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An Invasive Predator Substantially Alters Energy Flux Without Changing Food Web Functional State or Stability

Hayley C. Glassic[1,2] | James R. Junker[3] | Christopher S. Guy[4] | Lusha M. Tronstad[5] | Michelle A. Briggs[2] | Lindsey K. Albertson[6] | Dominique R. Lujan[5] | Travis O. Brenden[7] | Timothy E. Walsworth[8] | Todd M. Koel[9]

[1]Northern Rocky Mountain Science Center, United States Geological Survey, Bozeman, Montana, USA | [2]Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, Montana, USA | [3]Department of Biological Sciences, University of North Texas, Denton, Texas, USA | [4]Montana Cooperative Fishery Research Unit, Montana State University, United States Geological Survey, Bozeman, Montana, USA | [5]Wyoming Natural Diversity Database and Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA | [6]Department of Ecology, Montana State University, Bozeman, Montana, USA | [7]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, USA | [8]Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, Utah, USA | [9]Native Fish Conservation Program, Yellowstone National Park, Wyoming, USA

Correspondence: Hayley C. Glassic (hglassic@usgs.gov)

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ABSTRACT

Understanding how invasive species affect the stability and function of ecosystems is critical for conservation. Here, we quantified the effect of an actively suppressed invasive species on the Yellowstone Lake ecosystem using a food web energetics approach. We compared energy flux, functional state, and stability of four food web states: a pre-invasion network and three post-invasion networks undergoing active invasive species suppression, namely, initial invasion, expansion, and decline. Invasion caused ≥25% change (±) in energy flux for most consumers, and total flux increased twofold post-invasion. Flux to the species of conservation concern, Yellowstone cutthroat trout (*Oncorhynchus virginalis bouvieri*), was 2.8 times less post-invasion versus pre-invasion, whereas invasive lake trout (*Salvelinus namaycush*) flux was up to 17.3 times higher compared to the initial invasion network. The dominant functional state and food web stability did not change post-invasion, likely due to introduction of a generalist predator and the stabilizing effect of suppression. Lake trout invasion in Yellowstone Lake caused large changes to energy flux, shifting dominant fluxes away from the species of conservation concern, despite not changing functional state or stability. We demonstrate that changes in energy flux may signal invasions in ecosystems, but functional state or stability may not necessarily reflect the magnitude of invasion influences. For invaded fish communities, a better understanding of how the invasive species control the food web beyond just the direct influence on prey can be achieved by investigating energy flux, functional state, and food web stability. Furthermore, evaluating the effect of suppression beyond the invasive species can demonstrate the far-reaching value of suppression management actions for conservation.

1 | Introduction

To identify whether an ecosystem is stable, an understanding of the structure and dynamics of the ecological network is critical. However, many challenges exist in explaining or quantifying structure and dynamics in ecological networks (Gauzens et al. 2018). Food web research has a robust history of empirical and theoretical network analysis (Elton 1927; Lindeman 1942;

MacArthur 1955; May 1973; Paine 1966). Network research is an expanding field in modern ecology (McCann 2000), especially as threats to biodiversity, including habitat loss and fragmentation, climate change, and invasive species, become more common (Cameron, Vilà, and Cabeza 2016; Chapin, Sala, and Huber-Sannwald 2013; Sala et al. 2000; Vilà et al. 2011; Vitousek, Loope, and Westbrooks 2017).

Invasive species can rewire food webs (Goto et al. 2020; Ogorelec 2021), leading to substantial changes in nutrient and energy pathways. Indirect effects of biological invasions can include non-consumptive effects (Coverdale et al. 2013; Heins, Knoper, and Baker 2016; Kindinger and Albins 2017), trophic cascades (Doody et al. 2017; Gallardo et al. 2016; Kimbro et al. 2009; Walsh, Carpenter, and Van Der Zanden 2016), and even species evolution (Lau 2012). Due to the influence of invasive species beyond predator–prey interactions, studying whole food webs can further elucidate consequences of species invasions (Baiser, Russell, and Lockwood 2010; Cameron, Vilà, and Cabeza 2016; DeVore and Maerz 2014; Pearson 2009; Smith and Schmitz 2015).

Disruptions by invasive species can operate over long time periods and shift food web dynamics (e.g., energy flux, dominant energetic pathways and stability; Neutel, Heesterbeek, and de Ruiter 2002). Using networks (Berlow et al. 2004) to describe natural communities, such as the food web energetics approach (De Ruiter, Neutel, and Moore 1995; Hunt et al. 1987), can aid in quantifying energy flux post-invasion. The dominant energetic pathway or functional state (i.e., herbivory, detritivory or carnivory) of a food web can regulate susceptibility to invasion (Sperfeld et al. 2010) and may be altered post-invasion (Higgins and Vander Zanden 2010; Johnson and Bunnell 2005; Knight, O'Malley, and Stockwell 2018), leading to less resilience. The loss or addition of a species can influence the stability and functioning of ecosystems (McCann 2000), where, generally, weak trophic interactions stabilize community dynamics by dampening potentially destabilizing, strong interactions (Odum 1953). Therefore, conserving species to maintain stabilizing trophic interactions is important (O'Gorman and Emmerson 2009) because stability can regulate the resilience of food webs to perturbations such as invasions. Furthermore, applying the food web energetics approach while comparing functional states and stability pre- and post-invasion may provide broader insight into how invaders affect community dynamics beyond more than predator–prey interactions alone.

An apex predator, lake trout *Salvelinus namaycush*, was discovered in Yellowstone Lake, Yellowstone National Park, Wyoming, USA, in the early 1990s (Kaeding, Boltz, and Carty 1996; Koel et al. 2020). Following population expansion in the 1990s, lake trout caused a trophic cascade (Tronstad et al. 2010). Lake trout reduced the abundance of their preferred prey item, Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri*, a species of conservation concern and a keystone species in the Greater Yellowstone Ecosystem (Koel et al. 2019). Yellowstone cutthroat trout are accessible to predators during their spawning migrations to tributary streams and are a seasonal food source for terrestrial species (Baril et al. 2013; Felicetti et al. 2004; Koel et al. 2005). Lake trout are not an ecological substitute for Yellowstone cutthroat trout because lake trout live deep within the lake and do not spawn in tributaries, reducing vulnerability to most terrestrial predators (Baril et al. 2013; Felicetti et al. 2004; Koel et al. 2005). The reduction in Yellowstone cutthroat trout abundance also resulted in a reduced proportion of lake trout diet consisting of the Yellowstone cutthroat trout (Glassic, Lujan, et al. 2023; Syslo, Guy, and Koel 2016). A lake trout gillnetting suppression programme began in 1995 and effort was increased annually but did not cause population decline until 2012 (Koel et al. 2020). Lake trout biomass peaked in 2012 and has been declining since due to the intensive gillnetting suppression programme (Koel et al. 2020; Syslo et al. 2020).

In this study, we combined recent estimates of biomass and diet composition with published estimates of biomass, metabolic demand, ecological efficiencies, and diet composition to compare the energetic fluxes, functional state, and stability of four food web states. We compared food webs characterizing a pre-invasion network with an apex zooplanktivore, Yellowstone cutthroat trout (Jones et al. 1993) and an invaded network including an invasive apex piscivore, lake trout (Koel et al. 2019; Syslo, Guy, and Koel 2016; Syslo et al. 2020). The invaded network consisted of three states from (1) initial invasion (initial discovery of lake trout; low lake trout biomass; earliest state with lake trout present) to (2) expansion (climax of lake trout biomass) and finally to (3) decline (decline of lake trout biomass, most contemporary state). Using this framework, we answered the following questions: (1) Did lake trout invasion change the overall energy flux throughout the food web in Yellowstone Lake, (2) to what degree did the invasion of lake trout change the functional state of the food web, and (3) did the invasion of lake trout change the stability of the food web?

2 | Methods

2.1 | Study Site

Yellowstone Lake is in Yellowstone National Park in northwestern Wyoming, USA, and is the largest high elevation (above 2000 m; 2357 m) lake in North America. The lake has a surface area of 34,020 ha (Kaplinski 1991) and a maximum depth of 133 m (Morgan et al. 2003). Surface water temperatures during the ice-free season vary between 9°C and 18°C (Koel et al. 2019). Yellowstone Lake is mesotrophic (Kilham, Theriot, and Fritz 1996) and ice-covered from December through May (Gresswell and Varley 1988).

Yellowstone Lake has a low diversity of organisms given the lake is a high-elevation, cold-water system near the Continental Divide in western North America. The plankton assemblage in Yellowstone Lake is depauperate, but the species that are present are highly abundant. Phytoplankton are dominated by diatoms (*Stephanodiscus* spp., *Cyclotella bodanica*, *Aulacoseira subarctica* and *Asterionella formosa*; Interlandi, Kilham, and Theriot 1999). The zooplankton in Yellowstone Lake consist of two species of cladocerans (*Daphnia schødleri* and *Daphnia pulicaria*) and three species of copepods (*Diacyclops bicuspidatus thomasi*, *Leptodiaptomus ashlandi* and *Hesperodiaptomus shoshone*; Tronstad et al. 2010). The benthic invertebrate assemblage is more diverse than the plankton assemblage in Yellowstone Lake and includes the taxa Ephemeroptera, Trichoptera, Diptera (Chironomidae), Crustacea (*Gammarus lacustrus* and *Hyallela azteca*), Annelida (*Helobdella stagnalis*, *Erpobdella obscura* and Hirudinea) and Mollusca (Sphaeriidae and Planorbidae; Wilmot et al. 2016). The fish assemblage of Yellowstone Lake is composed of two native species (longnose dace and Yellowstone cutthroat trout), three non-native fishes that were introduced but do not cause measurable ecological damage (redside shiner *Richardsonius balteatus*: introduced 1950s, Varley and Schullery 1998; lake chub *Couesius plumbeus*: introduced 1960s, Cope 1958; and longnose sucker *Catostomus catostomus*: introduced 1930s, Brown and Graham 1954), and one invasive fish causing measurable ecological damage (lake trout: discovered in 1994; Kaeding, Boltz, and Carty 1996).

Due to the location of Yellowstone Lake within a national park and the population of ecologically important Yellowstone cutthroat trout, the organisms of the food web in Yellowstone Lake are well researched, with studies primarily focused on quantifying biomass of fishes, macroinvertebrates and, plankton, and diet composition of fishes before and after lake trout invasion (Benson 1961; Jones et al. 1993; Knight 1975; Theriot, Fritz, and Gresswell 1997; Tronstad et al. 2010; Tronstad, Hall, and Koel 2015; Wilmot et al. 2016). Four specific food webs were used for comparisons of energy flux, functional state, and stability: pre-invasion, initial invasion, expansion, and decline. The year 1980 represents the ecosystem in an unaltered state (pre-invasion) when Yellowstone cutthroat trout were the apex predator. The three subsequent periods represent times when biomass of Yellowstone cutthroat trout, lake trout, zooplankton, and phytoplankton varied because of invasion or suppression of lake trout with gillnets. The year 1998 represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout, and the resulting trophic cascade (Tronstad et al. 2010). The year 2012 represents the period when lake trout biomass peaked (expansion), lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016), and Yellowstone cutthroat trout biomass continued to decline. The year 2018 represents the period when lake trout biomass was declining (decline), lake trout shifted their diets (Glassic, Lujan, et al. 2023), and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020). The extensive historical and contemporary research regarding the invasion of lake trout provides a unique opportunity to apply a food web energetics approach to quantify the effects of an invasive species on an ecosystem.

2.2 | Food Web Years and Structure

Lake trout, Yellowstone cutthroat trout, and longnose sucker were separated into adult and juvenile groups based on ontogenetic diet shifts (Benson 1961; Furey et al. 2020; Glassic, Lujan, et al. 2023; Ruzycki, Beauchamp, and Yule 2003; Syslo, Guy, and Koel 2016) and susceptibility to predation (Yellowstone cutthroat trout only). Lake trout biomass was estimated for the population at the beginning of the ice-free season (Syslo et al. 2020; i.e., before suppression gillnetting began each season). For all groups except longnose sucker, we used Yellowstone Lake-specific, published biomass estimates for each year or biomass estimates derived from the literature in similar systems (Figure 1 and Table S1). Longnose sucker biomass estimates were not available from the literature but catch per unit effort (CPUE) was available (Koel et al. 2019).

2.3 | Assumptions

We assumed that the relationship between longnose sucker CPUE and biomass was similar to that of the relationship between Yellowstone cutthroat trout CPUE and biomass; the trend of longnose sucker CPUE and Yellowstone cutthroat trout CPUE are similar before and after lake trout invasion (Koel et al. 2019). As there were no longnose sucker biomass estimates available, we estimated longnose sucker biomass from CPUE using a linear model fit to Yellowstone cutthroat trout CPUE and biomass data from Walsworth and Gaeta (2020) (Table S1), assuming that size structure, gear selectivity and

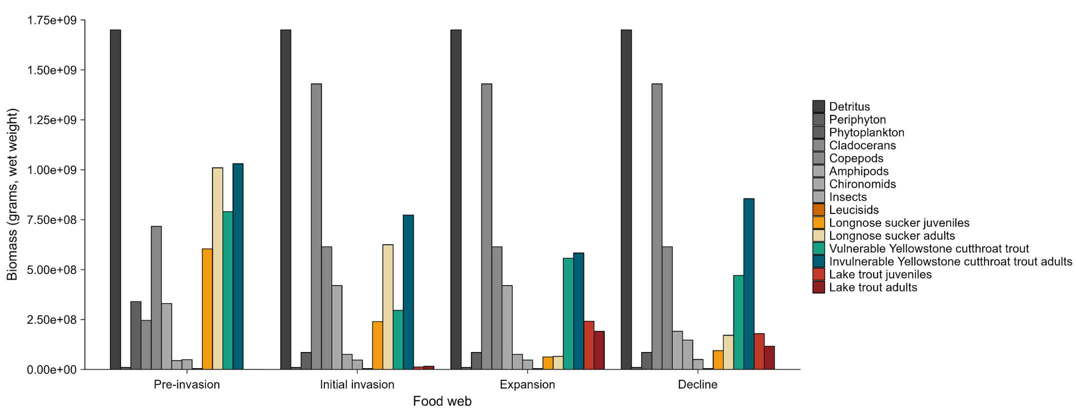

FIGURE 1 | Taxa biomass for the pre-invasion food web compared to each post-invasion food web with invasive lake trout suppression (initial invasion, expansion and decline) in Yellowstone Lake, Yellowstone National Park, Wyoming, USA. The food web naming describes the following: 'pre-invasion' before lake trout were introduced (1980); 'initial invasion' (1998) represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout and the resulting trophic cascade (Tronstad et al. 2010); 'expansion' (2012) represents the period when lake trout biomass peaked, lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016) and Yellowstone cutthroat trout biomass continued to decline; 'decline' (2018) represents the period when lake trout biomass was declining, lake trout shifted their diets (Glassic, Lujan, et al. 2023) and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020).

length–weight relationships of the two species were comparable. Leucisid biomass was estimated using relationships from Downing and Plante (1993). The food web energetics approach assumes ecosystem equilibrium (i.e., energy fluxes among nodes are calculated to balance the energetic demands of biomass stocks with energy outflow; Barnes et al. 2018). We assumed stable state conditions for each food web year despite the fishing pressure from the lake trout suppression gillnetting programme. For taxa other than lake trout and Yellowstone cutthroat trout, diets were assumed to constant over time due to lack of available temporal data. Metabolic rates were assumed to be only affected by body mass and whether the organism was an ectotherm vertebrate or invertebrate (consistent with methodology outlined within Gauzens et al. 2018). Assimilation efficiencies were assumed to be only affected by the type of organism consumed (consistent with methodology outlined within Gauzens et al. 2018).

2.4 | Energy Flux

We compared energy flux through the four food webs in Yellowstone Lake to quantify the influence of lake trout on the Yellowstone Lake food web beyond their prey base. The energy flux approach, also known as the food web energetics approach, uses measured biomass of stocks, energetic expenditure, and assimilation efficiencies to calculate energy flux F ($J\,y^{-1}$) between network nodes (Barnes et al. 2018; De Ruiter, Neutel, and Moore 1995; Hunt et al. 1987; O'Neill 1969). Network nodes, or direct feeding links, were established when Species A consumed Species B during one ice-free season in Yellowstone Lake. Individual metabolic demands derived from the literature were incorporated into network nodes to better account for taxonomy, body size structure and trophic topology (size and shape of tropic networks; Barnes et al. 2018). In the food web energetics approach, energy flux F ($J\,y^{-1}$) to each consumer node was calculated as

$$F = \frac{1}{e} \bullet (X + L), \qquad (1)$$

where e was the diet-specific assimilation efficiency (dimensionless; proportion), X was the estimated metabolic demands of individuals in a consumer node ($J\,y^{-1}$) and L was the loss of energy to higher trophic levels via consumption (e.g., predation or herbivory; $J\,y^{-1}$; Barnes et al. 2018). Data used to calculate energy flux food webs were (1) mean body masses for each network node (Table S2), (2) calculated individual metabolic rates using mass metabolism regressions (Table S3), (3) network topology including diet (Tables S4–S7), (4) calculated node metabolism (X) using biomasses (Table S8) for each node and (5) assimilation efficiencies (e) for each organism type (i.e., animal, plant and detritus; Table S9).

The data listed above were compiled through a combination of values published in the literature (Table S1). We used the R package *fluxweb* (Gauzens et al. 2018; Version 0.2.0) to estimate all food web energetics calculations. All analyses were conducted using R version 4.2.2 (R Core Team 2022). We compared the energy fluxes for the four food web states to quantify the influence of an invasive apex predator (lake trout) on food web structure. We compared the flux from unique prey to unique predator, total flux to unique predator from all prey combined, and total flux within a food web among the four networks. We used a Monte Carlo sampling approach to estimate uncertainty in flux for pre-invasion, initial invasion, expansion and decline food webs. We randomly sampled 10,000 values from a normal distribution with mean and standard deviation estimated from the empirical sample distribution of each node. When comparing the pre-invasion Yellowstone Lake network with the invaded networks (initial invasion, expansion and decline), we anticipated that a shift in energy flux towards lake trout would reduce energy flux to the other organisms (e.g., Yellowstone cutthroat trout) in Yellowstone Lake, but total flux within a food web would increase as biomass of lake trout increased.

2.5 | Food Web Functional State

After an energetic food web was established, we estimated food web functional state (i.e., herbivory, detritivory or carnivory). We compared functional state among the four food webs in Yellowstone Lake because we were interested in whether the dominant energetic pathway of the food web changed after lake trout invasion. Here, the functional states are defined according to Gauzens et al. (2018), with herbivory as the sum of fluxes outgoing from photosynthetic organisms, detritivory as the sum of fluxes outgoing from detritus, and carnivory as the sum of fluxes outgoing from heterotrophs. The functional state with the greatest sum of fluxes was the assigned functional state of the food web. We hypothesized that the lake trout invasion caused a shift towards a carnivory dominant functional state. We identified the dominant functional state for each food web and compared the percentage of total flux contributed by each functional state among the Yellowstone Lake food webs.

2.6 | Food Web Stability

We calculated stability metrics for each food web because we wanted to estimate whether the invasion of lake trout caused the food web to be less likely to return to equilibrium following disturbance. Stability of the food webs was calculated within the *fluxweb* package. Network stability was based on the Jacobian matrix adapted from Neutel et al. (2007). A food web was considered stable if dominant eigenvalues were negative, with more negative values representing greater stability. We used a Monte Carlo sampling approach to estimate uncertainty in stability values for pre-invasion, initial invasion, expansion and decline food webs. We randomly sampled 10,000 values from a normal distribution with mean and standard deviation estimated from the empirical sample distribution of each node. For each iteration, we estimated food web stability using the 'stability.value' function in the *fluxweb* package to construct a distribution of stability values for each food web to account for and incorporate variability in potential inputs that could result in variable stability outcomes. We hypothesized that the invasion of lake trout caused the food web to become less stable, or approach a stability value of zero, especially when lake trout biomass peaked during the expansion food web.

3 | Results

3.1 | Energy Flux

The pre-invasion food web was dominated by energy flux to copepods (Table 1). Total flux to cladocerans was the second greatest flux in the system but was still less than half of the total flux to copepods (Table 1). Flux to amphipods was an order of magnitude smaller than flux to copepods or cladocerans but was an order of magnitude larger than chironomids, Yellowstone cutthroat trout juveniles or adults, and longnose sucker juveniles or adults (Table 1). Yellowstone cutthroat trout adults had the largest estimated biomass pre-invasion of all fish nodes (Figure 1) and had the largest flux of all fish nodes (Table 1).

The invasion of lake trout caused more than a ±25% change in total energy flux for all organisms in Yellowstone Lake except copepods, chironomids, and other invertebrates, depending on the food web type (i.e., initial invasion, expansion and decline; Table 1), with many of these changes in energy flux mirroring changes in biomass estimates (Figure 1). Incorporating uncertainty (i.e., standard deviation around biomass estimates) allowed us to calculate confidence intervals around mean estimates of energy flux. The percent change in flux incorporating uncertainty again mirrored biomass estimates, however, provided insight into the potential variation in energy flux estimates. Flux to Yellowstone cutthroat trout juveniles was 64% (confidence interval: −66, −26%) less during initial invasion than pre-invasion, mirroring a decrease in biomass of 63% from pre-invasion to initial invasion, and flux to Yellowstone cutthroat trout adults was on average 55% less post-invasion (Table 1). We compared changes in flux to lake trout to initial invasion fluxes because lake trout were not present in pre-invasion. Lake trout juvenile flux in expansion and decline food webs was on average 1408% greater than the initial invasion food web, whereas biomass increased 20× compared to initial invasion (Figure 1). Lake trout adult flux peaked in the expansion food web and was 1065% (1036, 1096%) greater than in the initial invasion food web (Table 1), which mirrored the increase in biomass during expansion (Figure 1). Flux to longnose sucker juveniles and adults also decreased post-invasion. Compared to pre-invasion, flux to longnose sucker juveniles was on average 76% less post-invasion, and flux to longnose sucker adults was on average 72% less post-invasion (Table 1). Leucisid fluxes consistently decreased by 48% (−49, −47%) post-invasion (initial invasion, expansion and decline) compared to pre-invasion because biomass and diet were held constant for all post-invasion food webs (Table 1 and Figure 1). Cladoceran biomass increased sixfold between pre-invasion and initial invasion (Figure 1), and flux increased to cladocerans by 452% (301, 621%; Table 1). Copepod flux only decreased by 14% post-invasion (Table 1). Amphipod flux compared to

TABLE 1 | Total energy flux (J y^{-1}) for pre-invasion and percent change in total flux (confidence intervals based on 10,000 iterations varying biomass ± standard deviation) to specific taxa compared to pre-invasion for initial invasion, expansion and decline. For lake trout, total flux to that taxa are listed for initial invasion, and percent change in flux was compared to initial invasion because lake trout were not present in the ecosystem pre-invasion. For leucisids, biomass and diet were held constant for all years. The food web naming describes the following: 'pre-invasion' before lake trout were introduced (1980); 'initial invasion' (1998) represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout and the resulting trophic cascade (Tronstad et al. 2010); expansion (2012) represents the period when lake trout biomass peaked, lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016) and Yellowstone cutthroat trout biomass continued to decline; 'decline' (2018) represents the period when lake trout biomass was declining, lake trout shifted their diets (Glassic, Lujan, et al. 2023) and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020).

Taxa	Total flux 'pre-invasion'	Change in flux 'initial invasion'	Change in flux 'expansion'	Change in flux 'decline'
Yellowstone cutthroat trout juveniles	1.74E+08	−64% (−66, −26)	−35% (−37, −34)	−46% (−51, −48)
Yellowstone cutthroat trout adults	2.29E+08	−45% (−46, −44)	−68% (−69, 65)	−53% (−54, −51)
Lake trout juveniles	NA	2.43E+06 (total flux)	1629%[a] (1514, 1967)	1187%[a] (1045, 1436)
Lake trout adults	NA	1.66E+06 (total flux)	1065%[a] (1036, 1096)	593%[a] (576, 612)
Longnose sucker juveniles	1.68E+08	−56% (−58, −54)	−88% (−91, −85)	−84% (−87, −81)
Longnose sucker adults	2.12E+08	−38% (−39, −37)	−93% (−96, −91)	−84% (−86, −82)
Leucisids	5.29E+06	−48% (−49, −47)	−48% (−49, −47)	−48% (−49, −47)
Cladocerans	1.28E+10	452% (301, 621)	451% (269, 631)	453% (303, 661)
Copepods	3.52E+10	−14% (−27, −4)	−14% (−23, −7)	−13% (−21, −3)
Amphipods	1.18E+09	32% (2, 50)	39% (7, 60)	450% (424, 469)
Chironomids	8.40E+08	−19% (−31, −7)	−48% (−65, −31)	−7% (−49, 44)
Other invertebrates[b]	1.52E+08	17% (−8, 32)	19% (−7, 33)	339% (318, 353)

[a]Value compared to initial invasion.
[b]Other invertebrates are defined as in Syslo, Guy, and Koel (2016).

pre-invasion was on average 174% greater post-invasion, with the decline food web flux having the greatest increase of 450% (424, 469%; Table 1). Chironomids had only 1 year where flux was changed by ±25% post-invasion, with a decrease in flux of 48% (−65, −31%) in the expansion food web. Other invertebrate flux was changed by more than 25% in the decline food web, with an increase of 339% (318, 353%; Table 1).

Similar to overall flux, flux of different prey taxa to consumer taxa also changed post-invasion compared to pre-invasion (Figure 2). For Yellowstone cutthroat trout juveniles and adults, flux from amphipods increased by more than 138% post-invasion (Figure 2). Flux from amphipods to Yellowstone cutthroat trout juveniles peaked in the expansion food web with a 491% increase compared to pre-invasion (Figure 2) and peaked at 432% from amphipods to Yellowstone cutthroat trout adults in the decline food web (Figure 2). Juvenile lake trout in the expansion food web had the greatest change in flux from copepods compared to the initial invasion, with a 22,955% increase (Figure 2). Adult lake trout in the expansion food web had the greatest change in flux from cladocerans and amphipods compared to the initial invasion, with a 4795% increase for amphipods and a 5145% increase for cladocerans (Figure 2). Adult lake trout in the decline food web had a 581% increase in flux from juvenile Yellowstone cutthroat trout compared to the initial invasion (Figure 2).

Total flux in the food web varied by food web type, and the taxa with the greatest percentage of flux varied by food web type (Table 2). Total flux peaked post-invasion in the decline food web and was two times greater than pre-invasion (Table 2). Despite being the apex predator before lake trout invaded, flux to Yellowstone cutthroat trout adults and juveniles was < 1% of the total flux for all years and peaked pre-invasion (Table 2). Though invasion of lake trout caused a trophic cascade, changes in diets, and changes in individual fluxes to other taxa,

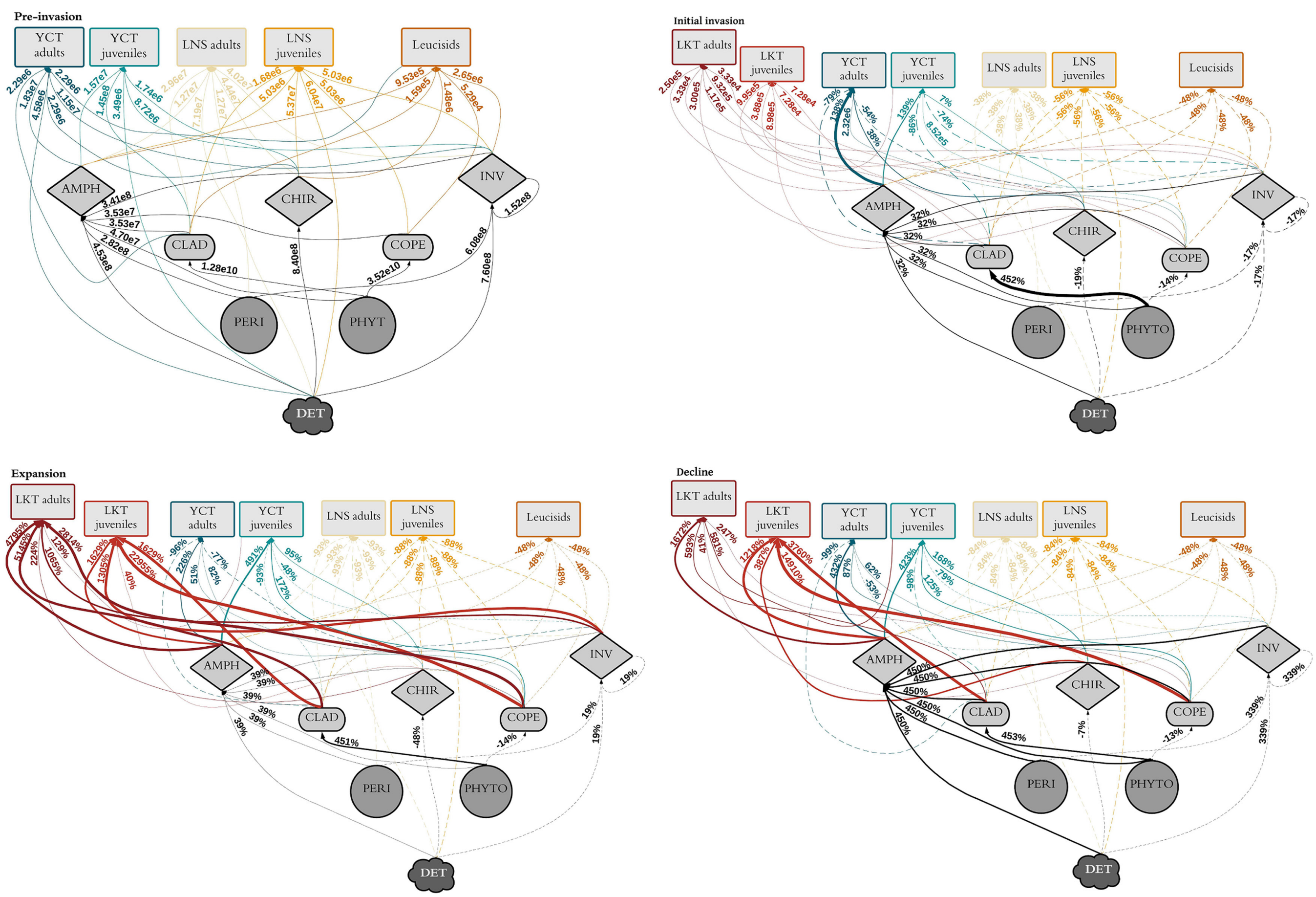

FIGURE 2 | Food web structure and energy flux for the pre-invasion food web and the percentage change in flux compared to pre-invasion for the post-invasion food webs (initial invasion, expansion and decline) in Yellowstone Lake, Yellowstone National Park, Wyoming, USA. Flux values for lake trout during initial invasion are not percentages because the first year of lake trout invasion was 1998. The width of the line represents the relative increase (solid line) or decrease (dashed line) in flux compared to pre-invasion. AMPH, amphipods; CHIR, chironomids; INV, other invertebrates; LKT, lake trout; LNS, longnose sucker; YCT, Yellowstone cutthroat trout (as described by Syslo, Guy, and Koel 2016); CLAD, cladocerans; COPE, copepods; DET, detritus; PERI, periphyton; PHTYO, phytoplankton. The food web naming describes the following: 'pre-invasion' before lake trout were introduced (1980); 'initial invasion' (1998) represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout and the resulting trophic cascade (Tronstad et al. 2010); expansion (2012) represents the period when lake trout biomass peaked, lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016) and Yellowstone cutthroat trout biomass continued to decline; 'decline' (2018) represents the period when lake trout biomass was declining, lake trout shifted their diets (Glassic, Lujan, et al. 2023) and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020).

TABLE 2 | Total flux ($J y^{-1}$) for the most dominant taxa in the Yellowstone Lake food web by food web type with percentage of total flux flowing to different taxa. The food web naming describes the following: 'pre-invasion' before lake trout were introduced (1980); 'initial invasion' (1998) represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout and the resulting trophic cascade (Tronstad et al. 2010); expansion (2012) represents the period when lake trout biomass peaked, lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016) and Yellowstone cutthroat trout biomass continued to decline; 'decline' (2018) represents the period when lake trout biomass was declining, lake trout shifted their diets (Glassic, Lujan, et al. 2023) and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020).

Energy flux to taxa	'Pre-invasion'	'Initial invasion'	'Expansion'	'Decline'
Total flux (compared to pre-invasion)	5.23E+10 (NA)	1.05E+11 (2.0×)	1.05E+11 (2.0×)	1.15E+11 (2.2×)
Yellowstone cutthroat trout adults	0.44%	0.12%	0.11%	0.09%
Yellowstone cutthroat trout juveniles	0.33%	0.06%	0.07%	0.08%
Lake trout adults	NA	0.00%	0.02%	0.02%
Lake trout juveniles	NA	0.00%	0.04%	0.03%
Cladocerans	24.43%	67.06%	67.16%	61.24%
Copepods	67.30%	28.73%	28.85%	26.44%
Amphipods	2.25%	1.47%	1.56%	5.60%

TABLE 3 | Total flux for the functional states of herbivory, detritivory and carnivory for four food web years in Yellowstone Lake, Yellowstone National Park, Wyoming, USA. Here, the functional states are defined according to Gauzens et al. (2018), with herbivory as the sum of fluxes outgoing from photosynthetic organisms, detritivory as the sum of fluxes outgoing from detritus and carnivory as the sum of fluxes outgoing from animals. The food web naming describes the following: 'pre-invasion' before lake trout were introduced (1980); 'initial invasion' (1998) represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout and the resulting trophic cascade (Tronstad et al. 2010); expansion (2012) represents the period when lake trout biomass peaked, lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016) and Yellowstone cutthroat trout biomass continued to decline; 'decline' (2018) represents the period when lake trout biomass was declining, lake trout shifted their diets (Glassic, Lujan, et al. 2023), and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020).

Food web state	'Pre-invasion'	'Initial invasion'	'Expansion'	'Decline'
Herbivory	94%	97%	97%	92%
Carnivory	2%	1%	1%	3%
Detritivory	4%	2%	2%	6%

percentage of total flux to lake trout juveniles and adults was <1% of the total flux for all years (Table 2). Flux to cladocerans was highest among all taxa post-invasion and peaked during the initial invasion and the expansion food webs at 67% of the total flux (Table 2). Flux to copepods was highest among all taxa pre-invasion with 67% of total flux. Flux to amphipods was 1%–6% for all food webs and peaked in the decline food web with 6% of total flux (Table 2).

3.2 | Food Web Functional State

Overall food web functional state did not change among food webs, but percentage of functional state contributing to total flux varied. Herbivory was the dominant food web functional state for all years examined, with the greatest percentage of flux from herbivory in initial invasion and the expansion food web (Table 3). Percentage of detritivory was highest in the decline food web, contributing to 6% of total flux, and flux from carnivory was also greatest in the decline food web at 3% (Table 3).

3.3 | Food Web Stability

Mean stability values were approximately equal, and distributions overlapped for all food webs. Therefore, no evidence existed to suggest that stability values differed among the four food webs (Figure 3).

4 | Discussion

Our research quantified important invasive species-driven changes to community and food web structure. We implemented a food web energetics approach to understand the effect of invasive lake trout on energy flux, expanding our understanding of how invasive species may influence the function and stability of ecosystems. We combined empirical measurements of energy flux, diets, and biomass to examine changes in a food web over time, driven by an invasive species. We showed that the addition of lake trout increased total flux through the food web (flux; $J y^{-1}$) twofold compared to pre-invasion. Lake trout also influenced the contributions

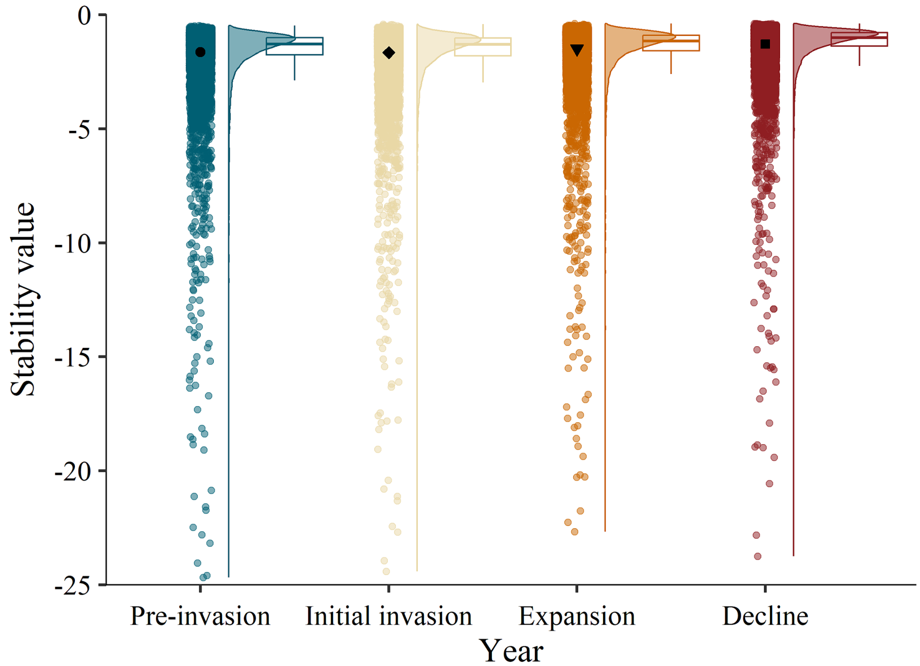

FIGURE 3 | Stability values for pre-invasion and post-invasion (initial invasion, expansion and decline) food webs in Yellowstone Lake, Yellowstone National Park, Wyoming, USA, calculated using methods from Gauzens et al. (2018). Black symbols represent the mean stability value for each year. We used a Monte Carlo sampling approach to estimate uncertainty in stability values for historical and contemporary food webs. Here, we randomly sampled 10,000 values from a normal distribution with mean and standard deviation estimated from the empirical sample distribution of each node. For each iteration, we estimated food web stability using the 'stability.value' function in the fluxweb package (Gauzens et al. 2018) to construct a distribution of stability values for each food web. Variability estimates in the food web stability values were quantified by calculating the 95% percentile intervals (2.5–97.5 percentiles) from the distribution of stability values for each model year. The food web naming describes the following: 'pre-invasion' before lake trout were introduced (1980); 'initial invasion' (1998) represents the initial invasion of lake trout in Yellowstone Lake, the initial decline in Yellowstone cutthroat trout and the resulting trophic cascade (Tronstad et al. 2010); expansion (2012) represents the period when lake trout biomass peaked, lake trout and Yellowstone cutthroat trout shifted their diet (Syslo, Guy, and Koel 2016) and Yellowstone cutthroat trout biomass continued to decline; 'decline' (2018) represents the period when lake trout biomass was declining, lake trout shifted their diets (Glassic, Lujan, et al. 2023) and Yellowstone cutthroat trout biomass began to increase (Koel et al. 2020).

of dominant taxa in sustaining these fluxes. Differences in stability of the post-invasion food webs compared to the pre-invasion food web could not be detected, potentially due to a steadying mechanism by lake trout suppression efforts, or the omnivorous feeding of lake trout, which may counteract otherwise destabilizing forces associated with species invasion. The functional states of pre- and post-invasion food webs were dominated by herbivory, though detritivory increased in the final post-invasion food web in contrast to the pre-invasion food web, which may represent an adaptive state where ecosystem function persisted given the omnivorous feeding of lake trout and assistance from lake trout suppression.

4.1 | Energy Flux

From our analysis, we concluded that post-invasion (initial invasion, expansion, and decline), the Yellowstone Lake ecosystem was driven by top-down effects from the invasion of lake trout. The lake trout invasion caused widespread change in overall flux in the ecosystem and within individual fluxes from producers to consumers. Very few studies quantify the effect of invasive species on food web energy flux; however, some research has quantified the effect of fish introductions on nutrient flux (Collins et al. 2016; Tronstad, Hall, and Koel 2015). Invasive species are known to modify energy flow in ecosystems (Baxter et al. 2004; Charles and Dukes 2008; Gherardi 2007; Rodda and Savidge 2007), but comparisons to our study are best related to shifted production post-invasion. Reduced capacity to support native fish can occur post-invasion (Rush et al. 2012), which we observed in decreased post-invasion energy flux to Yellowstone cutthroat trout. Overall energy flux in our system increased post-invasion, similar to increased net primary production when comparing invaded to non-invaded systems (Caraco et al. 2000; Huryn 1998; Lucero, Allen, and McMillan 2015; South et al. 2016).

One of our objectives was to investigate the effects of an invasive apex predator on the flux of energy through the food web. However, we acknowledge that factors other than species invasion (e.g., temperature, nutrient cycling and trophic cascade) can be important in regulating energy flux through food webs, potentially confounding our comparisons. Temperature is known to influence ectotherm performance (e.g., growth, metabolism, ingestion rate and reproduction; Pörtner and Farrell 2008; Pörtner and Peck 2010). Warming has occurred in the Greater Yellowstone Ecosystem region since 2000 (Heeter, Rochner, and Harley 2021; Hostetler et al. 2021), and Yellowstone Lake surface water temperature has increased by 0.45°C per decade between 1976 and 2018 (Koel et al. 2019).

Increasing water temperatures could have been approaching an optimum metabolic window for lake trout and Yellowstone cutthroat trout over the past decades (Al-Chokhachy et al. 2013), possibly contributing to increased energy flux not solely explained by lake trout invasion. Additionally, lake trout invasion altered nutrient cycling in Yellowstone Lake and its tributaries (Tronstad, Hall, and Koel 2015), which can also influence energy flux in food webs (Cross, Wallace, and Rosemond 2007).

Although energy fluxes can be a useful tool for comparing food webs, energy fluxes should be compartmentalized as comparative values rather than precise representations of food web energy flow (Jochum et al. 2021). In that context, the comparisons of flux calculated for Yellowstone Lake pre- and post-invasion food webs are valid. Although the overall effect of lake trout invasion on total energy flux may be largely explained by the trophic cascade (Koel et al. 2019; Tronstad et al. 2010) and changes to trout diets through time (Glassic, Lujan, et al. 2023; Jones et al. 1993; Ruzycki, Beauchamp, and Yule 2003; Syslo, Guy, and Koel 2016), flux values from species that did not have a change in biomass (i.e., leucisids) or diet (i.e., longnose sucker and leucisids) are likely a result of a redundancy of functional or trophic states (Nelson et al. 2020). For taxa other than the lake trout and Yellowstone cutthroat trout, we did not change diet through time due to lack of available temporal data. Although some biomass data were available for the periods of our study, other biomass data were estimated or derived from the literature (e.g., longnose sucker, leucisids, benthic invertebrates, some zooplankton and phytoplankton data), which is why some fluxes remained constant post-invasion. The lack of Yellowstone Lake or network-specific (pre-invasion, initial invasion, expansion and decline) biomass data affects our ability to describe changes in fluxes to these groups and affects our accuracy in creating networks and estimating fluxes that may more closely resemble dynamics that occurred in Yellowstone Lake.

4.2 | Food Web Functional State

This study is one of the first to investigate food web stability in relation to functional states, particularly within the context of environmental perturbations such as biological invasion. The herbivore-dominated food web in Yellowstone Lake may have made the ecosystem more susceptible to invasion and lake trout expansion—herbivory has been identified as the driving factor for invasion in other communities (Sperfeld et al. 2010). The increased functional detritivory in the decline food web was due to a 450% increase in flux to amphipods compared to the non-invaded food web and suggests that the ecosystem may be approaching a new equilibrium (Bezerra et al. 2018) where lake trout are integrated into the food web instead of causing large network disturbances. The increase in detritivory in the decline food web could also be attributed to the increase in biomass of amphipods during that year; amphipods were released from predation when Yellowstone cutthroat trout biomass decreased after invasion (Wilmot et al. 2016). Furthermore, the shift towards greater reliance on detritivory follows a growing body of evidence supporting benthification or trophic downgrading in freshwater lakes after invasion (Bezerra et al. 2018, 2019; Mills et al. 2013), though the shift observed in Yellowstone Lake did not cause a complete shift in food web functional state.

The decrease in carnivory flux following the invasion of the piscivorous lake trout seemed counterintuitive given lake trout are an apex predator, but is likely due to the diet of lake trout adults and the biomass of consumed taxa during the post-invasion food webs. During the initial invasion, lake trout adults were highly piscivorous, with Yellowstone cutthroat trout juveniles comprising 56% of their diet (Ruzycki, Beauchamp, and Yule 2003). However, the biomass of lake trout adults during that period was not large enough to overwhelm the herbivory flux of other taxa (i.e., cladocerans and copepods). Although lake trout are characterized as apex piscivores, the species in Yellowstone Lake is not an obligate piscivore (Glassic, Lujan, et al. 2023; Ruzycki, Beauchamp, and Yule 2003; Syslo, Guy, and Koel 2016), nor is the species in their native range (Martin and Olver 1980; Vinson et al. 2020). The dynamics we observed between biomass and diet, and more specifically diet plasticity in an apex invasive fish (Glassic, Lujan, et al. 2023), highlights the complexity surrounding dominant functional states in invaded food webs. Comparisons of food web functional states in relation to ecosystem invasion are rarely examined; further investigations between functional states and stability could advance our understanding and management of invaded ecosystems.

4.3 | Food Web Stability

We could not detect a difference in stability metrics of the food webs in Yellowstone Lake over time likely due to the prey-switching life-history strategy and the generalist feeding behaviour of lake trout (Glassic, Lujan, et al. 2023; Ruzycki, Beauchamp, and Yule 2003; Syslo, Guy, and Koel 2016) and generalist feeding strategies by other fishes in Yellowstone Lake (Furey et al. 2020; Glassic, Guy, and Koel 2021; Syslo, Guy, and Koel 2016). Lake trout exhibit diet plasticity, buffering time spent on search image processing and increasing consumption efficiency when multiple prey types are present (Kratina, Vos, and Anholt 2007). The diet plasticity behaviour may maintain food web stability in Yellowstone Lake, despite causing a trophic cascade (Koel et al. 2019; Tronstad et al. 2010). The invasion of lake trout introduced a generalist consumer into the food web, and all fishes in Yellowstone Lake were omnivores post-invasion, which stabilized food web dynamics because feeding occurred across different trophic levels (Kondoh 2003; McCann, Rasmussen, and Umbanhowar 2005; Wolkovich et al. 2014). Furthermore, the adaptive foraging behaviour of lake trout increased food web complexity post-invasion, which may enhance community resilience to further environmental fluctuations (Kondoh 2003).

Predator–prey dynamics between lake trout and Yellowstone cutthroat trout also maintained food web stability. After invasion, the Yellowstone Lake food web had heightened states of fast (high biomass turnover due to suppression and high recruitment, lake trout) and slow (low biomass turnover, Yellowstone cutthroat trout) energy channels, leading to asynchronous resource dynamics, thereby maintaining stability (Rooney et al. 2006; Rooney and McCann 2012). The resulting asynchronous resource dynamics produced a stabilizing resource base for the invasive predator, allowing for a rapid but inhibited expansion (Fowler 2009; Rooney et al. 2006; Rooney and McCann 2012). The relationship between lake trout and Yellowstone cutthroat trout also represents an example of asymmetrical intraguild predation; the species experience direct competition as well as predator–prey interaction, with lake trout not only consuming Yellowstone cutthroat trout but also consuming amphipods (Ruzycki, Beauchamp, and Yule 2003; Syslo, Guy, and Koel 2016; Glassic, Lujan, et al. 2023). Intraguild predation can be linked to destabilization (Huxel, McCann, and Polis 2002; Tanabe and Namba 2005), but for Yellowstone Lake, intraguild predation may be linked to post-invasion food web stability (Kuijper et al. 2003) because ongoing lake trout suppression is regulating intraguild predation dynamics (Hall 2011).

4.4 | Implications for Conservation

Our research provides a comprehensive empirical assessment of how an invasive species can influence energy flux in a large lake food web undergoing intensive invasive species suppression. We provide novel estimation of energy flux at different time periods to understand how invasive species may influence food web stability from initial invasion to expansion and decline. Although no overall change in ecosystem stability or functional state was detected after invasion in our study, we believe that this framework could be useful in examining the effect of invasive species in ecosystems with more complexity or different taxa. Additionally, the lack of change in functional state or stability highlighted the importance of invasive suppression in its contribution to preventing ecosystem collapse (Glassic, Chagaris, et al. 2023); without suppression, the possibility exists that the reduced flux to the native fishes due to lake trout invasion would have destabilized the ecosystem. Efforts to combine biomass estimates with mechanistic models of organism metabolism represent an important step towards closing the gap (Barnes et al. 2018) in studying ecosystems by viewing invasive species beyond solely a predator–prey focus. Here, we clearly demonstrate that invasive species can cause more than declines in native species abundance. The consideration of energy flux, functional state, and food web stability will ultimately characterize how invasive species can affect the distribution of energy flux in food webs beyond their prey base alone.

Author Contributions

Hayley C. Glassic conceived the study, performed the analyses, interpreted results and wrote the manuscript. Christopher S. Guy secured funding, conceived the study, discussed results and implications and edited earlier manuscripts. Lusha M. Tronstad provided data, discussed results and implications and edited earlier manuscripts. Michelle A. Briggs provided data, discussed results and implications and edited earlier manuscripts. Lindsey K. Albertson provided data, discussed results and implications and edited earlier manuscripts. Dominique R. Lujan provided data, discussed results and implications and edited earlier manuscripts. Travis O. Brenden provided data, discussed results and implications and edited earlier manuscripts. Timothy E. Walsworth provided data, discussed results and implications and edited earlier manuscripts. Todd M. Koel secured funding, discussed results and implications and edited earlier manuscripts.

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Ethics Statement

All fieldwork and lab work were conducted under Yellowstone National Park permit 8048. This study was performed under the auspices of Institutional Animal Care and Use Protocol 2018-72 at Montana State University.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this manuscript are available in the Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.