Plasticity in the reproductive biology of Yellowstone cutthroat trout Oncorhynchus virginalis bouvieri in Yellowstone Lake following lake trout Salvelinus namaycush invasion

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Plasticity in the reproductive biology of Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri* in Yellowstone Lake following lake trout *Salvelinus namaycush* invasion

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Abstract

Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri* in Yellowstone Lake are the focus of intensive conservation efforts due to the threat of predation by invasive lake trout *Salvelinus namaycush*. Suppression gillnetting has reduced the abundance of predatory lake trout, and the Yellowstone cutthroat trout population is recovering. Long-term monitoring indicates the size structure of the population shifted following lake trout invasion, suggesting that reproductive demographic rates of Yellowstone cutthroat trout may have changed. Length at 50% probability of maturity, as assessed using histological analysis of gonadal tissue, was 479 mm (95% confidence interval [CI] 467–490 mm) for females and 406 mm (95% CI 386–430 mm) for males, compared to 330 mm for males and females historically. Currently, age at 50% probability of maturity is 6.6 for females and 5.4 for males. The rate of skipped spawning was 3% for females and 38% for males. Mean absolute fecundity was 2897 ovarian follicles/individual at present compared to 1141 ovarian follicles/individual before lake trout invasion. Mean relative fecundity was 2157 ovarian follicles/kg. This research illustrates the plasticity in the reproductive strategies of fishes as a result of an invasive species. Understanding the reproductive biology of fish populations is vital for effective fisheries management, and these results are integral to a population model that can be used to develop new conservation benchmarks for Yellowstone cutthroat trout.

KEYWORDS
fecundity, maturity, reproductive structure, spawning

1 | INTRODUCTION

Understanding reproductive biology is a fundamental component of fisheries conservation (Kjesbu, 2009; Lowerre-Barbieri, 2009). The age at which fish become sexually mature, the proportion of the population that spawns annually and individual fecundity influence the productivity of fish populations (Corriero et al., 2021; Rideout et al., 2005); thus, understanding fish reproduction is vital for assessing population dynamics and for developing predictive population models. Reproductive biology can also influence how fish populations respond to anthropogenic disturbances, including harvest and invasive species predation (Black et al., 2014; Lowerre-Barbieri et al., 2011; Morgan, 2008). Fecundity and age at maturity in fishes vary considerably among populations and change in response to environmental and biotic conditions (Blanck &

Lamouroux, 2007; Lobon-Cervia et al., 1997; Massey et al., 2022). Thus, contemporary, population-specific studies of reproduction are critical for effective fisheries management.

Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri* in Yellowstone Lake (Yellowstone National Park, Wyoming, USA) are the focus of one of the largest native fish conservation programs in North America (Koel et al., 2020). These fish occupy high-quality, protected habitat within Yellowstone National Park and represent the largest remaining nonhybridized population of Yellowstone cutthroat trout. Thus, the population is of the highest conservation priority for the subspecies (Al-Chokhachy et al., 2018; Gresswell, 2011). Additionally, Yellowstone cutthroat trout are considered a keystone species in the Yellowstone Lake ecosystem and are a food source for numerous terrestrial and avian predators, such as grizzly bears *Ursus arctos horribilis*, otters *Lontra canadensis* and osprey *Pandion haliaetus* (Koel et al., 2019). Yellowstone cutthroat trout in Yellowstone Lake are threatened by the presence of invasive lake trout, which were first discovered in Yellowstone Lake in 1994 (Kaeding et al., 1996). The Yellowstone cutthroat trout population experienced a precipitous decline in abundance due to predation by invasive lake trout (Koel et al., 2005, 2020).

To conserve Yellowstone cutthroat trout in Yellowstone Lake, the National Park Service implemented a lake trout suppression program in 1995, which consists primarily of gillnetting (Koel et al., 2020). Intensive gillnetting effort, paired with extensive research to increase suppression efficacy, has successfully reduced the abundance of predatory lake trout, and the Yellowstone cutthroat trout population has responded positively to lake trout suppression (Glassic et al., 2023; Koel et al., 2020; Syslo et al., 2020). Yellowstone cutthroat trout catch per effort in annual assessment netting has increased since it reached a minimum in 2010 (Koel et al., 2020, 2023). Additionally, the size structure of the population has shifted following lake trout invasion. Individuals attain larger body sizes, and fish greater than 400 mm in length comprise a greater proportion of the population than before lake trout invasion (Koel et al., 2020). Age at maturity and fecundity were estimated for the population prior to the onset of intensive lake trout suppression (Kaeding & Koel, 2011), but reproduction may have changed due to the altered size structure and changes in abundance in the past two decades.

Future conservation of Yellowstone cutthroat trout in Yellowstone Lake will require knowledge of demographic rates, including reproductive metrics, to develop a population model and predict future responses to management actions. Studying the reproductive biology of Yellowstone cutthroat trout in Yellowstone Lake also provides a unique opportunity to investigate how changes in abundance and size structure, caused by the introduction of an invasive apex predator, may alter reproductive biology in a native fish population. Our research questions are: what are the population reproductive structure (defined as the proportion of the population in different reproductive phases) and reproductive demographic rates of Yellowstone cutthroat trout in Yellowstone Lake, and how have reproductive demographic rates changed since the introduction of lake trout? To address these questions, we focus specifically on length and age at maturity, spawning periodicity and fecundity.

2 | METHODS

2.1 | Study area and focal population

Yellowstone Lake is in Yellowstone National Park at an elevation of 2357 m. With a surface area of 340 km^2, it is the largest high-elevation lake in North America and is generally ice-covered from late December to mid-May or early June (Tronstad et al., 2024). Yellowstone Lake is a mesotrophic lake that thermally stratifies in the summer and mixes twice per year (Kilham et al., 1996). It has complex bathymetry, with a mean depth of 43 m, a maximum depth of 148 m and geothermal features distributed throughout the northern and western regions of the lake (Koel et al., 2020). Water temperatures during the ice-free season vary from approximately 6 to 16°C at the surface and from 6 to 12°C at a depth of 10 m, and water temperature is approximately 3°C during the ice-covered season (Koel et al., 2020). Yellowstone Lake has two native fish species: Yellowstone cutthroat trout and longnose dace *Rhinichthys cataractae*, and four established non-native species: lake trout, longnose sucker *Catostomus catostomus*, redside shiner *Richardsonius balteatus* and lake chub *Couesius plumbeus*.

Yellowstone cutthroat trout exhibit lacustrine-adfluvial and allacustrine life histories in Yellowstone Lake (Gresswell et al., 1994) and have been observed spawning in 60 of 126 known tributaries (lacustrine-adfluvial) and in the Yellowstone River immediately downstream of the lake outlet (allacustrine) (Gresswell et al., 1994; Reinhart, 1990). Yellowstone cutthroat trout spawn in the spring and early summer, with peak spawning occurring from mid-May to mid-June (Gresswell et al., 1994). Juvenile Yellowstone cutthroat trout emerge about 30 days after egg deposition and outmigrate to Yellowstone Lake at ages varying from 2 months to >1 year (Gresswell & Varley, 1988). Yellowstone cutthroat trout exhibit synchronous oocyte development and determinant fecundity, and they are physiologically capable of annual spawning (Gresswell, 2011; Piper et al., 1982).

2.2 | Maturity and spawning periodicity

Gonad samples were collected from Yellowstone cutthroat trout that were inadvertently killed as bycatch in lake trout suppression gillnets from 6 to 30 June 2022. Suppression gillnets were set throughout Yellowstone Lake, and mesh sizes varied from 25- to 64-mm bar measure. The target sample size was six to 10 samples per 10-mm size class. The smallest size class was 190 mm, which is the smallest size of fish captured in 25-mm bar measure gillnets. Additional samples were collected from Yellowstone cutthroat trout caught during annual assessment netting conducted from 1 to 7 August 2022. During assessment netting, 24 sites distributed throughout Yellowstone Lake were sampled using variable mesh gillnets, targeting all size classes of Yellowstone cutthroat trout ≥200 mm (Koel et al., 2020). Gonad samples were collected from specific size classes of Yellowstone cutthroat trout (350–429 mm) that were not adequately represented in suppression gillnetting bycatch. All fish sampling was conducted under Montana State University IACUC Protocol 2022–190.

During sample collection, each fish was measured (total length, nearest mm) and weighed (nearest g). Gonads were removed and weighed (nearest 0.01 g), and a subsample of gonadal tissue was weighed and preserved in 10% buffered formalin. In the laboratory, gonadal tissue was dehydrated and cleaned, embedded in paraffin, sectioned at 5 μm and stained by Periodic Acid Schiff reagent following standard histological techniques. Slides were examined under a compound microscope (Leica DM 2000, 40× to 400×), and germ cells were examined to determine sex and to assign the reproductive phase and stages of gamete development as defined in Brown-Peterson et al. (2011) and Crossman et al. (2022) (Table 1). The most advanced gamete stage was used to assign reproductive phase. Spawning markers in both sexes included

TABLE 1 Descriptions of sex-specific reproductive phases and stages of gonadal development used to describe Yellowstone cutthroat trout sampled in Yellowstone Lake.

Reproductive phase	Gamete stage	Spawn this season (Y/N)	Histological indicators
Females			
Immature (IMM)	Oogonial proliferation (OP)	N	Clusters of oogonia; no evidence of previous spawning or mass follicular atresia
Immature (IMM)	Primary growth (PG)	N	Oogonia and primary growth oocytes; no evidence of previous spawning or mass follicular atresia
Early developing (DEV)	Cortical alveolar (CA)	N	Primary growth oocytes with cortical alveoli on periphery of the oocytes or distributed throughout the ooplasma; follicular layer formed; thin zona radiata may be present; atresia from the past cycle or atresia from natural fecundity regulation may be evident
Developing (DEV)	Primary vitellogenic (PV)	N	Yolk granules accumulating in the oocyte; cortical alveoli appear in a central position of the oocytes; zona radiata thickening and together the oocyte with its full complement of follicular layers and zona radiata may be referred to as an ovarian follicle; atresia from natural fecundity regulation may be evident
Developing (DEV)	Secondary vitellogenic (SV)	N	Yolk globules accumulating toward centre or may be present throughout the oocytes; cortical alveoli and lipid droplets move toward the periphery of oocyte; zona radiata thickening; atresia from natural fecundity regulation may be evident
Spawning capable (SPC)	Tertiary vitellogenic (TV)	Y	Yolk fusing into larger globules throughout the oocytes; zona radiata development complete; central germinal vesicle or slightly offset; atresia from natural fecundity regulation may be evident
Spawning capable (SPC)	Oocyte maturation (OM)	Y	Yolk coalesced; offset germinal vesicle or germinal vesicle may be broken down; atresia from natural fecundity regulation may be evident
Regressing (REG)	Postovulatory follicles (PO)	Y	Ovaries contain numerous postovulatory follicles and the next generation of oocytes or ovarian follicles
Regressing (REG)	Mass astresia (AT)	N	>50% of ovarian follicles undergoing follicular atresia
Regenerating (RGN)	Regenerating (RN)	N	Primary growth oocytes; degenerating postovulatory follicles may be present; atretic ovarian follicles may be present
Males			
Immature (IMM)	Spermatogonial proliferation (SG)	N	Spermatogonia undergoing mitosis; absence of lumens in testicular cysts
Developing (DEV)	Early spermatogenesis (ES)	N	Spermatocysts may contain spermatogonia, spermatocytes, spermatids, and/or few spermatozoa; spermatozoa not present in cyst lumen or in sperm ducts; germinal epithelium continuous throughout
Spawning capable (SPC)	Mid- to late spermatogenesis (ML)	Y	Spermatocysts contain few spermatogonia and spermatocytes, spermatids, and spermatozoa; spermatozoa present in cyst lumen and/or sperm ducts; germinal epithelium continuous or discontinuous
Spawning capable (SPC)	Ripe (SZ)	Y	Only spermatozoa visible; germinal epithelium discontinuous; spermatozoa in lumens and ducts
Regressing (REG)	Post-spermiation (RG)	Y	Residual spermatozoa in cyst lumen and sperm ducts; spermatocysts near periphery contain spermatogonia, spermatocytes, spermatids, and/or spermatozoa; regeneration of germinal epithelium
Regenerating (RGN)	Regenerating (RN)	N	No residual spermatozoa may be evident but cyst lumens open; proliferation of spermatogonia throughout testes; germinal epithelium continuous

Note: Abbreviations of reproductive phases and stages are provided in parentheses and modified from Brown-Peterson et al. (2011) and Crossman et al. (2022). Histological analysis was based on the most advanced gamete stage and gonadal structure based on Lowerre-Barbieri et al. (2023). Spawning markers in both sexes included consideration of the cold-water temperatures in Yellowstone Lake and spawning streams and collection time to identify Yellowstone cutthroat trout that spawned within the 2022 season (spawn this season Y = yes or N = no). Atresia from natural fecundity regulation refers to the downregulation of fecundity through ovarian follicular atresia (Treanor et al., 2024).

consideration of the cold-water temperatures in Yellowstone Lake and spawning streams and collection time to identify Yellowstone cutthroat trout that spawned in 2022 (Lowerre-Barbieri et al., 2023). Individuals were considered sexually mature if the reproductive phase indicated that spawning was imminent (spawning capable), had occurred earlier in spring 2022 (regressing) or if the gonadal tissue showed evidence of past spawning (regenerating). Females were classified as having undergone mass follicular atresia if histological signs of atresia were evident in >50% of the secondary or tertiary vitellogenic ovarian follicles (Hunter & Macewicz, 1985). Ovarian follicles herein refer to the oocyte and the encompassing follicular layers (see Grier et al., 2009; Patiño & Sullivan, 2002). Gonadosomatic index (GSI) was calculated for each individual as the weight of the gonad divided by the weight of the fish multiplied by 100.

Logistic regression was used to estimate the predicted probability of maturity by length for female and male Yellowstone cutthroat trout. Models were fit using the glm function in R version 4.4.1 (R Core Team, 2024). Maturity was used as a binary response variable, with each fish considered immature (maturity = 0) or sexually mature (maturity = 1). Total length and sex were included as interacting covariates. Sagittal otoliths were obtained from all Yellowstone cutthroat trout that were lethally sampled during annual assessment netting in 2022. Otoliths were embedded in resin, cut into cross-sections and mounted onto slides. Cross-sections of otoliths were used to estimate ages for three individuals per 20-mm length class ($n = 66$). A von Bertalanffy growth model was fit to the length and age data for Yellowstone cutthroat trout and used to estimate the age at length for the total lengths associated with 50% and 95% probabilities of maturity for female and male Yellowstone cutthroat trout (Ogle & Isermann, 2017). The length at 50% maturity was compared to an estimate of length at 50% maturity from Kaeding and Koel (2011), which was estimated using visual examination of gonads of approximately 19,000 Yellowstone cutthroat trout sampled in gillnets set at 11 sites throughout Yellowstone Lake from 1969 to 2005.

Reproductive stage was used to determine the percentage of mature males and females that were skipped spawners. For females, individuals were considered skipped spawners if they showed evidence of mass follicular atresia in the tertiary vitellogenic stage in 2022 (Table 1; Lowerre-Barbieri et al., 2023) or were assigned to the regenerating reproductive phase with no indication of spawning during the current year. Males were considered skipped spawners if they were assigned to the regenerating reproductive phase with no spermatozoa present but open testicular lumens (Lowerre-Barbieri et al., 2023). The number of females that underwent mass follicular atresia in their first reproductive cycle was assessed. These females had initiated vitellogenesis based on the size and presence of yolk granules/globules, had no evidence of past spawning and went atretic (McBride et al., 2022; Rideout & Tomkiewicz, 2011).

2.3 | Fecundity

Fecundity was estimated using gonad samples collected from 47 spawning capable female Yellowstone cutthroat trout in spring 2022 ($n = 3$), 2023 ($n = 21$) and 2024 ($n = 23$). Spawning capable female Yellowstone cutthroat trout were captured in lake trout suppression nets and by angling. Most fecundity samples ($n = 42$) were collected from the southeast arm of Yellowstone Lake near the inlet of the Yellowstone River, where spawning capable fish congregate in late May before migrating upstream in the Yellowstone River to spawn. Collecting spawning capable females in Yellowstone Lake is logistically difficult because ice cover prevents sampling the lake during the beginning of the spawning period, and the southeast arm was the only area where spawning capable females could be consistently collected. During sampling, fish were measured (total length, nearest mm) and weighed (nearest g). Gonads were removed and weighed (nearest 0.01 g). Six gonad subsamples were collected from each fish. Subsamples (approximately 60–90 ovarian follicles each) were collected from the anterior, middle and posterior sections of the right and left gonads. Gonad subsamples were weighed (nearest 0.01 g) and preserved in 70% ethanol. In the laboratory, the number of ovarian follicles in each subsample was counted to estimate absolute and relative fecundity (Heredia et al., 2021); oocytes in the primary growth stage were not counted. Linear regression was used to evaluate the relationship between length and fecundity. Linear models were fit using total length as the predictor variable and either absolute or relative fecundity as the response variable. Absolute fecundity was compared to measurements of fecundity from fish collected in 1950–1951 and 1984 (Kaeding & Koel, 2011).

To assess individual variation in fecundity, we measured ovarian follicle diameters of a subset of fecundity samples ($n = 13$). Fifteen ovarian follicles were removed from each gonad subsample ($n = 90$ ovarian follicles per fecundity sample). The ovarian follicles were photographed using a dissecting scope and ovarian follicle diameter was measured using Image-Pro software (Bioimager, Inc). Mean ovarian follicle diameter was calculated for each fecundity sample. Linear regression was used to evaluate the relationship between fecundity and mean ovarian follicle diameter, and the relationship between fish length and mean ovarian follicle diameter.

3 | RESULTS

3.1 | Reproductive structure, maturity and spawning periodicity

Gonad samples were collected from 300 Yellowstone cutthroat trout. Lengths varied from 194 to 582 mm. Of the individuals sampled, 152 were identified as female, 147 were identified as male and one was identified as intersex (Figures 1 and 2). For females, 40 individuals (26%) were immature (Table 2 and Figure 1a). Sixty-eight females (44%) were in the developing phase (Figure 1b,c) and 44 females (29%) were in the regressing phase (Figure 1d). All females in the regressing phase showed evidence of re-entering the developing phase with the presence of either cortical alveolar or primary vitellogenic follicles. No spawning capable females were sampled, indicating that females that were reproductively active in 2022 had completed spawning or may have been actively spawning in tributaries during the sampling period. No sampled females were in the regenerating phase. Thirty-nine

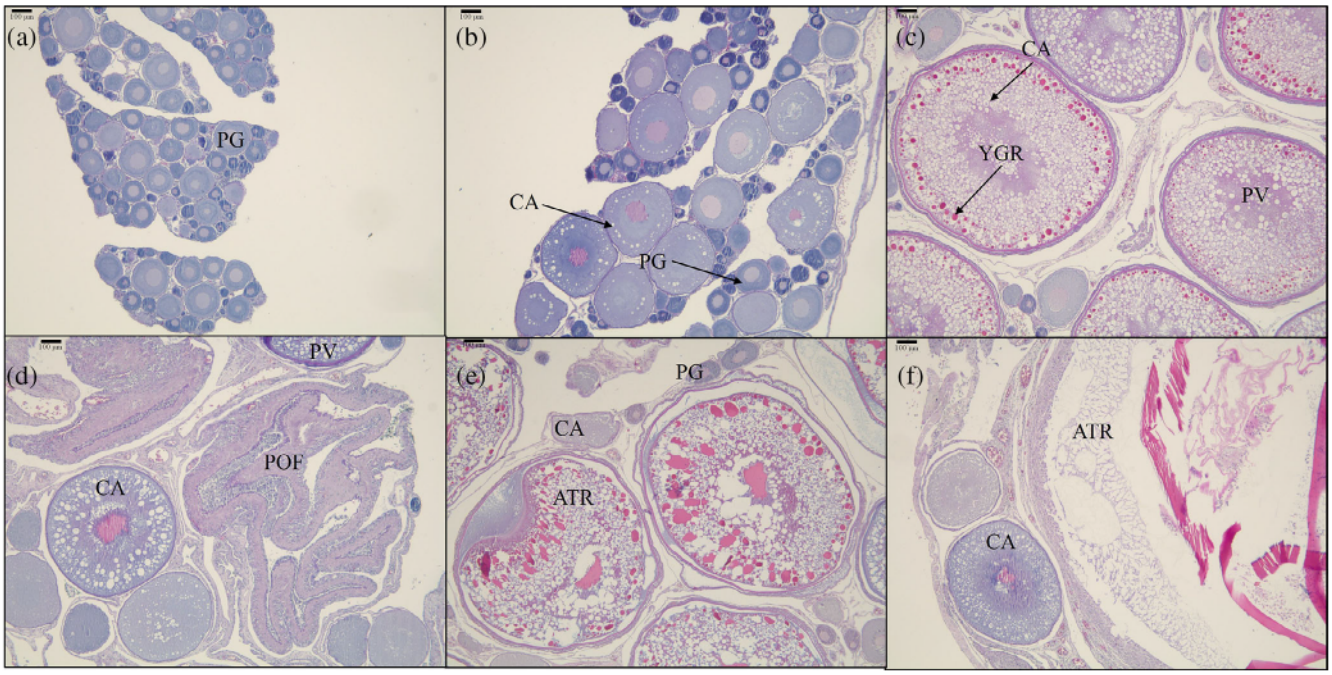

FIGURE 1 Photomicrographs of histological sections of Yellowstone cutthroat trout ovarian tissue (described in Table 1) from Yellowstone Lake. (a) Primary growth (PG) oocytes (immature phase); (b) PG oocytes with cortical alveoli (CA) (developing phase); (c) primary vitellogenic (PV) ovarian follicles with yolk granules (YGR) accumulating in the oocyte and CA (developing phase); (d) postovulatory follicles (POF) with the presence of CA oocytes and PV ovarian follicles (regressing phase); (e) atretic (ATR) vitellogenic ovarian follicles with the presence of PG and CA oocytes (regressing phase); f) atretic (ATR) tertiary vitellogenic ovarian follicles classified as mass atresia with the presence of CA oocytes (regressing phase). Oogonial proliferation, secondary vitellogenic, tertiary vitellogenic, oocyte maturation and regenerating stages are not shown. Tissue stained with Periodic Acid Schiff reagent. Scale bars indicate 100 μm for all panels.

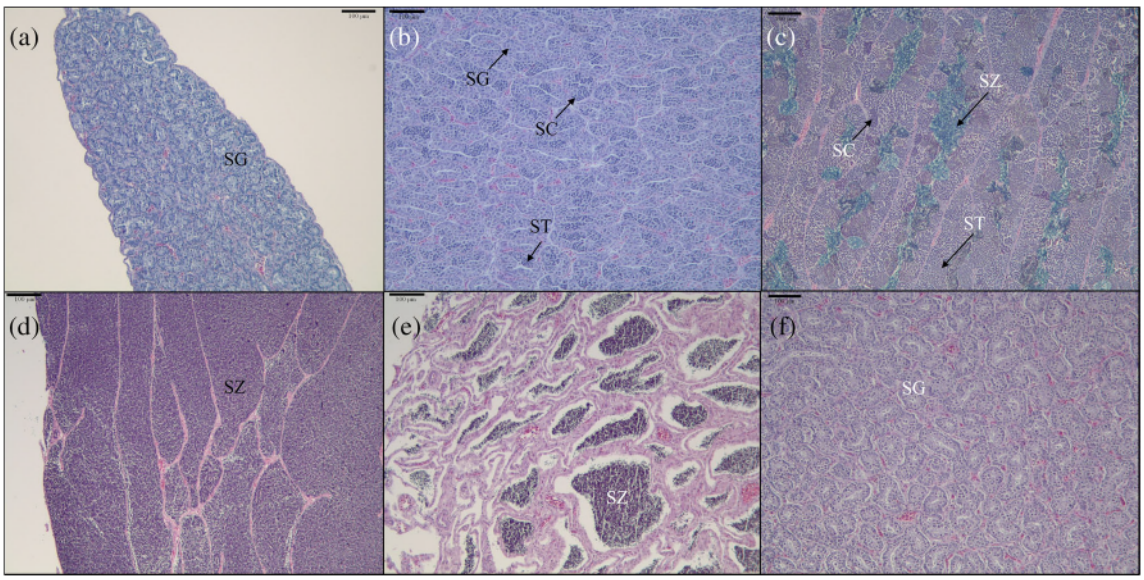

FIGURE 2 Photomicrographs of histological sections of Yellowstone cutthroat trout testicular tissue (described in Table 1) from Yellowstone Lake. (a) Spermatogonia (SG) undergoing mitosis in the immature phase; (b) SG, spermatocytes (SC) and spermatids (ST) (developing phase); (c) SC, ST and spermatozoa (SZ) with continuous germinal epithelium (spawning capable phase); (d) SZ with discontinuous germinal epithelium (spawning capable phase); (e) residual SZ in lumen of lobules and sperm ducts with regeneration of germinal epithelium in the regressing phase; and (f) proliferation of SG in testicular cysts with open lumens throughout testes (regenerating phase). Tissue stained with Periodic Acid Schiff reagent. Scale bars indicate 100 μm for all panels.

TABLE 2 The number of individuals, percentage of the individuals, mean length (mm) and mean weight (g), and mean gonadosomatic index (GSI) by reproductive phase and stage for Yellowstone cutthroat trout, sampled in Yellowstone Lake, Yellowstone National Park in 2022, as identified by histological analysis of gonadal tissue.

Reproductive phase	Gamete stage	*n*	Percentage	Mean length (standard error) (mm)	Mean weight (standard error) (g)	Mean GSI (standard error)
Females						
Immature	Primary growth	40	26	264.6 (6.0)	191.6 (15.1)	0.088 (0.004)
Developing	Cortical alveolar	40	26	320.4 (6.2)	344.9 (23.6)	0.115 (0.008)
	Primary vitellogenic	21	14	446.8 (6.9)	1004.4 (42.5)	0.319 (0.026)
	Secondary vitellogenic	7	4	442.9 (16.1)	1109.0 (134.0)	0.604 (0.069)
Regressing	Regressing mass atresia, first cycle	4	3	407.5 (21.5)	847.5 (125.6)	0.415 (0.063)
Regressing	Regressing with post-ovulatory follicles	39	26	518.2 (4.8)	1332.6 (45.0)	1.169 (0.069)
Regressing	Regressing mass atresia, previous spawn	1	1	517.0	1260	0.637
Males						
Immature	Spermatogonial proliferation	62	42	294.0 (6.4)	274.5 (21.6)	0.050 (0.002)
Developing	Early spermatogenesis	16	11	463.4 (15.3)	1232.8 (121.5)	0.171 (0.052)
Spawning capable	Mid- to late spermatogenesis	4	3	395.8 (9.0)	725.5 (62.5)	0.846 (0.406)
	Ripe	20	14	507.0 (14.1)	1423.9 (115.2)	1.818 (0.107)
Regressing	Post-spermiation	19	13	471.3 (14.7)	1177.4 (102.7)	0.224 (0.049)
Regenerating	Regenerating	26	18	445.3 (10.1)	1025.3 (64.7)	0.085 (0.007)

Note: Females within the regressing phase were further classified as having undergone mass follicular atresia during their first reproductive cycle, having spawned successfully as seen by the presence of post-ovulatory follicles or having undergone mass follicular atresia with evidence of a previous spawning event (skipped spawning).

females (26%) had successfully spawned in 2022, determined by the presence of post-ovulatory follicles, and one female underwent mass follicular atresia during the tertiary vitellogenic stage, suggesting skipped spawning. Four females showed evidence of mass follicular atresia during primary or secondary vitellogenesis with no evidence of past spawning (Figure 1e). These four females were not considered sexually mature in our analysis because they did not contribute to reproduction in 2022 or in previous years. For males, 62 individuals (42%) were immature (Figure 2a) and 16 (11%) were assigned to the developing phase (Table 2 and Figure 2b). Twenty-four males (16%) were spawning capable ($n = 4$ mid- to late spermatogenesis, $n = 20$ ripe), 19 (13%) were regressing and 26 (18%) were regenerating (Table 2 and Figure 2c,f). Sixty-nine males (47%) had reached sexual maturity and were assigned to the spawning capable, regressing and regenerating phases.

Fish length ($p < 0.0001$), sex ($p = 0.0010$) and the interaction between fish length and sex ($p = 0.0016$) were significantly related to the probability of maturity. Females had a 50% probability of being sexually mature at 479 mm and a 95% probability of being sexually mature at 513 mm (Table 3 and Figure 3), corresponding to ages 6.6 and 7.2 years, respectively. Males had a 50% probability of being sexually mature at 406 mm and a 95% probability of sexual maturity at 557 mm (Table 3 and Figure 3), corresponding to ages 5.4 and 8.3 years, respectively. Length at maturity has increased for males and females when compared to historical estimates but has shown a greater increase for females. Historical sampling used visual observation of gonads to assess the maturity of Yellowstone cutthroat trout from 1969 to 2007, and results indicated that approximately 50% of female and male fish were mature at 330 mm and 95% of fish were mature at 400 mm (Kaeding & Koel, 2011). Thus, the length at 50% maturity has increased by 149 mm for females and 76 mm for males.

Of the 44 females in the regressing phase, one (3% of regressing females) was identified as a skipped spawner and showed evidence of mass follicular atresia (reabsorbing skipped spawning) during the tertiary vitellogenic stage. This female had evidence of reaching sexual maturity in the past (e.g. thick ovarian wall; Lowerre-Barbieri et al., 2023; Figure 1f). Twenty-six males were identified as skipped spawners. These fish were assigned to the regenerating phase; males that were in the regenerating phase did not spawn in 2022 but had reached sexual maturity and showed evidence of past spawning (histological indicators included open lumens in the testicular lobules; Figure 2f). Skipped spawners represented 38% of the mature males.

3.2 | Fecundity

Fecundity samples were collected from 47 females varying in length from 446 to 566 mm and weight from 890 to 2183 g. No spawning capable females smaller than 446 mm were observed during the 3 years of sample collection, and the length range of fish sampled for fecundity represents the length range of spawning capable females in the population. Absolute fecundity varied from 1855 to 4423 ovarian follicles per individual, with a mean value of 2897 ovarian follicles per

TABLE 3 Predicted lengths and ages at 50% and 95% probability of maturity for female and male Yellowstone cutthroat trout sampled in Yellowstone Lake, Yellowstone National Park in 2022.

	Female		Male	
Probability of maturity	Length (mm)	Age (years)	Length (mm)	Age (years)
50%	479 (467–490)	6.6 (6.2–7.1)	406 (386–430)	5.4 (5.2–5.8)
95%	513 (499–547)	7.2 (6.8–8.1)	557 (517–626)	8.3 (7.5–10.9)

Note: Confidence intervals (95%) are shown in parentheses.

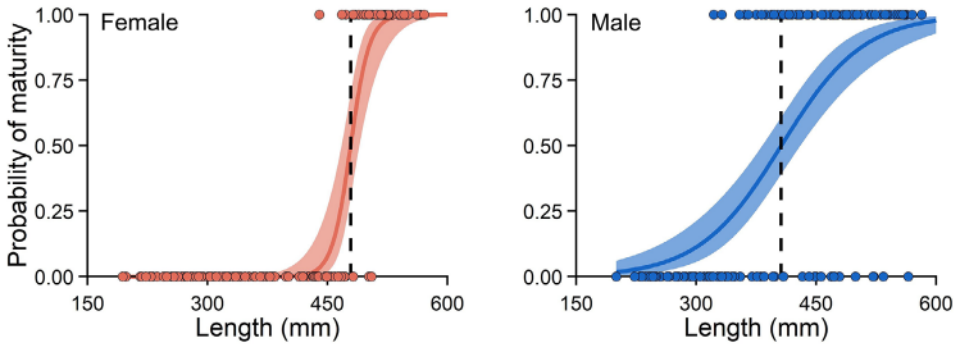

FIGURE 3 Results of a logistic regression showing the probability of maturity for female and male Yellowstone cutthroat trout in Yellowstone Lake as a function of length. The line indicates the predicted probability of maturity and the band indicates the 95% confidence interval. Each point indicates an individual fish sampled; points on the *x* axis indicate fish that were immature ($y = 0$) and points at $y = 1$ indicate fish that were mature. The vertical dashed line indicates the length at a 50% probability of maturity.

individual. Relative fecundity varied from 1264 to 2981 ovarian follicles/kg with a mean value of 2157 ovarian follicles/kg. There was a weak, positive relationship between fish length and fecundity ($p = 0.07$, $r = 0.27$; Figure 4a), and a negative relationship between fish length and relative fecundity ($p = 0.02$, $r = -0.34$; Figure 4b). Fish length explained little variation in absolute and relative fecundity, with R^2 values of 0.07 and 0.12, respectively. Ovarian follicle diameter varied from 3.95 to 6.30 mm, and the mean ovarian follicle diameter per individual varied from 4.73 to 5.27 mm. No relationship was detected between mean ovarian follicle diameter and fish length ($p = 0.47$, $r = 0.22$, $r^2 = 0.05$) or between mean ovarian follicle diameter and fecundity ($p = 0.53$, $r = -0.19$, $r^2 = 0.04$) (Figure 5).

Absolute fecundity has increased when compared to historical samples. Measurements of fecundity were collected in 1950–1951 ($n = 40$) and in 1984 ($n = 68$) from fish varying in length from 295 to 428 mm (Figure 4a; Kaeding & Koel, 2011). Mean absolute fecundity from historical samples was 1141 ovarian follicles per individual, and historical samples showed a stronger relationship between fish length and fecundity than contemporary samples ($p < 0.0001$, $r = 0.49$, $r^2 = 0.24$; Figure 4a; Kaeding & Koel, 2011). Mean absolute fecundity from the current study is 2.5 times greater than the mean absolute fecundity measured from historical samples, and reproductive females from the contemporary sample are larger in size than those in the historical sample.

4 | DISCUSSION

We observed plasticity in the reproductive characteristics of Yellowstone cutthroat trout in Yellowstone Lake, which were a result of an invasive species. For example, length at maturity and fecundity increased for Yellowstone cutthroat trout since the introduction of lake trout. The plasticity in reproductive demographic rates underscores the importance of using contemporary estimates for populations that have experienced changes in biotic or abiotic conditions.

Size at maturity has increased for female and male Yellowstone cutthroat trout as compared to historical data (Kaeding & Koel, 2011). It is likely that the reduction in the abundance of Yellowstone cutthroat trout due to predation by lake trout resulted in release from density dependence, allowing Yellowstone cutthroat trout to attain larger sizes. Allocating energy toward increased growth may benefit Yellowstone cutthroat trout because vulnerability to lake trout predation decreases at larger sizes, and predation of Yellowstone cutthroat trout >350 mm is rare (Ruzycki et al., 2003). Changes in size and age at maturity in fish populations have most often been documented in response to harvest, which typically causes a decline in the size at maturity due to size-selective harvest of large individuals (De Roos et al., 2006; Morita & Fukuwaka, 2007). However, release from density dependence can cause an increase in the size at maturity in fish populations because individuals are able to grow faster (Pollock, 1995). The relative changes in size and age at maturity may elucidate mechanisms causing changes in maturation, such as release from density dependence, temperature and fisheries-induced evolution (De Roos et al., 2006). Age structure was not quantified for Yellowstone cutthroat trout in Yellowstone Lake prior to 2010, so we are uncertain if age at maturity has increased, decreased or remained constant as the size at maturity changed. We hypothesize that release from density dependence as abundance declined caused faster individual growth of Yellowstone cutthroat trout, resulting in a larger size at maturity and stable or decreasing age at maturity (Morgan, 2008).

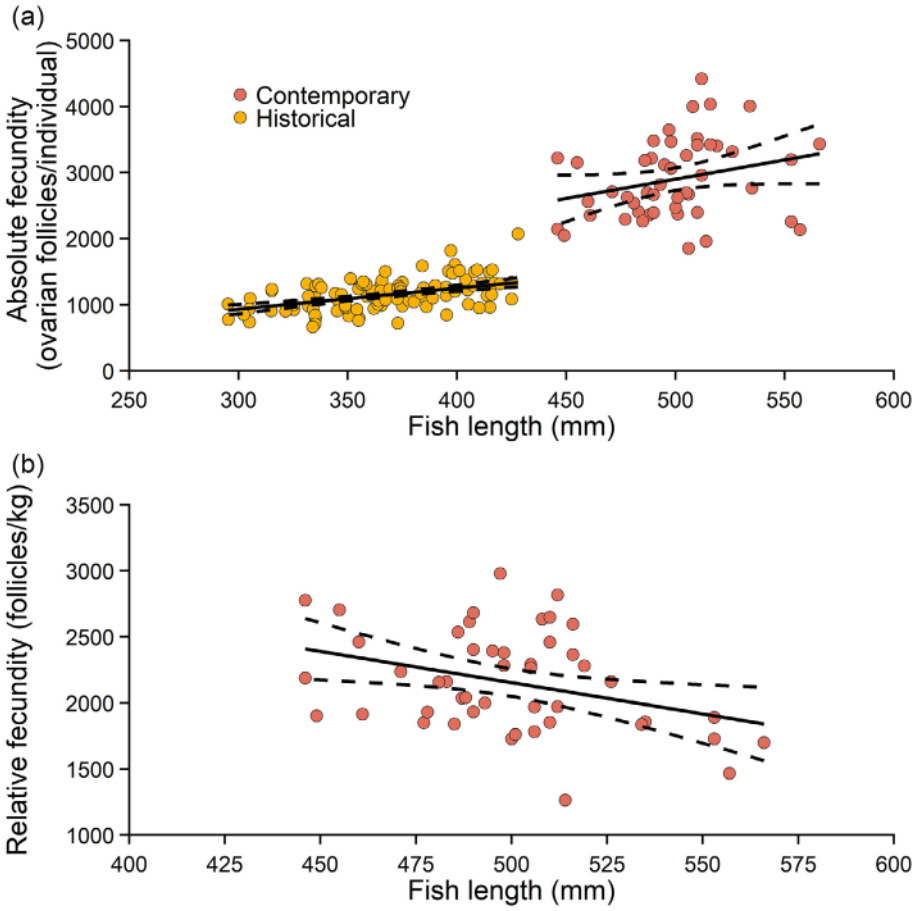

FIGURE 4 (a) Fecundity for Yellowstone cutthroat trout in Yellowstone Lake measured from fish collected in 1950, 1951 and 1984 (historical) and 2022–2024 (contemporary). The black lines indicate the slope and 95% confidence intervals of linear regressions using fish length to predict fecundity, fit separately to each sampling period. Historical data reproduced from Kaeding and Koel (2011). (b) Relative fecundity for Yellowstone cutthroat trout in Yellowstone Lake measured from fish collected in 2022–2024. The black lines indicate the slope and 95% confidence interval of a linear regression using fish length to predict relative fecundity.

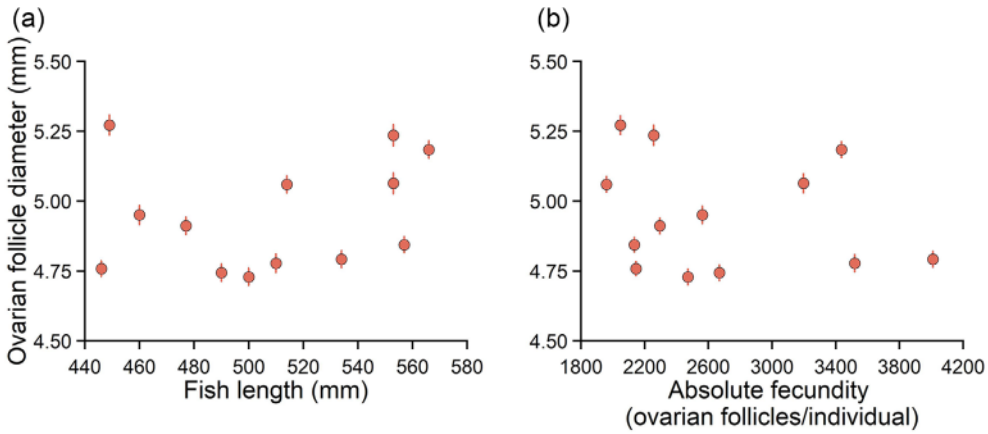

FIGURE 5 Mean ovarian follicle diameter from 13 Yellowstone cutthroat trout in Yellowstone Lake collected in 2022–2023 shown in relation to (a) fish length and (b) fecundity. The error bars indicate the standard error of ovarian follicle diameter.

However, the relationship between changes in size and age at maturity are unknown for this population, and we are uncertain how size and age at maturity may change as lake trout suppression continues in the future.

Skipped spawning, or non-annual spawning by sexually mature individuals that are physiologically capable of annual spawning, has been documented in numerous species of fish (Rideout et al., 2005). We documented skipped spawning in female (3%) and male Yellowstone cutthroat trout (38%) in 2022. Skipped spawning is often attributed to poor body condition or low food availability; skipped spawning may also be an adaptively favourable life-history strategy that may maximize lifetime reproductive success (Haraldstad et al., 2018; Jørgensen et al., 2006; Rideout et al., 2005; Rideout & Tomkiewicz, 2011). Skipped spawning is prevalent in some populations of anadromous, iteroparous fish, such as brown trout *Salmo trutta* and steelhead *Oncorhynchus mykiss*, in which 40–55% of mature fish have been observed skipped spawning (Copeland et al., 2019; Haraldstad et al., 2018). In this study, we observed skipped spawning in a single female; the mechanism underlying the skipped spawning was mass follicular atresia in the tertiary vitellogenic stage

(reabsorbing skipped spawning). Rates of mass follicular atresia in wild populations increase in response to low food availability, stress or poor environmental conditions (Corriero et al., 2021; Rideout et al., 2000). In Yellowstone Lake, mass follicular atresia was more common in females in their first reproductive cycle than in females that had spawned previously. These females were smaller (mean length = 408 mm, standard error = 21.5 mm) than the reabsorbing skipped spawner (517 mm length) and the regressing females that did successfully spawn (mean length = 518 mm, standard error = 4.8 mm). Smaller, younger females may be less likely to have sufficient energy reserves to undertake migration and spawning, resulting in mass follicular atresia during the first reproductive cycle (Jørgensen et al., 2006).

Skipped spawning has been studied more often in female fish than in male fish because of the assumption that recruitment is limited by egg production rather than sperm production and because assessing skipped spawning in males is difficult (Rideout & Tomkiewicz, 2011). However, skipped spawning in males has been observed in multiple fish species, including lake trout, humpback chub *Gila cypha* and brown trout (Haraldstad et al., 2018; Morbey & Shuter, 2013; Pearson et al., 2015). Smaller, younger males may have a higher rate of skipped spawning; the mean length of Yellowstone cutthroat trout male skip spawners was 445 mm (standard error = 10.1 mm), which is smaller than the mean length observed in other mature reproductive phases (mean length = 481 mm, standard error = 10.4 mm). Male bull trout *Salvelinus confluentus* increased their rate of skipped spawning in response to increasing population density, indicating that non-consecutive reproduction may be related to competition for food resources or competition among males for mates (Johnston & Post, 2009). Higher spawning return rates have been observed for females than for males in iteroparous, anadromous fish, including steelhead and taimen *Parahucho perryi* (Fukushima & Rand, 2021; Keefer et al., 2008), and lower return rates in males have been attributed to high energetic investment in spawning due to competition for females and nest defence (Fleming, 1998). In Yellowstone Lake, spawning runs of Yellowstone cutthroat trout have been documented with higher proportions of females than males (Ball & Cope, 1961; Kaeding & Koel, 2011), and historical work suggests skipped spawning was more common than spawning in consecutive years (Ball & Cope, 1961). In Yellowstone Lake, it is unlikely that resource limitations are inducing skipped spawning in males, so skipped spawning may be a response to high energetic investment in reproduction due to the cost of competition among males. Males may also spend more time at spawning sites than females and can participate in spawning events with more than one female (Blanchfield & Ridgway, 1997; Evans, 1994). However, the factors influencing the rate of skipped spawning in male Yellowstone cutthroat trout remain uncertain.

Individual absolute fecundity for Yellowstone cutthroat trout in Yellowstone Lake has increased when compared to historical samples (Kaeding & Koel, 2011). The increase in fecundity was most likely caused by the larger body size that females currently attain, however, relative fecundity may have changed over time as well. All individuals in the historical fecundity sample were smaller than the individuals in the contemporary sample (Kaeding & Koel, 2011). The increase in length at maturity provides additional evidence that reproductive Yellowstone cutthroat trout are larger than in the past. Individual fecundity was variable, and the relationship between fish length and fecundity was weak. Fecundity in fishes often increases with length, but this was not apparent in Yellowstone cutthroat trout in Yellowstone Lake. The weak relationship between length and fecundity may be due to the narrow range of fish lengths in the dataset. Females in the contemporary dataset varied from 446 to 566 mm in length. Strong relationships between length and fecundity have been identified for cutthroat trout, but these typically depend on the inclusion of individuals from multiple populations and a wider range of lengths (Downs et al., 1997; Meyer et al., 2003). High variation in fecundity has been observed in migratory populations of Yellowstone cutthroat trout from the South Fork of the Snake River, Idaho (Meyer et al., 2003) and westslope cutthroat trout *Oncorhynchus lewisi* from Hungry Horse Reservoir, Montana (Downs et al., 1997). In Yellowstone Lake, observed variability in individual growth (Koel et al., 2020) may contribute to the variation observed in absolute fecundity.

Ovarian follicle diameter was measured for a subset of individuals to determine if a relationship exists between egg size and fecundity for Yellowstone cutthroat trout in Yellowstone Lake. Fish may exhibit a trade-off between ovarian follicle size and fecundity (Jonsson & Jonsson, 1999). Specifically, fish may produce larger eggs to increase the survival rate for their offspring at the cost of producing fewer eggs (Duarte & Alcaraz, 1989). The relationship between ovarian follicle size and fecundity in salmonids may be related to growth conditions throughout the life of the individual as well as life-history characteristics (Beacham & Murray, 1993; Quinn et al., 2011). The lack of relationship between ovarian follicle size and fecundity in Yellowstone cutthroat trout in Yellowstone Lake indicates that although individual fecundity is variable, ovarian follicle size is consistent within the population and suggests that variation in reproductive investment in females is apparent in absolute fecundity rather than ovarian follicle size.

Comparison with historical data provided an opportunity to assess how reproductive metrics changed over time; however, limitations exist when comparing contemporary and historical studies. Kaeding and Koel (2011) used visual analysis to assign maturity to male and female Yellowstone cutthroat trout. Visual examination of gonadal tissue does not allow for the identification of regenerating males, which comprised 38% of mature males in the contemporary study. Additionally, identification of regressing and regenerating females using visual analysis can be difficult. Thus, the historical estimates of length at maturity are likely less precise than the contemporary estimates, which used histological analysis of gonadal tissue. Estimation of fecundity also had limitations for both the historical and contemporary study. Historical fecundity sampling was limited to two spawning tributaries sampled in 1984 and 1950–1951 (Kaeding & Koel, 2011). When conducting contemporary fecundity sampling, we attempted to collect spawning capable females from locations throughout Yellowstone Lake. However, due to the onset of spawning in the spring when Yellowstone Lake remains ice-covered, collection

of spawning capable females was logistically difficult. We were only able to consistently collect fecundity samples from a single location in the southeast arm of Yellowstone Lake, and fish collected in this location represent 89.3% of the contemporary fecundity samples. Thus, neither historical nor contemporary fecundity estimates are based on samples with even spatial distribution around the lake. Although Yellowstone Lake is large (340 km^2 surface area), Yellowstone cutthroat trout move throughout the lake (Ertel et al., 2017), and it is unlikely that fecundity would exhibit strong spatial differences within the population.

The results presented here provide contemporary descriptions of reproductive metrics of Yellowstone cutthroat trout in Yellowstone Lake. Comparison with historical data illustrates the plasticity in reproductive demographic parameters following lake trout invasion. Larger length at maturity and higher fecundity reflect the altered size structure of the population, which includes a higher proportion of large individuals (Koel et al., 2020). The results provide a unique example of how invasive species and their subsequent removal may alter the reproductive biology of native fish populations and will inform future conservation efforts for this iconic population.

AUTHOR CONTRIBUTIONS

Conceptualization: all authors. Methodology: all authors. Investigation: M.A.B. and M.A.H.W. Formal analysis: M.A.B. Writing – original draft preparation: M.A.B. and M.A.H.W. Writing – review and editing: all authors. Funding acquisition: C.S.G. and T.M.K.

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