Lake trout–induced spatial variation in the benthic invertebrates of Yellowstone Lake

Invasive lake trout indirectly increased biomass and body mass of amphipods

Figure 1. Lake trout were illegally introduced to Yellowstone Lake around 1985 and have been a disruptive influence to the lake ecosystem since.

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Abstract

Invasive predators can induce trophic cascades in the open water of lakes; however, much less is known about their effect on benthic invertebrates, which inhabit the lake bottom, or benthic zone. Lake trout (*Salvelinus namaycush*) were introduced to Yellowstone Lake, Wyoming, and reduced the Yellowstone cutthroat trout (*Oncorhynchus clakrii bouvieri*) population. We predicted that lake trout indirectly reduced predation of benthic invertebrates through cutthroat trout. To estimate how the benthic invertebrate assemblages differed under cutthroat trout– versus lake trout–dominated food webs, we collected benthic invertebrate samples from two areas of Yellowstone Lake in 2004 using a Ponar sampler and compared them with stomach contents from cutthroat trout. Cutthroat trout selectively ate benthic invertebrates with the largest body sizes. The amphipod genus, *Gammarus*, had the highest biomass of all benthic invertebrates. *Gammarus* biomass was higher in West Thumb (6,000 mg/m^2 [0.02 oz/ft^2]) where lake trout dominated and lower in South Arm (3,160 mg/m^2 [0.01 oz/ft^2]) where cutthroat trout dominated ($p = 0.01$). Additionally, individual body mass of *Gammarus* was greater in West Thumb (1.6 mg/individual [0.000056 oz/individual]) than in South Arm (1.1 mg/individual [0.000039 oz/individual; $p = 0.01$). Our results suggest that lake trout predation on cutthroat trout indirectly reduced predation on *Gammarus* in West Thumb, leading to a relative increase in the local *Gammarus* biomass and body mass. Monitoring the benthos of Yellowstone Lake may allow managers to understand the food web dynamics at higher trophic levels.

Key words

diet, invasive species, invertebrates, trophic cascade, Yellowstone cutthroat trout

LAKE TROUT (*SALVELINUS NAMAYCUSH*) HAVE BEEN widely introduced, both legally and illegally, throughout the western United States (Martinez et al. 2009) (fig. 1). These fish are considered apex predators in lakes because they occupy the top trophic level (Post et al. 2000). Lake trout have been successful invaders in many lakes and can alter ecosystems through competition, hybridization, predation, and trophic cascades, described below (Martinez et al. 2009). For example, lake trout in two Idaho lakes reduced bull trout (*Salvelinus confluentus*) populations through competition, and lake trout can hybridize with other trout, such as brook trout (*Salvelinus fontinalis*; Behnke 2002). These piscivores (fish predators) have reduced the native fish populations in many lakes and reservoirs (Martinez et al. 2009), which can lead to a trophic cascade that alters the structure of the pelagic (open water) food web (Tronstad et al. 2010). The effects of trophic cascades have been studied thoroughly in the pelagic zone of lakes, but few studies have examined trophic cascades in the lake benthos (life associated with the bottom substrate of aquatic habitats; fig. 2, next page).

Introduced lake trout can change lower trophic levels through direct and indirect effects (Tronstad et al. 2010). Trophic cascades are naturally occurring processes in ecosystems where

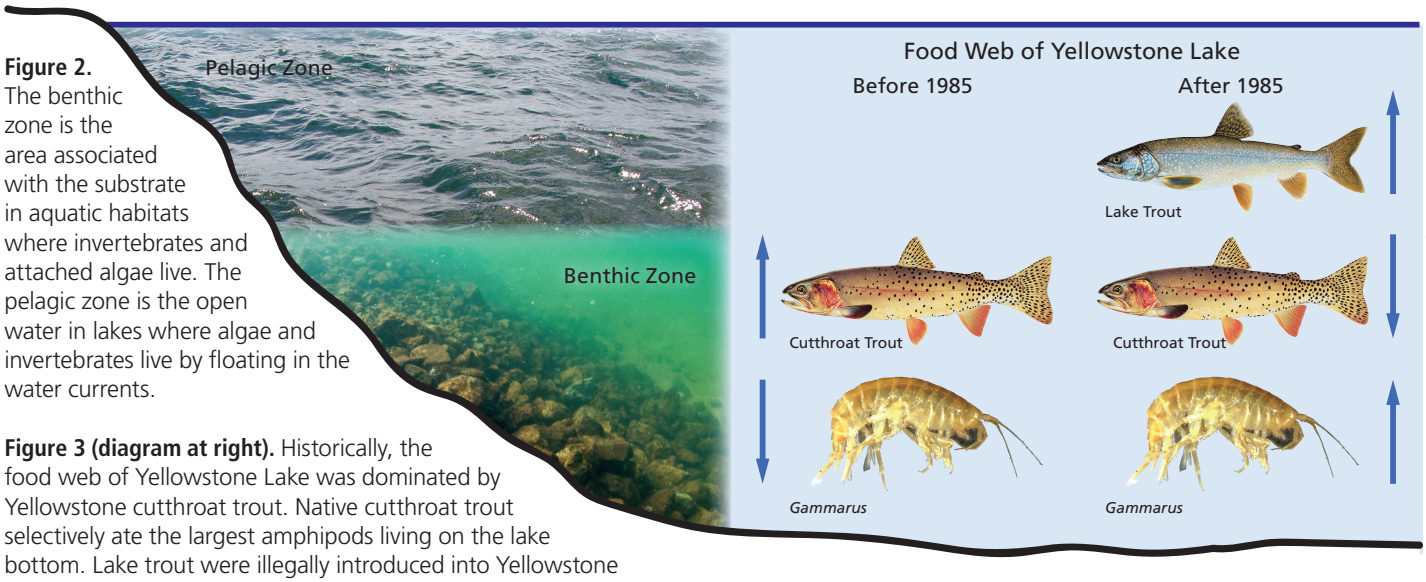

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Figure 2. The benthic zone is the area associated with the substrate in aquatic habitats where invertebrates and attached algae live. The pelagic zone is the open water in lakes where algae and invertebrates live by floating in the water currents.

Figure 3 (diagram at right). Historically, the food web of Yellowstone Lake was dominated by Yellowstone cutthroat trout. Native cutthroat trout selectively ate the largest amphipods living on the lake bottom. Lake trout were illegally introduced into Yellowstone Lake around 1985 and these fish likely caused a trophic cascade where the biomass (weight; arrows) of animals alternates between trophic levels. Lake trout have reduced cutthroat trout and increased the biomass and body size of amphipods (*Gammarus*) in areas where these invasive predators are abundant. Our study used South Arm as a representation of the pre–lake trout assemblages and West Thumb for the post–lake trout assemblages.

top predators control the biomass of lower trophic levels (the position an organism occupies in the food web). These top-down effects create a pattern of alternating biomass from high to low between trophic levels (e.g., Carpenter et al. 1987; fig. 3). Trophic cascades also alter the body size of herbivores. For example, the introduction of northern pike (*Esox lucius*) in a Canadian lake reduced the abundance of plankton-eating fish, increased the body size of zooplankton (microscopic invertebrates that live in the pelagic zone of lakes), and decreased phytoplankton (algae that live in the pelagic zone of lakes) biomass (Findlay et al. 2005). Introducing a species that occupies a new trophic level can alter the structure of the food web when interactions among trophic levels are strong.

Trophic cascades can occur when predators eat a variety of organisms, but predators can still affect lower trophic levels when they eat specific prey. For example, specialist fish predators preferentially fed on and drastically reduced specific prey taxa but had less of an effect on other benthic invertebrates (Brönmark 1994). Despite reducing only prey taxa, these fish indirectly increased benthic primary production. Current knowledge of benthic trophic cascades is based on enclosure manipulations (Brönmark et al. 1992; Brönmark 1994) and observations in ponds (Brönmark and Weisner 1996). Carpenter and Kitchell (1993) recommend conducting in situ studies on the lake benthos to better understand food web dynamics.

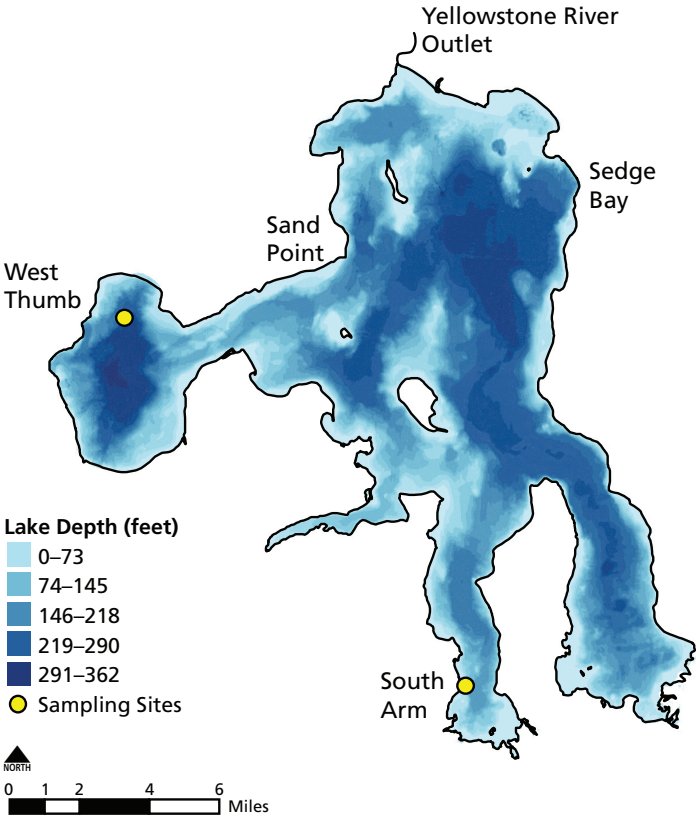

Figure 4. Map of Yellowstone Lake showing our study sites.

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Figure 5. We compared invertebrates living on the lake bottom in two areas of Yellowstone Lake: Carrington Island in West Thumb (left) and South Arm (right).

Yellowstone Lake ecosystem

Indigenous fish species within Yellowstone Lake include Yellowstone cutthroat trout (*Onchorynchus clarkii bouveri*) and longnose dace (*Rhinichthys cataractae*; Gresswell et al. 1997). Lake trout were illegally introduced into Yellowstone Lake around 1985 (Munro et al. 2005) and discovered in 1994 (Kaeding et al. 1996). In addition to lake trout, redside shiner (*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and longnose sucker (*Catostomus catostornus*; Gresswell and Varley 1988) have been introduced to Yellowstone Lake. Lake trout and cutthroat trout are the dominant fish in the lake and the other species occur in much lower abundances. After their introduction, lake trout flourished and decreased the abundance of native Yellowstone cutthroat trout through predation (Koel et al. 2005). Lake trout feed heavily upon cutthroat trout and can attain relatively large body sizes (e.g., 120 cm [47 in] and 11 kg [25 lb]; Behnke 2002), allowing them to eat more and larger cutthroat trout. Additionally, Ruzycki et al. (2003) estimated that lake trout can eat cutthroat trout up to 57% of their body length. In the Yellowstone Lake food web, lake trout filled a new niche (fourth trophic level) and induced a four-level trophic cascade in the pelagic zone of Yellowstone Lake (Tronstad et al. 2010; see fig. 3). The introduction of lake trout indirectly increased the biomass and body size of zooplankton, resulting in lower biomass of phytoplankton.

Despite an altered pelagic food web, the degree to which lake trout disrupted the benthic or lake bottom food web of Yellowstone Lake has not been studied before. Benthic invertebrates may have been altered indirectly by the lake trout invasion because cutthroat trout feed heavily on amphipods within the littoral or nearshore zone that is less than 20 m (66 ft) deep (Tronstad et al. 2015; see fig. 2). Amphipods or scuds are small crustaceans that are abundant in Yellowstone Lake. *Gammarus* is the most common amphipod in the lake. Our goal was to estimate the degree to which lake trout indirectly altered the benthic invertebrates of Yellowstone Lake. We studied two sites within Yellowstone Lake (figs. 4 and 5) with varying densities of cutthroat trout and lake trout. This was necessary as a space-for-time substitution because benthic invertebrates were not collected when cutthroat trout were abundant. South Arm has higher cutthroat trout densities than West Thumb (fig. 6, next page) and is considered the last spatial refuge for this native trout within Yellowstone Lake (Koel et al. 2004). Our specific questions were: (1) How did the biomass of invertebrates compare between sites with different trout abundances? (2) To what degree did amphipod biomass and size differ between sites? (3) How did the assemblage and body mass of invertebrates in cutthroat trout diets compare with benthic samples? And (4) How strong were the interactions between lake trout, Yellowstone cutthroat trout, and amphipods?

Material and methods

Study area

Yellowstone Lake is located in Yellowstone National Park in northwestern Wyoming and is the largest lake in North America above an elevation of 2,000 m (6,562 ft; Gresswell et al. 1997). The lake has a surface area of 340.0 km^2 (131.3 mi^2) and a mean depth of 43 m (141 ft; Kaplinski 1991). The littoral zone of Yellowstone Lake occupies 81.0 km^2 (31.3 mi^2) and encompasses about 24% of the lake (Benson 1961). Ice covers the lake from December through May (Gresswell and Varley 1988) and the primary productivity is mesotrophic (moderate productivity by algae; Kilham et al. 1996).

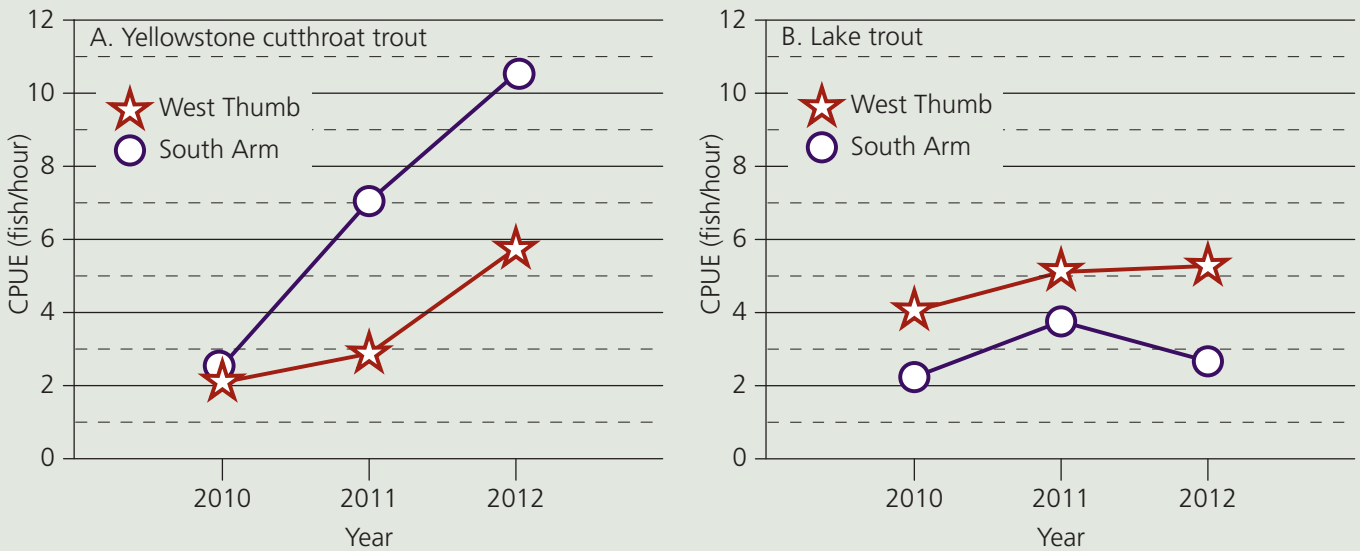

Figure 6. (A) Catch per unit effort (CPUE) of Yellowstone cutthroat trout was higher in South Arm than in West Thumb over a three-year period. (B) CPUE of lake trout was higher in West Thumb than in South Arm over a three-year period.

Patterns of habitat use differ between lake trout and cutthroat trout. Lake trout live deep within the pelagic zone, feeding on invertebrates as juveniles and preying on fish as adults (Ruzycki et al. 2003). In Yellowstone Lake, lake trout have large home ranges and move throughout the lake in search of food (T. Koel and J. Arnold, personal observation). Juvenile cutthroat trout are thought to live in the pelagic zone (Gresswell and Varley 1988), which may make them more vulnerable to predation by lake trout. Adult cutthroat trout move into the littoral zone of the lake and feed on both zooplankton and benthic macroinvertebrates (Benson 1961).

Shortly after the discovery of lake trout in Yellowstone Lake, fisheries managers at Yellowstone National Park initiated an aggressive removal program in an attempt to conserve cutthroat trout (Koel et al. 2005). These efforts have progressively increased since implementation. Using gill nets, resource managers removed approximately 25,000 lake trout from Yellowstone Lake in 2004 and more than 200,000 in 2011 (Koel et al. 2012*b*)

Sampling and laboratory analysis

We collected invertebrate samples in the littoral zone of West Thumb and South Arm during the ice-free months of June to November 2004 to estimate their density and biomass. The West Thumb site was near Carrington Island and the South Arm site was near the southern end of the lake at the edge of the motorless zone (figs. 4 and 5). We collected four samples from each site on six dates: 30 June, 14 July, 29 July, 30 August, 23 September, and 21 October. We sampled the benthos using a Ponar grab sampler (524 cm^2 [81 in^2] sampling area) attached to a winch and a crane mounted on a boat (fig. 7). We sieved samples with 500 µm (0.02 in) mesh and preserved samples in approximately 75% ethanol.

We removed invertebrates from the debris in the laboratory and identified individuals under a dissecting microscope using dichotomous keys (Merritt et al. 2008; Thorp and Covich 2010). We counted all individuals in each sample to calculate density. Additionally, we measured the first 20 haphazardly chosen individuals of each taxon to calculate biomass (ash-free dry mass [AFDM] of all animals per unit area of the lake bottom). We estimated invertebrate biomass for most taxa using previously published length-mass regressions (Benke et al. 1999; Johnson et al. 2012). For taxa that did not have published length-mass regressions, we calculated biomass using other methods. For leeches, we randomly selected five individuals from each species and dried them in an oven at 65°C (149°F) for 18 hours. The leeches were placed in a desiccator for 1 hour before weighing. To calculate biomass for oligochaetes, ostracods, copepods, nematodes, and acari we estimated a mean length and width based on individuals in the samples, and we assumed a specific gravity of 1.13 and a dry mass–to–wet mass conversion of 0.25 (Feller and Warwick 1988).

We measured the density and biomass of trout stomach contents to estimate the degree to which cutthroat trout feed on benthic invertebrates. We were unable to use historical information because biomass of stomach contents was not previously calculated (Benson 1961; Jones et al. 1990). We caught seven cutthroat trout

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Figure 7. Ponar sampler and winch attached to a boat used to collect aquatic invertebrates from the littoral zone (<20 m [66 ft] depth) of Yellowstone Lake.

Our goal was to estimate the degree to which lake trout indirectly altered the benthic invertebrates of Yellowstone Lake.

at Sand Point in June 2004 and flushed their stomachs to identify and measure what they were eating. Invertebrates in stomach contents were identified to the lowest possible taxonomic level, counted, and measured. We examined gut contents under a dissecting microscope and calculated individual and total biomass of gut contents using the same principles as for the benthic fauna analysis above (e.g., Benke et al. 1999).

We used the method by Cross et al. (2011) to compare the species impact of cutthroat trout and lake trout on *Gammarus*. The species impact is the production of *Gammarus* (accumulation of *Gammarus* biomass over time) consumed by trout divided by *Gammarus* biomass in the benthos of Yellowstone Lake. Cross et al. (2011) found an annual production-to-biomass ratio of 3.3/year for rainbow trout (*Onchorynchus mykiss*) in Lake Powell (Glen Canyon National Recreational Area, Utah and Arizona). This finding means that rainbow trout produce 3.3 times as much mass in a year relative to the mass of all these fish at a given time. We assumed that this value was similar for cutthroat trout and lake trout in Yellowstone Lake.

We multiplied annual trout production-to-biomass ratio by trout biomass in each area of the lake (g/m^2) to estimate annual fish consumption (g/m^2/yr, or grams per meter squared per year). We used mean individual size to estimate trout biomass for cutthroat trout (350 mm [14 in] total length; 85 g [3 oz] dry mass; Tronstad et al. 2015) and lake trout (500 mm [20 in] total length; 264 g [9 oz] dry mass; Syslo et al. 2011) in Yellowstone Lake. We multiplied annual fish production by the proportion of *Gammarus* in trout stomach contents to estimate the production of trout from *Gammarus* (Pgam; g/m^2/yr). In other words, we calculated the amount of trout biomass that is produced annually from eating *Gammarus*. *Gammarus* made up 9.8% of lake trout stomach contents by volume (Ruzycki et al. 2003). The proportion of cutthroat trout diet from *Gammarus* was calculated based on biomass of *Gammarus* in each stomach sample divided by total biomass in each stomach.

The number of lake trout and cutthroat trout in each study area was estimated based on total population size and catch in each area. In 2004, the total cutthroat trout population in Yellowstone Lake was estimated at 1.4 million individuals (Tronstad et al. 2015) and the total lake trout population was approximately 125,000 individuals (Syslo et al. 2011). We calculated the number of lake trout and cutthroat trout in West Thumb and South Arm using proportions based on catch per unit effort (CPUE) values throughout the lake in 2010 (Koel et al. 2012*a*); however, previous years did not have estimates of lake trout CPUE. The littoral zone area was calculated for South Arm (11.0 km^2 [4.2 mi^2]) and West Thumb (8.6 km^2 [3.3 mi^2]) using ArcMap and bathymetry (underwater depth; unpublished data, Yellowstone National Park). Using total cutthroat trout and lake trout biomass, we calculated total biomass for each species per unit area of the littoral zone for both study sites. We calculated the species impact for cutthroat trout and lake trout on *Gammarus* in West Thumb and South Arm by dividing the production of trout from *Gammarus* (Pgam) by the biomass of *Gammarus* from benthic samples (g/m^2).

We used R version 3.0.0 (R Core Development Team 2013) for calculations and statistical analyses. We used the Wilcoxon signed rank test to test for differences in density, biomass, and individual body mass between South Arm and West Thumb, because our data were not normally distributed. We subtracted South Arm values from West Thumb values and tested whether the difference was significantly greater than zero, because we predicted that biomass and body size would be higher in West Thumb where lake trout are more abundant. We estimated error by "bootstrapping" 95% confidence intervals (CI; the region between the 2.5% and 97.5% quantiles), because our data were not normally distributed and contained many zeros for rare taxa (e.g., Huryn 1996).

Bootstrapping uses the data we collected to estimate the uncertainty in our measures without making any assumptions about the distribution of our data. We sampled with replacement 10,000 times from the four replicate samples and six dates for each taxon at each site (i.e., 24 samples total from each site).

Results

We collected 23 taxa of invertebrates in three phyla in the benthos of Yellowstone Lake. Noninsects (6,100 individuals/m² [600 individuals/ft²]) had lower density than insects (8,900 individuals/m² [800 individuals/ft²]), but they also had much higher biomass (7,100 mg/m² [0.02 oz/ft²]) than insects (500 mg/m² [0.002 oz/ft²]; table 1). Of the noninsects, amphipods had the highest density (2,500 individuals/m² [200 individuals/ft²]) and biomass (2,500 mg/m² [0.008 oz ft²]), followed by oligochaetes (500 individuals/m² [50 individuals/ft²] and 1,200 mg/m² [0.004 oz/ft²]). We collected three orders of insects, including Ephemeroptera (mayflies), Trichoptera (caddisflies), and Diptera (true flies). The family Chironomidae (nonbiting midges) had by far the highest density (8,800 individuals/m² [800 individuals/ft²]) and biomass (400 mg/m² [0.001 oz/ft²]; table 1).

Although values for density and biomass of most taxa were higher in West Thumb than in South Arm, the differences were not statistically significant ($p > 0.05$). Total density ($p = 0.81$) and biomass ($p = 0.10$) of invertebrates was similar between sites (table 1). Conversely, Ephemeroptera density ($p < 0.01$) and biomass ($p < 0.01$) were greater in West Thumb than in South Arm. Noninsects had marginally higher biomass in West Thumb ($p = 0.06$; table 1). This pattern is driven primarily by slightly higher biomass of crustaceans ($p = 0.04$), and specifically *Gammarus* ($p = 0.01$), in West Thumb where lake trout are more abundant.

Gammarus was a dominant taxon in the benthos of Yellowstone Lake and their biomass differed between sites. *Gammarus* comprised 69% of the assemblage in West Thumb and 49% of the assemblage in South Arm based on biomass. We collected 75% higher biomass of *Gammarus* in West Thumb than in South Arm ($p = 0.01$; fig. 8A). Individual *Gammarus* body mass was 50% greater in West Thumb than in South Arm ($p < 0.01$; fig. 8B).

Gammarus makes up a large proportion of the invertebrates that cutthroat trout eat in Yellowstone Lake. This amphipod (52%) dominated invertebrate biomass in cutthroat trout stomachs, followed by *Daphnia* (water fleas; 29%), Chironomidae (midges; 12%), Ephemeroptera (mayflies; 2%), and Copepoda (copepods; 2%). The individual body mass of invertebrates in cutthroat trout stomachs was larger than in individuals in benthic samples. Mean *Gammarus* body mass was 9.6 mg/individual (0.0003 oz/individual) in cutthroat trout stomachs compared to 1.3 mg/individual (0.00005 oz/individual) in benthic samples. Mean body mass of Ephemeroptera in cutthroat trout stomachs was 2.7 mg/individual

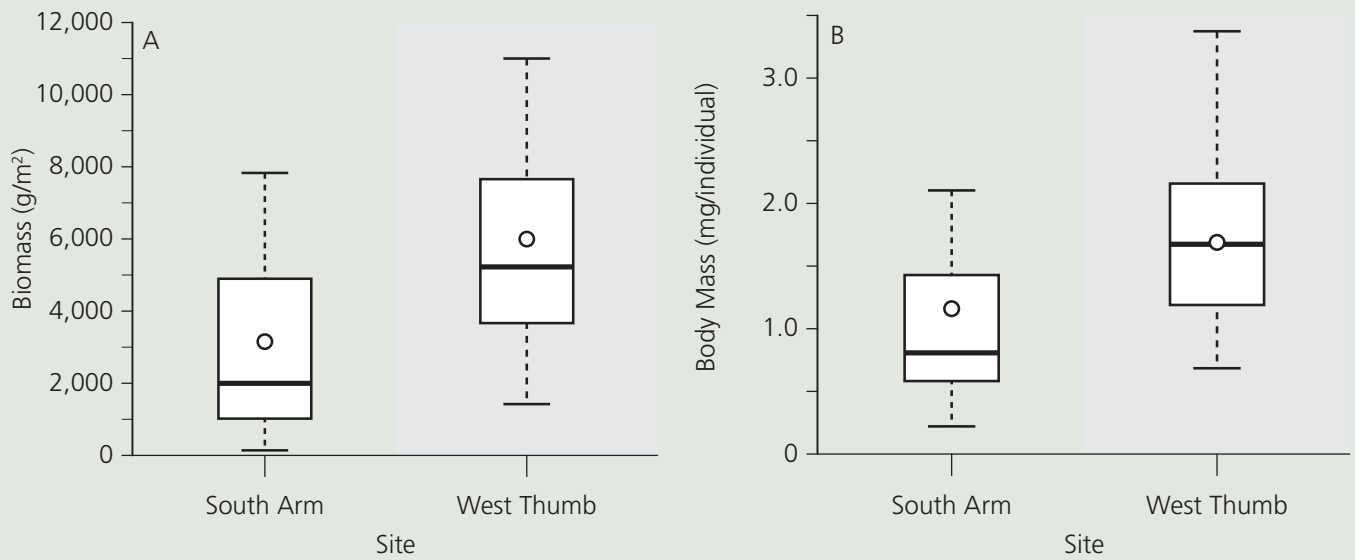

Figure 8. (A) Total biomass of *Gammarus* in South Arm and West Thumb, and (B) individual body mass of *Gammarus* in South Arm and West Thumb. Bold lines represent median values, and upper and lower edges of the boxes represent the 75th (top) and 25th (bottom) percentiles. Bars are minimum and maximum values and circles represent mean values.

Table 1. Mean density and biomass of benthic invertebrates in South Arm and West Thumb of Yellowstone Lake

	Density (individuals/m²)		Biomass (mg/m²)	
Taxon[a]	**South Arm**	**West Thumb**	**South Arm**	**West Thumb**
Ephemeroptera	**11 (0–32)**	**94 (0–248)**	**10 (0–51)**	**67 (0–206)**
Trichoptera	22 (0–76)	38 (0–97)	17 (0–91)	15 (0–54)
Diptera	9,289 (3,463–17,132)	8,319 (2,738–20,108)	522 (185–1,138)	372 (106–857)
Chironomidae	9,259 (3,420–16,949)	8,223 (2,565–19,676)	522 (185–1,137)	372 (108–866)
Crustacea	4,897 (2,359–7,749)	5,216 (2,165–9,762)	**3,880 (1,340–7,402)**	**5,998 (2,793–10,995)**
Gammarus	2,902 (1,342–5,163)	3,452 (2,186–6,255)	**3,160 (957–6,597)**	**5,500 (3,403–10,262)**
Hyallela	1,923 (498–3,788)	1,699 (32–4,751)	671 (99–2,113)	486 (7–1,540)
Annelida	657 (152–1,483)	756 (173–1,710)	1,848 (535–3,774)	2,099 (594–4,254)
H. stagnalis[b]	36 (0–119)	70 (0–281)	34 (0–115)	68 (0–262)
N. obscura[b]	105 (22–206)	124 (54–303)	670 (139–1,316)	797 (346–1,939)
Oligochaeta	514 (54–1,342)	552 (76–1,483)	1,141 (120–2,979)	1,225 (168–3,316)
Mollusca	283 (11–844)	139 (0–541)	171 (0–568)	100 (0–473)
Sphaeriidae	267 (0–823)	114 (0–509)	45 (0–223)	6 (0–22)
Planorbidae	14 (0–54)	11 (0–54)	126 (0–471)	94 (0–471)
Insect	9,321 (3,528–17,262)	8,450 (2,813–20,022)	549 (198–1,167)	453 (152–954)
Noninsect	6,044 (2,825–10,649)	6,255 (2,565–11,970)	5,901 (2,488–9,895)	8,199 (3,929–14,208)
Total	15,365 (7,835–24,535)	14,705 (6,050–27,803)	6,450 (2,869–10,542)	8,652 (4,301–14,884)

Note: Boldfaced taxa represent summed means for all individuals within a group. Bootstrapped confidence intervals are in parentheses and boldfaced values represent significant differences where p-values ≤ 0.05. Bootstrapping uses the data we collected to estimate the uncertainty in our measures without making any assumptions about the distribution of our data.

[a]We omitted taxa with biomass <10 mg/m² from the table, but we included these taxa in totals. Taxa not listed in the table were Ephemeroptera (Baetis, Ephemerella, Ephemerellidae, and Serratella), Trichoptera (Apatania, Brachycentrus, Molanna, and Oecetis), Diptera (Culicoides), Crustacea (Ostracoda and Harpacticoida), Annelida (*Glossiphonia complanata*), Mollusca (Planorbidae and Physidae), and Arachnida.

[b]*Helobdella stagnalis* and *Nephelopsis obscura*.

(0.0001 oz/individual) compared to 0.8 mg/individual (0.00003 oz/individual) in benthic samples. Chironomidae mean body mass in cutthroat trout stomachs was 0.3 mg/individual (0.000001 oz/individual) compared to 0.05 mg/individual (0.000002 mg/individual) in the benthos.

Cutthroat trout strongly interacted with *Gammarus* in South Arm where these fish are numerous. They had a larger species impact on *Gammarus* in South Arm than in West Thumb, as we predicted based on cutthroat trout numbers and food web dynamics (table 2, next page). Conversely, lake trout had a much smaller species impact on *Gammarus* at both sites (table 2, next page). Assuming the annual production-to-biomass ratio for *Gammarus* in Yellowstone Lake is 5 per year (Benke and Huryn 2007), cutthroat trout ate half of *Gammarus* production in South Arm and 17% of *Gammarus* production in West Thumb. Lake trout ate far less *Gammarus* production at both sites (< 5%).

Table 2. Parameters for calculating species impact of Yellowstone cutthroat trout and lake trout on *Gammarus* in South Arm and West Thumb of Yellowstone Lake

Fish Species	Site	Trout Biomass[a] in Littoral Zone (g DM/m²)	*Gammarus* consumed by trout (g DM/m²/yr)	Production of Trout from *Gammarus* Consumption (g DM/m²/yr)	Species Impact
Yellowstone cutthroat trout	South Arm	4.4	15	7.7	2.4
	West Thumb	2.9	10	5.2	0.9
Lake trout	South Arm	0.8	3	0.3	0.1
	West Thumb	1.9	6	0.6	0.1

[a]Biomass is the dry weight of animals, production is the accumulation of biomass over time, and units are in dry mass (DM) (Syslo et al. 2011; Koel et al. 2012*a*).

Discussion

Invasive lake trout reduced the abundance of cutthroat trout in Yellowstone Lake (Koel et al. 2005), which increased the mean biomass and body size of cutthroat trout's dominant food source, *Gammarus*. Lake trout directly reduced cutthroat trout through predation and indirectly released *Gammarus* from predation by cutthroat trout (fig. 3). Cutthroat trout reduced *Gammarus* biomass and body size in South Arm where these fish are still relatively abundant (fig. 8). In contrast, *Gammarus* populations show greater biomass and greater individual body mass in West Thumb where lake trout dominated.

Our results suggest that cutthroat trout are eating the largest *Gammarus* in Yellowstone Lake, inducing spatial variation in the benthic invertebrate assemblage. Cutthroat trout feed heavily on *Gammarus* and higher abundances of native trout mean fewer and smaller *Gammarus*. Unfortunately, benthic invertebrate samples were not collected in the past when cutthroat trout were abundant throughout the lake, but differences in *Gammarus* biomass and individual body mass may be even greater in pre– versus post–lake trout invasion samples had they been available for comparison. We collected samples after lake trout invaded Yellowstone Lake and cutthroat trout had drastically declined. We used variation in present trout densities to assess the degree to which a benthic trophic cascade may have occurred. Based on our results, lake trout likely induced a benthic trophic cascade whereby fewer cutthroat trout released *Gammarus* from predation.

Fish selectively feed on larger amphipods (Newman and Waters 1984; Wellborn 1994; Laudon et al. 2005). Newman and Waters (1984), for example, observed that brook trout, brown trout (*Salmo trutta*), rainbow trout, and sculpins (*Cottus cognatus*) selectively fed on larger *Gammarus* in a Minnesota stream, despite seasonal variation in mean body size of amphipods. Mean and median sizes of *Gammarus* in stomach samples from these fish species were much larger than those in the benthos. Similarly, invertebrates in the stomach contents of cutthroat trout were larger than invertebrates in benthic samples from Yellowstone Lake. Furthermore, *Gammarus* had greater mean individual body mass in West Thumb than in South Arm, suggesting that size-selective predation differed between sites. Cutthroat trout ate the largest available *Gammarus* in Yellowstone Lake, but these amphipods did not grow as large in South Arm because cutthroat trout were more abundant and collectively ate more.

The diet of cutthroat trout in Yellowstone Lake has been sampled extensively in the past. Despite our small sample size, past studies support our diet results. The stomach contents of cutthroat trout were collected in 1957 and 1958 (Benson 1961; $n = 344$ and 429 respectively), 1970 (Dean 1971; $n = 81$), 1974 (Scott 1977; $n = 56$), and 1989 (Jones et al. 1990; $n = 132$). These studies report that amphipods comprised between 4% and 40% of stomach contents based on number of individuals in each stomach sample. Tronstad et al. (2015) showed that percentage of amphipods in the diet of cutthroat trout was a function of cutthroat trout abundance. Cutthroat trout numbers varied over time from low abundances in the 1940s and 1950s, when egg-taking and liberal creel limits reduced the fish population, to the 1970s and 1980s, when the cutthroat trout abundance peaked (Koel et al. 2005). When cutthroat trout are less abundant they have more amphipods in their diet, perhaps because these crustaceans are more available. Similarly, our results showed that amphipods, specifically *Gammarus*, made up a large fraction of cutthroat trout diet and our results are similar to past studies when cutthroat trout were less abundant.

Most studies have investigated trophic cascades in the pelagic zone of lakes, but few studies have shown top-down effects on lake benthos. Trophic cascades were observed in benthic communities by manipulating organisms using enclosure and exclosure experiments in which the removal of pumpkinseeds (*Lepomis gibbosus*) altered the biomass of benthic algae in two Wisconsin

Based on our results, lake trout likely induced a benthic trophic cascade whereby fewer cutthroat trout released Gammarus *from predation.*

lakes (Brönmark et al. 1992). While we did not artificially manipulate fish densities in Yellowstone Lake, we used variation in the present densities of cutthroat and lake trout in two study areas as a space-for-time substitution. We did this to draw conclusions about the degree to which the invasion of lake trout and the subsequent decline of cutthroat trout altered benthic invertebrates in Yellowstone Lake.

Benthic trophic cascades have been observed less frequently in natural ecosystems. Brönmark and Weisner (1996) surveyed 44 ponds with two to four trophic levels in southern Sweden. Ponds with two or three trophic levels had strong interactions among organisms, but piscivores (fourth trophic level) weakly interacted with lower trophic levels. This is likely because piscivorous fishes could not eat their prey because they were too large. In contrast, we observed strong interactions among trophic levels in Yellowstone Lake. Differences in the benthic fauna in our study suggest lake trout prey heavily upon cutthroat trout. Change in body size of benthic fauna provides strong evidence that a trophic cascade occurred (Carpenter et al. 2001; Findlay et al. 2005) and we observed the predicted changes in body size of *Gammarus* (i.e., smaller in areas of more intense predation) in the benthos of Yellowstone Lake.

Alternative hypotheses

Differences in the benthic invertebrate assemblages may be due to factors other than the introduction of lake trout. The differences we observed between our sites may be attributed to hydrothermal inputs. West Thumb is located within the Yellowstone caldera where the presence of hydrothermal activity alters the chemistry of the lake (Morgan et al. 2003), whereas South Arm is outside the caldera. Ammonium-nitrogen concentrations (464 ppb) from hydrothermal waters in Sedge Bay of Yellowstone Lake were much higher than in ambient lake water (2 ppb; Klump et al. 1988). This nutrient input affected the biota immediately surrounding the thermal vents where microorganisms and oligochaetes flourished (Klump et al. 1988). Additionally, amphipods have been observed at high densities around the hydrothermal vents located in shallow areas of Yellowstone Lake (Morgan et al. 2003). Balistrieri et al. (2007) estimated fluid input from hydrothermal vents to be 16–25 million liters/day (4.2–6.6 million gallons/day). Given the average discharge of the Yellowstone River was about 3.5 billion liters/day (9.2 billion gallons/day; U.S. Geological Survey data, available at http://waterdata.usgs.gov; gage 06186500), the contribution of hydrothermal water into the lake is relatively low (< 1%). Therefore, nitrogen inputs from hydrothermal vents probably do not contribute a substantial amount of nitrogen to the lake. Furthermore, hydrothermal water is transported and mixed throughout the lake (Balistrieri et al. 2007), suggesting that water chemistry does not vary significantly from location to location. We do not attribute higher biomass and larger body mass of *Gammarus* to hydrothermal activity in West Thumb.

Lake trout may alter the biomass and body size of amphipods because these fish also feed on invertebrates. Amphipods comprised 25% of the diet of juvenile lake trout in Yellowstone Lake (Ruzycki et al. 2003). Although juvenile lake trout feed upon amphipods, they do so only for the first few years of their lives. Conversely, cutthroat trout feed on amphipods throughout their lives, suggesting that these fish eat far more amphipods than do lake trout. These differences are reflected in the species impacts on *Gammarus*, whereby the interaction between *Gammarus* and cutthroat trout is much stronger than the interaction between lake trout and *Gammarus*. Lake trout ate about 2% of *Gammarus* production at both of our sites in Yellowstone Lake. Therefore, the difference in amphipod biomass between our sites is probably not due to lake trout feeding on amphipods.

Management implications

Lake trout can indirectly affect lower trophic levels in the pelagic (Tronstad et al. 2010) and benthic zones of Yellowstone Lake. However, the effects of introduced lake trout may reach much further and actually alter nutrient cycling in tributary streams (Tronstad et al. 2015). Lake trout spawn within the lake and live deep in the water column, making them relatively inaccessible to avian and terrestrial predators. Conversely, cutthroat trout spawn in the shallow tributary streams of Yellowstone Lake and are more vulnerable to these kinds of predators. Historically, avian and terrestrial predators relied heavily on cutthroat trout as a food source (Koel et al. 2005). Currently, lower abundances of spawning cutthroat trout correlate with declining bear activity around Yellowstone Lake (Koel et al. 2005). Evidence suggests that the introduction of lake trout caused a trophic cascade that

began in Yellowstone Lake and rippled into tributary streams (Tronstad et al. 2015) and the surrounding terrestrial ecosystems (Middleton et al. 2013).

In an attempt to suppress the lake trout, the National Park Service implemented an aggressive removal program to conserve cutthroat trout. Although removal of lake trout has increased every year since their introduction (Koel et al. 2005), this highly invasive species has proven to be difficult to remove because they live deep in the pelagic zone, and Yellowstone Lake is relatively large and deep. Monitoring the benthic invertebrates of Yellowstone Lake, specifically *Gammarus*, may help managers to assess food web dynamics occurring at higher trophic levels. Combining benthic invertebrate and trout data will yield stronger and more informative results than either separately.

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