Received: 5 July 2022 | Revised: 30 July 2023 | Accepted: 28 October 2023
DOI: 10.1002/aff2.141

AQUACULTURE, FISH and FISHERIES Open Access
WILEY

ORIGINAL ARTICLE

Spawning interactions between hatchery-reared and wild naturalized rainbow trout (*Oncorhynchus mykiss*, Walbaum, 1792) in high-altitude tropical streams, Kenya

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Funding information
Kenya Fisheries Service, Grant/Award Number: GOK/KeFS/2021

Abstract

Rainbow trout (*Oncorhynchus mykiss*) is among the most widely translocated fish species in the world. The current study evaluated the spawning interactions between naturalized and wild rainbow trout from two high-altitude second-order streams, in Kenya. Data on total length, weight, condition factor, fecundity, fertilization, egg diameter and fry survival were collected on spawning rainbow trout between March and December 2021. Length–weight relationship showed parabolic equations as $W = 0.0144L^{2.900}$, $W = 0.0069L^{3.0285}$ and $W = 0.00027L^{3.175}$ for wild fish stock, hatchery-reared and wild × hatchery-reared rainbow trout, respectively. Total fecundity differed significantly among the hatchery-reared, wild fish and the cross of the two ($p < 0.05$). The fertilization rate showed significant differences ($p < 0.05$), with no discernable difference observed between the hatchery-reared and crossed (wild × hatchery-reared). There was a positive correlation among the total fecundity to female egg weight, female body weight, fertilization rate and eyed egg survival in all the populations. Relative fecundity was significantly different among the three groups of fish ($p < 0.05$), but the differences between the hatchery and the crossed (wild × hatchery-reared) fish showed no significant differences. We recommend the use of crossed (wild × hatchery-reared) populations for fry production for use in aquaculture as they presented the highest fecundity and gave the best outcome of fry with high survival.

KEYWORDS
aquaculture, fecundity, interactions, naturalized rainbow trout, tropical streams

1 | INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss*) has received a lot of research attention due to its translocations to many parts of the world (Stanković et al., 2015). Endemic populations of rainbow trout are found in Pacific coastal watersheds from California to Alaska except for the Yukon River system. They were first introduced outside their native range in 1874. Since then their range has been extended from western North America to include waters on all continents except Antarctica and its populations have established in at least 53 of those countries' fields (Fausch, 2007; MacCrimmon, 1971).

Rainbow trout were first introduced in Kenya particularly in Mt. Kenya Rivers (River Gura) during the colonial period for sport fishing and other recreational needs in 1905. In the year 1910, trout

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were introduced into the Nairobi and Nanyuki Rivers. In the year 1920, trout were stocked in most rivers originating from Mt. Kenya. The naturalized population of rainbow trout later spread to all cold-water rivers in the Central and Western part of the country due to flooding (Ngugi & Green, 2007). The offsprings from these trout were later liberated in streams on the Southwestern slope of Mount Kenya (Van Someren, 1952). The naturalized population of rainbow trout were later translocated into cold-water streams in central and western regions of Kenya (Copley, 1940). By 1927, rainbow trout had been transplanted into the most suitable cold-water streams, particularly those around Mount Kenya and the Aberdare ranges for sport fishing and other recreational needs (Ngugi, 1999). Since then the species has been naturalized in many rivers of highland regions through hatchery programmes, enabling it to become integrated into these aquatic systems (Ngugi & Green, 2007). The success of translocation of the species can be ascribed to: the significance of rainbow trout as a valued game fish, the manipulation of life histories through selective breeding, rapid growth and suitability for hatchery cultivation and, consequent on those, its economic importance in food production (Woynarovich et al., 2011).

Hatcheries have played an important role in supporting the harvest and conservation of rainbow trout, and hatchery-reared fish now make up large proportions of the rainbow trout stock in most parts of the world (Crichigno & Cussac, 2019; Pulcini et al., 2014). Nevertheless, hatchery use has become increasingly controversial because of the potential for negative interactions between hatchery-reared (hatchery) and naturally spawned (wild) fish (Crichigno et al., 2021; Pinter et al., 2019; Scott et al., 2015). Fish stocks from the hatcheries when released to the wild can negatively affect wild fish through genetic contamination, predation, competition, induction of premature migration, mixed-stock exploitation problems, predator attraction and disease transmission (Anderson et al., 2020; Fast et al., 2015). Most intervening breeding programmes take place in established hatcheries which rely on fish broodstock from the wild. Currently, several private and public hatcheries have been established to enable the efficient cultivation of naturalized *O. mykiss* in Kenya. As a result, the viability and fitness of the wild population relative to hatchery fish may differ substantially due to adaptability in the wild and hatchery conditions. The population of rainbow trout from River Sagana is at risk because the migration of rainbow trout upstream to spawn each year has reduced due to issues of ecosystem degradation. High maximum temperatures (21.5°C) have also been registered in the river affecting the fish. Management of broodstock in the hatcheries can improve reproductive performance to produce fries which can be used in subsequent restocking activities, either in the River Sagana or its tributaries for the conservation of the species. Currently, there is inadequate knowledge on spawning behaviour and survival potential of naturalized hatchery-reared fish that are later released into the streams to maintain rainbow trout populations in Kenya. This study aims to evaluate spawning interactions between wild and hatchery-reared naturalized *O. mykiss* from the Rivers Sagana and Thego in Kenya to describe their performance and to explore the variables that could determine condition factors, fecundity and fertilization in addition to egg survival and size for improved performance under culture conditions.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out along the River Sagana, the streams and the Kiganjo National Trout Hatchery. Both the Sagana and Thego are second-order streams flowing from Mount Kenya (Figure 1). The sampling stations are labelled S1, S2 and S3 for River Sagana and T1, T2 and T3 for River Thego. The two streams originate from the Southeastern slopes of Mt. Kenya at an altitude of approximately 4000 m above sea level. The catchment stretches from latitude 0°13′S to 0°22′S to longitude 37°16′E to 37°03′E draining a watershed area of approximately 2256 km^2 (Ngugi & Green 2007).

2.2 | Experimental fish

The study was conducted between March and December 2021 where wild fish were collected from six sites along River Sagana (Figure 1). The fishing sessions were always carried out using landing nets to capture breeders in the pools or riffles and the runs, where the presence of adult specimens was noted. A total of 219 fish were collected, which included 104 males and 116 females. Fish were maintained in breeding ponds in Kiganjo Trout Hatchery, until the spawning phase. After ovulation and spawning, which were performed once, breeders were released back to the breeders' ponds no later than 24 h after their reproductive management. In some cases, fish were kept for several days in the hatchery ponds, to enable the conclusion of their maturation process and to proceed with the spawning activity. Using a ratio of three females to one male during propagation, wild male trout were bred with wild female trout and hatchery-grown female trout, whereas hatchery male trout were bred with hatchery female trout (Figure 2).

2.3 | Morphometric investigations and indices

2.3.1 | Determination of length–weigh relationship and condition factor

Length–weight relationship (LWR): The relationship between the length and weight of fish was analysed by measuring the fork length and wet weight of fish samples collected for the study at the time they were captured from the river and the hatchery, respectively. The statistical relationship between these parameters used the parabolic equation by Froese (2006) that takes the equation $W = a L^b$. The relationship between length and weight for mean samples was used to calculate Fulton's condition factor index (K) estimated using the equation $CF = (W/L^3) \times 100$, where W is the weight (g) and L is the total length (cm), a is the regression slope, and b is the y-intercept.

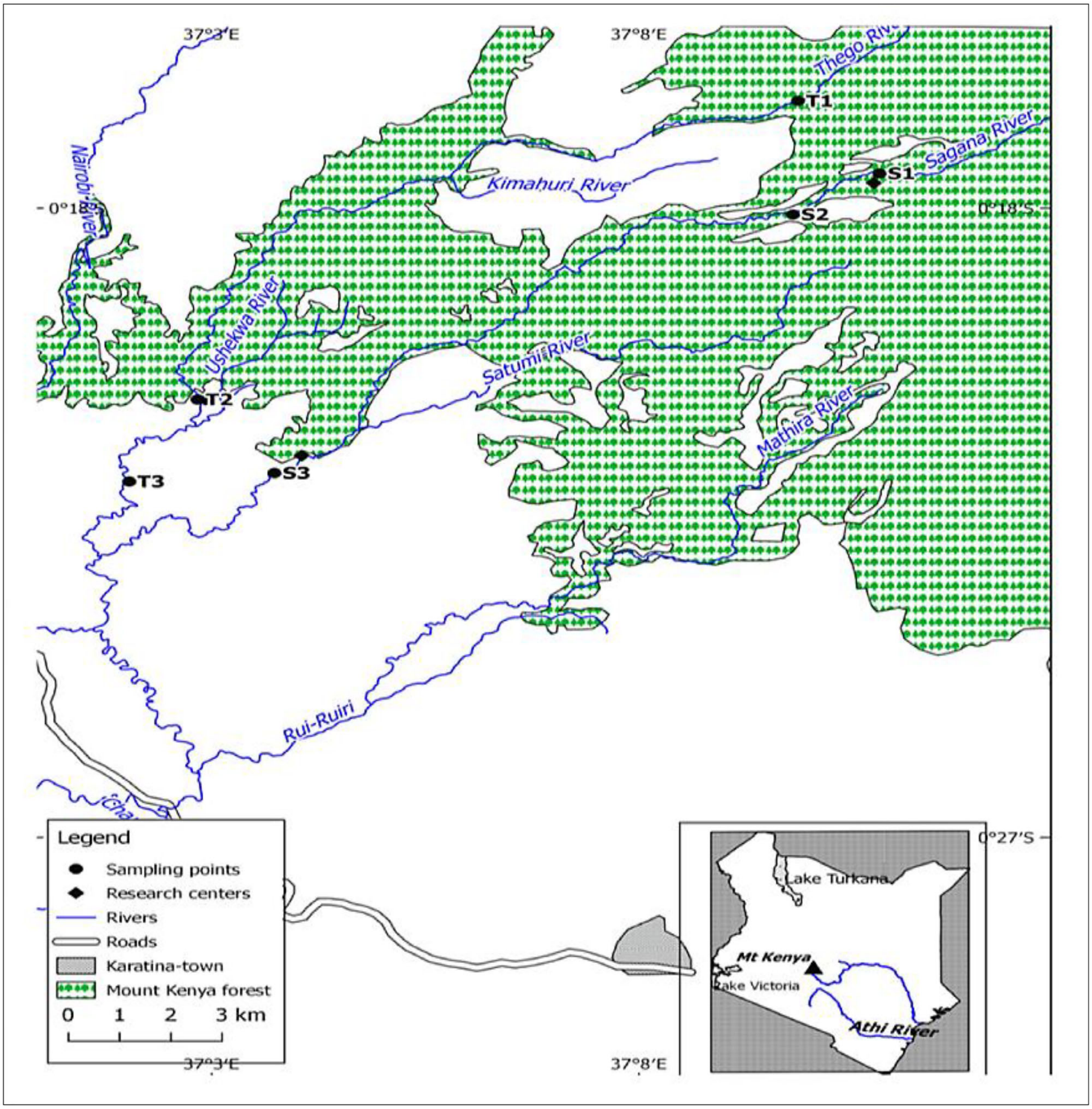

FIGURE 1 Location of the Sagana and Thego second-order streams flowing from the Southeastern slopes of Mount Kenya showing the study site as S1–S3 and T1–T3, respectively.

2.3.2 | Broodstock management and artificial propagation

Broodstock were monitored every week for the timing of ovulation and spermiation, before the spawning process. Females were palpated weekly to assess the distended abdomen in gravid breeders for timely detection of ovulation to ensure optimum egg quality during each spawning session. Before stripping, females and males were anaesthetized for 2–3 min with 40 ppm of benzocaine solution. The eggs of each female were collected in individual bowls. When egg batches presented impurities such as blood, broken eggs and traces of yolk, the ovarian fluid was drained over a strainer and washed using a 0.8% saline solution. Subsequently, they were returned to their bowl, and the eliminated fluid was replaced by Billard's sperm diluent (Billard, 1992) before being fertilized. Males were selected when milt had an appropriate external feature (intense white colour) and texture (semi-creamy and homogeneous). Fertilization was done with 3 mL of pooled semen obtained from three to four males. This number of males was used in each spawning session, which ranged from five to seven during each reproductive season. It should be mentioned that all males were spawned only once; they were not reused in successive spawning sessions and were from the same origin as females. After fertilization, the eggs were rinsed several times with incubation water to remove sperm remnants and then left for 15 min to facilitate egg hardening. The eggs

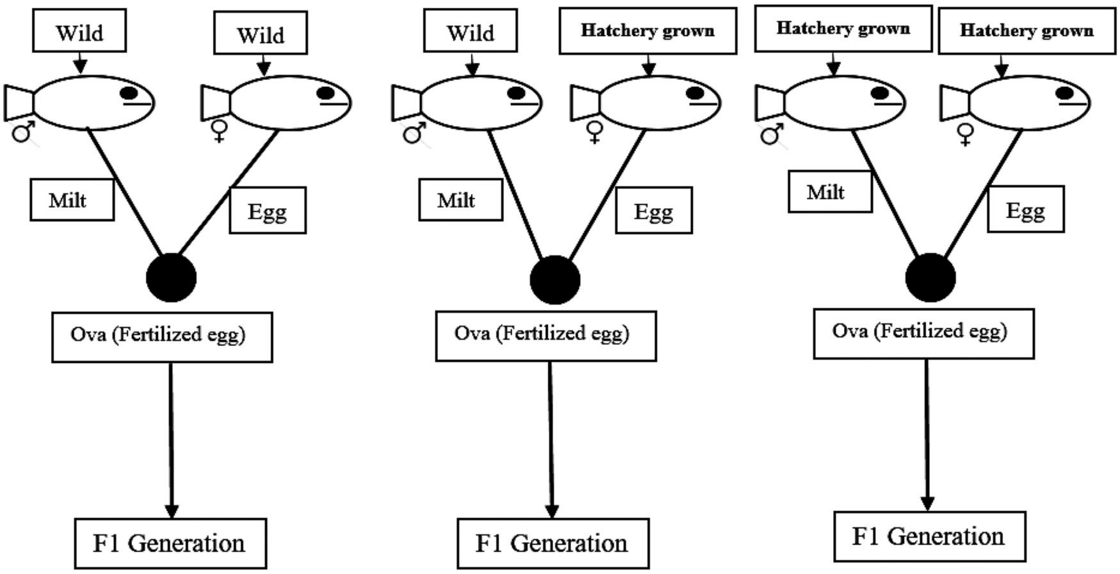

FIGURE 2 Schematic diagram showing how fish breeding was done in the hatchery.

of each female were individually incubated to allow the traceability of reproductive variables. The incubation process was performed in fibreglass punts with a spring water supply at a temperature of between 7 and 8°C and a constant flow of 20 L/min.

A wet method of fertilization was used in this trial; where fertilization is allowed to occur in a moist environment. The fertilized ova were placed in incubation trays within the incubation troughs. Silt-free clear cold water (7–8°C) flows through the troughs at a flow rate of 5 L/s and was maintained throughout the incubation period. The fish were held in a brooder pond, removed when ripe, and stripped. For the male, milt was collected from ripe males and eggs stripped from females. Once fertilization occurred, the eggs become fertilized ova ready for growth and maturation. Trout eggs were incubated until the “eyed” stage was reached, in hatching troughs, hatching and rearing troughs were 40–50 cm wide, 20 cm deep and up to about 4 m in length. Two layers of eggs were placed in screened trays supported 5 cm above the bottom, and water passed through the tray (3–4 L^{-min}). As the eggs hatched in approximately 4–14 weeks, the fry dropped through the mesh to a bottom trough. The time taken for hatching varied depending on water temperature, taking 100 days at 3.9°C and 21 days at 14.4°C. The dead (white) eggs were removed regularly to limit bacterial and fungal infections. Fungal infections were controlled using formalin (37% solution of formaldehyde) in the inflow water at 1:600 dilutions for 15 min daily, but not within 24 h of hatching. After hatching, the trays were removed and the trough water depth is kept shallow (8–10 cm) with a reduced flow until the fry reach the ‘swim-up’ stage, the yolk sac was absorbed, and active food searching began.

2.3.3 | Rearing of fry

Live feeds (*Daphnia*; which is zooplankton) were offered to wean the hatched free-swimming fry to juveniles for 2 weeks after which formulated feed of 50% protein was offered to the fry at a daily ration of 7% of the body weight. Survival for the ova, alevins and free-swimming fry was recorded as growth performance progressed. The feed used in the study were made into pellets by formulating the diet in the laboratory. The feed was formulated by mixing fish meal (80%), fish oils and grains to contain approximately 50% protein and 12%–15% fat. Vitamins (A, D and E), minerals (calcium, phosphorus and sodium) and a pigment to achieve pink flesh were used as additives to the feed. The feed was nutritionally balanced to encourage the growth of rainbow trout. Pellets of 1–2 mm were made using a pelletizer machine in the laboratory, and feeds were stored in airtight containers for use. Feeding commenced when fry were 15–25 mm long, based on published charts, and was related to temperature and fish size. As growth continued, dissolved oxygen was monitored and fish were moved to larger tanks to reduce density, as the fries grew to fingerlings.

2.4 | Biometry and reproductive traits

The body weight (g), total body length (cm) and condition factor (*K*) of each fish were recorded before gamete collection. At 100 accumulated thermal units (ATUs) of incubation, a sample of 50 eggs treated with a 20% acetic acid solution was taken from each incubation to record the fertilization rate (%). Total fecundity (number of eggs/female) and relative fecundity (number of eggs/kg of female) were also recorded. The number of eggs was estimated by the gravimetric method, using three pieces of approximately 0.02 g each from the anterior, medial and posterior positions of both ovarian lobes. The relative fecundity index was calculated as RF = F/BW, where F is absolute fecundity, and BW is total body weight (Patimar & Safari, 2010). At 200 ATUs, eyed egg survival (%) was determined in each incubation by subjecting eggs to a shock process to induce the mortality of the weak and infertile eggs. In contrast, viable eggs were shiny orange and translucent, with visible pigmented eyes. The sum of live and dead egg classes represented total fecundity per female. Fecundity and egg survival was quantified gravimetrically by weighing a sample of 500 eggs obtained from a counting paddle, in a digital balance, to determine the mean egg weight of each female. The mean egg weight was used to estimate the total egg number, by dividing the total egg weight recorded in each female by the mean egg weight value. Mean egg diameter (mm) was obtained by determining the number of eggs arranged on a 300 mm ruler, and then dividing the ruler length by the number of resulting eggs, as described by Von Bayer (1950).

2.5 | Statistical analysis

The biometric and reproductive data of breeders which were based on their common spawning period were pooled and considered a single stock for statistical analysis. Reproductive traits were modelled as a function of female breeder traits using general linear mixed models (GLMMs) to explore the relationships between female reproductive and other breeder traits to identify all the potential combinations that could be linked to specific female reproductive traits, such as total fecundity, relative fecundity, egg diameter, fertilization rate and eyed egg survival. Regression models were fitted to all independent variable combinations of biometric and reproductive traits before statistical analysis, and the variables were analysed for normality and homogeneity of variance using the Kolmogorov–Smirnov (K–S) and Levene's tests, respectively. One-way ANOVA was used to evaluate the statistical significance among the measured parameters at $p < 0.05$. Analysis of covariance was performed to test for significant differences in length–weight–length relationships (Yazıcıoğlu, 2016). The degree to which *b* differed from the three was tested by using earlier developed equations (Pauly, 1984). All statistical analyses were done using the MINITAB version 18 programme.

3 | RESULTS

3.1 | Biometric parameters between hatchery and wild rainbow trout brooders

During this study, meristic counts were taken from pooled samples of 32 fish each from the hatchery-reared, wild and crossed fish (wild × hatchery-reared). The fish traits were assessed for the relationship between body length and weight. The examined specimens exhibited total length and weights varying between 21.0–37.5 cm and 153.00–758.70, respectively. The largest fish were recorded from the crossed population that had a mean of 48.9 ± 7.5 cm. The smallest fish had a mean of 35.4 ± 5.0 cm and was recorded from the wild population. The weight of most fish caught was above 400 g. The biometric parameters for the fry of the naturalized rainbow trout population from River Sagana registered during the sampling seasons are provided in Table 1. The LWR was calculated by transforming the real data to the linear equation (log Wt = log a + b log TL). The values of a = −1.843, −2.159, −2.573 and b = 2.900, 3.029, 3.175 were better fitted at r^2 = 0.95, 0.95 and 0.96, respectively (Table 1).

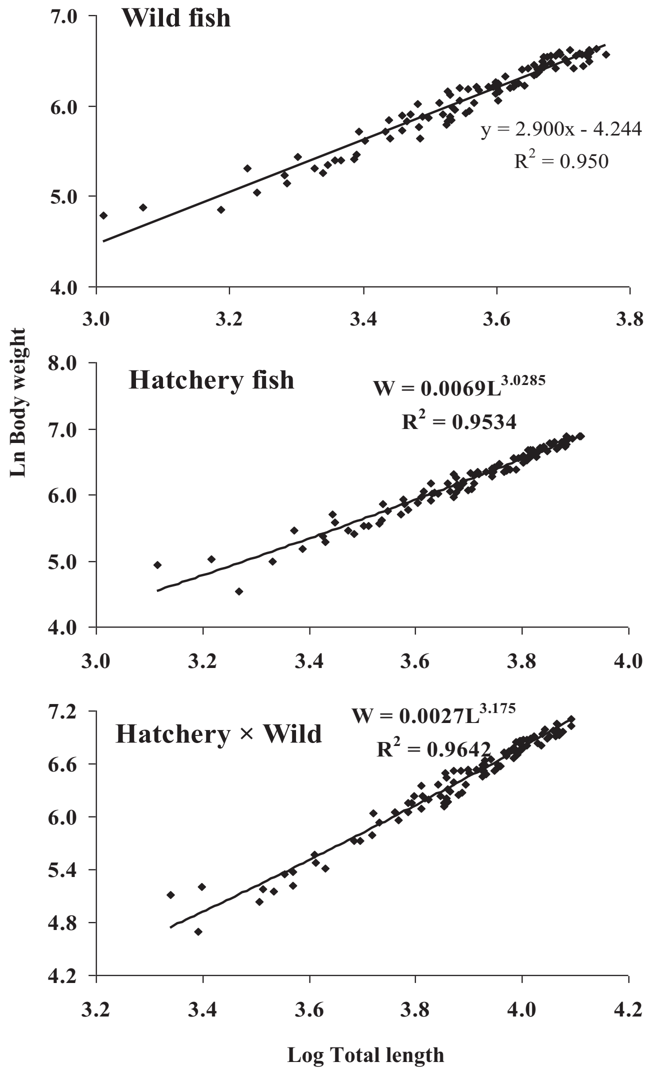

FIGURE 3 Length–weight relationship (LWR) of three different rainbow trout populations under hatchery conditions.

Then these values were transformed into parabolic form, and the equations obtained were $W = 0.0144L^{2.900}$, $W = 0.0069L^{3.0285}$ and $W = 0.00027L^{3.175}$, respectively (Figure 3). The graphs of the value of *a* in all show positive allometric growth. There were no significant differences in the LWR and r^2 in the male and female rainbow trout of the different groups ($p > 0.05$) (Table 1). All the *b* values were almost 3, indicating that *O. mykiss* has an isometric form of growth in weight. Furthermore, the r^2 value of LWR of *O. mykiss* was relatively high indicating a strong relationship between the length and weight of the three groups.

3.2 | Reproductive traits among hatchery, wild and crossed rainbow trout

The reproductive trait between the hatchery and wild rainbow trout brooders is shown in Table 1. Total fecundity of the broodstock is

TABLE 1 Biometric and reproductive parameters for the naturalized wild and hatchery-reared rainbow trout populations from River Sagana registered during the sampling seasons.

Parameters	Wild fish stock	Hatchery-reared	Wild × hatchery-reared
Female weight (g)	0.52 ± 0.04^a	0.91 ± 0.11^b	1.02 ± 0.15^c
Female total length (cm)	0.31 ± 0.04^a	0.45 ± 0.13^b	0.46 ± 0.12^b
Female condition factor (*K*)	1.2 ± 0.04^a	1.4 ± 0.04^a	1.4 ± 0.04^a
Male weight (g)	0.41 ± 0.02^a	0.40 ± 0.04^b	0.48 ± 0.04^c
Male total length (cm)	0.28 ± 0.04^a	0.40 ± 0.10^b	0.43 ± 0.11^b
Male condition factor (*K*)	1.1 ± 0.04^a	1.2 ± 0.04^a	1.2 ± 0.04^a
(R^2)	0.953^a	0.950^a	0.964^a
Survival of fry (%)	61.4 ± 10.2^a	84.5 ± 5.6^b	86.7 ± 5.9^b
Total fecundity (no. of eggs/female)	2134 ± 335^a	3245 ± 234^b	3745 ± 316^c
Relative fecundity (no. of eggs per/kg female)	6275 ± 876^a	7211 ± 925^b	7201 ± 1005^b
Fertilization rate (%)	82.2 ± 6.7^a	93.4 ± 4.5^b	94.9 ± 4.1^b
Egg diameter (mm)	5.1 ± 0.13^a	5.6 ± 0.12^b	5.9 ± 0.14^c
Egg weight (mg)	74.2 ± 3.4^a	81.3 ± 3.1^b	88.4 ± 2.7^c
Eyed egg survival, EES (%)	78.3 ± 5.6^a	87.4 ± 7.8^b	87.1 ± 6.4^b

Note: Values are Mean ± S.E. Means having the same letter in the same row are not significantly different at $p < 0.05$.

significantly different among the wild strain, hatchery-reared and the (wild × hatchery-reared) stock ($p < 0.05$). Total fecundity also increased with an increase in body weight and a similar trend was reported in egg weight (Table 1). Bivariate linear regression between the total fecundity against the female body weight and egg weight in the wild, hatchery reared and wild × hatchery naturalized rainbow trout from River Sagana are shown in Figure 4. Regression lines (solid lines) fitted by ordinary least squares are shown. There was a significant ($p < 0.05$) positive correlation between total fecundity and female body weight for only the wild × hatchery naturalized population, such correlations were not significant ($p > 0.05$) for the wild fish as well as hatchery-reared fish. There was a negative significant correlation between total fecundity and egg weight in wild fish, whereas for the wild × hatchery naturalized population, the relationship was positive and significant ($p < 0.05$). The total numbers of eggs spawned were not significantly ($p > 0.05$) affected by female body weight and egg weight for the hatchery-reared fish. Moreover, the fecundity of the brood-stock was consistent with the average weight of the brooders where the wild × hatchery-reared fish provided superior performance.

Relative fecundity was significantly different among the three groups of fish ($p < 0.05$) (Table 1) but the differences between the hatchery and wild × hatchery-reared fish showed no significant differences. Bivariate linear regression between the relative fecundity against female body weight and egg weight in wild, hatchery reared and wild × hatchery naturalized rainbow trout from River Sagana are shown in Figure 5. Regression lines were fitted by ordinary least squares. There were significant ($p < 0.05$) positive correlations between relative fecundity and female body weight for the hatchery-reared and wild × hatchery naturalized population. Relative fecundity was also positively correlated with egg weight in hatchery-reared and wild × hatchery naturalized rainbow trout fish ($p < 0.05$).

The fertilization rate showed significant differences among fish in the three experimental groups ($p < 0.05$), with no discernable difference observed between the hatchery and wild × hatchery-reared. Meanwhile, egg diameter showed consistent significant differences among fish in the three experimental fish groups ($p < 0.05$). Consistent with egg diameter is the egg weight which showed concomitant significant differences among the fish in the three cohorts. Eyed egg survival was lowest among the wild fish but showed no significant differences between the hatchery and wild × hatchery traits (Table 1). Bivariate relationships between LN eyed egg survival (%) against female body weight and egg weight in naturalized rainbow trout from River Sagana are shown in Figure 6. Survival of the eyed eggs was significantly affected positively by female body weight and egg weight in the hatchery-raised and wild × hatchery naturalized rainbow trout but in the wild stock.

The variance component for the spawning year was low, accounting for only between 0.34% and 14.82% of the total variance; therefore, this factor did not represent a significant effect (Wald *Z*-test: $p > 0.37$) to be considered a random factor in the GLMM analysis. Thus, the models were fitted considering a sample size of the full data set ($n = 133$).

4 | DISCUSSION

This study provides new information on how biometric and reproductive traits of rainbow trout are linked with fecundity and early life-history characteristics. Fecundity also referred to as total or absolute fecundity is concerned with the total number of oocytes possibly laid by an individual brood fish during its breeding period (Ganias & Lowerre-Barbieri, 2018). Meanwhile, relative fecundity is the

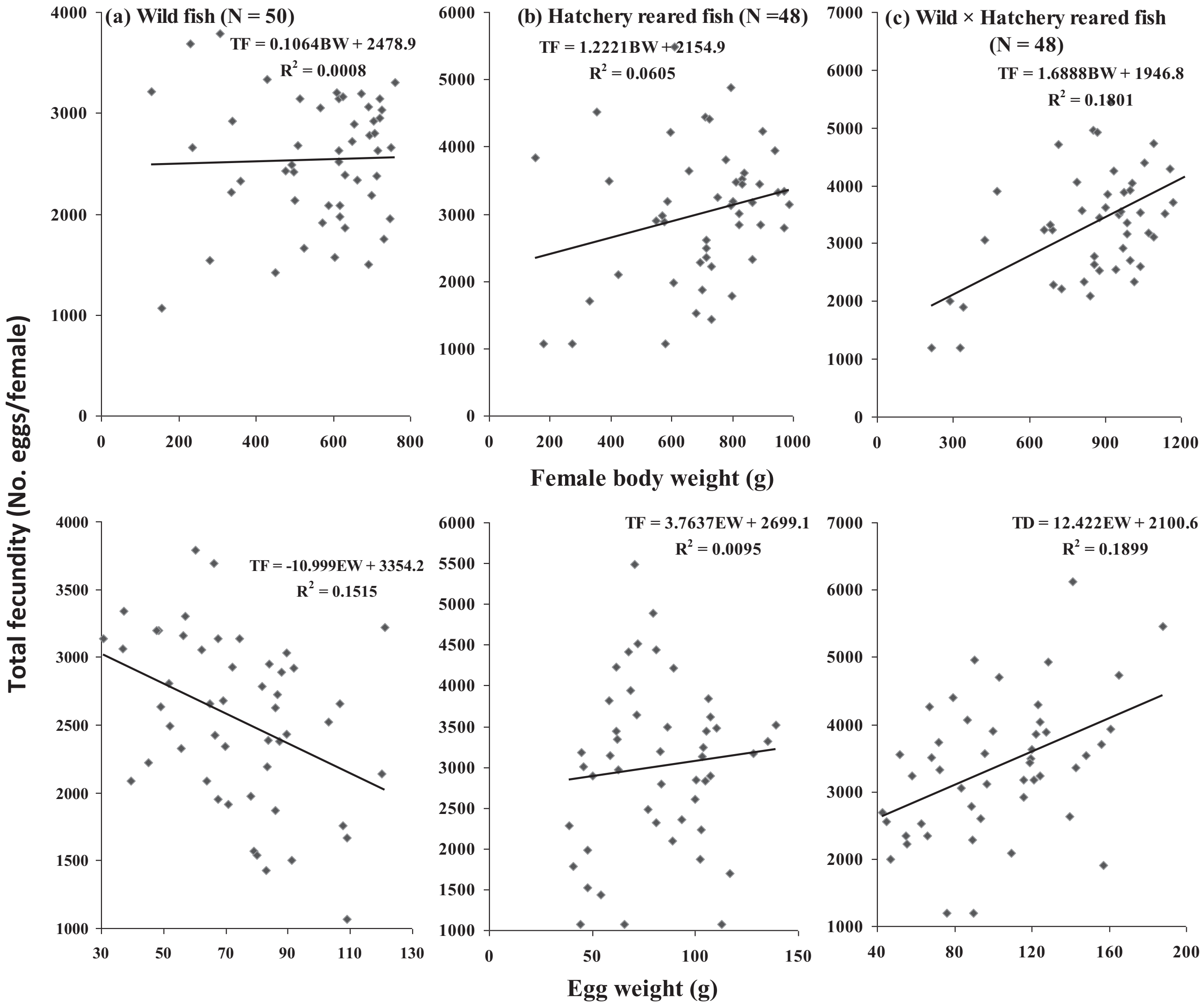

FIGURE 4 Bivariate linear regression between total fecundity (No. of eggs/female) against female body weight and egg weight (g) in (a) wild population, (b) hatchery reared population and (c) wild × hatchery reared population of rainbow trout.

number of mature oocytes in a female divided by the total weight of that female (Armstrong & Witthames, 2012). In this study, total and relative fecundity was largely affected by female body weight in the naturalized population, but not in the wild fish population. The total fecundity parameters were within the range (TF = 2170–3195) reported for naturalized rainbow trout populations in other regions of the world (Wetzlar, 1979). This has also been reported in species of trout (Alp et al., 2003) including rainbow trout (Chandra et al., 2018; Cakmak et al., 2019; Yousuf & Razak, 2022). This could be attributed to the fact that the naturalized population in the hatchery had access to more nutritious feeds and wasted less energy which positively influenced their fecundity compared to the wild stock (Miller et al. 1988). Nevertheless, negative relative fecundity has also been reported for body mass for the wild anadromous brown trout *Salmo trutta* (Rinaldo, 2020). The study established that the total and relative fecundity of the broodstock was highest for the fish where a cross was done between hatchery and wild rainbow trout. Hatchery-raised rainbow trout typically have a morphology that is quite distinct from their wild counterparts (Pulcini et al., 2014). However, some phenotypic traits associated with hatchery-raised genotypes and a captive-rearing environment can be lost following release into the wild (Fleming, 1994). Likely, the probability of the wild × hatchery fish acquiring superior reproductive traits is higher through consistent breeding programmes in the hatchery. Other reproductive parameters such as fertilization rate, egg diameter, egg weight and eyed egg survival showed significant differences among fish in the three experimental groups, with wild traits having inferior traits, whereas hatchery-raised and wild × hatchery raised fish showed similarity in their traits. Atlantic salmon (*Salmo salar*) offsprings of pure domestic or hybrid parentage tend to have lower survival than offspring of pure wild parentage (Skaala et al., 1996).

The LWR of the naturalized rainbow trout presented r^2 values greater than 0.95. This high coefficient of determination values obtained in the assessment of LWRs means a good quality of the

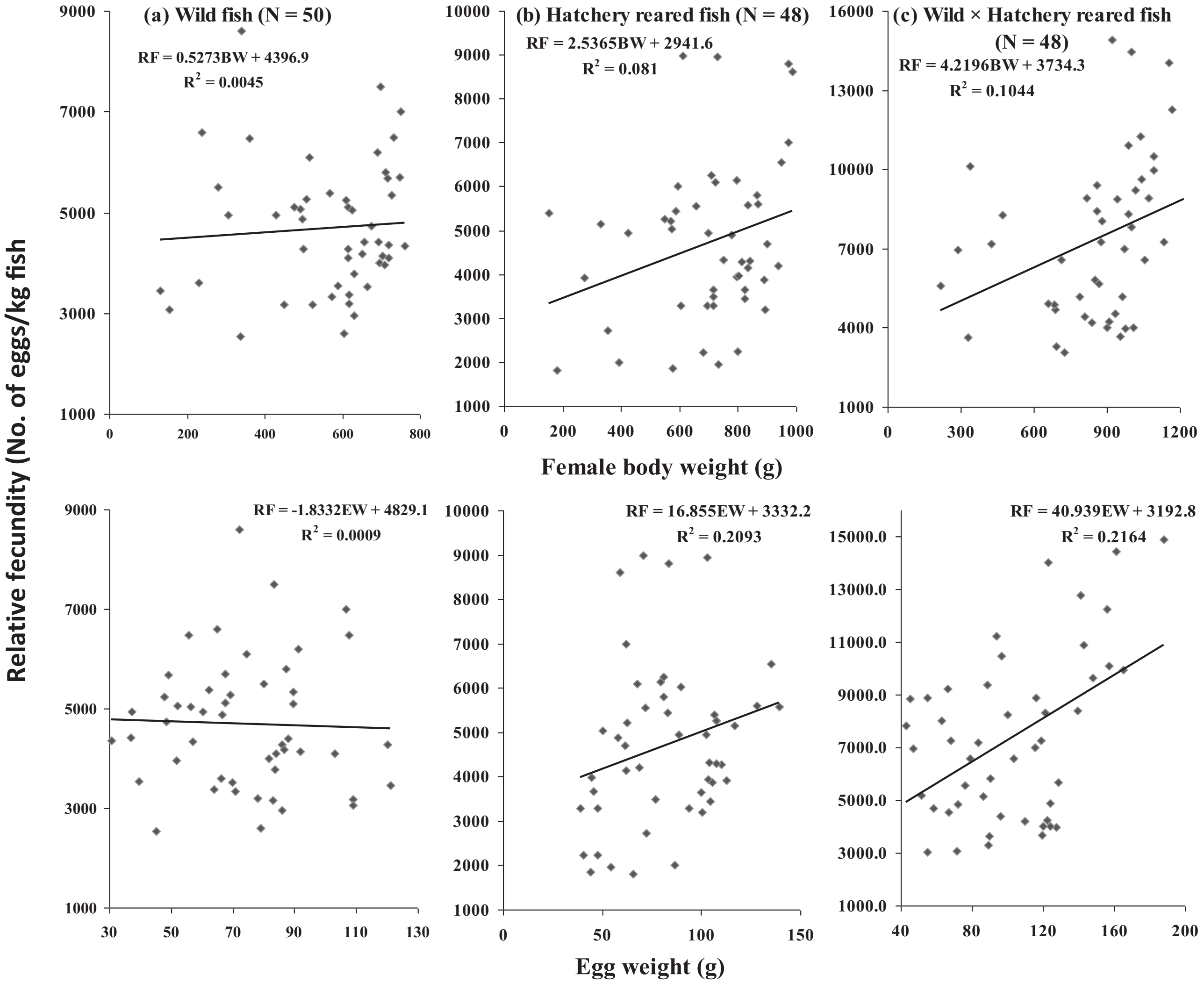

FIGURE 5 Bivariate linear regression between relative fecundity (no. of eggs/kg fish) against female body weight and egg weight (g) in (a) wild population, (b) hatchery reared population and (c) wild × hatchery reared population of rainbow trout in Sagana.

prediction of linear regression for the analysed fish species and suggested that extrapolation in future catches can be done in that geographical spot for this size range. A significant correlation was observed for all tested species. The negative allometric growth deduced for wild analysed fish suggested that these species have a relatively slow growth rate and tend to be thinner compared to hatchery-raised fish which had a positive allometry.

In this study, total fecundity was significantly affected by the interaction between female body weight and egg weight, whereas relative fecundity is affected by the combination of female body length and egg weight. In addition, a positive correlation was observed between female body weight and total fecundity, whereas an inverse association was recorded between relative fecundity and female body length. This trend indicates that the population analysed fits well with the general reproductive trade-off pattern between egg number and fish size described for the species (Neira & Fernandez, 1994). Likewise, mean total fecundity and relative fecundity fall within the range of, or were close to, data reported for other tropical riverine environments (Estay et al., 2004). However, regression equations output suggests that the reproductive performance of the River Sagana population has a more depleted fecundity in comparison either with naturalized populations or with cultured stocks of this species, suggesting that this population may have a particular reproductive performance pattern which has not been reported in other populations globally.

However, the fundamental fecundity-weight relationship for wild-caught trout could not explain the link between fecundity (total and relative) and body weight in the wild trout population in the current study. The presence of varying selective pressures in the wild (Hutchings & Ferguson, 1992; Knudsen et al., 2005) may be one of the factors responsible for the distortion of fecundity-weight relationships which suggest the presence of negative environmental factors that may distort the reproductive performance of wild population of rainbow trout. We observed massive human activities along the river ecotones, and therefore, their impacts on reproductive biology need further confirmation. The total fecundity was also affected by egg weight in the naturalized population which agrees with studies in other fish species

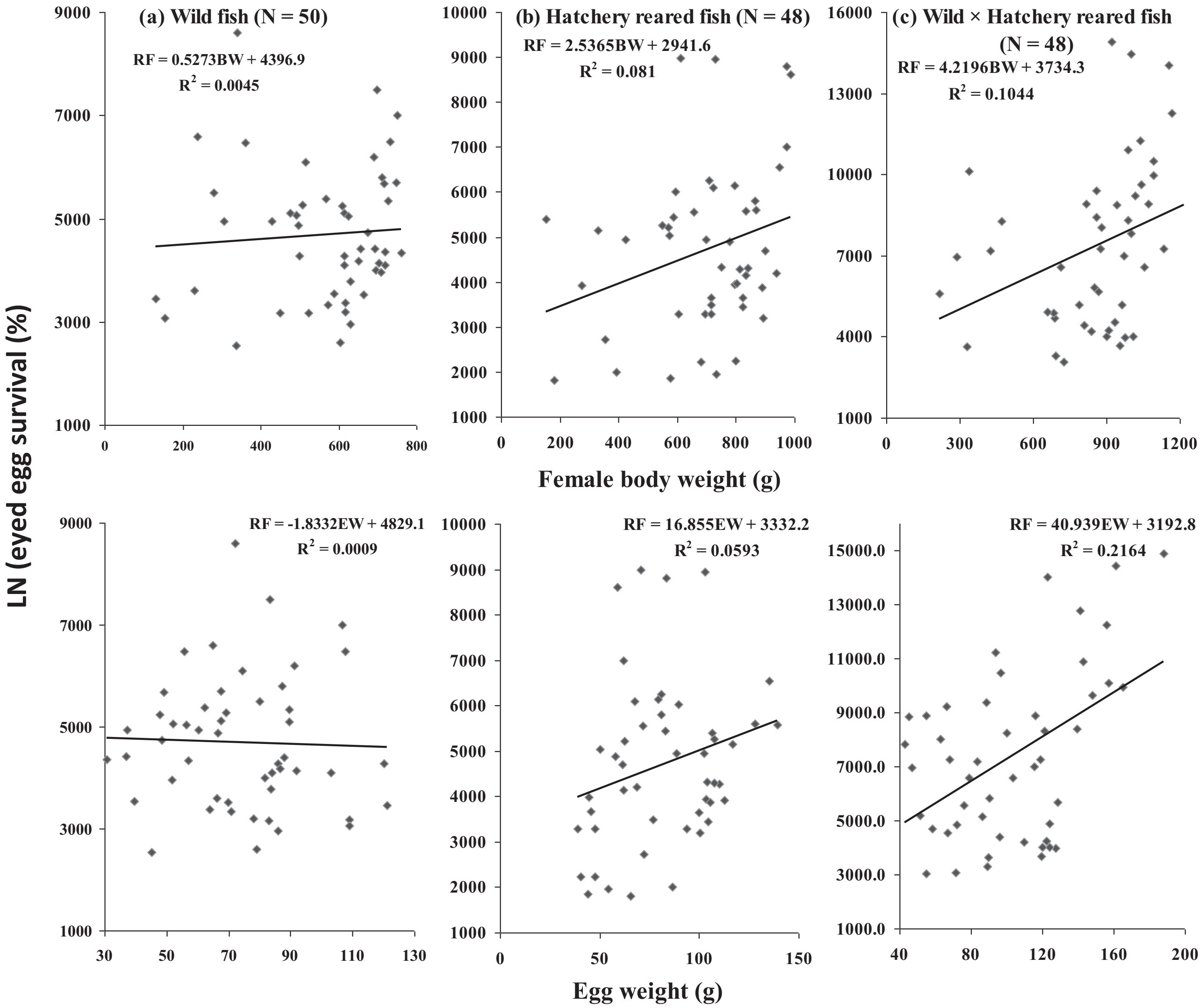

FIGURE 6 Bivariate linear regression between Natural logarith (LN) of eyed egg survival (%) against fertilization rates and relative fecundity (no. of eggs/kg fish) in (a) wild population, (b) hatchery reared population and (c) wild × hatchery reared population of rainbow trout in Sagana. Eyed egg survival data were log-transformed based on the equation $y = \text{LN}(y/(100^{-y}))$. Regression lines fitted by ordinary least-squares are shown.

such as the pool barb, *Puntius sophore* (Kant et al., 2016), zig-zag eels and *Mastacembelus armatus* (Rashid & Dobriyal, 2020). In many studies, the positive correlation between total fecundity and egg weight seems to be the rule, rather than the exception. A puzzling observation, however, was that the number of eggs spawned was negatively correlated with egg weight in wild fish populations.

The increased fecundity and reduced egg weight in wild fish populations could be linked to the possibility that if wild trout undergo ontogenetic habitat shifts in spawning habitat, egg size may be affected or even decreased according to abiotic conditions (Armstrong & Nislow, 2006; Winemiller & Rose, 1992). In addition, studies have reported trade-offs in some populations between fecundity and egg weight; where fish in some populations produced fewer but heavier eggs (Jonsson & Jonsson, 1999) and in others, females produced more eggs but of a smaller size (Jensen et al., 2019; Lobon-Cervia et al., 1997; Nicola & Almodóvar, 2002). The trade-offs occur due to trout growth as a function of environmental conditions (Braun et al., 2013). Second, the reproductive strategy could shift from one strategy for small individuals to another strategy for large individuals (Nevoux et al., 2019), which support the idea that small individuals fish populations have low fecundity compared to their large conspecifics and will strive to gain higher fitness on numerous small eggs and favourable environmental conditions. In this study, the hatchery-reared and naturalized hatchery × wild population appeared to invest in more eggs wiled the wild population appeared to invest their energy in larger egg sizes rather than numbers which have higher chances of survival. This may be a phenotype-response to the environment caused by resource availability and homogeneity (Rinaldo, 2020), which may be supported by the idea that egg size in trouts is partly plastic and may develop in response to maternal growth or spawning habitat (Nevoux et al., 2019).

Models for egg size reveal that this variable is affected by egg weight and also by body length or body weight, all with positive correlations. This result concurs with observations reported for other naturalized populations of rainbow trout, and with other salmonids, further supporting evidence that larger females of this species usually produce larger eggs than smaller females (Estay et al., 2021). The size of the eggs is generally linked to a greater change in the survival of the larvae. As already demonstrated in other fish species (Berkeley et al., 2004; Heinimaa & Heinimaa, 2004; Nazari et al., 2009; Trippel et al., 1997; Vallin & Nissling, 2000), the bigger larvae are hatched from larger eggs, spawned by larger females. Studies on the early life stage showed that a greater amount of yolk reserves are positively correlated with the survival of the larvae during the first days after hatching and with the growth rate (Mehault et al., 2010). Indeed the larger larvae may use a wider range of prey, and therefore, they have greater facility in finding food, wasting less energy (Miller et al., 1988).

The significant positive effect of fertilization rate and relative fecundity on embryo survival reported in this study is consistent with data available for cultured stocks of rainbow trout (Estay et al., 1994). However, the positive effect of relative fecundity on egg survival is an unexpected result, given that insignificant correlations between these variables have been found at least in cultured stocks of this species. This result suggests that rainbow trout females of River Sagana that yield large egg numbers have an increasing trend towards better egg viability. The survival of the eyed eggs was positively affected by female body weight and egg weight in the hatchery-reared and wild × hatchery naturalized rainbow trout as the size of the eggs in the hatchery was somewhat larger than egg size in the wild and naturally larger egg sizes can survive much longer (Leblanc et al., 2023). The survival of the eyed eggs at a higher body weight of the broodstock may be attributed to the maternal fitness which enables them to spawn healthier and larger eggs that survive much longer. In the wild, survival of the eyed stage may be limited by their interactions with environmental cues which lower reproductive fitness (Alix et al., 2020). Therefore, egg survival appears to be controlled by female body weight and egg size.

Most studies of interactions between captive-bred and wild fish have focused on hatchery populations stocked into areas containing native populations of the same species, particularly for the commonly artificially propagated species of the family *Salmonidae* (Einum & Fleming, 2001; Fleming & Petersson, 2001; Reisenbichler & Rubin, 1999; Waples et al., 2007). We found that biometric traits vary as a function of sex and that various types of relationship trends may explain the variation of reproductive traits across experimental units. It is hypothesized that fish length or weight is positively correlated with egg size and total fecundity, but relative fecundity showed an opposite trend. Our results support these expectations, as, in all experimental units analysed, the highest ranking models for total fecundity included the predictor variable female body weight, with a positive effect, combined with egg weight with a negative effect. In the case of relative fecundity, top-ranking models included negative significant relationships with female body length along with egg weight.

In the River Sagana population of rainbow trout, there was a positive correlation between female body weight and total fecundity and an inverse association with relative fecundity. Total fecundity increasing with body weight in naturalized females of rainbow trout is not an unexpected result, as this trend has been observed in several naturalized populations of the Unites States of America (Johnston et al., 2016). This trend is also following data reported in cultured strains of rainbow trout (Kanyilmaz et al., 2016). Therefore, our results suggest that, under natural conditions, the introduced populations of rainbow trout from the River Sagana follow a general reproductive trade-off pattern. However, when we use the regression equation obtained in our analysis to calculate expected total and relative fecundity at specific body length and weight, including the egg weight, the River Sagana population presents lower values for these reproductive parameters than other naturalized populations in the United States of America. For example, in Brule River and Pikes Creek, Wisconsin in the United States, Dubois et al. (1989) while studying females measuring 63.9 and 59.1 cm body length and with a mean egg weight of 63 mg reported relative fecundity values of 2195 and 2414, respectively; in contrast, our analyses indicate only 1680.0 and 1834.7 eggs/kg female, respectively, using the regression equation for relative fecundity. The same pattern is observed when the expected total fecundity as a function of female body weight is compared to the reproductive performance of cultured stocks.

Kanyilmaz et al. (2016) observed a mean number of 3483 and 5530 eggs/female for individuals with a body weight of 1720 g (mean egg weight = 64.4 mg) and 2784 g, respectively. In our case, the regression equation indicates a reduction in the total fecundity, as numbers of 3382.9 and 5073.3 eggs/female are expected, respectively, based on the regression equation for total fecundity. Thus, this result suggests depleted fecundity in the naturalized rainbow trout of River Sagana in comparison with naturalized populations in the United States or with cultured stocks of this species.

Available data indicate that genetics and environmental factors may affect the reproductive performance of fish (Izquierdo et al., 2001). Moreover, from the energy point of view, diet is highly relevant as fish reproduction usually demands a large energetic cost. In the case of salmonids, the energetic expenditures for all reproduction processes can reach up to 80% of the total body energy, depending on whether the species are iteroparous (resident) or semelparous (anadromous) (Fleming & Reynolds, 2004). It is plausible that differences in fecundity among populations of rainbow trout could be related to diet differences, especially if we consider that in the natural environment, this factor varies. Moreover, as the fecundity of rainbow trout is largely size-dependent (Johnston et al., 2016), it is expected that different growth rates among populations may yield different reproductive performances for this parameter.

Egg size showed a positive relationship with egg weight, and also with body length and body weight. Our regression equation predicts that females with a body length of 40 and 50 cm will present an egg size of 4.97 and 5.24 mm, respectively. The positive correlation between egg size and body length coincides with previous reports of other salmonids, such as brown trout (Estay et al., 2004) where egg size typically increases with female size, in a strong and consistent relationship. In naturalized rainbow trout from the Great Lakes in North America, a positive association between both female length and egg size has also been recorded (Dubois et al., 1989). Therefore, our result is following observations reported for different salmonids species in which larger females usually produce larger eggs.

Based on early egg survival analysis of the River Sagana population, we were able to estimate the level of embryo viability in a self-sustaining population of an introduced species. These data, collected under controlled conditions in a hatchery facility, have not been obtained for other naturalized rainbow trout populations in River Sagana. In the United States, this approach has been applied to analyse survival at the hatching stage in pure and hybrid crosses of naturalized strains (Negus, 1999). A specific comparison of our data on survival at the "eyed" egg stage with data published for some cultured stocks of rainbow trout reveals an interesting trend as survival performance in River Sagana is higher than that of the cultured populations (83.4%–88.8% vs. 63.2%–79.6%). Thus, these comparisons support the proposal that the River Sagana population has a higher survival performance in early development than cultured stocks.

Models relating eyed egg survival to reproductive traits indicate the effect of fertilization rate and relative fecundity, both with a positive effect on the response variable. Also of interest was the significant positive effect of relative fecundity on egg survival. Our result suggests that rainbow trout females in River Sagana yielding large egg numbers will have increasing egg viability. Moreover, given that in this population total fecundity was negatively correlated with egg size, this reduction trend in egg size would appear to be beneficial, rather than detrimental for egg survival. Existing evidence indicates that fecundity can vary as a function of female breeder growth rate, a process that can affect egg biometry. Furthermore, available evidence indicates that variation in the egg size-fecundity relationship may be affected by environmental factors, such as food availability (Jonsson et al., 1996). Thus, females reared in a food-rich environment will have higher fecundity than those inhabiting poor environments. Further research, for example, estimating the energy allocated to reproduction or somatic growth will be required to explore whether fecundity variations are associated with egg survival and whether weight found in the naturalized rainbow trout breeders of River Sagana could be related to their nutritional conditions. Although egg size has been related to embryo survival (Negus, 1999), no consistent relationship has been found. In our case, this reproductive parameter was mostly affected by the combination of fertilization rate and relative fecundity, which ranked highest in the model. This result is consistent with available data indicating that more than egg size, egg content, such as lipid and essential fatty acid content, seems to play an important role in embryo survival, both showing an ontogenetic trend (Johnston et al., 2016).

5 | CONCLUSION

The wild × hatchery-reared fish proved to have superior reproductive traits such as fertilization rate, egg diameter, egg weight, eyed egg survival and viability of the eggs compared with the fish from the wild and hatchery-reared populations, with wild fish having inferior traits. This study provides new information on how biometric and reproductive traits of rainbow trout are linked with fecundity and early life-history characteristics. The positive attributes in the wild × hatchery-reared populations can be adopted in the rainbow trout hatcheries for the production of fry or fingerlings for aquaculture activities and restocking of threatened rivers of rainbow trout in the Mount Kenya region.

AUTHOR CONTRIBUTIONS

Justus N. Njue: Conceptualization; data curation; formal analysis; investigation; methodology; resources; validation; visualization; writing—original draft; writing—review and editing. **Charles C. Ngugi**: Conceptualization; formal analysis; investigation; methodology; supervision; writing—original draft; writing—review and editing. **Mucai Muchiri**: Conceptualization; investigation; methodology; project administration; supervision; writing—original draft. **Mary A. Opiyo**: Data curation; methodology; validation; writing—original draft; writing—review and editing.

ACKNOWLEDGEMENTS

The authors sincerely thank the State Department of Fisheries, Aquaculture and Blue Economy through Kenya Fisheries Service (KeFS) and Kenya Marine and Fisheries Institute (KMFRI) for their contribution to this study. We especially thank the Masters Class lecturers at Karatina University for their visionary guidance towards the completion of this academic work. We appreciate the Wildlife Research and Training Institute (WRTI) for the design and training of research assistants, field data collection and analysis. We also thank the staff of Kiganjo Trout Hatchery for their assistance during the data collection for this study.

CONFLICT OF INTEREST STATEMENT

The authors state that there are no conflicts of interest to declare.

ETHICS STATEMENT

The study was conducted following the standard operating procedures (SOPs) of the Kenya Marine and Fisheries Research Institute (KMFRI) guidelines for handling animals registered with the National Commission for Science, Technology and Innovation (NACOSTI) registration number NACOSTI/2016/05/001. The SOPs comply with the Prevention of Cruelty to Animals Act 1962, CAP 360 (Revised 2012) of the laws of Kenya and the EU regulation (EC Directive 86/609/EEC).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/aff2.141.

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How to cite this article: Njue, J.N., Ngugi, C.C., Muchiri, M., & Opiyo, M.A. (2023) Spawning interactions between hatchery-reared and wild naturalized rainbow trout (*Oncorhynchus mykiss*, Walbaum, 1792) in high-altitude tropical streams, Kenya. *Aquaculture, Fish and Fisheries*, 1–13. https://doi.org/10.1002/aff2.141