lake

The zooplankton assemblage in 1977–1980 differed from the 2004 assemblage in terms of both individual size and species composition. Zooplankton shifted from an assemblage dominated by small copepods in 1977–1980 (large species comprised 24% of biomass) to an assemblage with higher abundance and biomass of large species in 2004 (large species comprised 51% of biomass; bootstrapped 95% CI for the mean change = −55.1 to −34.7 mg DM/m³; Figure 4A). Total biomass was two times higher in 2004 compared with 1977–1980 (bootstrapped 95% CI for the mean change = −65.6 to −26.1 mg DM/m³), probably because of the increase in the proportion of large species.

Length of individual zooplankton and the assemblage changed between 1977–1980 and 2004. The length of individual zooplankton species averaged 17% greater in 2004 (Figure 4B). Because the zooplankton assemblage shifted to larger species in 2004, the mean length of an individual zooplankter in the assemblage

\[
\log_e \text{GRS} = -10.7(\pm 0.5) + 1.8(\pm 0.1) \times \log_e \text{TL}\]  

\((r^2 = 0.70, df = 153, P < 0.0001; \pm 95\% \text{ CIs})\), showing that larger fish had larger GRSs and could filter only large zooplankton (Figure 2A). Zooplankton sizes significantly differed among the species. *Diacyclops*, *Leptodiaptomus*, and nauplii were smaller than 0.4 mm in width, with nauplii being significantly smaller than the two other groups. *Hesperodiaptomus* and *Daphnia schodleri* were between 0.5 and 1.0 mm in width, whereas *Daphnia pulicaria* were significantly larger, with mean width exceeding 1.3 mm. Therefore, a 200-mm TL Yellowstone cutthroat trout with a mean GRS of 0.32 mm could filter individual zooplankton of all species in Yellowstone Lake except *Diacyclops* and nauplii, but a 400-mm TL fish with a mean GRS of 1.11 mm could only filter *Daphnia pulicaria*.
increased from 0.40 mm in 1977–1980 to 0.55 mm in 2004 (t-test: \( t = 2.62, \text{df} = 33, P = 0.01 \)), and the frequency of individuals in each size-class changed between the two time periods (Kolmogorov–Smirnov test: \( d_{\text{max}} = 13.3, k = 20, P < 0.05 \), where \( d_{\text{max}} \) is the test statistic and \( k \) is the number of categories; Figure 4C).

Production of small zooplankton was 45% higher in 1977–1980 than in 2004. Production of large zooplankton was 150% higher in 2004 than in 1977–1980 (Figure 4D). However, total zooplankton production was similar between the two periods. The \( b \) for *Daphnia schröderi* was higher in 2004 (0.04 per day) than in 1977–1980 (0.01 per day). For *Daphnia pulicaria*, \( b \) was similar between periods (0.12 per day). Zooplankton daily production : biomass ratio (turnover rate) was slightly higher in 1977–1980 (0.055 per day) than in 2004 (0.046 per day).

**Phytoplankton in Yellowstone Lake**

Phytoplankton biomass in Yellowstone Lake was lower after the introduction of lake trout. Chlorophyll-\( a \) concentration, an indicator of phytoplankton biomass, was twice as high in 1972 (Knight 1975) compared with 2004 and 2005 (t-test: \( t = 4.8, \text{df} = 16, P = 0.0002 \); Figure 5A) in the West Thumb. The total density of phytoplankton in Yellowstone Lake during 2004 was intermediate to the densities in 1996 and 1997 (Figure 5B).
Conversely, total phytoplankton biovolume in Yellowstone Lake was three times higher in 1972 (Knight 1975; before lake trout introduction) compared with 2004 and 2005 (postintroduction). Total phytoplankton density (cells/mL; ±95% confidence interval [CI]) was similar in 1996, 1997, and 2004, but the diatom density was greater in 2004 than in 1996–1997. Total phytoplankton biovolume (mm³/m³; ±95% CI) was three times higher in 1972 and 1996 and nearly seven times higher in 1997 than in 2004. Taxon-specific changes to phytoplankton biovolume depended on the species (not all phytoplankton species are shown). Biovolume of *Asterionella* was higher in 2004 than in 1972; biovolumes of *Anabaena*, *Stephanodiscus yellowstonensis*, *Aulacoseira*, and *Rhodomonas* were lower in 2004 than in 1972; and biovolumes of *S. jamiesonii* and *S. minutus* were similar between the pre- and postintroduction periods.

Differences in the phytoplankton assemblages were taxon specific. Total density of diatoms was 2.5 times higher in 2004 (sequential differences, 95% CI of change = -740 to -175 cells/mL for 1996 and -733 to -223 cells/mL for 1997) compared with 1996 and 1997 because of higher densities of *Stephanodiscus*, *Syedra*, and *Cyclorella*; there was no difference between 1996 and 1997 (sequential differences, 95% CI of change = -141 to 162 cells/mL; Figure 5B). The differences were mainly driven by the density of small phytoplankton (greatest axial linear dimension < 30 μm).
Biovolumes of the taxa *Stephanodiscus yellowstonensis*, *Anabaena*, *Aulacoseira*, and *Rhodomonas* were higher in 1972, whereas *Asterionella* had higher biovolume in 2004 (Figure 5D).

Water clarity increased between 1976 and 2006 (15 July–15 September; Figure 6). Secchi depths showed little first-order (DW test statistic = 1.84) or higher-order autocorrelation. Year (df = 84, P = 0.0033) and Julian day (df = 84, P < 0.0001) explained 26% of the variation in Secchi depth. According to the relationship, Secchi depth increased by 0.053 m each year (±95% CI):

\[
\text{Secchi depth} = [0.053(\pm 0.03) \times \text{year}] + [0.045(\pm 0.02)] \times \text{day} - 105(\pm 68).
\]

Secchi depths were 1.6 m (0.7–2.5 m) deeper in 2006 compared with 1976. Deeper Secchi depths indicated a decrease in phytoplankton biomass:

\[
\log_e(\text{Secchi depth}) = -0.44(\pm 0.09) \times \log_e C + 1.7(\pm 0.07)
\]

(df = 29, \(R^2 = 0.44, P < 0.0001\)), where \(C\) is chlorophyll-a concentration (µg/L; Figure 6 inset).

**Discussion**

**Evidence of a Trophic Cascade in Yellowstone Lake**

Reduced abundance and increased mean body size of Yellowstone cutthroat trout altered the assemblage of zooplankton in Yellowstone Lake through consumption. Yellowstone cutthroat trout size structure likely affected the removal of zooplankton because the number of large fish increased, simultaneously increasing GRS. Similarly, Post et al. (2008) showed that two subpopulations of alewives *Alosa pseudoharengus* filtered different sizes of zooplankton, which resulted...
in trophic cascades of different strengths. Additionally, reduced Yellowstone cutthroat trout abundance produced changes in the Yellowstone cutthroat trout diet, thereby altering the zooplankton assemblage. Tronstad, Hall, and Koel (unpublished data) observed that in years when Yellowstone cutthroat trout were abundant in Yellowstone Lake, their diet was largely composed of zooplankton, whereas in the years after their decline they consumed more benthic invertebrates. Similarly, Hodgson and Kitchell (1987) observed that zooplankton constituted a larger fraction of the diet for adult largemouth bass Micropterus salmoides when these fish were more abundant.

The introduction of lake trout into Yellowstone Lake had a small effect on zooplankton production. We calculated that zooplankton production was only 13% higher when Yellowstone cutthroat trout dominated Yellowstone Lake. Using modeling, Scavia et al. (1988) calculated that zooplankton production was five times higher in Lake Michigan when the abundance of planktivorous alewives was high than when alewife abundance was low. We expected higher zooplankton production in 1977–1980 because turnover rates of smaller individuals are faster (Gillooly 2000; Huryn and Benke 2007). However, trophic cascade theory does not predict changes in zooplankton secondary production.

Phytoplankton biomass was lower after lake trout introduction into Yellowstone Lake. Whole-lake experiments demonstrated that phytoplankton biovolume (Carpenter et al. 1987; Findlay et al. 2005) and chlorophyll a (Carpenter et al. 2001) were about three times higher when planktivores dominated. Similarly, biovolumes of phytoplankton in Yellowstone Lake were 3.0–6.5 times higher and chlorophyll-a concentrations were two times higher prior to the invasion of lake trout. Although interannual variability of total phytoplankton biovolume was large and varied with local climate (Kilham et al. 1996), phytoplankton biovolume after the introduction of lake trout was significantly lower than all pre-introduction estimates. Furthermore, the density of small phytoplankton taxa increased in Yellowstone Lake after the introduction of lake trout. Similarly, the density of small phytoplankton increased in Bighorn Lake, Banff National Park, Alberta, after the removal of planktivorous fish (i.e., number of trophic levels was reduced from three to two; Parker and Schindler 2006). Large phytoplankton taxa were also lost from the assemblage after the addition of largemouth bass and removal of minnows (northern redbelly dace Phoxinus eos, finescale dace P. neogaeus, and central mudminnow Umbra limi) in Tuesday Lake, Michigan (Carpenter et al. 1987). Smaller individual biovolumes or a larger proportion of smaller phytoplankton taxa may explain why total phytoplankton biovolume in Yellowstone Lake was lower but density was similar in 2004.

A sparser phytoplankton assemblage after the introduction of lake trout into Yellowstone Lake (number of trophic levels was increased to four) increased water clarity by 1.6 m. Similarly, lakes dominated by Daphnia pulex, a large zooplankton species that often predominates in lakes with an even number of trophic levels, had deeper water clarity than lakes dominated by smaller zooplankton (Kasprzak et al. 1999). Eliminating fish in a Norwegian lake (two trophic levels after fish removal) also increased water clarity by 3 m (Reinertsen et al. 1990).

Multiple lines of evidence suggested that the Yellowstone Lake food web changed from three to four trophic levels, ultimately lowering phytoplankton biomass. Individually, each measurement contained low inference because any one data point is likely to be unreliable. However, the support of multiple hypotheses can indicate lake trout-induced change. Together, 90% of the hypotheses (Figure 1) were in the predicted direction based on trophic cascade theory and only 10% were inconclusive, providing strong evidence that the food web of Yellowstone Lake effectively changed to four trophic levels (Table 1). The calculated effect size of zooplankton and phytoplankton in Yellowstone Lake (2.2 times difference between the pre- and postintroduction periods) were within the range reported for herbivores (1.4–17.3 times) and primary producers (1.1–18.0 times) from multiple ecosystem types (Schmitz et al. 2000; Shurin and Seabloom 2002). Furthermore, Polis and Strong (1996) suggested that when the ratio of direct to indirect effects of predators is greater than 1, the effects of predation attenuate down the food chain. Conversely, when the ratio is less than 1, predator effects intensify down the food chain. The ratio of direct effects (2.0; Yellowstone cutthroat trout) to indirect effects (mean = 2.2; zooplankton and phytoplankton) in Yellowstone Lake suggests that predation by lake trout was nearly equally transmitted down the food chain, indicating strong interactions at each trophic level. Lake trout are specialist piscivores that tend to be apex predators with the longest food chains (Post et al. 2000). The strength of the cascading trophic interactions in Yellowstone Lake may be attributable to the lake’s biota, including ectothermic predators, invertebrate herbivores, and small primary producers, which can facilitate a trophic cascade (Borer et al. 2005; Shurin and Seabloom 2005; Shurin et al. 2006). Compared with many lakes inhabited by lake trout, Yellowstone Lake contains few other fish species and lacks nonnative mysid shrimp Mysis relicta. Thus, the observed interactions may have been stronger.
Table 1.—Responses of Yellowstone cutthroat trout (YCT), zooplankton, and phytoplankton to the introduction of lake trout into Yellowstone Lake. Based on trophic cascade theory, we predicted the response of variables to the addition of lake trout. Means and 95% confidence intervals (MoE = margin of error) of the response variables are reported. The mean and MoE of zooplankton biomass were bootstrapped, and phytoplankton biovolume was calculated from sequential differences. We calculated significant differences in zooplankton and phytoplankton based on changes between the pre- and postintroduction periods (see Methods). We compared the response variables for the past (before 1998) and present (after 2003) using a log response ratio of means ($\log_{10}(X_{\text{present}}/X_{\text{past}})$). Lake trout enhanced the variable when the ratio was positive and reduced the variable when the ratio was negative; ratios near zero indicate that the variable was similar between the two time periods. The conclusion column states whether the data fit the prediction (yes), produced the opposite finding as expected (no), or were inconclusive (?). Asterisks indicate that the two time periods were significantly different and agreed with the hypothesis (after Hebblewhite et al. 2005).

<table>
<thead>
<tr>
<th>Variable Description</th>
<th>Prediction</th>
<th>Past</th>
<th>Present</th>
<th>P-value</th>
<th>Log ratio</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>YCT abundance (fish/net)</td>
<td>–</td>
<td>15.5</td>
<td>19</td>
<td>6.2</td>
<td>1.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Zooplankton individual length (mm; Daphnia pulicaria)</td>
<td>+</td>
<td>1.88</td>
<td>0.088</td>
<td>2.24</td>
<td>0.076</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Zooplankton assemblage length (mm)</td>
<td>+</td>
<td>0.40</td>
<td>0.04</td>
<td>0.55</td>
<td>0.01</td>
<td>0.0095</td>
</tr>
<tr>
<td>Zooplankton biomass (mg dry mass [DM]/m$^3$)</td>
<td>+</td>
<td>49.7</td>
<td>10.4</td>
<td>97.8</td>
<td>2.97</td>
<td>0.30</td>
</tr>
<tr>
<td>Large zooplankton biomass (mg DM/m$^3$)</td>
<td>+</td>
<td>16.6</td>
<td>4.6</td>
<td>63.3</td>
<td>2.3</td>
<td>0.58</td>
</tr>
<tr>
<td>Cladoceran biomass (mg DM/m$^3$)</td>
<td>+</td>
<td>13.9</td>
<td>3.9</td>
<td>46.9</td>
<td>2.3</td>
<td>0.53</td>
</tr>
<tr>
<td>Zooplankton production (mg DM/m$^3$)</td>
<td>–</td>
<td>5.4</td>
<td>4.8</td>
<td>–0.05</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Phytoplankton biovolume (mm$^3$/m$^3$)</td>
<td>–</td>
<td>214</td>
<td>40</td>
<td>74</td>
<td>9</td>
<td>0.47</td>
</tr>
<tr>
<td>Chlorophyll $a$ (ug/L)</td>
<td>–</td>
<td>1.9</td>
<td>0.2</td>
<td>0.8</td>
<td>0.4</td>
<td>0.0002</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>+</td>
<td>10.0</td>
<td>11.6</td>
<td></td>
<td></td>
<td>0.0033</td>
</tr>
</tbody>
</table>

* Index of YCT abundance from fall gillnetting surveys (Figure 3) in 1977 and 2006.
* Confidence intervals were not calculated for secondary production estimates.
* Past phytoplankton biovolume was from 1972 (Knight 1975).
* Secchi depth was calculated using the model in Figure 6 based on a date of 15 August (Julian day 228) in 1976 and 2006.

because there are few fish to replace the role of Yellowstone cutthroat trout in the food web of Yellowstone Lake.

Alternative Hypotheses

Other factors besides the introduction of lake trout may have altered the trophic structure of Yellowstone Lake. For example, surface water temperatures increased by 0.29°C per decade in Yellowstone Lake during the past 30 years (i.e., 1976–2006; Tronstad, Hall, and Koel, unpublished data). Such temperature increases could directly influence the zooplankton and phytoplankton of the lake. Similar to Yellowstone Lake, March–June water temperatures in Lake Washington, Washington, increased by 0.35°C per decade during the past 40 years (i.e., 1962–2002; Winder and Schindler 2004). The altered thermal regime in Lake Washington caused asynchrony in Daphnia and phytoplankton blooms. As a result, densities of Daphnia declined, but there were no increases in adult size (Winder and Schindler 2004). In addition, Winder and Schindler (2004) observed higher juvenile Daphnia mortality with increasing temperatures, suggesting low food availability. In contrast with Lake Washington, Daphnia in Yellowstone Lake have become both more abundant and larger, suggesting reduced predation pressure rather than responses to water temperatures and low food availability (e.g., Brooks and Dodson 1965). We suggest that the observed changes in the Yellowstone Lake zooplankton assemblage are more likely due to the introduction of lake trout and loss of Yellowstone cutthroat trout than to increased temperature.

Climate change may also affect the phytoplankton assemblage in Yellowstone Lake by altering precipitation and nutrient availability. Using experiments and observations, Interlandi and Kilham (1998) predicted that increasing atmospheric nitrogen deposition would shift the phytoplankton assemblage from diatoms to green and blue-green algae. Despite increasing atmospheric nitrogen deposition at Tower, Yellowstone National Park (NADP 2007; http://nadp.sws.uiuc.edu/), we observed higher diatom densities in 2004 compared with those observed in 1996–1997. However, a zooplankton assemblage dominated by large individuals (four trophic levels) decreased the biovolume of large phytoplankton (Carpenter et al. 1987) because of an increased capacity to handle and consume larger phytoplankton taxa (Bergquist et al. 1985). Similarly, the decrease in Stephanodiscus yellowstonensis, a large centric diatom (mean biovolume $\approx 2,480$ μm$^3$/individual), was probably caused by altered zooplankton grazing. Conversely, the colonial diatom Asterionella increased when the zooplankton assemblage was dominated by cladocerans (four trophic levels; Bergquist et al. 1985), similar to our observations in
Yellowstone Lake. Finally, we did not observe the *Anabaena* sp. (blue-green algae) bloom in Yellowstone Lake during 2004 (0 mm$^3$/m$^3$ on 26 August 2004), whereas such blooms were observed prior to the introduction of lake trout (360 mm$^3$/m$^3$ on 25 August 1972; Knight 1975). Likewise, Scavia et al. (1988) noted a high biomass of blue-green algae under three trophic levels and extremely low biomass under two trophic levels. Our data suggest that the decreases in phytoplankton biomass and biovolume were more likely due to increased grazing pressure of a zooplankton assemblage dominated by large cladocerans than to climate change or increasing nitrogen deposition.

Drought may reduce Yellowstone cutthroat trout abundance and alter the trophic structure of Yellowstone Lake. During drought years, low water levels in small spawning streams can kill juvenile Yellowstone cutthroat trout (Koel et al. 2005). To estimate the degree to which drought caused the Yellowstone cutthroat trout decline, we compared discharge of the Yellowstone Lake outlet with indices of Yellowstone cutthroat trout abundance over time (Figure 3). Abundance decreased during both wet and dry years; thus, we attribute most of the loss of Yellowstone cutthroat trout to lake trout predation.

**Management Implications**

The ecosystem consequences of introducing predators are more easily understood when a single perturbation occurs, such as the loss of an apex oceanic predator as occurred in the Scotian Shelf ecosystem (Frank et al. 2005). The effects of numerous invasive predators and perturbations can be difficult to untangle, such as in the Great Lakes (e.g., Scavia et al. 1988; Kitchell et al. 2000; Mills et al. 2003). However, studying the effects of an invasive predator in an otherwise relatively undisturbed ecosystem is opportune. We demonstrated that lake trout likely induced a four-level trophic cascade and decreased primary producer biomass. Lake trout have been introduced into over 200 lakes and reservoirs in the western United States (Martinez et al. 2009), and these piscivores may induce trophic cascades and change energy flow in water bodies with native salmonids.

In Yellowstone Lake, the impacts of lake trout predation have resulted in a population decline from which the Yellowstone cutthroat trout may be unable to fully recover. The effects of lake trout predation were transmitted down the food web, indicating strong interactions at each trophic level. However, the interaction between humans and lake trout is weak. Even with intensive lake trout suppression efforts by the NPS, evidence suggests that lake trout continue to regulate Yellowstone cutthroat trout and maintain an altered trophic structure within Yellowstone Lake. Future research should address how much lake trout removal is needed to allow recovery of Yellowstone cutthroat trout and reversion of the Yellowstone Lake food web to its historic configuration.

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**References**


Link, J., and M. H. Hoff. 1998. Relationships of lake herring (Coregonus artedii) gill raker characteristics to retention...