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ARTICLE

Invasive Lake Trout Reproduction in Yellowstone Lake under an Active Suppression Program

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Abstract

In Yellowstone Lake, predation by invasive Lake Trout *Salvelinus namaycush* has caused significant abundance declines in native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*. Lake Trout suppression has been ongoing since 1995; assessment and simulation modeling are used to measure suppression effectiveness and guide efforts. Lake Trout reproduction demographics are linked to these modeling efforts via quantification of the population stock–recruitment relationship. To improve estimation of this relationship for Lake Trout in Yellowstone Lake, we assessed reproduction demographics by quantifying spawning periodicity, size at maturity, and female fecundity. Histological assessment suggested that females with a gonadosomatic index (GSI) >3.0 and males with a GSI >1.0 were capable of spawning. Approximately 65% of mature females appeared to have spawned on an annual cycle. In 2015, the mean absolute and relative fecundities were 4,612 eggs and 1,535 eggs/kg, respectively; temporal differences in relative fecundity (1996, 2006, 2007, and 2015) were not statistically significant. Lake Trout population fecundity has declined from a peak in 2010 due to reduction in abundance of spawners. The estimated population fecundity of approximately 4.7 million eggs in 2020 represents an 81% decline from the mean estimate of previous samples and an 87% reduction from peak population fecundity. Despite declines in population fecundity, age-2 recruitment has increased in recent years; our results suggest these increases are not related to changes in reproductive demographics, but rather are related to increased prerecruitment survival. Our results provide information for understanding temporal variation in spawning stock biomass of Lake Trout in Yellowstone Lake and the capacity of the population to

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respond to suppression. When responding to an invasive species, fishery managers should recognize that population characteristics (e.g., reproduction demographics, population dynamics) in invaded systems may differ from those in the species' native range; such differences can influence the effectiveness of management actions and policies.

The Lake Trout *Salvelinus namaycush* is a salmonine predator found throughout much of North America. In some portions of their native range, such as the Laurentian Great Lakes, the species is diminished and being managed for recovery by federal, state, provincial, and tribal agencies (Crawford 2001). However, where introduced, Lake Trout are often actively suppressed by fishery management agencies to protect or restore native fauna (e.g., Martinez et al. 2009; Hansen et al. 2016; Fredenberg et al. 2017). Within their native range, the species exhibits diverse life history strategies that can vary by morphotype, latitude, and physical conditions of lakes (Trippel 1993; Morbey and Shuter 2013; Muir et al. 2016). Comparable knowledge about life history strategies for introduced or invasive populations of Lake Trout is limited.

Within their native range, Lake Trout typically spawn from September through December (Martin and Olver 1980; Goetz et al. 2011) when epilimnetic temperatures decrease to 12°C (Casselman 1995), although deepwater populations of the siscowet morphotype near Isle Royale, Lake Superior can spawn in either spring or fall (Goetz et al. 2017). For lean Lake Trout, spawning often occurs on steep slopes of rocky shoals in shallow regions of lakes, where embryos become lodged in interstitial spaces (Marsden et al. 2005). Both annual spawning and nonannual spawning (skipped spawning; Rideout et al. 2005) have been reported in the native range. Rideout and Tomkiewicz (2011) defined skipped spawning as "the failure to spawn in a given year." In a study of five lakes in Algonquin Provincial Park, Ontario, skipped spawning among male Lake Trout was not observed in any of the lakes, but skipped spawning among females in one population ranged from 25% to 75%, depending on body size (Trippel 1993). In Lake Superior, estimates of skipped spawning among female Lake Trout were 58% and 12% in siscowet and lean morphotypes, respectively (Sitar et al. 2014). Goetz et al. (2011) reported that skipped spawning was more common in female than male Lake Trout for both lean and siscowet morphotypes.

Lake Trout were discovered in Yellowstone Lake, Wyoming in 1994 (Varley and Schullery 1995). The prevailing hypothesis suggests that the population originated from one or more illegal stocking events that occurred in the 1980s, ostensibly with fish from an introduced population in Lewis Lake, Wyoming (Munro et al. 2005). Lake Trout population abundance rapidly expanded in Yellowstone Lake (Syslo et al. 2020), and predation by the nonnative invader led to significant reductions in the abundance of native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* (Koel et al. 2020). The decline in abundance of Yellowstone Cutthroat Trout caused cascading effects throughout Yellowstone National Park and affected abundances of a variety of terrestrial wildlife and avian populations, including grizzly *Ursus arctos horribilis* and black bear *Ursus americanus*, elk *Cervus canadensis*, bald eagle *Haliaeetus leucocephalus*, and osprey *Pandion haliaetus* (Tronstad et al. 2010; Gresswell and Tronstad 2013; Koel et al. 2019). Since the mid-1990s, biologists with the U.S. National Park Service have been engaged in an aggressive Lake Trout suppression program meant to reverse these effects.

Through a combination of direct observation and telemetry studies, some aspects of Lake Trout spawning in Yellowstone Lake have been well-documented. For example, littoral habitat in Yellowstone Lake is abundant (Bigelow 2009), and numerous Lake Trout spawning locations have been identified (Ruzycki et al. 2003; Gutowsky et al. 2020; Williams et al. 2020). Lake Trout spawning in Yellowstone Lake occurs from September to early October, with the greatest proportion of spawning-capable (a fish capable of spawning within the current reproductive cycle, Brown-Peterson et al. 2011) females generally captured in the last week of September. However, there are numerous other aspects about the reproductive structure (e.g., rate of gonadal development and frequency of skipped spawning) of Lake Trout in Yellowstone Lake that remain unknown or poorly understood. Knowledge of these reproduction demographics could be beneficial to efforts to suppress Lake Trout. For example, assessment and simulation modeling are used to determine the response of Lake Trout to the suppression program and to guide future efforts to meet conservation targets that have been established for recovery of Yellowstone Cutthroat Trout in the lake. Data on reproduction demographics of Lake Trout could improve understanding of the underlying stock–recruitment relationship for the population and ultimately determine the level of effort necessary for the suppression program to achieve conservation targets in a timely manner.

The goal of this study was to assess the reproduction demographics of Lake Trout in Yellowstone Lake by quantifying spawning periodicity, size at maturity, and female fecundity. Information from this study will provide insight into the population growth potential of invasive Lake Trout in Yellowstone Lake and expand our understanding of life history variation of the species in novel environments.

METHODS

Study area.— At an elevation of 2,357 m, Yellowstone Lake is the largest high-elevation lake in North America (>2000 m; Gresswell et al. 1997), with a surface area of 341 km^2 and a maximum depth of 133 m (Kaplinski 1991; Morgan et al. 2003). This mesotrophic (Theriot et al. 1997), dimictic lake is typically ice-covered from late December until late May and stratified from July through September (Benson 1961). Yellowstone Cutthroat Trout use 68 of 124 tributaries and the lake outlet for spawning from May to July (Gresswell and Varley 1988). The only other native fish species in Yellowstone Lake is the Longnose Dace *Rhinichthys cataractae* (Benson 1961). Previously identified nonnative fishes include Longnose Sucker *Catostomus catostomus*, Redside Shiner *Richardsonius balteatus*, and Lake Chub *Couesius plumbeus* (Benson 1961).

Gonadosomatic index and gonadal development.— In 2014 and 2015, we obtained Lake Trout captured by suppression crews (Hickey Brothers, LLC) in gill nets set throughout the lake (mesh sizes = 25, 32, 38, 44, 51, 57, and 64 mm, bar measure). Nets varied in height from 1.2 to 1.8 m and were 91 m in length. Male and female Lake Trout were captured during the ice-free season of 2014 for gonadosomatic index (GSI) assessment and histological staging of gonadal tissue. The sample periods for 2014 were June (June 18 to 25), July (June 30 to July 16), August (July 30 to August 1), September (September 2 to 22), and October (October 1 to 2).

All sampled Lake Trout were measured (nearest mm, TL) and weighed (nearest g). Gonadal lobes were removed, weighed (nearest 0.1 g), and a subsample was stored in phosphate-buffered formalin for histological analysis. The GSI ([gonad weight/body weight] × 100) was calculated for each individual. We classified Lake Trout as capable of spawning if GSI was ≥1.0 and 3.0 for males and females, respectively (Goetz et al. 2011; Sitar et al. 2014).

In the lab, gonadal tissue was embedded in paraffin, sectioned at 5 μm, and stained by periodic acid–Schiff reagent (Luna 1968). Slides were examined under a compound microscope (Leica DM 2000, 50× to 400×), and germ cells were scored for stage of maturation (Figures 1 and 2) according to the modified protocol of Goetz et al. (2011; Table 1). To standardize terminology according to Brown-Peterson et al (2011), females that were in stages 1 (previtellogenic), 2 (early vitellogenic), and 3 (mid-vitellogenic) were considered developing; those in stages 4 (late vitellogenic) and 5 (ripe) were considered spawning capable, and females in stages 6 (ovulating) and 7 (post-ovulation) were considered to be spawning at capture or to have successfully spawned prior to capture (regressing). Males that were in stage 1 (prespermatogenic) were immature, stages 2 (early spermatogenic) and 3 (mid-spermatogenic) were developing, stages 4 (late spermatogenic) and 5 (ripe) were spawning capable, and stage 6 (post spermiation) were regressing. Mean GSI and percent change in histological stage were subsequently compared across sample periods.

Differences in length and weight between male and female Lake Trout were summarized and compared using *t*-tests ($\alpha = 0.05$). We assessed the relationship between histological stage and GSI separately for female and male Lake Trout using one-way ANOVA ($\alpha = 0.05$). We $\log_e$ transformed the GSI values of female Lake Trout prior to analysis to meet the assumptions of normality. Pairwise comparisons between histological stages were further analyzed after Bonferroni adjustments (*P*-values adjusted for multiple comparisons, $\alpha = 0.05$).

Fecundity.— Fecundity was estimated from ovarian follicles (hereafter referred to as "eggs") collected from 44 spawning-capable female Lake Trout during September and early October of 2015. To account for potential spatial variation in fecundity and spawning behavior, individuals were captured by gillnetting in numerous locations around the lake. Within 10 h of capture, we recorded fish weight and removed and weighed each ovary. Ovaries were placed in ethanol and stored for processing at a later date. In the lab, we weighed preserved gonads (nearest 0.1 g), removed three subsections from each ovary (middle, anterior, and posterior), weighed the subsections, and counted the number of eggs in each subsection.

We estimated absolute fecundity (Nikolsky 1963; Bagenal 1978) for each female Lake Trout using the equation:

$$\text{Absolute fecundity} = \frac{\left[\sum_i \frac{O_i}{W_i}\right]}{n}(W_{\text{ovaries}}),$$

where O_i was the subsample ovarian follicle count, W_i was the subsample weight, n was number of subsamples, and W_{ovaries} was the combined weight of both ovaries. Relative fecundity was estimated by dividing absolute fecundity by the total body weight (kg; Nikolsky 1963; Bagenal 1978; Liermann et al. 2004). We used regression analysis with $\log_{10}$ transformations to further explore the relationships between absolute fecundity and weight and absolute fecundity and length of Lake Trout. Because the predictor variables (length or weight) in these equations were subject to natural variability, geometric mean (GM) functional regressions and confidence limits were also derived for each according to Ricker (1975). We used ANCOVA to compare slope and intercept estimates from the current study with previous Lake Trout fecundity relationships from Yellowstone Lake (1996, 2006, and 2007). Prior estimates were obtained volumetrically in 1996 (Ruzycki et al. 2003; $n = 10$) and gravimetrically in 2006 and 2007 (Syslo 2010; $n = 119$ and $n = 77$, respectively). Slopes of GM regressions were evaluated by comparing the confidence intervals

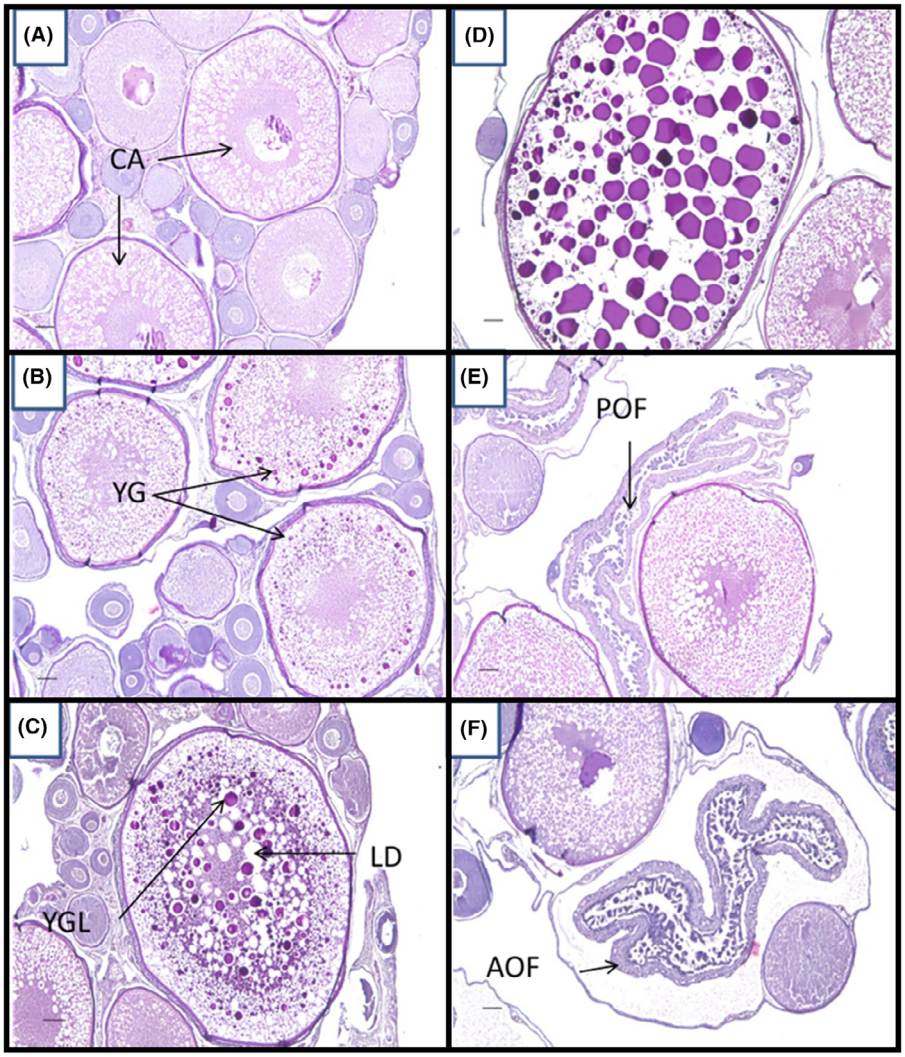

FIGURE 1. Lake Trout ovarian histology: **(A)** stage 1, oocytes in cortical alveolus stage (CA); **(B)** stage 2, yolk granules (YG) accumulating in the periphery of oocytes; **(C)** stage 3, YG beginning to coalesce into yolk globule (YGL) and lipid droplets (LD) present; **(D)** stage 4, YGL continue to coalesce and ovarian follicle diameter increases; **(E)** stage 7, postovulatory follicle (POF) and oocytes in the CA stage; **(F)** stage 8, atretic ovarian follicle (AOF) and oocytes in the CA stage. Stages 5 and 6 are not shown. Photos captured with a 5× objective, and scale bar is 1 μm. [Color figure can viewed at afsjournals.org.]

among years. Finally, we used one-way ANOVA to compare the relative fecundity among sample years.

To estimate population fecundity (number of eggs potentially laid by all females in the population; Bagenal 1978) and changes through time for Lake Trout in Yellowstone Lake, the relative fecundity data were incorporated into the statistical catch-at-age assessment model (Syslo et al. 2011, 2020) that has been used to guide the Lake Trout suppression program on Yellowstone Lake. Mean relative fecundity and measures of uncertainty in the means were then estimated in the assessment model along with other parameter values. Based on these model estimates, we then calculated population-level fecundity at different time periods within the assessment model, which allowed for propagation of the uncertainties in both population biomass and relative fecundity estimates. We did not calculate population fecundity in 1996 because the initial year of the assessment model was 1998; thus we lacked population biomass estimates for that year. We assumed that fish age 6 and older were capable of spawning, and we assumed a 1:1 sex ratio based on the results of Syslo et al. (2011). Based on our histological results (see below), we assumed that 65% of the female Lake Trout were spawning capable on an annual basis, and the estimated number of females ≥age 6 was adjusted accordingly. Confidence limits for the population fecundity estimates for each sample year were calculated by likelihood profiling as implemented in AD Model Builder (Fournier et al. 2012), which is the software used to fit the Lake Trout assessment model for Yellowstone Lake.

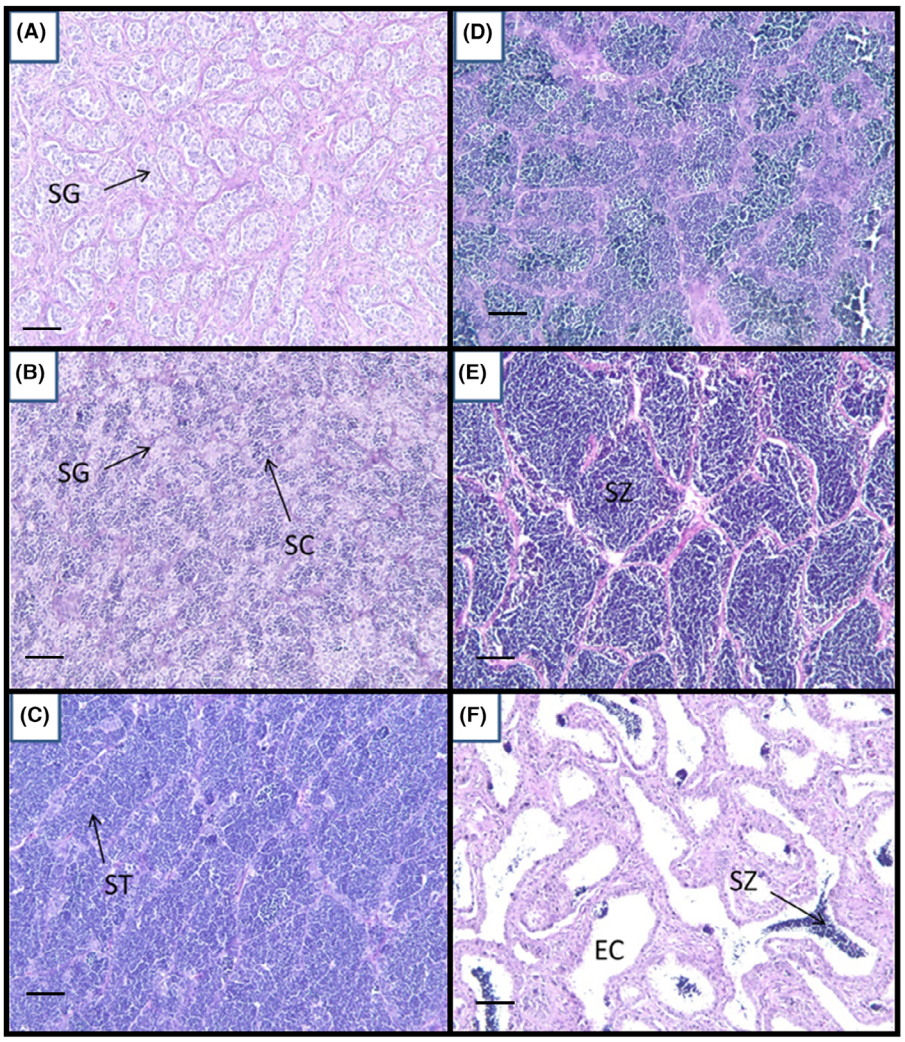

FIGURE 2. Lake Trout testicular histology: **(A)** stage 1, only spermatogonia (SG) present; **(B)** stage 2, SG and spermatocytes (SC) present; **(C)** stage 3, few cysts contain SG, >50% of the cysts contain SC and spermatids (ST), few cysts may contain spermatozoa (SZ); **(D)** stage 4, predominately SC, ST, and >25% cysts contain SZ; **(E)** stage 5, SZ present in >75% of cysts; **(F)** stage 6, emptying testicular cysts (EC) and residual SZ. Photos captured using a 10× objective, and scale bar is 1 μm. [Color figure can viewed at afsjournals.org.]

RESULTS

Between June 18 and October 2, 2014, we captured 222 female and 133 male Lake Trout. Mean length and weight of females were 575 mm (range = 330–901 mm) and 2,197 g (range = 375–8,732 g), respectively. Mean length and weight of males were 511 mm (range = 301–836 mm) and 1,549 g (range = 285–8,850 g), respectively. Length ($t = 1.97$, $P < 0.001$) and weight ($t = 1.97$, $P < 0.001$) differed significantly between sexes, with females generally longer and heavier than males.

Gonadosomatic Index and Histology

Mean GSI for females increased from 0.4 (range = <0.1–4.3) in June to a maximum of 5.7 (range = <0.1–17.7) in September; male GSI increased from 0.5 (range = <0.1–2.4) to 2.9 (range = 0.2–6.1) during the same period (Table 2). Gonadosomatic index estimates for female Lake Trout over the entire sample period ranged from <0.1 to 20.9 (mean = 3.6); in general, values for female Lake Trout were close to 0.0 until individuals reached 490 mm (the length of the smallest individual with a GSI indicating the potential to spawn, GSI ≥3; Figure 3). For example, estimates for females <490 mm (range = 330–489 mm; mean = 438 mm; $n = 34$) ranged from <0.1 to 0.7 (mean = 0.1), and GSI for individuals in that size group remained low throughout the study. In contrast, the GSI of larger individuals (≥490 mm) were highly variable, and mean estimates increased through time. From June through August, GSI for females ≥490 mm (range = 492–850 mm; mean = 578 mm; $n = 78$) ranged from <0.1 to 7.4 (mean =

TABLE 1. Stages of gonadal development identified from gonadal biopsies of Lake Trout caught in Yellowstone Lake. Germ cells were scored for stage of maturation according to the modified protocol of Goetz et al. (2011).

Developmental phase	Stage	Description
		Females
Previtellogenic	1	Oocytes in cortical alveolus stage.
Early vitellogenic	2	Yolk granules accumulating in periphery of developing oocytes.
Mid-vitellogenic	3	Yolk globules present, nucleus central.
Late vitellogenic/ spawning capable	4	Yolk coalescing throughout oocyte, nucleus off center, much larger in size.
Ripe/spawning capable	5	Yolk entirely coalesced, nucleus has migrated to animal pole, and follicular layer is intact.
Ovulated	6	Yolk entirely coalesced, nucleus has undergone germinal vesicle breakdown, and a few postovulatory follicles may be present.
Postovulatory	7	Postovulatory follicles present with oocytes in cortical alveolus stage.
Atretic	8	Greater than 75% atretic ovarian follicles, no postovulatory follicles present with oocytes in cortical alveolus stage.
		Males
Prespermatogenic	1	Only spermatogonia present.
Early spermatogenic	2	Spermatogonia and spermatocytes present.
Mid-spermatogenic	3	Few cysts contain spermatogonia, >50% of the cysts contain spermatocytes and spermatids, few cysts may contain spermatozoa.
Late spermatogenic/ spawning capable	4	Predominately spermatocytes, spermatids, and >25% cysts contain spermatozoa.
Ripe/spawning capable	5	Greater than 75% of cysts contain spermatozoa.
Postspermiation	6	Residual spermatozoa and empty testicular cysts.

TABLE 2. Mean, range, and sample size of gonadosomatic index by month for Lake Trout caught in Yellowstone Lake.

	June	July	August	September	October
			Females		
Mean	0.4	1.6	1.7	5.7	5.6
Range	<0.1–4.3	0.1–7.4	0.1–6.8	<0.1–17.7	<0.1–20.9
n	30	56	17	67	52
			Males		
Mean	0.5	1.9	2.8	2.9	2.5
Range	<0.1–2.4	0.3–3.3	1.2–4.4	0.2–6.1	0.4–6.7
n	32	20	18	32	31

1.7). During the spawning season, GSI for females ≥490 mm (range = 490–901 mm; mean = 615; $n = 110$) ranged from <0.1–20.9 (mean = 6.1). The female with the highest GSI (20.9) was only 640 mm. During the spawning season, 63% (69/110) of female Lake Trout ≥490 mm had a GSI >3.0.

Overall, GSI for male Lake Trout was highly variable (Figure 4); estimates for male Lake Trout ranged from <0.1 to 6.7 (mean = 2.1; $n = 133$). The smallest individual with a GSI indicating the potential to spawn (GSI ≥1.0) was 395 mm. Estimates for males <395 mm (range = 301–390 mm; mean = 352; $n = 13$) ranged from <0.1 to 0.9 (mean = 0.2). Prior to the spawning season, GSI for males ≥395 mm (range = 395–680 mm; mean = 495 mm; $n = 57$) ranged from <0.1–4.4 (mean = 1.8). During the spawning season, GSI for males ≥395 mm (range = 450–836 mm; mean = 558; $n = 63$) ranged from 0.2 to 6.7 (mean = 2.7). Fifty-eight (92%) of the males sampled in this period had a GSI ≥1.0. Histological analysis revealed two of the five males with GSI <1 had testicular cysts with spermatozoa (ripe/spawning capable), but it was evident that spermiation had begun as indicated by emptying testicular cysts. However, the volume of spermatozoa within cysts was high enough to assign these males as spawning capable. Finally, GSI values for all males >600 mm suggested imminent spawning, a trend not observed in females of the same size.

Histological analyses were completed for 110 female and 77 male Lake Trout captured in 2014. Gonadal development was restricted to the previtellogenic (stage 1) and vitellogenic stages (stages 2–4) for female Lake Trout captured in June, July, and August, but development had advanced further by September (Table 3). In June, 67% of females ≥490 mm were in the mid-vitellogenic stage (stage 3). However, as the season progressed the percentage of fish in this stage decreased and percentages increased in the later stages of gametogenesis (stages 4–8; Table 3). By September and October, female Lake Trout ≥490 mm exhibited a wide range of developmental stages, and many

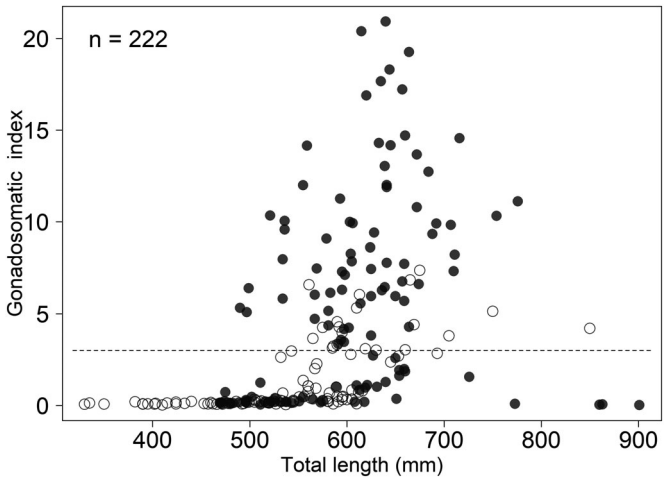

FIGURE 3. Female Lake Trout gonadosomatic index (GSI) by length. Solid gray circles represent fish caught during the spawning season (September and October) and hollow circles represent fish caught prior to the spawning season. The dashed line represents GSI value of 3.

individuals were still in the early to mid-vitellogenic stages (stages 2 and 3; 27% in September and 18% in October; Table 3). Five of the six previtellogenic females ≥490 mm were captured in September and October. In contrast, 65% of females ≥490 mm collected in September had reached the late vitellogenic, ripe, or ovulated stage (stages 4–6), suggesting they were spawning capable, were spawning, or had spawned. By October, 64% had reached the late vitellogenic, ripe, ovulated, or postovulated stage (stages 4–7). Not considered spawning capable, 9% ($n = 2$, lengths = 654 and 664 mm) were undergoing follicular atresia, hence they failed to spawn prior to capture.

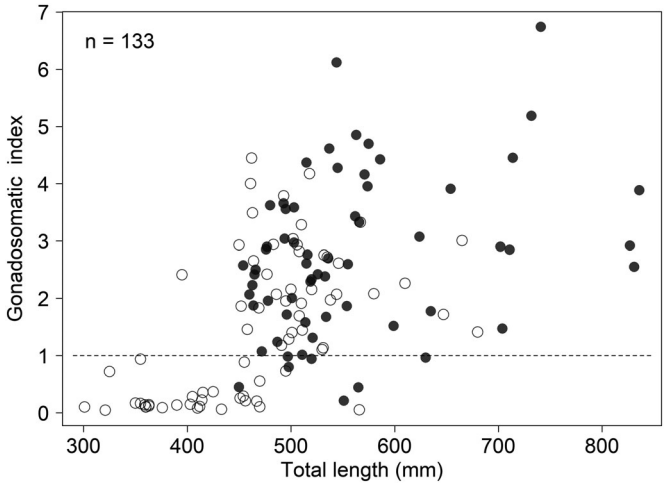

FIGURE 4. Male Lake Trout gonadosomatic index (GSI) by length. Solid gray circles represent fish caught during the spawning season (September and October) and hollow circles represent fish caught prior to the spawning season. The dashed line represents GSI value of 1.

Finally, during the spawning season the proportion of spawning-capable females increased with length between 450 and 749 mm, but three of the four largest females captured (all ≥750 mm) were not spawning capable (Figure 5).

Gonadal development in male Lake Trout advanced from early spermatogenic (stage 2) in June to late spermatogenic/spawning capable (stage 4) in August and ripe/spawning capable (stage 5) in September and October (Table 4). In contrast to female Lake Trout, all males of a potentially mature size (≥395 mm) that were caught from August through October exhibited gonadal development indicative of spawning (stages 4–6; $n = 48$; Table 4), suggesting that after male Lake Trout reach reproductive maturity, they spawn annually.

Gonadosomatic index and gonadal development.— The GSI for female Lake Trout exhibited a strong relationship with histological stage, as illustrated by an increase in values at the late vitellogenic stage (stage 4; Figure 6). Mean GSI was <1.0 for all females sampled in the previtellogenic, early vitellogenic, or mid-vitellogenic stages (stages 1–3); $\log_e$ transformed GSI values for these stages were significantly different than those for late vitellogenic, ripe, and ovulated females (stages 4–6; one-way ANOVA $F_{6,101} = 198$, $P < 0.001$; for pairwise comparisons $P < 0.001$). Mean GSI was 6.8 (range = 1.4–17.2) and 8.8 (range = 3.8–14.1) for the late vitellogenic and ripe females (stages 4 and 5), respectively. Mean GSI reached a maximum during ovulation (stage 6) at 11.7 (range = 7.5–14.7), but this group consisted of only three individuals (Figure 6). Mean GSI for postovulated (stage 7) females was 2.7 (range = 1.0–7.4); these fish were captured during the spawning season and had released eggs prior to capture. Three of the 33 female Lake Trout with GSI <3.0 were designated as late vitellogenic, and all three were captured prior to the spawning season (i.e., July or August). The two atretic (stage 8) females were not included in the statistical comparisons because of insufficient sample size.

Gonadosomatic index estimates for male Lake Trout increased during the late spermatogenic (stage 4) and ripe (stage 5) stages (Figure 7). Log_e transformed GSIs of males sampled in the early (stage 2) and mid-spermatogenic (stage 3) stages were significantly different from those in the late spermatogenic and ripe stages (one-way ANOVA $F_{3,72} = 24.9$, $P < 0.001$; for all pairwise comparisons $P < 0.01$). Mean GSI during the mid-spermatogenic stage (stage 3) was 0.8 (range = 0.1–2.2), but mean estimates increased to 2.7 (range = 0.6–6.1) and 3.0 (range = 0.5–6.7) in the late spermatogenic and ripe stages (stages 4 and 5), respectively. We captured only one male in the postspermiation stage (stage 6), but it was not included in the statistical analysis because of small sample size. Two of the 36 males in the late spermatogenic stage/

TABLE 3. Stage of maturity (%) by month for female Lake Trout ≥490 mm TL captured in Yellowstone Lake. Numbers in bold indicate the stage with the highest proportion of individuals per month. Stages 4 and 5 were considered spawning capable during the spawning season.

Month	*n*	Previtellogenic (stage 1)	Early vitellogenic (stage 2)	Mid-vitellogenic (stage 3)	Late vitellogenic (stage 4)	Ripe (stage 5)	Ovulated (stage 6)	Postovulation (stage 7)	Atretic (stage 8)
June	9		22%	**67%**	11%				
July	15	7%	13%	33%	**47%**				
August	11		18%	27%	**55%**				
September	34	9%	12%	15%	**44%**	18%	3%		
October	22	9%	9%	9%	18%	14%	9%	**23%**	9%

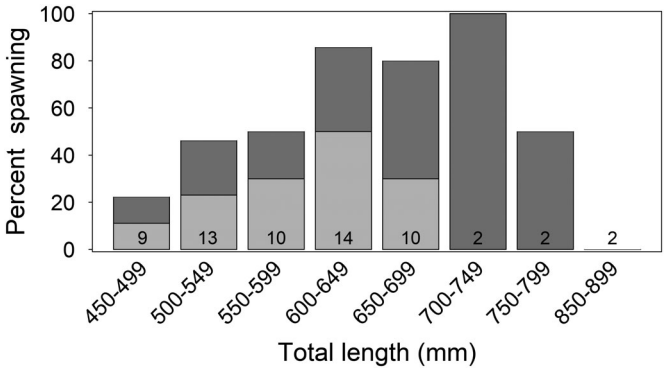

FIGURE 5. Percent of spawning-capable female Lake Trout caught during the spawning season (September and October) based on histological analysis. Dark gray indicates fish in the late vitellogenic stage (stage 4), and light gray indicates fish caught in the ripe, ovulated, or postovulatory stages (stages 5–7). Two atretic (stage 8) individuals (654 and 664 mm TL) considered not spawning capable were not included in this figure. Size group sample sizes are shown at the bottom of each group.

spawning capable (stage 4) and two of the 25 ripe/spawning-capable (stage 5) males had GSI <1.0; however, the latter two individuals showed signs of spermiation as indicated by the initiation of emptying testicular cysts.

Fecundity

We captured 44 female Lake Trout in the fall of 2015 for fecundity estimates. Total length ranged from 477 to 826 mm (mean = 626 mm), and weight ranged from 1,300 to 6,421 g (mean = 2,929 g). Absolute fecundity ranged from 1,287 eggs in a female that was 2,169 g to 10,514 eggs in an individual that was 6,421 g (mean absolute fecundity = 4,612 eggs). Mean relative fecundity was 1,535 eggs/kg (range = 593–2,827 eggs/kg). Among years, mean relative fecundity varied from 1,535 eggs/kg (2015) to 1,557 eggs/kg (2007), but differences in relative fecundity among years were not statistically significant (ANOVA, $F_{3,247} = 0.02$, $P = 1.00$; Figure 8). Although $\log_{10}$–$\log_{10}$ relationships between absolute fecundity and both length ($r^2 = 0.56$) and weight ($r^2 = 0.67$) were statistically significant for female Lake Trout sampled in 2015, weight explained over 10% more of the variation in absolute fecundity (Tables 5 and 6).

Initial screening of data from 1996 (Ruzycki et al. 2003) and 2006–2007 (Syslo et al. 2011) detected an extreme outlier (>4.6× interquartile range) in the estimated number of eggs for a female from 1996; consequently, we removed this individual from further analysis. Subsequent analyses revealed that slopes for regressions of absolute fecundity and both length and weight (all variables $\log_{10}$ transformed) varied among sample years (Figure 9); however, differences were not statistically significant (ANCOVA, $P > 0.05$). Furthermore, confidence intervals for the slopes of the GM regressions for absolute fecundity and weight overlapped (Tables 5 and 6), suggesting that differences among slopes were not statistically

TABLE 4. Stage of maturity (%) by month for male Lake Trout ≥395 mm TL captured in Yellowstone Lake. Numbers in bold indicate the stage with the highest proportion of individuals per month. Stages 4 and 5 were considered spawning capable during the spawning season.

Month	*n*	Early spermatogenic (stage 2)	Mid-spermatogenic (stage 3)	Late spermatogenic (stage 4)	Ripe (stage 5)	Postspermatogenic (stage 6)
June	14	**43%**	29%	29%		
July	11		9%	**82%**	9%	
August	14			**100%**		
September	15			47%	**53%**	
October	19			16%	**79%**	5%

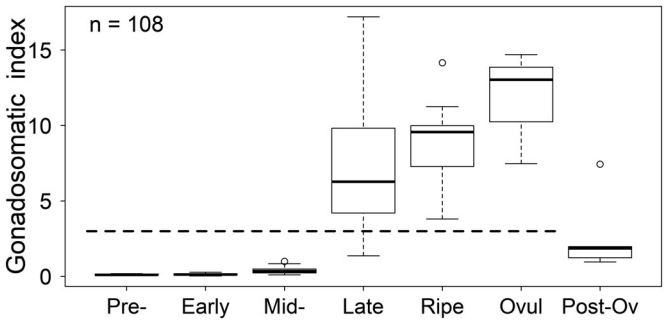

FIGURE 6. Female gonadosomatic index (GSI) as a function of stage of oogenesis. Thick lines inside the boxes indicate medians, boxes indicate the lower and upper quartiles, and whiskers extend to up to 1.5× the interquartile ranges. Outliers are indicated with open circles. The two fish caught while undergoing follicular atresia were not used in the figure due to low sample size. The first four abbreviations ("Pre-," "Early," "Mid-," and "Late") refer to the stages of vitellogenesis. Abbreviations "Ovul" and "Post Ov" refer to ovulated and postovulated fish. The horizontal dashed line represents GSI = 3.

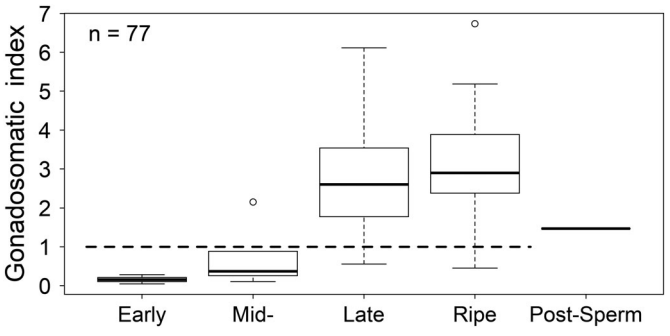

FIGURE 7. Male gonadosomatic index (GSI) as a function of spermatogenesis stage. Thick lines inside the boxes indicate medians, boxes indicate the lower and upper quartiles, and whiskers extend to up to 1.5× the interquartile ranges. Outliers are indicated with open circles. The first three abbreviations ("Early," "Mid-," and "Late") refer to the stages of spermatogenesis. The abbreviation "Post-Sperm." refers to postspermiation. The horizontal dashed line represents GSI = 1.

significant. In contrast, only some pairs of the confidence limits for the GM regression slope for absolute fecundity and length overlapped, and interpretation was inconclusive.

Based on our estimate of relative fecundity and estimates of population biomass from the statistical catch-at-age assessment model used as part of the Lake Trout suppression program, population fecundity was approximately 21.508 million eggs (95% confidence limits [CL]: 13.596–30.348 million eggs) in 2015. This estimate was less than population fecundity calculated for 2006 (26.834 million eggs; 95% CL: 20.317–34.077 million eggs) and 2007 (27.656 million eggs; 95% CL: 20.889–35.169 million eggs), but confidence limits for the three estimates

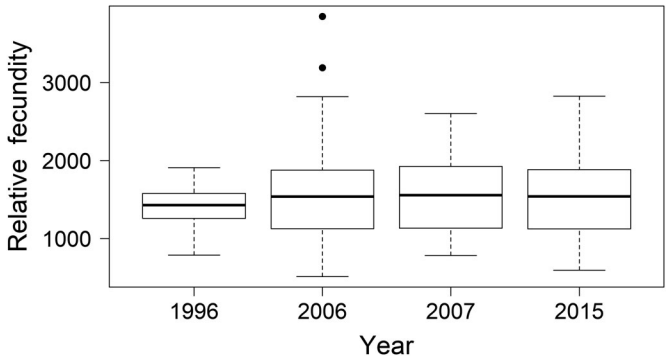

FIGURE 8. Box-and-whisker plot of relative fecundity by year for female Lake Trout in Yellowstone Lake. Thick lines inside the boxes indicate medians, boxes indicate the lower and upper quartiles, and whiskers extend to up to 1.5× the interquartile ranges. Outliers are indicated with open circles. Data for 1996 were provided from Ruzycki et al. (2003), and data for 2006 and 2007 were provided from Syslo et al. (2011).

overlapped. Population fecundity associated with the peak Lake Trout abundance in 2010 was 35.092 million eggs (95% CL: 26.286–44.196 million eggs); estimates declined to 4.735 million eggs (95% CL: 2.332–7.506 million eggs) for 2020 (using 2015 relative fecundity estimates).

DISCUSSION

Our results suggest that although the Lake Trout suppression program has likely reduced population fecundity, it may have had limited influence on life history demographics at the individual level. Relative fecundity has remained constant for the duration of the program and sex-specific differences in the frequency of skipped spawning are comparable to those found within the species' native range. The vast majority (92%) of male Lake Trout were spawning capable on an annual cycle, while only around two-thirds of females were spawning capable, which suggests that it may take longer than a year for some females to develop viable eggs following a successful spawning event. Both GSI indices and histological data suggested that male Lake Trout attain maturity at smaller sizes (approximately 395 mm) than females (approximately 490 mm). Our estimates of fecundity, rates of skipped spawning, and size at maturity will aid in future estimates of population growth.

Part of our motivation for conducting this study was to determine whether recent increases in Lake Trout recruitment levels in Yellowstone Lake could be related, at least in part, to changes in reproduction demographics of the species, possibly as an unintended consequence of the ongoing and aggressive suppression program. Population assessment results indicate that suppression efforts intended to reduce Lake Trout abundance and increase

TABLE 5. Least squares (LS) and geometric mean (GM) regression coefficients for the relationships between $\log_{10}E$ (eggs) and $\log_{10}L$ (length) for female Lake Trout captured in Yellowstone Lake during the 1996, 2006, 2007, and 2015 sample years, where B and V are slopes, and A and A' are intercepts.

Year	n	r^2	LS regression		GM regression		SE	95% CI V (+/−)	Mean $\log_{10}E$	Mean $\log_{10}L$
			B	A	V	A'				
1996	10	0.87	4.4384	−8.89676	4.7588	−9.8046	0.6069	1.3996	3.6780	2.8332
2006	119	0.66	2.9911	−4.79054	3.6882	−6.7257	0.1995	0.3951	3.5126	2.7760
2007	77	0.75	3.6259	−6.55099	4.1797	−8.0959	0.2401	0.4782	3.5645	2.7898
2015	44	0.56	4.0000	−7.57626	5.3477	−11.3416	0.5477	1.1052	3.5997	2.7940
All	250	0.68	3.2987	−5.63874	4.0110	−7.6230	0.1449	0.2854	3.5505	2.7857

TABLE 6. Least squares (LS) and geometric mean (GM) regression coefficients for the relationships between $\log_{10}E$ (eggs) and $\log_{10}W$ (weight) for female Lake Trout captured in Yellowstone Lake during the 1996, 2006, 2007, and 2015 sample years, where B and V are slopes, and A and A' are intercepts.

Year	n	r^2	LS regression		GM regression		SE	95% CI V (+/−)	Mean $\log_{10}E$	Mean $\log_{10}W$
			B	A	V	A'				
1996	10	0.88	1.3346	−1.0488	1.4207	−1.3540	0.1722	0.3972	3.6780	3.5419
2006	119	0.66	0.9689	0.2663	1.1947	−0.4902	0.0646	0.1280	3.5126	3.3503
2007	77	0.75	1.1746	−0.4208	1.3540	−1.0295	0.0778	0.1549	3.5645	3.3930
2015	44	0.67	1.2906	−0.8371	1.5808	−1.8349	0.1409	0.2843	3.5997	3.4379
All	250	0.69	1.0635	−0.0511	1.2768	−0.7729	0.0449	0.0884	3.5505	3.3866

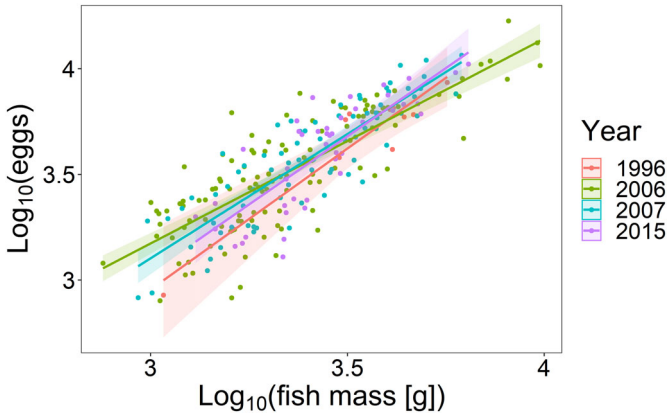

FIGURE 9. Relationship between eggs and fish mass (both $\log_{10}$ transformed) for Lake Trout in Yellowstone Lake. Shaded regions indicate 95% confidence intervals. Data for 1996 were provided from Ruzycki et al. (2003), and data for 2006 and 2007 were provided from Syslo et al. (2011). [Color figure can viewed at afsjournals.org.]

Yellowstone Cutthroat Trout abundance have dramatically affected both abundance and age composition of the invasive population (Syslo et al. 2011, 2020). Despite experiencing nearly exponential population growth through the first decade of the 21st century, Lake Trout abundance since 2011 has declined, with the largest reductions in abundance for age-6 and older individuals (Syslo et al. 2020). Since the mid-2010s, age-6 and older individuals have been estimated to compose less than 5% of the age-2 and older Lake Trout population (Syslo et al. 2020). Despite these reductions in population abundance, recent assessment modeling results have suggested that recruitment of the Lake Trout population in Yellowstone Lake has slightly increased (Syslo et al. 2020), the mechanism for which remains unclear.

The hypothesis that elevated Lake Trout recruitment levels could be due to changes in reproduction demographics such as female fecundity was not supported by the results of this study. Estimates of mean relative fecundity in Lake Trout were stable over the assessed time periods ranging from a low of 1,535 eggs/kg to a high of 1,557 eggs/kg. Conversely, the amount of gill-net suppression effort during roughly this same time period increased from approximately 1,000 100-m net nights to nearly 77,000 100-m net nights (Syslo et al. 2020). When compared with populations from other lakes, fecundity of the Yellowstone Lake population does appear to be above average. Mean relative fecundity of Lake Trout for all samples collected from Yellowstone Lake (1,550 eggs/kg) was greater than the mean estimate for 23 lakes in North America (1,396 eggs/kg; Hansen et al. 2021). The mean relative fecundity estimate for Lake Trout in Yellowstone

Lake was just under the 75th percentile (1,599 eggs/kg) of relative fecundity values compiled by Hansen et al. (2021). Interestingly, Hansen et al. (2021) reported that the difference in relative fecundity between native and nonnative Lake Trout populations was not statistically significant, which suggests there are conditions specific to Yellowstone Lake that are perhaps contributing to higher reproductive potential in the lake; however, identifying those conditions may be difficult (Goetz et al. 2021).

Rates of skipped spawning in Lake Trout in Yellowstone Lake appear also to have not changed since the early phases of the suppression program and reported rates for the lake are similar to those found in the native range Lake Trout, which further supports the conclusion that the suppression program is not having unintended effects on reproduction demographics. Ruzycki et al. (2003) examined fish gonads during the spawning season in Yellowstone Lake and reported that after attaining maturity, male Lake Trout spawned annually and females spawned in alternate years, which is fairly consistent with our estimates that 92% of males and 65% of females were capable of spawning. Our estimates of skipped spawning were supported by our observations that females were collected during the spawning season in every stage of ovarian development—a clear indication that some females had developing oocytes that had not completed vitellogenesis. Conversely, male Lake Trout began the summer in the early stages of gonadal development and nearly all individuals proceeded to a ripe/spawning-capable stage prior to spawning season. In Lake Superior, 42% of female siscowet Lake Trout morphotypes and 88% of female lean morphotypes appeared to be capable of spawning in the year sampled, whereas all female lean Lake Trout >680 mm and all female siscowet Lake Trout >720 mm were capable of spawning (Sitar et al. 2014). In a separate study from Lake Superior, Goetz et al. (2011) used GSI criteria to determine that 58% of female siscowets and 46% of female lean Lake Trout would spawn in the year sampled, and the majority of female Lake Trout skip spawners were between 500 and 750 mm. Approximately 80% of male lean and siscowet Lake Trout were spawning capable in Lake Superior (Goetz et al. 2011). These sex-specific differences in skipped spawning are consistent with life history theory that suggests that females require a higher rate of energy investment for reproduction than males (Nikolsky 1969; Fleming and Reynolds 2004).

Skipped spawning has been identified as a reproductive strategy that balances trade-offs between reproduction, growth, and mortality rates of populations and can occur under conditions of poor or good growth (Jørgensen et al. 2006; Shaw and Levin 2013). When condition is poor or food availability is limited, skipped spawning becomes more prevalent because there is too little energy intake for gonad development to proceed (Rideout et al. 2000; Jørgensen et al. 2006). Skipped spawning has also been associated with exploitation, with greater levels occurring when fishing mortality at the spawning grounds is high or when fishing mortality at feeding grounds is low (Jørgensen et al. 2006). In Yellowstone Lake, Lake Trout suppression has been conducted throughout the lake during the ice-free season but fall gillnetting effort has been heavily concentrated on known spawning locations, using larger mesh sizes to target spawning capable (>500 mm) females (Syslo et al. 2011). Passive and active tracking of acoustically telemetered Lake Trout have also been used to identify movement corridors to spawning locations and to target aggregations that are proximal or moving towards these grounds through a "Judas fish" technique (Gutowsky et al. 2020; Williams et al. 2020). Based on assessment modeling results, annual exploitation levels of Lake Trout fully selected to suppression gill nets (≥4 years of age) has exceeded 50% since the mid-2010s (Syslo et al. 2020). Despite this targeted effort on the spawning grounds and high exploitation rates in recent years, the finding that skipped spawning rates have not changed between our study and that of Ruzycki et al. (2003) suggest that suppression is unlikely related to the extent of skipped spawning but rather may be linked to Lake Trout growth.

Fecundity estimates of Lake Trout in Yellowstone Lake peaked in 2010 (Syslo et al. 2020) and have steadily declined since then as abundance of spawning-capable Lake Trout has decreased. Although there was considerable overlap in confidence intervals in population fecundity for 2006, 2007, and 2015, it was not stable in intervening years. The estimated population fecundity for 2020 of approximately 4.7 million eggs represents an 81% decline from the mean of estimates in 2006, 2007, and 2015 and an 87% reduction from the peak spawning stock biomass in 2010. Despite this reduction in spawning stock biomass, Lake Trout recruitment levels have increased by an average of approximately 7,300 fish over the last 10 years (T. O. Brenden, unpublished data). As previously indicated, our results suggest that these changes are probably not related to changes in reproductive demographics. Rather, we attribute this increase to an increase in prerecruitment survival—perhaps attributable to a reduction in recruitment compensation caused possibly by factors such as reduction in cannibalism of new recruits by older fish (Syslo et al. 2020). According to Simard et al. (2020), early life stages of Lake Trout in Yellowstone Lake benefit from the depauperate fish community in the lake, which allows them to more freely take advantage of available food resources in the lake and which presumably leads to better survival than in most other systems in the species' native range.

One of the major challenges that fishery management agencies must confront when attempting to control,

suppress, or eradicate an invasive species is lack of information on the behavior, life history, ecology, demographics, and dynamics of the species in the invaded system. Upon initial detection of an invasive species, rapid initiation of suppression efforts is of paramount importance (Simberloff 2003). However, if these initial efforts prove unsuccessful and the population continues to expand or becomes established, assessment or simulation modeling may be useful for formulating the strategies to meet management objectives (Hansen et al. 2010; Syslo et al. 2013; DuFour et al. 2021). When relevant data are limited, life history, demographic, and dynamic estimates from the species' native range may be the only alternative for conducting these modeling exercises. However, it is important to recognize these estimates may not accurately reflect conditions in novel systems, and differences may have major consequences on the best courses of action. For example, preliminary modeling efforts for the Lake Trout population in Yellowstone Lake using information from the species' native range suggested that an annual suppression effort of 29,000 units (1 unit = 100 m of gill net set for 1 night) would be sufficient to prevent the population from expanding (Syslo et al. 2011). However, the actual amount of suppression to accomplish this goal was closer to 50,000 units, primarily because of high early-life survival (Syslo et al. 2020). Although we did not find major differences in reproduction demographics (spawning periodicity, size at maturity, and female fecundity) in Yellowstone Lake compared to systems within the native range of Lake Trout, these data have provided new information integral to understanding this specific situation and for maximizing the potential for success with the Lake Trout suppression program, and it serves as a model for the use of such information in other areas where suppression of invasive species is a priority management strategy.

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