

Supplementary Materials for

Predatory fish invasion induces within and across ecosystem effects in Yellowstone National Park

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Supplementary Text

Yellowstone Lake is located on the Yellowstone Plateau (2357-m) in southeastern Yellowstone National Park, Wyoming (fig. S1). The lake lies partially within the Yellowstone caldera (66) and is mesotrophic (67) with a surface area of 341-km², an average depth of 48.5-m, and 239-km of shoreline (68). Yellowstone Lake remains ice-covered from December through May. The lake is dimictic with summer stratification occurring from mid-July to mid-September. During the ice-free season, surface water temperatures range from 3°C after ice-off to 18°C in mid-summer, dissolved oxygen ranges from 7–11 mg/L, the water is slightly basic pH (7.2–8.3), and conductivity is low (69–96 µS/cm).

Geology of the lake and surrounding basin is mainly rhyolite, with northern and eastern areas composed of andesite (69). Climate in the region is characterized by short summers with an average temperature of 11.8°C during July and long, cold winters with an average temperature of –10.8°C during December. The region receives approximately 513-mm of precipitation during the year, most of which falls as snow during the winter months. Yellowstone Lake tributary basins are predominantly subalpine and contain lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), whitebark pine (*Pinus albicaulis*), and Douglas-fir (*Pseudotsuga menziesii*) forest types and abundant open meadows. A wide range of stream lengths, bed gradients, slope aspects, and unique geothermal features greatly influence the timing and magnitude of snowmelt runoff and stream thermal characteristics. A large portion of the Yellowstone Lake watershed has been burned by multiple wildfires over the past three decades.

The fish assemblage in Yellowstone Lake includes two native species, Yellowstone cutthroat trout and the less abundant minnow, longnose dace (*Rhinichthys cataractae*) (70). Yellowstone cutthroat trout exhibit an adfluvial life history (71, 72). During spring (May–June) the cutthroat trout spawn in ~68 tributaries around Yellowstone Lake. In autumn or the following spring after hatching, juvenile cutthroat trout emigrate from the streams. Juvenile cutthroat trout in Yellowstone Lake are pelagic, feeding on zooplankton, whereas adult fish move to the littoral zone and feed on benthic macroinvertebrates and zooplankton. The cutthroat trout have been affected by *Myxobolus cerebralis* (the parasite that causes whirling disease) in a few spawning tributaries (15, 73, 74). Discharge and temperature variations of spawning streams are also considered to be important drivers of cutthroat trout year-class strength (48).

Other fish species that were intentionally introduced by managers to Yellowstone Lake and subsequently established reproducing populations include longnose sucker, redbelt shiner (*Richardsonius balteatus*), and lake chub (*Couesius plumbeus*) (70). There is no evidence that these introduced species negatively impacted the native cutthroat trout. Lake trout were inadvertently introduced to Yellowstone Lake, either illegally, or by invasion from Jackson Lake in the upper Snake River via the natural connection of Pacific and Atlantic creeks at Two Ocean Pass (fig. S1). Lake trout are the only piscivorous fish in Yellowstone Lake. As lake trout complete their entire life history within the lake and preferentially utilize deep water, they are inaccessible to consumers and do not serve as an ecological substitute for cutthroat trout in the system.

The zooplankton in Yellowstone Lake consist of three copepods (*Diacyclops bicuspidatus thomasi*, *Leptodiaptomus ashlandi*, and *Hesperodiaptomus shoshone*) and two cladoceran species (*Daphnia schødleri* and *Daphnia pulicaria*). Phytoplankton are dominated by the diatoms *Stephanodiscus* spp., *Cyclotella bodanica*, *Aulacoseira subarctica*, and *Asterionella formosa* (75). Cyanobacteria, Chlorophytes, Chrysophytes, and flagellated algae also inhabit the lake.

Twenty avian and terrestrial species are known to prey upon or scavenge cutthroat trout in Yellowstone Lake or its tributaries (76). Birds include American dipper (*Cinclus mexicans*), American white pelican, Barrow's goldeneye (*Bucephala islandica*), bald eagle, belted kingfisher (*Megaceryle alcyon*), bufflehead (*Bucephala albeola*), California gull, Caspian tern, common loon, common merganser (*Mergus merganser*), common raven (*Corvus corax*), double-crested cormorant, eared grebe (*Podiceps nigricollis*), great blue heron (*Ardea herodias*), great horned owl (*Bubo virginianus*), and osprey. Mammals include American black bear, grizzly bear, mink (*Mustela vison*), and river otter. Because they typically live at deep depths and spawn within the lake (not tributary streams), there are no predators known to prey upon lake trout adults or juveniles.

Supplementary Figures

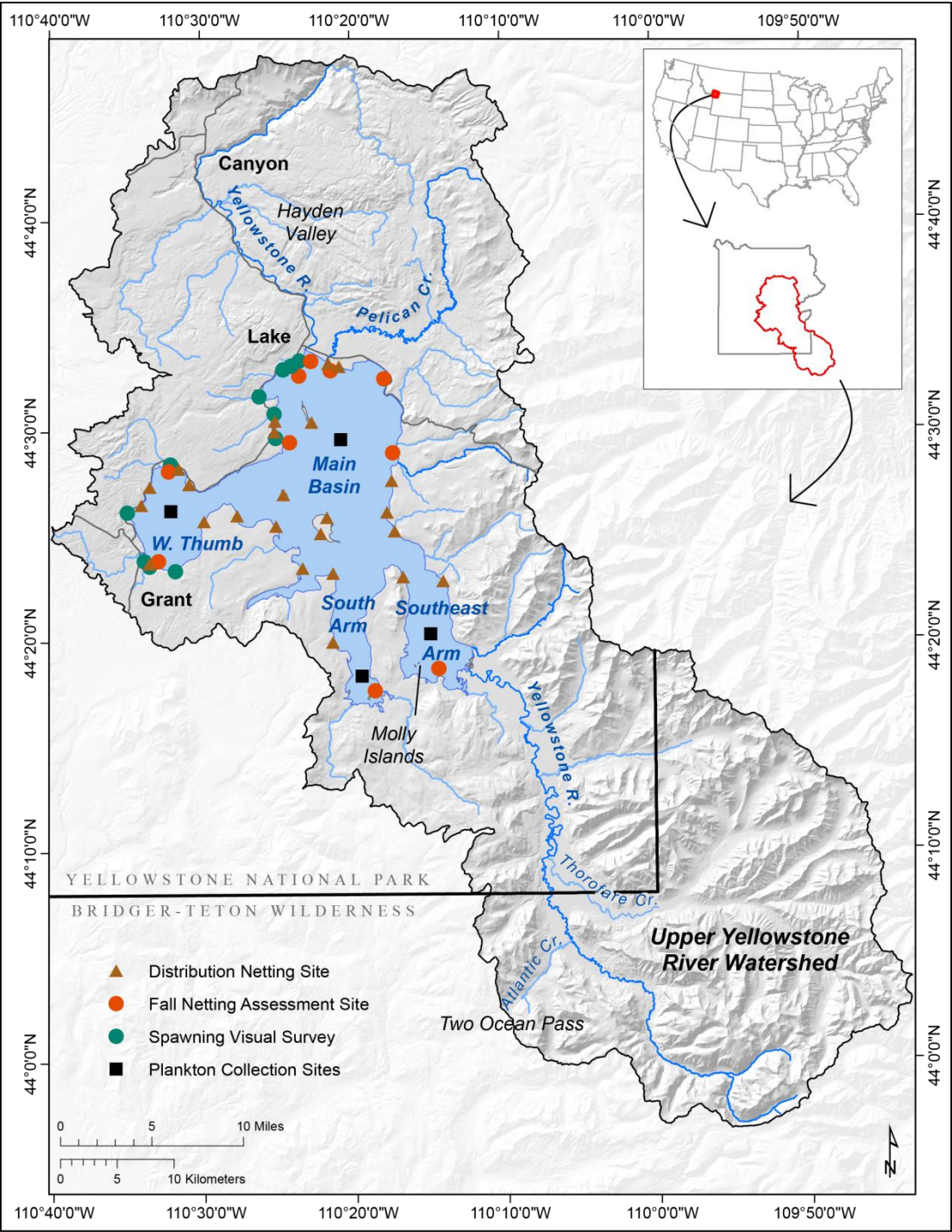


Fig. S1. The watershed (>3200 km²) of Yellowstone Lake and tributary streams in Yellowstone National Park and the Bridger-Teton wilderness, Wyoming. Shown are locations of annual fish population netting assessment (fall netting and distribution netting) sites; plankton monitoring sites; and tributaries visually-surveyed for spawning cutthroat trout and activity by bears.

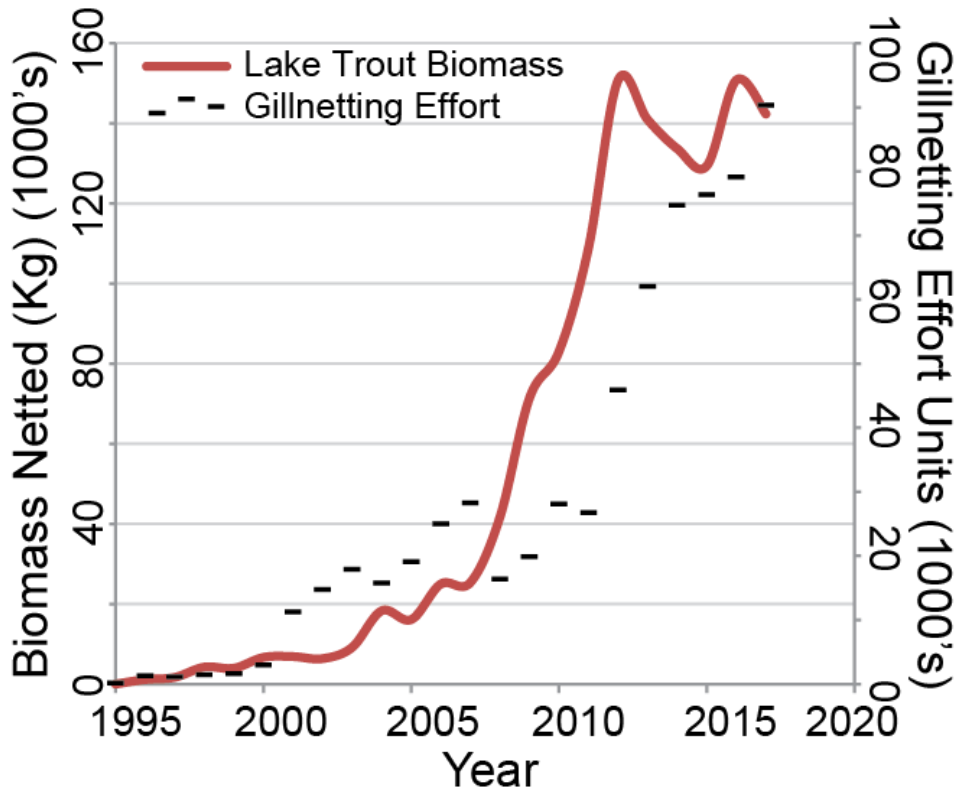


Fig. S2. Gillnetting effort expended and biomass of lake trout netted. The biomass of lake trout killed and returned to deep (>65-m) areas of Yellowstone Lake dramatically increased as the total gillnetting suppression effort increased (effort unit = 100-m net per night) during 1995–2012. During 2012–2017 the average biomass of lake trout killed annually was >140,000-kg.

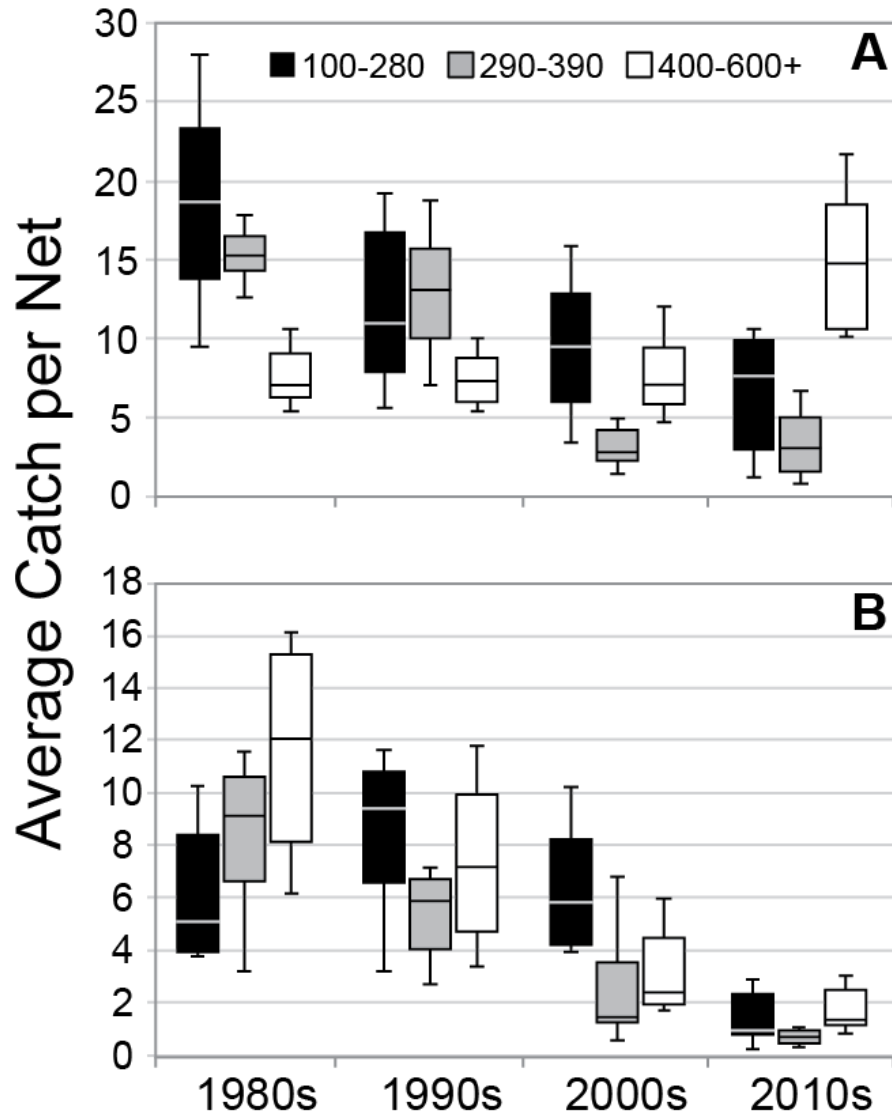


Fig. S3. Shift in size structure of prey fish populations during the period of lake trout invasion. Average catch per net (100-m net per night) is from standardized fish population assessment netting during each decade (1980–2017) for each of three fish length groups (mm). Prior to invasion by lake trout, the (A) cutthroat trout population was dominated by small individuals (100–280 mm) and the (B) sucker population by large individuals (400–600+ mm). As lake trout invaded and expanded throughout the lake, the small cutthroat trout declined and the population became dominated by large individuals. All length groups of longnose sucker declined.

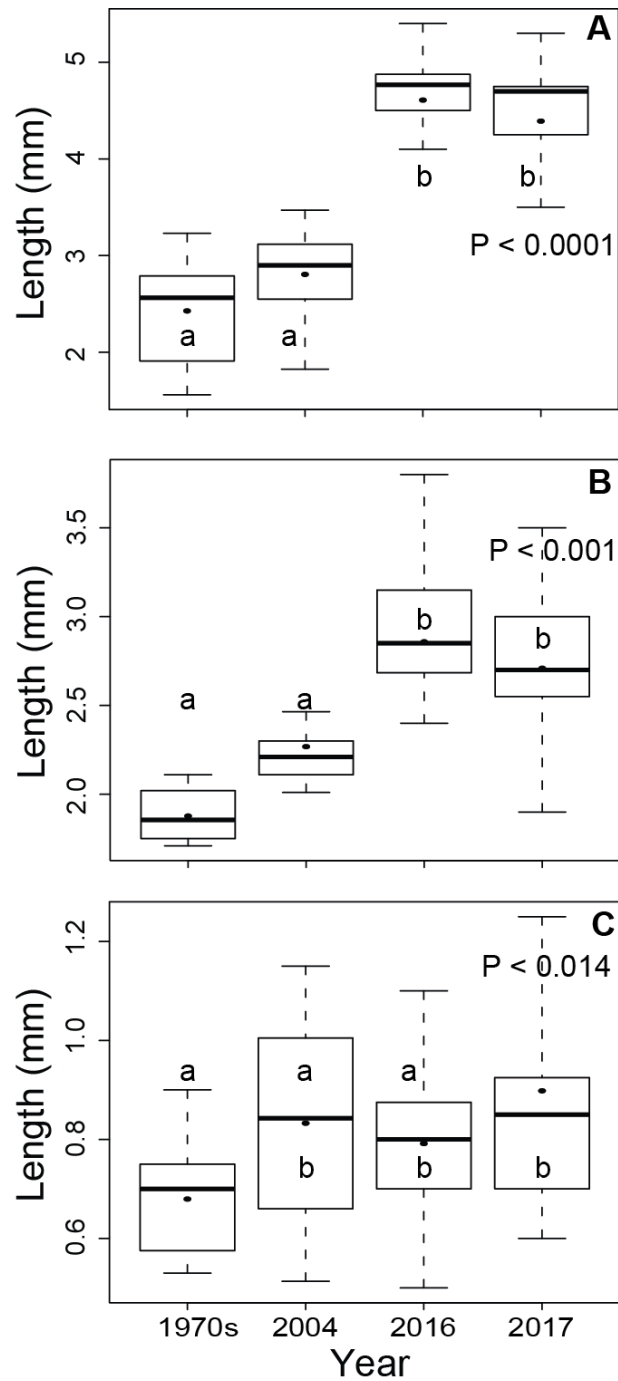


Fig. S4. Changes in plankton due to decline of planktivorous cutthroat trout.

Between 1977–1980 (prior to lake trout introduction), 2004 (10 years after lake trout were discovered), and 2016–2017 (>20 years later), the length of the (A) large zooplankton, *Hesperodiptomus shoshone* and (B) *Daphnia pulicaria*, was longer after lake trout invaded Yellowstone Lake. (C) The length of the small copepod, *Leptodiptomus ashlandi*, which is not efficiently consumed by cutthroat trout, only slightly changed.

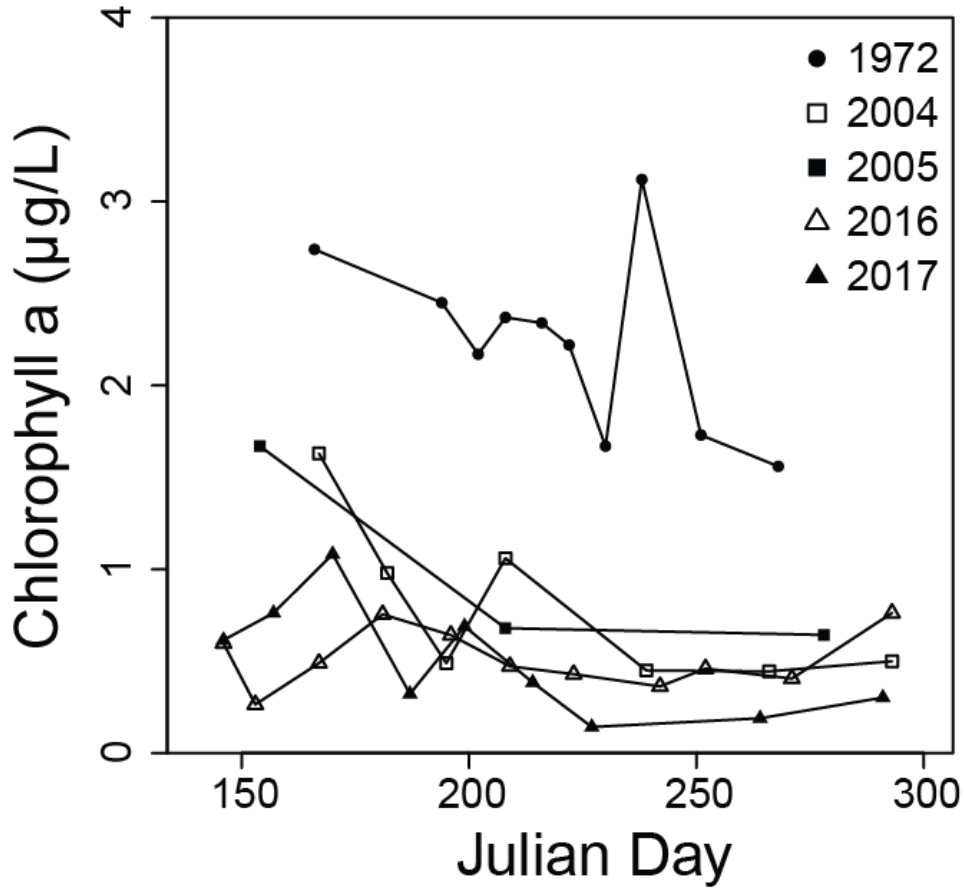


Fig. S5. Phytoplankton biomass in the West Thumb of Yellowstone Lake. Phytoplankton biomass (chlorophyll-*a* concentrations; µg/L) through the open water season was twice as high prior to lake trout invasion in 1972 (17) than after invasion during 2004–2005 (56) and 2016–2017.

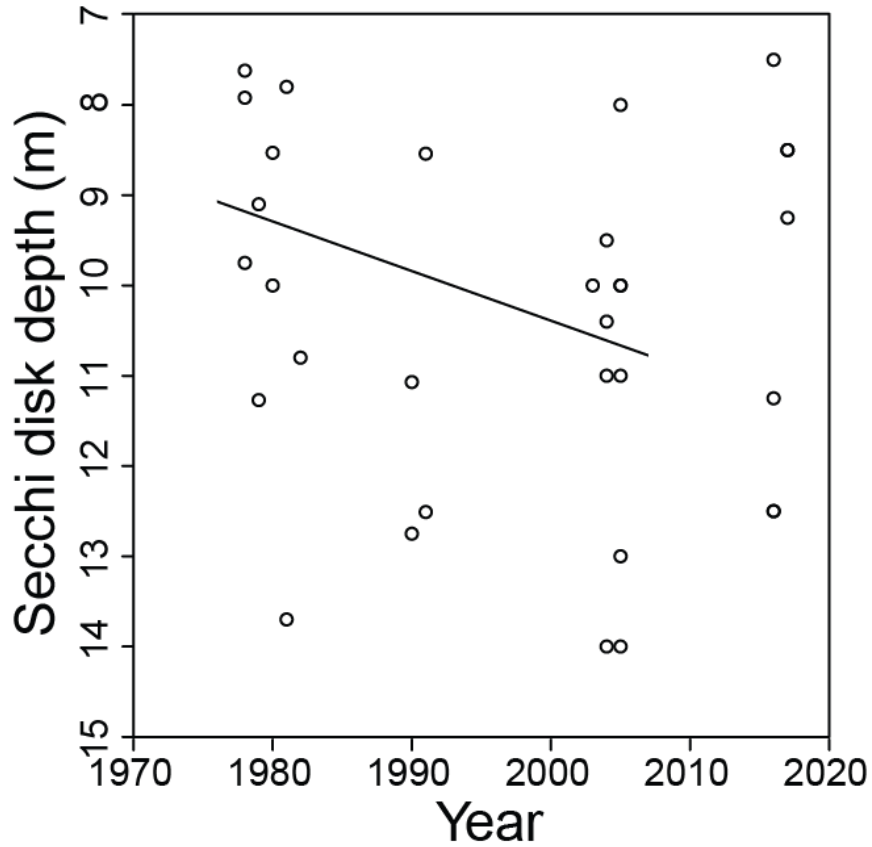


Fig. S6. Secchi disk depths in the West Thumb of Yellowstone Lake. Secchi disk depths (m) became 1.6-m deeper between 1976 (before lake trout invasion) and 2005 (after lake trout invasion; $P = 0.05$). Deeper Secchi disk depths indicated a decrease in phytoplankton biomass. $\text{Secchi disk depth (m)} = -113.11(\pm 52.96) + 0.055(\pm 0.027) \times \text{Year} + 0.063(\pm 0.017) \times \text{Julian}$.

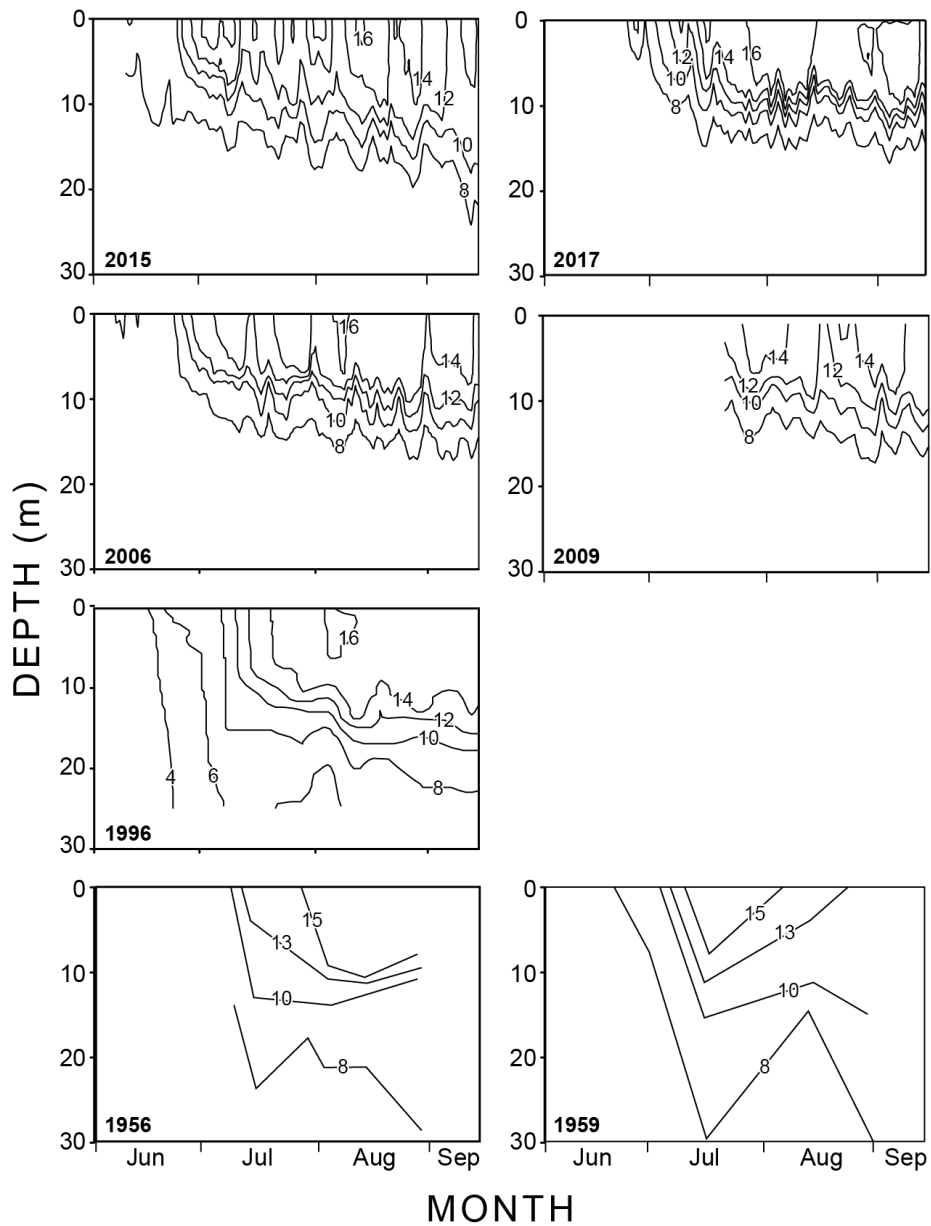


Fig. S7. Depths of isotherms (°C) in the West Thumb of Yellowstone Lake. Temperatures of Yellowstone Lake were measured in the West Thumb in 1956 and 1959 using a bathythermograph (77), and in 1996, 2006, 2009, 2015, and 2017 using a multiparameter sonde (Hydrolab Surveyor). The thermal structure of Yellowstone Lake is typically unstable with a weak and variable thermocline. Graphs for 1956–1959 are recreated from Benson (77) and for 1996 from Interlandi et al. (75).

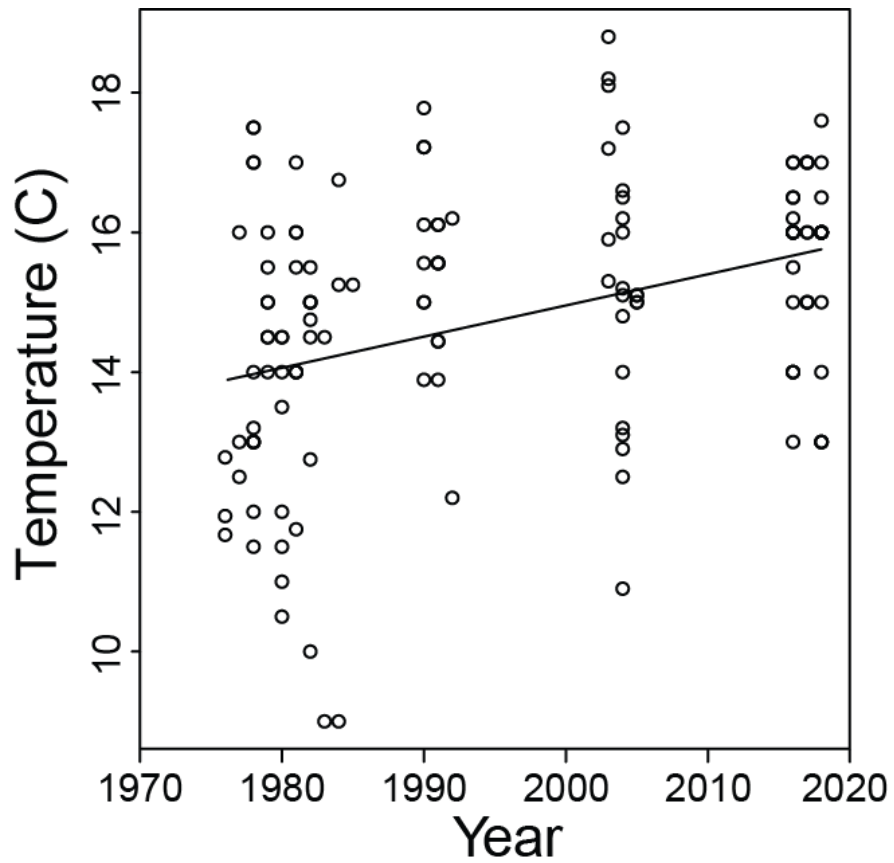


Fig. S8. Surface water temperatures of Yellowstone Lake. During the stratified period (15 July–15 September) surface water temperatures lake wide have increased 0.45°C per decade between 1976 and 2018. The line is drawn for a Julian day of August 15 (227). Surface water temperature (°C) = $-69.85 + 0.0446 \times Year - 0.0198 \times Julian$.

Supplementary Tables

Table S1. Results of Prais-Winsten time series regressions. Time series analyses were used to explore the relationships of cutthroat trout (YCT) and longnose sucker (LNS; explanatory variables) with bears, osprey and bald eagles (response variables). Significant relationships $Pr(>|t|)$ are in bold and marked (*).

| Explanatory | Response | | | | |
|------------------------------------|-------------------|----------------------------|------------------|--------------------------------|-----------------|
| | Bear Frequency | Osprey Count Success | | Bald Eagle Count Success | |
| YCT Spawning Visual Surveys | | | | | |
| Intercept Coefficient | | | | | |
| Estimate | 0.07603 | 4.46621 | 0.027708 | 3.2677 | 0.22269 |
| Std. Error | 0.03276 | 0.91496 | 0.035137 | 0.26702 | 0.08101 |
| t value | 2.321 | 4.881 | 0.789 | 12.238 | 2.749 |
| Pr(> t) | *0.0281 | *4.19E-05 | 0.437 | *1.58E-12 | *0.0105 |
| YCT Coefficient | | | | | |
| Estimate | 0.04891 | 0.01595 | 0.059612 | -0.02866 | 0.02771 |
| Std. Error | 0.00804 | 0.13875 | 0.008934 | 0.05670 | 0.01874 |
| t value | 6.084 | 0.115 | 6.673 | -0.506 | 1.478 |
| Pr(> t) | *1.70E-06 | 0.909 | *3.67E-07 | 0.617 | 0.1509 |
| Adjusted R-squared | 0.856 | 0.5362 | 0.8395 | 0.9095 | 0.5565 |
| F-statistic | 87.22 | 17.77 | 76.83 | 146.6 | 19.19 |
| DF | 27 | 27 | 27 | 27 | 27 |
| Rho t | 0.1896 | 0.8155 | -0.2038 | 0.6016 | 0.4414 |
| YCT Assessment Netting CPUE | | | | | |
| Intercept Coefficient | | | | | |
| Estimate | 0.116214 | 4.93778 | -0.047352 | 3.52347 | 0.142245 |
| Std. Error | 0.098521 | 1.180 | 0.095485 | 0.37952 | 0.114873 |
| t value | 1.180 | 4.185 | -0.496 | 9.284 | 1.238 |
| Pr(> t) | 0.248 | *0.00024 | 0.62369 | *1.83E-10 | 0.2249 |
| YCT Coefficient | | | | | |
| Estimate | 0.004988 | -0.01391 | 0.010345 | -0.01695 | 0.006783 |
| Std. Error | 0.003546 | 0.02564 | 0.003398 | 0.01211 | 0.003942 |
| t value | 1.407 | -0.543 | 3.045 | -1.40 | 1.721 |
| Pr(> t) | 0.171 | 0.591495 | *0.00492 | 0.172 | 0.0953 |
| Adjusted R-squared | 0.5703 | 0.4273 | 0.6517 | 0.8977 | 0.6789 |
| F-statistic | 20.24 | 12.57 | 30.01 | 145.8 | 35.89 |
| DF | 27 | 29 | 29 | 31 | 31 |
| Rho t | 0.5029 | 0.8712 | 0.0791 | 0.06326 | 0.2021 |
| LNS Assessment Netting CPUE | | | | | |
| Intercept Coefficient | | | | | |
| Estimate | 0.18099 | 3.26456 | 0.071863 | 2.954361 | 0.342254 |
| Std. Error | 0.05978 | 0.62925 | 0.061919 | 0.277036 | 0.084505 |
| t value | 3.027 | 5.188 | 1.161 | 10.660 | 4.050 |
| Pr(> t) | *0.00537 | *1.50E-05 | 0.2553 | *6.75E-12 | *0.00032 |
| LNS Coefficient | | | | | |
| Estimate | 0.00516 | 0.10537 | 0.011214 | 0.005055 | -0.00088 |
| Std. Error | 0.00316 | 0.03525 | 0.003832 | 0.011486 | 0.004881 |
| t value | 1.633 | 2.990 | 2.926 | 0.440 | -0.181 |
| Pr(> t) | 0.11407 | *0.00564 | *0.0066 | 0.663 | 0.857405 |
| Adjusted R-squared | 0.5285 | 0.8287 | 0.645 | 0.8419 | 0.573 |
| F-statistic | 17.26 | 76.00 | 29.16 | 88.87 | 23.15 |
| DF | 27 | 29 | 29 | 31 | 31 |
| Rho t | 0.5784 | 0.4375 | 0.0799 | 0.7096 | 0.3308 |

Table S2. Fish explanatory variables used in time series and trend analyses. Mean number of cutthroat trout observed during visual surveys of tributary spawning streams, mean catch-per-unit-effort (CPUE) of cutthroat trout and longnose sucker during fish population netting assessments, and lake trout abundance (1000's) estimated by statistical catch-at-age analysis.

| Year | Cutthroat trout | | Longnose sucker | Lake Trout |
|------|-----------------|-----------|-----------------|----------------|
| | Mean Count | Mean CPUE | Mean CPUE | Est. Abundance |
| 1980 | | 34.2 | 26.3 | |
| 1981 | | 62.8 | 23.9 | |
| 1982 | | 27.8 | 34.7 | |
| 1983 | | 47.5 | 29.9 | |
| 1984 | | 50.4 | 35.3 | |
| 1985 | | 37.5 | 16.4 | |
| 1986 | | 44.1 | 27.2 | |
| 1987 | | 48.7 | 26.3 | |
| 1988 | | 42.2 | 20.6 | |
| 1989 | 71.8 | 37.8 | 14.9 | |
| 1990 | 74.2 | 31.3 | 28.3 | |
| 1991 | 62.8 | 37.2 | 27.9 | |
| 1992 | 28.9 | 28.0 | 10.2 | |
| 1993 | 26.1 | 35.0 | 17.9 | |
| 1994 | 7.4 | 41.9 | 25.6 | |
| 1995 | 16.4 | 37.0 | 24.9 | |
| 1996 | 7.8 | 36.9 | 17.3 | |
| 1997 | 23.6 | 29.1 | 16.4 | |
| 1998 | 42.0 | 26.1 | 20.5 | 79.7 |
| 1999 | 21.9 | 21.3 | 21.9 | 94.3 |
| 2000 | 26.6 | 19.0 | 12.7 | 101.5 |
| 2001 | 7.9 | 17.2 | 22.4 | 99.6 |
| 2002 | 4.3 | 16.1 | 15.1 | 101.2 |
| 2003 | 3.7 | 19.5 | 6.8 | 112.8 |
| 2004 | 0.5 | 19.3 | 7.3 | 147.7 |
| 2005 | 0.4 | 19.7 | 10.3 | 217.0 |
| 2006 | 0.4 | 15.8 | 9.5 | 299.4 |
| 2007 | 0.2 | 23.8 | 15.2 | 368.0 |
| 2008 | 0.3 | 24.2 | 9.0 | 455.1 |
| 2009 | 1.0 | 25.1 | 14.9 | 550.9 |
| 2010 | 1.2 | 11.9 | 2.6 | 670.6 |
| 2011 | 2.4 | 12.7 | 1.6 | 801.4 |
| 2012 | 2.8 | 19.9 | 4.7 | 953.0 |
| 2013 | 3.5 | 23.8 | 4.1 | 863.2 |
| 2014 | 4.4 | 28.4 | 6.0 | 836.1 |
| 2015 | 7.0 | 19.4 | 2.8 | 853.5 |
| 2016 | 7.5 | 18.3 | 5.0 | 853.7 |
| 2017 | 4.2 | 20.4 | 5.1 | 813.1 |

Table S3. Bear and bird response variables used in time series analyses. Proportion (frequency) of annual spawning stream visual surveys where evidence of use by bears (e.g. tracks, scat, sightings) was found, and nest counts and success (%) of ospreys and bald eagles.

| Year | Bear | Osprey | | Bald Eagle | |
|------|-----------|--------|-------------|------------|-------------|
| | Frequency | Count | Success (%) | Count | Success (%) |
| 1985 | | | | 5 | 40 |
| 1986 | | | | 6 | 50 |
| 1987 | | 39 | 62 | 6 | 67 |
| 1988 | | 43 | 49 | 7 | 86 |
| 1989 | 0.43 | 42 | 55 | 8 | 38 |
| 1990 | 0.48 | 39 | 77 | 8 | 63 |
| 1991 | 0.55 | 25 | 52 | 8 | 63 |
| 1992 | 0.38 | 50 | 76 | 9 | 44 |
| 1993 | 0.46 | 54 | 56 | 11 | 73 |
| 1994 | 0.34 | 62 | 66 | 12 | 33 |
| 1995 | 0.31 | 38 | 37 | 12 | 58 |
| 1996 | 0.15 | 40 | 30 | 12 | 50 |
| 1997 | 0.29 | 51 | 47 | 14 | 57 |
| 1998 | 0.23 | 50 | 76 | 10 | 60 |
| 1999 | 0.23 | 53 | 36 | 13 | 31 |
| 2000 | 0.35 | 56 | 48 | 14 | 57 |
| 2001 | 0.30 | 60 | 38 | 15 | 20 |
| 2002 | 0.22 | 47 | 9 | 15 | 27 |
| 2003 | 0.06 | 28 | 18 | 16 | 44 |
| 2004 | 0.07 | 19 | 11 | 14 | 43 |
| 2005 | 0.07 | 14 | 14 | 14 | 21 |
| 2006 | 0.03 | 10 | 40 | 13 | 23 |
| 2007 | 0.14 | 7 | 14 | 12 | 33 |
| 2008 | 0.01 | 5 | 0 | 4 | 25 |
| 2009 | 0.03 | 4 | 0 | 9 | 0 |
| 2010 | 0.14 | 5 | 0 | 9 | 33 |
| 2011 | 0.07 | 4 | 0 | 10 | 40 |
| 2012 | 0.21 | 5 | 20 | 11 | 64 |
| 2013 | 0.15 | 3 | 66 | 9 | 78 |
| 2014 | 0.11 | 4 | 25 | 7 | 71 |
| 2015 | 0.30 | 3 | 33 | 11 | 73 |
| 2016 | 0.18 | 3 | 0 | 6 | 50 |
| 2017 | 0.41 | 3 | 33 | 5 | 80 |