

Efficacy of dopamine antagonists in stimulating ovulation and spermiation of Caspian kutum (*Rutilus frisii*) under controlled conditions

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Abstract

The present study compared the effectiveness of dopamine antagonists and commercial hormonal agents containing GnRH analogs combined with dopamine antagonists for inducing ovulation and spermiation in Caspian kutum (*Rutilus frisii*) spawners. For this purpose, females ($n = 15$ for each treatment) and males ($n = 10$ for each treatment) were treated with different agents as follows: (1) Ovulin (sGnRHa combined with domperidone), (2) Ovopel (mGnRHa combined with metoclopramide), (3) domperidone, (4) metoclopramide, and (5) 0.9% saline solution (control group). During the study, ovulation success, latency time, reproductive performance, egg quality, sperm quality parameters, seminal plasma characteristics, relationships between sperm quality parameters and seminal plasma characteristics, and the performance of the freshly hatched larvae were

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recorded. There were no differences in the latency time of ovulation, which ranged from 340 to 450 degree-hours (DH) in treated groups ($p > 0.05$). Ovulation and spermiation rates were similar ($p > 0.05$) after treatment with hormonal agents (Ovulin or Ovopel) and dopamine antagonists (domperidone or metoclopramide). The number of stripped oocytes ($116.1\text{--}137.3 \text{ g female}^{-1}$), fertilization success (86.9%–92.3%), and larvae survival rates (73.4%–81.1%) were comparable across all treatments ($p > 0.05$). However, MET-treated fish had the highest hatching rate at 90.8%, which was significantly higher than DOM (81.0%) and Ovopel (75.4%) treatments ($p < 0.05$). Moreover, lower larval malformation rates (1.1%–1.2%) were observed in domperidone and metoclopramide-treated groups ($p < 0.05$). The results of sperm volume, spermatozoa concentration, motility, and total sperm produced in dopamine antagonist-treated fish were within favorable ranges with no notable differences compared to the samples from the hormonal-treated groups ($p > 0.05$). The osmolality of seminal plasma was highest following application of hormonal treatments ($252.2\text{--}260.7 \text{ mOsmol L}^{-1}$), which did not significantly differ from those stimulated with the dopamine antagonists ($238.7\text{--}241.3 \text{ mOsmol L}^{-1}$) ($p > 0.05$). Together, these results demonstrated that both dopamine antagonists, domperidone and metoclopramide, were effective in inducing spawning of Caspian kutum without the addition of GnRHa. Therefore, their application can be suggested as efficient induction agents for controlled reproduction and conservation programs of Caspian kutum in hatchery centers.

KEYWORDS

broodstock management, cypriniformes, dopamine inhibition, offspring quality, reproduction, stimulation

1 | INTRODUCTION

Reproductive dysfunctions (absence of final maturation, ovulation, spermiation, spawning) are primary challenges in captive breeding of wild and captive fish, which are more prevalent in female spawners (Imanaga et al., 2014; Król et al., 2024). These problems arise from alterations in natural environmental cues, including temperature (TEMP), light, water currents, substrate, and social interactions, which directly influence the hypothalamic–pituitary–gonadal

(HPG) axis and trigger the neuroendocrine cascade necessary for normal gamete production (Mylonas et al., 2010; Wang et al., 2003; Zohar et al., 2010). Loss or disruption of these signals in captivity causes chronic stress, which leads to the inappropriate release of gonadotropin-releasing hormone (GnRH) and suppressed secretion of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) (Schreck, 2010). This endocrine disruption is intensified by strong dopaminergic inhibition, as dopamine generally suppresses GnRH-stimulated release of gonadotropins (Fontaine et al., 2013). Consequently, these disruptive processes described above could act as a physiological brake on final oocyte maturation (FOM) and ovulation in females, as well as spermiation in males (Cejko & Kucharczyk, 2015; Nowosad et al., 2014). Hormonal manipulation is often used to overcome the inhibitory endogenous mechanisms and initiate the reproductive process (Akbari Nargesi, Gorouhi, & Abbasi Mesrdashti, 2025; Akbari Nargesi, Gorouhi, Alavi, & Falahatkar, 2025; Kucharczyk et al., 2024). One general technique involves the direct administration of hormonal agents in the form of analogues (GnRHa). This approach is most effective in overcoming endocrine barriers in captive species when combined with a dopamine antagonist (Dufour et al., 2010). In this regard, hormonal manipulation is crucial for triggering normal gonadotropin release and effectively inducing FOM, ovulation, and spermiation in species that normally face reproductive challenges in captivity.

The Caspian kutum (*Rutilus frisii*) is a unique endemic fish species belonging to the family Leuciscidae found in the Caspian Sea (Eagderi et al., 2022). This species is anadromous, and its reproductive migration begins in early March and continues until late April (Akbari Nargesi et al., 2024). Because the Caspian kutum is an important prey for higher predators (e.g., sturgeons, seals) and a competitor/consumer among cyprinids and other benthic feeders, its population fluctuations can impact food webs and socio-ecological systems (Moëzzi et al., 2024). Consequently, it is vital to maintain river connectivity, protect spawning grounds, and align fishing practices with Caspian kutum aggregation patterns to ensure the stability of the Caspian Sea ecosystem. In recent years, the natural reproduction of Caspian kutum has been affected by river pollution and the destruction of spawning sites. To deal with this problem, one of the primary goals of the Iranian Fisheries Organization has been to focus on artificial reproduction and the restoration of stocks of this valuable species (Akbari Nargesi et al., 2024; Falahatkar et al., 2013). Under the restocking program, broodstock are caught at the river inlets (mainly from the Sepid-Rood River) during the reproductive migration and then transferred to hatchery centers. Following the controlled reproduction process, the larvae are raised in earthen ponds and released into rivers once they reach the fingerling stage. Therefore, implementing practical controlled reproduction strategies and restoring natural populations of Caspian kutum is crucial for maintaining the stability of the Caspian Sea ecosystem and ensuring the sustainability of the local fishing industry.

Hormonal induction has proven essential for reliably stimulating FOM, ovulation, and spermiation in Caspian kutum spawners under controlled hatchery conditions (Dorafshan & Heyrati, 2006; Falahatkar et al., 2013; Heyrati et al., 2007; Koohilal et al., 2017). Initially, artificial reproduction of the Caspian kutum was carried out using a two-stage injection of carp pituitary homogenate (CPH). This protocol involves an initial injection of females equal to ~10% of the total hormonal agent dose, followed by a secondary injection ~12 h later, delivering the remaining 90% of the dose (Abdollahy et al., 2011). Males were typically induced with half the hormonal dose given to females at the second injection time, or received no hormonal injection (Akbari Nargesi et al., 2024). Recent studies have demonstrated that a single-stage injection can achieve maximum fertilization rates (100%) (Heyrati et al., 2007), and as a result, this method has been used to induce spawning in this fish over the past few years. Like species of the family Cyprinidae, application of dopamine antagonists is crucial to overcome the natural inhibition of LH release by dopamine, thereby ensuring a synchronized and favorable spawning response for the Caspian kutum.

Previous studies have documented that the use of synthetic GnRHa, especially sGnRHa in combination with domperidone (DOM, commercial Ovaprim hormone), can achieve the highest spawning success rates, as well as improve sperm quality at latency periods typically lower than 24 h following injection at 12–13°C (Falahatkar et al., 2013). In contrast, independent treatments (without a dopamine antagonist administration) with various hormonal agents such as human chorionic gonadotropin (hCG) (Falahatkar et al., 2013), sGnRHa (Heyrati et al., 2007),

and LHRHa2 (Falahatkar et al., 2013), have shown low efficacy and spawning percentages. Recent studies have shown that catecholaminergic agents, such as Salbutamol and Olanzapine, can enhance the stimulating effects of GnRH α , while Metoprolol may inhibit these effects (Koochilal et al., 2017), which highlights the importance of selecting efficient treatments to optimize controlled reproduction outcomes. Considering the above-mentioned results, the key role of dopamine antagonists in the successful induction of Caspian kutum spawners is undeniable. A recent study has shown that the induction with a metoclopramide (MET) dopamine antagonist resulted in higher hatching rates and fewer deformed embryos in the crucian carp (*Carassius carassius*) compared with a commercial complex containing GnRH α and a dopamine antagonist (Ovopel) (Cejko & Kucharczyk, 2015). In this regard, application of a dopamine antagonist alone may also successfully stimulate final maturation in Caspian kutum spawners and lead to optimized reproductive manipulation under controlled conditions. This method has significant potential for evaluation as it could facilitate the creation of an effective and cost-efficient protocol for artificially reproducing Caspian kutum spawners in commercial hatchery centers.

The objective of this study was to compare the effectiveness of dopamine antagonists with commercial hormonal strategies for the induction and controlled reproduction of Caspian kutum spawners. To achieve this, two dopamine antagonists, DOM and MET, were compared with two commercial hormonal agents, Ovulin and Ovopel, for evaluation of ovulation and spermiation success in this species. The efficiency of each agent was evaluated in hatchery conditions with respect to latency time, oocyte quantity, egg and larval quality, sperm quantity and quality parameters, and relationships among spermatological parameters. Because the effect of dopamine antagonists alone (without combination with hormonal agents) has not yet been studied for controlled reproduction of Caspian kutum, exploring this approach could assist in developing a practical procedure for advanced conservation and restoration goals of this valuable species.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

This study was conducted in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (National Research Council, 2011).

2.2 | Fish origin and maintaining conditions

Caspian kutum spawners were captured in late March (at a water TEMP of 12°C) during the natural reproductive migration using a beach seine net in the Sepid-Rood River (Guilan, Iran). Immediately after capture, the fish were separated by sex (female: $n = 110$; male: $n = 97$) and transported to the hatchery center at the Shahid Ansari Teleost Fish Restocking and Genetic Conservation Center (Rasht, Guilan, Iran). The fish were kept in 4000 L tanks at a maximum density of 40 kg of fish per tank.

The broodstock were assessed for sexual maturity 24 h after arriving at the hatchery. Females with soft, enlarged bellies and males that released milt following gentle abdominal pressure were selected for experimental treatment. Females ($n = 75$, five groups) and males ($n = 50$, five groups) were randomly assigned to experimental groups (see Table 1), and each treatment fish (female: $n = 15$; male: $n = 10$) was placed into a separate 2000 L tank, then subjected to experimental treatment. Only healthy mature spawners with no visible body damage were used in the study. During the experiment, fish were kept in natural river water from the Sepid-Rood River source, with an average TEMP of $12.5 \pm 0.9^\circ\text{C}$ (the optimal TEMP for kutum spawning), and the photoperiod followed natural conditions (12L:12D). Before any experimental manipulation, fish were anesthetized in a solution of 200 mg L $^{-1}$ clove (*Syzygium aromaticum*) powder extract (Akbari Nargesi et al., 2024).

TABLE 1 Characteristics (mean $\pm$ SEM) of Caspian kutum (*Rutilus frisii*) spawners selected for reproduction under controlled conditions.

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Group of fish					
Spawners	I	II	III	IV	V
Females (n)	15	15	15	15	15
Body weight (g)	1003.3 $\pm$ 51.6	1026.7 $\pm$ 31.9	1088.3 $\pm$ 45.9	1063.3 $\pm$ 48.2	1011.7 $\pm$ 48.7
Males (n)	10	10	10	10	10
Body weight (g)	718.0 $\pm$ 50.1	695.5 $\pm$ 57.0	688.5 $\pm$ 61.8	705.0 $\pm$ 36.0	722.0 $\pm$ 34.5

2.3 | Experimental design

The experimental design schematic for this study is shown in Figure 1. After a 3-day acclimatization period, both female and male subjects received different doses of hormonal agents (Ovulin and Ovopel) and dopamine antagonists (DOM and MET) through a single injection (see Table 2). Each milliliter of Ovulin (Ningbo Fonland Biotech, Zhejiang, China) contains 20 μ g of salmon sGnRHa and 10 mg of DOM, which acts as a dopamine receptor antagonist. Each pellet of Ovopel (Unic-trade, Budapest, Hungary) contains $\sim$ 18–20 μ g of mammalian mGnRHa and 8–10 mg of MET, also a dopamine receptor antagonist (Horváth et al., 1997). All spawning agents and saline solution were injected intraperitoneally with a 2 mL syringe (22-gauge needle) at the base of the pectoral fin. The control group was injected with 0.9% NaCl. The water TEMP at the injection time was 12.6°C.

2.4 | Oocyte collection and management

Ovulation signs were first evaluated 16 h after the injection of all preparations, followed by assessments at 2-h intervals. Females that had not ovulated were monitored for potential ovulation up to 72 h after the injection. Oocytes were manually stripped using gentle massage and pressure on the abdomen of each female individually and stored in dry plastic containers. The number of ovulated females and their latency times were recorded for each treated group. Before fertilization, the eggs were kept at room TEMP for no more than 15 min.

2.5 | Sperm collection and management

Sperm was collected, and the total volume of sperm was determined using 5 mL plastic syringes calibrated at 0.1 mL. It should be noted that sperm collection was performed after signs of ovulation in females, ensuring fresh sperm were always available for fertilization in each treated group. Care was taken during sampling to prevent contamination of the sperm with urine, feces, blood, or mucus. Prior to fertilization and during analysis, fresh sperm were stored on ice at a TEMP of +4°C, with a maximum storage time of 1 h.

2.6 | Sperm motility, spermatocrit, and spermatozoa concentration

For motility analysis ($n = 2$ per male), approximately 10 μ L of sperm was activated with 100 μ L of hatchery water at the same TEMP and then immediately observed under a light microscope at 40 $\times$ magnification (Olympus Corporation, Tokyo, Japan). The time from activation until the cessation of movement was recorded as the duration of motility (motility duration) (Falahatkar et al., 2022).

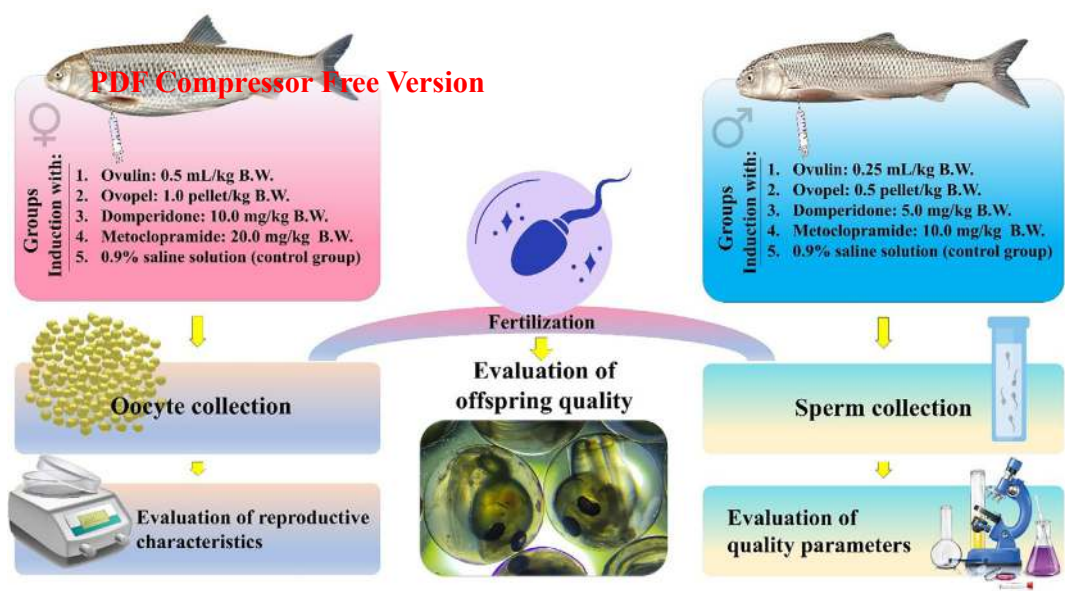


FIGURE 1 A representative schematic outlining the experimental design of this study. Each milliliter of Ovulin (Ningbo Fonland Biotech, Zhejiang, China) contains 20 µg of salmon GnRH analog and 10 mg of domperidone. Each pellet of Ovopel (Unic-trade, Budapest, Hungary) contains approximately 18–20 µg of mammalian GnRH analog and 8–10 mg of metoclopramide.

TABLE 2 Preparations used for stimulation of ovulation and spermatation in the Caspian kutum (*Rutilus frisii*) spawners under controlled conditions.

	Group of fish				
	I	II	III	IV	V
Selected preparations	0.9% NaCl	[(D-Arg6, Pro9NET)-sGnRH + domperidone]	[(D-Ala6, Pro9NET) mGnRH-a + Metoclopramide]	1-[3-(Piperidin-1-yl)propyl]-1,3-dihydro-2H-benzimidazol-2-one	4-Amino-5-chloro-N-(2-(diethylamino)ethyl)-2-methoxybenzamide
Commercial name	Control	Ovulin	Ovopel	Domperidone	Metoclopramide
Dose (b.w.)		0.5 mL kg ⁻¹	1.0 pellet kg ⁻¹	10.0 mg kg ⁻¹	20.0 mg kg ⁻¹
Availability	Samen (Iran)	Ningbo Fonland Biotech (China)	Unic-trade (Hungary)	PAS (Iran)	Daroupakhsh (Iran)

Note: Each milliliter of Ovulin contains 20 µg of salmon GnRH analog (sGnRH_a) and 10 mg of DOM, which acts as a dopamine receptor antagonist. One pellet of Ovopel typically contained 18 to 20 µg mammalian GnRH analogue (mGnRH_a) and 8 to 10 mg of the dopamine antagonist metoclopramide.

Spermatoctrit, which is the ratio of the volume of sperm to the total volume of milt multiplied by 100, was determined ($n = 2$ per male) according to Munkittrick and Moccia (1987). Briefly, sperm were centrifuged (Hawksley & Sons Ltd., Lancing, United Kingdom) for 7 min at 3500g. After centrifugation, spermatoctrit was calculated by measuring the length of the packed sperm cell layer and the total length of cells and seminal plasma with a ruler (accurate to 1.0 mm). The results were then expressed as a percentage.

Spermatozoa concentration ($\times 10^9 \text{ mL}^{-1}$) was determined using a hemocytometer counting chamber. Two replicates were considered for each sample. First, the sperm sample was diluted 10^4 -fold with 0.9% NaCl. Next, 10 μL of the diluted sperm was placed in the chamber. Spermatozoa cells were then counted, and the concentration was calculated according to Akbari Nargesi, Gorouhi, and Abbasi Mesrdashti (2025), Akbari Nargesi, Gorouhi, Alavi, and Falahatkar (2025), and Hatef et al. (2007).

Total sperm volume and spermatozoa concentration were used to assess sperm quantity (SQ, sperm volume kg^{-1} fish) and total sperm production (TSP) (Akbari Nargesi & Gorouhi, 2025).

2.7 | Artificial insemination

For the fertilization test, 100 g of stripped oocytes from each female was fertilized with pooled sperm collected from males of the same group to ensure consistent fertilization conditions. To estimate the number of oocytes g^{-1} , a 1.0 g sample of collected oocytes was weighed and counted in triplicate for each treatment, and the average (280 oocytes g^{-1}) was considered for the calculations related to the fertilization test. A similar concentration of spermatozoa was used to fertilize the oocytes in the fertilization test of different treatments, equating to $\sim 5.0 \times 10^9 \text{ mL}^{-1}$ spermatozoa cells per 100 g of oocytes (Akbari Nargesi et al., 2024).

For the fertilization test, sperm samples were added to oocytes, and the gametes were gently mixed before adding hatchery water (TEMP = 12.9, DO = 6.9, pH = 7.6) to activate the sperm and start the fertilization (dry fertilization method). The eggs were stirred for 5 min after adding hatchery water, and the water containing sperm was then completely drained. Egg samples were washed with hatchery water for an extra 45 min to eliminate stickiness. Afterward, eggs were kept motionless for 30 min to allow for water hardening. Following this, the fertilized eggs were transferred to Weiss incubators, maintaining a flow rate of 2.5 L min^{-1} .

After hatching (~ 96 – 98 DH after fertilization), the larvae from each treatment group were transferred to different 120.0 L horizontal flow incubators with a flow rate of 5.0 L min^{-1} , until the yolk sac was completely absorbed. Oxygen concentrations and pH levels were recorded twice daily, while TEMP measurements were taken every 2 h throughout the experiment. The average TEMP, dissolved oxygen level, and pH during the experimental period were $12.8 \pm 1.2^\circ\text{C}$, $6.7 \pm 0.3 \text{ mg L}^{-1}$, and 7.5 ± 0.2 , respectively.

2.8 | Reproductive characteristics

Reproductive traits were assessed, focusing on spawning performance and the quality parameters of eggs and larvae as follows (Abdissa et al., 2020; Akbari Nargesi, Gorouhi, & Abbasi Mesrdashti, 2025; Akbari Nargesi, Gorouhi, Alavi, & Falahatkar, 2025):

- Ovulation success (%) = $100 \times (\text{number of ovulated females} / \text{number injected females})$
- Latency period (DH) = number of days until ovulation $\times$ mean water TEMP from injection until ovulation
- Stripped oocyte amount (number of eggs fish^{-1}) = total weight of released eggs in g $\times$ the number of eggs g^{-1}
- Relative fecundity (number of eggs kg^{-1} fish) = Stripped oocyte amount / fish body weight (kg)
- Fertilization success (%) = $100 \times [(\text{total number of incubated eggs} - \text{number of estimated eggs with abnormal embryonic stage}) / \text{total number of incubated eggs}]$
- Embryonic survival rate until the eyed-egg stage (%) = $100 \times [(\text{total number of incubated eggs} - \text{total number of fungal-infected eggs at the eyed stage}) / \text{total number of incubated eggs}]$
- Hatching rate (%) = $100 \times (\text{number of estimated hatched larvae} / \text{total number of estimated fertilized eggs})$
- Survival up to absorbing yolk sac (%) = $100 \times (\text{total number of estimated larvae after absorbing yolk sac} / \text{total number of the estimated larvae after hatching})$

The fertilization rate was estimated using a dissecting microscope ~24 h after fertilization (at the blastula stage). The hatching rate was measured immediately after the larvae hatched. To assess fertilization and hatching rates, about 2.0 g of randomly collected eggs and larvae were counted in three aliquots, with ~600 eggs and larvae per sample, taken from each incubator. The percentage of abnormal larvae was calculated by comparing their numbers to the normal larvae in the aliquot samples. For this evaluation, noticeable morphological malformations, such as spinal cord, head, and caudal fin deformities, were identified at the larval stage and expressed as a percentage of the total number of abnormal larvae (Nowosad et al., 2018).

2.9 | Seminal plasma parameters

Seminal fluid was obtained by centrifuging sperm samples twice at 10,000g for 10 min. The supernatant from the first centrifugation was then centrifuged again to ensure the absence of spermatozoa cells in the seminal plasma. After this process, the supernatant was stored frozen at -80°C for further analysis.

Osmotic pressure and pH of the seminal plasma were measured using a Roebling osmometer (Messtechnik GmbH & Co., Berlin, Germany) and a WTW-537 pH meter (Xylem, Munich, Germany), respectively.

2.10 | Statistical analysis

The Chi-square test was employed to analyze the success rates of spawning and spermiation. The normality of data and the homogeneity of variances were confirmed by the Shapiro-Wilks and Levene's tests, respectively. The differences between the means of the groups for each variable were assessed using a one-way analysis of variance (ANOVA), followed by Tukey's post hoc test for comparing groups. A significance level of $p < 0.05$ was used to determine statistical significance. The analyses for percentage data were conducted using the arcsin-square root transformation. Following transformation, data were subjected to parametric analysis using a One-way nested ANOVA, and mean separations were conducted using Tukey's test. Pearson's linear correlation was applied to identify the relationship between sperm quality parameters and seminal plasma characteristics. The heatmap of correlation coefficients was created using the GraphPad Prism software (GraphPad Software Inc., California, USA). All analyses were conducted using SPSS software (version 23.0; IBM Corporation, Armonk, USA). Results for the experimental groups are reported as mean values with standard errors of the mean ($\pm$ SEM).

3 | RESULTS

3.1 | Ovulation rate and latency time

All female fish in the Ovulin, Ovopel, and MET treatments successfully ovulated after injection, resulting in a 100% ovulation success rate (Table 3). In the DOM treatment, only one fish did not ovulate after injection, leading to a spawning success rate of 93.3%. In the control group, one fish (1/15) ovulated, resulting in a spawning success rate of 6.7%. Consequently, there was no significant difference in spawning success rates between females treated with hormonal agents (Ovulin and Ovopel) and those treated with dopamine antagonists (DOM and MET) ($p > 0.05$). However, all treatments showed a significant difference when compared with the control group ($p < 0.05$).

The shortest latency time between injection and ovulation was observed when Ovulin (340.0 ± 45.0 DH) and Ovopel (400.0 ± 45.5 DH) were used as the spawning stimulating strategies. There were no differences between fish treated with hormonal agents and those treated with dopamine antagonists (latency time: $428.6\text{--}450.0$ DH) in the case of latency time after treatment applications ($p > 0.05$, Table 3).

TABLE 3 Results of the reproduction of Caspian kutum (*Rutilus frisii*) female spawners after treatments with different preparations.

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Selected parameters	Treatment groups				
	Control	Ovulin	Ovopel	Domperidone	Metoclopramide
Ovulation rate (%)	6.7	100	100	93.3	100
Latency time (degree-hour)	nd	340.0 ± 45.0	400.0 ± 45.5	428.6 ± 66.4	450.0 ± 60.4
Stripped oocyte amount (g female ⁻¹)	nd	137.3 ± 9.2	128.7 ± 9.4	116.1 ± 6.9	122.0 ± 9.5
Relative fecundity (× 10 ³)	nd	38.4 ± 1.6 ^a	34.0 ± 1.7 ^{ab}	32.1 ± 1.5 ^b	34.6 ± 1.6 ^{ab}

Note: Data in rows with different letters are statistically different ($p < 0.05$). All data are presented as mean ± SEM. Abbreviation: nd, values were not included in the comparison because of the small sample size ($n = 1$).

3.2 | Reproductive performance and offspring quality

There were no significant differences in the stripped oocyte amount, which ranged from 116.1 to 137.3 g female⁻¹, among treatment groups ($p > 0.05$, Table 3). However, the relative fecundity was higher in the group treated with Ovulin compared to the DOM treatment ($p < 0.05$). The Ovopel and MET treatments did not differ significantly from the Ovulin and DOM groups ($p > 0.05$, Table 3).

3.3 | Sperm quality parameters

Sperm was successfully collected from all males in both the experimental treatments and the control group, resulting in a 100% spermiation success rate. Consequently, no significant differences were noted in spermiation success ($p > 0.05$, Table 4).

The use of hormonal agents and dopamine antagonists positively influenced sperm volume and quantity, which were significantly higher in comparison to the control fish ($p < 0.05$). However, there were no significant effects of these treatments on total spermatozoa motility or motility duration ($p > 0.05$, Table 4).

Spermatoctrit values and sperm concentrations in the treated groups were the same as those of the control fish ($p > 0.05$, Table 4). Nevertheless, the application of hormonal agents and dopamine antagonists resulted in a significant ($p > 0.05$) increase in total sperm production, with the highest produced sperm in the treated groups (ranging from 131.0 to 135.4 × 10⁹) compared to the control group (81.3 × 10⁹).

3.4 | Seminal plasma parameters

Seminal plasma osmolality increased ($p < 0.05$) after Ovulin and Ovopel administrations (260.7 and 252.2 mOsmol L⁻¹, respectively), in comparison with the control group (225.7 mOsmol L⁻¹, Table 4). pH (range: 8.21–8.51) was at constant levels without remarkable differences between hormonal and non-hormonal treated fish ($p > 0.05$, Table 4).

3.5 | Relationships between sperm quality parameters and seminal plasma characteristics

In the control group, notable correlations were observed (Figure 2) between sperm volume and total sperm production ($r = 0.830$, $p < 0.01$), as well as between spermatoctrit value and both spermatozoa concentration ($r = 0.870$, $p < 0.01$) and total sperm production ($r = 0.640$, $p < 0.05$).

TABLE 4 Sperm quality parameters in Caspian Kutum, *Rutilus frisii* broodstock after treatments with different preparations ($n = 10$ for each treatment; mean $\pm$ SEM).

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Selected parameters	Treatment groups				
	Control	Ovulin	Ovopel	Domperidone	Metoclopramide
Spermated fish (%)	100	100	100	100	100
Sperm volume (mL)	4.1 $\pm$ 0.35 ^b	7.6 $\pm$ 0.54 ^a	6.9 $\pm$ 0.63 ^a	6.8 $\pm$ 0.73 ^a	7.1 $\pm$ 0.60 ^a
Sperm quantity (sperm volume kg ⁻¹ fish)	5.8 $\pm$ 0.45 ^b	11.0 $\pm$ 0.39 ^a	10.1 $\pm$ 0.27 ^a	9.5 $\pm$ 0.69 ^a	9.7 $\pm$ 0.52 ^a
Total spermatozoa motility (%)	90.0 $\pm$ 5.53	97.5 $\pm$ 2.50	92.5 $\pm$ 5.34	95.0 $\pm$ 5.00	95.0 $\pm$ 3.30
Motility duration (s)	51.2 $\pm$ 2.47	57.1 $\pm$ 4.43	52.5 $\pm$ 2.66	53.9 $\pm$ 2.59	55.6 $\pm$ 2.34
Spermatocrit (%)	49.0 $\pm$ 1.46	43.2 $\pm$ 2.04	44.3 $\pm$ 1.69	46.9 $\pm$ 1.80	45.5 $\pm$ 1.94
Sperm concentration ($\times 10^9$ mL ⁻¹)	19.8 $\pm$ 1.46	17.9 $\pm$ 1.01	18.9 $\pm$ 0.76	19.5 $\pm$ 0.67	18.8 $\pm$ 0.88
Total sperm produced ($\times 10^9$)	81.3 $\pm$ 9.7 ^b	135.4 $\pm$ 11.1 ^a	131.0 $\pm$ 12.5 ^a	132.1 $\pm$ 13.9 ^a	133.1 $\pm$ 13.4 ^a
pH	8.21 $\pm$ 0.07	8.51 $\pm$ 0.08	8.34 $\pm$ 0.11	8.37 $\pm$ 0.06	8.29 $\pm$ 0.08
Osmolality (mOsmol L ⁻¹)	225.7 $\pm$ 6.1 ^b	260.7 $\pm$ 7.1 ^a	252.2 $\pm$ 5.7 ^a	238.7 $\pm$ 3.7 ^{ab}	241.3 $\pm$ 7.7 ^{ab}

Note: Data in rows with different letters are statistically different ($p < 0.05$). All data are presented as mean $\pm$ SEM.

In the Ovulin-treated group, significant correlations were found among various parameters (Figure 2), specifically between body weight and both sperm volume ($r = 0.909$, $p < 0.01$) and total sperm production ($r = 0.827$, $p < 0.01$); sperm volume and total sperm production ($r = 0.760$, $p < 0.05$); spermatocrit value with both spermatozoa concentration ($r = 0.898$, $p < 0.01$) and sperm quantity ($r = 0.643$, $p < 0.05$); total sperm production with total sperm motility ($r = 0.677$, $p < 0.05$) and spermatocrit value ($r = 0.661$, $p < 0.05$); and between osmolality and motility duration ($r = 0.686$, $p < 0.05$).

In the Ovopel-treated group, significant correlations were observed among various parameters (Figure 2), including between body weight and sperm volume ($r = 0.946$, $p < 0.01$), total sperm production ($r = 0.830$, $p < 0.01$), and osmolality ($r = 0.774$, $p < 0.01$); sperm volume with sperm quantity ($r = 0.876$, $p < 0.01$), total sperm production ($r = 0.933$, $p < 0.01$), and osmolality ($r = 0.791$, $p < 0.01$); spermatocrit value and spermatozoa concentration ($r = 0.814$, $p < 0.01$); and between total sperm production and osmolality ($r = 0.818$, $p < 0.01$).

In the DOM-treated group, significant correlations (Figure 2) were observed between body weight and sperm volume ($r = 0.835$, $p < 0.01$); sperm volume and total sperm production ($r = 0.968$, $p < 0.01$); spermatocrit value and spermatozoa concentration ($r = 0.827$, $p < 0.01$); and between total sperm production and sperm quantity ($r = 0.829$, $p < 0.01$).

In the MET-treated group, significant correlations were observed among various parameters (Figure 2), particularly between body weight and both sperm volume ($r = 0.837$, $p < 0.01$) and total sperm production ($r = 0.759$, $p < 0.05$); between sperm volume and both sperm quantity ($r = 0.852$, $p < 0.01$) and total sperm production ($r = 0.903$, $p < 0.01$); between spermatocrit value and spermatozoa concentration ($r = 0.835$, $p < 0.01$); and between total sperm production and both sperm quantity ($r = 0.762$, $p < 0.05$) and pH ($r = 0.749$, $p < 0.05$).

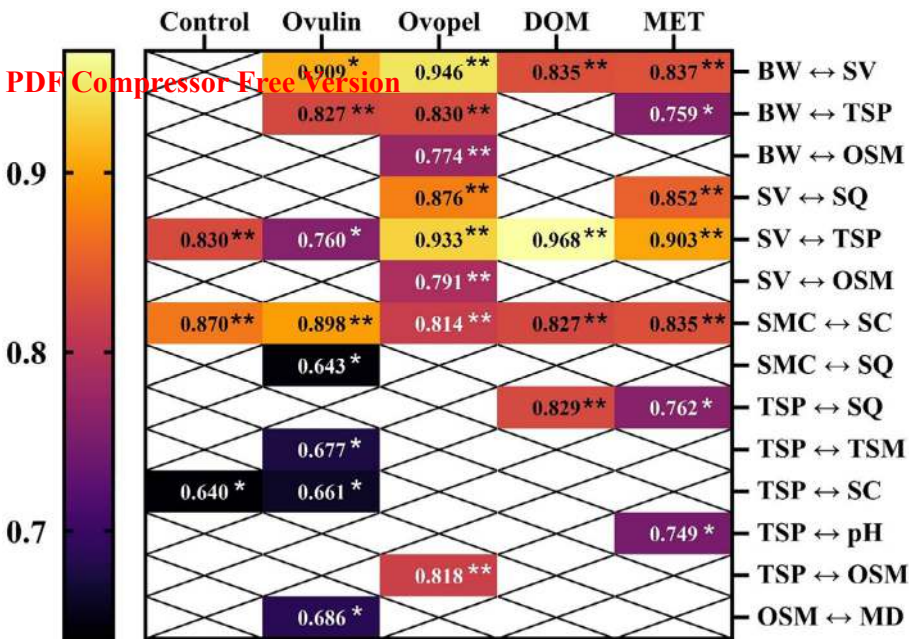


FIGURE 2 The relationship between sperm quality parameters of Caspian kutum (*Rutilus frisii*) following treatments with Ovulin, Ovopel, domperidone (DOM), and metoclopramide (MET). Statistically significant differences are marked with asterisks (Pearson's linear correlation; * $p < 0.05$; ** $p < 0.01$; $n = 10$). BW, body weight; MD, motility duration; OSM, osmolality; SC, spermatozoa concentration; SMC, spermatocrit; SQ, sperm quantity; SV, sperm volume; TSM, total sperm motility; TSP, total sperm production.

3.6 | Reproduction outcomes

The fertilization success rate in treated groups ranged from 86.9% to 92.3%, and applied treatments did not significantly affect fertilization success ($p > 0.05$; Figure 3a). The highest hatching rate was observed in MET-treated fish (90.8%), and showed a significant difference compared to DOM (81.0%) and Ovopel (75.4%) treatments ($p < 0.05$; Figure 3b). There was no influence of applied hormonal and dopamine antagonist treatments on the survival rate of larvae up to the eyed-egg stage ($p > 0.05$; Figure 3c). The rate of larval malformation in all treated groups was less than 3.0%, with the lowest observed rate of 1.1%–1.2% ($p < 0.05$) in the offspring of fish treated with dopamine antagonists (i.e., DOM and MET; Figure 3d).

4 | DISCUSSION

In the present study, the induction success and reproductive performance of Caspian kutum spawners were compared following injection of dopamine antagonists (MET and DOM) and hormonal agents (Ovulin and Ovopel) that contain dopamine antagonists. The results indicated that both MET and DOM alone can effectively induce ovulation and spermiation in this fish species. In most reproductive parameters, the results obtained in dopamine antagonist-treated fish were similar to those of fish treated with hormonal agents. These findings highlight, for the first time, the potential of dopamine antagonists to induce artificial reproduction of Caspian kutum during the spawning season.

In most cyprinid and their subfamily species, including Caspian kutum, it is impossible to obtain mature oocytes from female fish in hatchery conditions without hormonal stimulation (Król et al., 2024; Mylonas

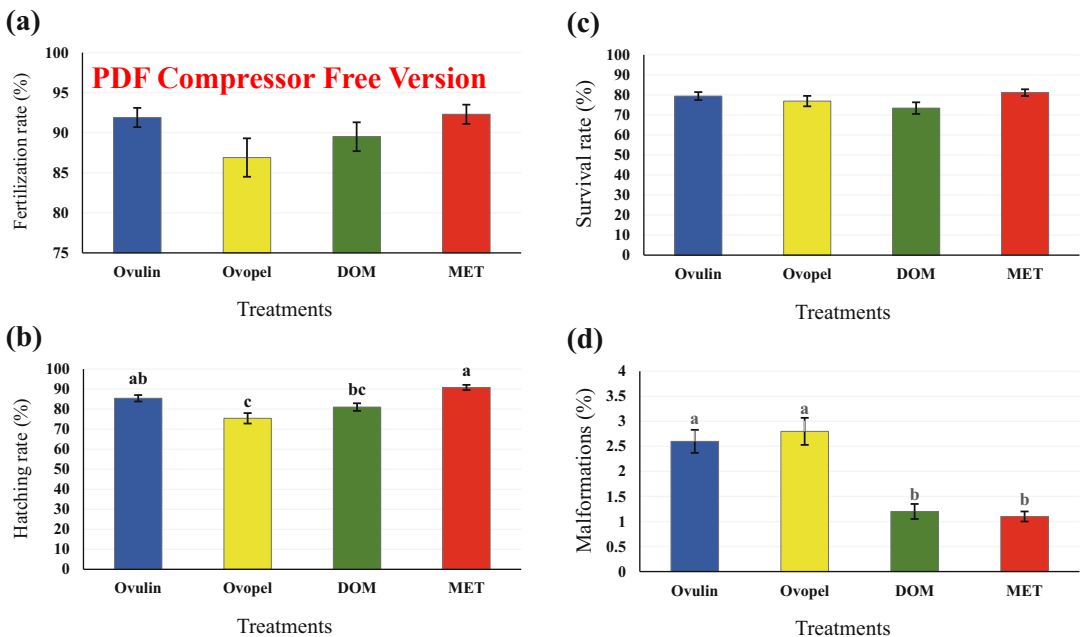


FIGURE 3 Results of the reproduction performance of Caspian kutum (*Rutilus frisii*) female spawners: Fertilization rate (a), hatching rate (b), survival of larvae (c), larvae malformations (d), following treatments with Ovulin, Ovopel, domperidone (DOM), and metoclopramide (MET). Different superscript letters indicate significant differences between experimental treatments (one-way ANOVA; $p < 0.05$; mean $\pm$ SEM; $n = 15$).

et al., 2010; Podhorec & Kouril, 2009). Consequently, artificial reproduction and hormonal induction are considered practical practices in the aquaculture operations of these fish species. Nowadays, various types of hormonal agents are used to induce artificial reproduction of Caspian kutum spawners. Ovaprim (sGnRH α + DOM) and CPH (carp pituitary homogenate), with ovulation rates of 100% (Akbari Nargesi et al., 2024; Falahatkar et al., 2013) and 60%–80% (Falahatkar et al., 2013; Heyrati et al., 2007), respectively, are the most successful applied hormonal treatments reported so far. Injections of other hormonal agents, including LhRH α 2, sGnRH α , hCG, and their combinations, have resulted in ovulation rates of zero (after hCG injection) up to 60% (after injection of LhRH α 2 in combination with hCG) (Falahatkar et al., 2013). It is noteworthy that injection of sGnRH α alone resulted in an ovulation rate of 20%–40% (Dorafshan & Heyrati, 2006; Falahatkar et al., 2013; Heyrati et al., 2007), while after injection in combination with the optimal dose of MET or DOM, the ovulation rate of 90% (Dorafshan & Heyrati, 2006) and 100% (Heyrati et al., 2007) has been reported, respectively. The reported results demonstrate the key role of dopamine antagonists in the successful induction of Caspian kutum females. Consistent with previous studies, this study recorded a maximum ovulation rate of 100% following the injection of sGnRH α + DOM (Ovulin) and mGnRH α + MET (Ovopel). Interestingly, the present results represent ovulation rates of 93.3% after treatment with MET and 100% after treatment with DOM, both of which were given alone without hormonal agents. Additionally, there were no significant differences in spawning success between females treated with hormonal agents (Ovulin and Ovopel) and those treated with dopamine antagonists alone (DOM and MET). Hence, in the stimulation of ovulation in Caspian kutum, MET and DOM injections are as effective as Ovulin and Ovopel. In line with the results of the present study, Cejko and Kucharczyk (2015) also found no differences in ovulation success after injecting Ovopel (80% success) or MET (90% success) to stimulate crucian carp females. In contrast, injecting MET alone did not induce ovulation in the tench *Tinca tinca* (Podhorec et al., 2012). Accordingly, different

species' responses to induction may be influenced by the maturation stage of spawners, form of spawning (single vs. multiple batch), and the type and dosage of injected dopamine antagonist, which can be considered in future studies. **PDF Compressor Free Version**

So far, no studies have investigated the potential of induction and artificial reproduction of Caspian kutum using only a dopamine antagonist. In the present study, following injection of dopamine antagonists (DOM and MET), no significant difference was observed in latency time and stripped oocyte amount compared to hormonal-induced female breeders. The results observed in the present study regarding latency time and stripped oocyte amount are within the range documented in previous studies on Caspian kutum after induction with various hormonal treatments (Dorafshan & Heyrati, 2006; Falahatkar et al., 2013; Heyrati et al., 2007; Koohilal et al., 2017). Cejko and Kucharczyk (2015) have reported similar results after inducing crucian carp with MET and Ovulin. In contrast, the highest relative fecundity observed in this study was recorded following Ovulin (sGnRH α + DOM) treatment, with a notable difference compared to the fish treated with DOM. The results of previous studies also indicate that the combination of sGnRH α + DOM achieves the highest level of relative fecundity in Caspian kutum compared to other hormonal treatment strategies (Falahatkar et al., 2013; Koohilal et al., 2017). It is worth noting that induction with MET yields similar results to the injection of Ovulin and Ovopel in terms of the relative fecundity of this fish, as has also been reported in crucian carp after induction with MET and Ovopel (Cejko & Kucharczyk, 2015). These results demonstrate the potential of dopamine antagonists to effectively stimulate Caspian kutum females, achieving comparable reproductive performance results to common hormonal treatments when administered at the appropriate type and dosage.

In successful artificial reproduction, the effectiveness of an induction strategy is evaluated not only by high ovulation and fecundity rates but also by the production of high-quality offspring in hatchery conditions (Brzuska, 2021; Mechaly et al., 2024). Therefore, monitoring egg and embryo quality parameters (i.e., fertilization success, hatching rate, larval survival, and malformations) can be a highly valuable approach for comparing the biological quality of eggs and embryos at different developmental stages. In this study, the quality parameters of eggs and embryos were evaluated after treatment with commercial hormonal agents and dopamine antagonists, aiming for a more accurate comparison of the quality of the produced offspring. The results showed that the treatments did not differ in terms of fertilization percentage and larval survival. Nevertheless, there are fewer larval deformities in the MET and DOM treatments than in the hormonally treated groups. Moreover, the MET group demonstrated better hatching success compared to the DOM and Ovopel-treated fish. In line with these results, Cejko and Kucharczyk (2015) also observed a better hatching rate and fewer abnormalities in the MET-induced crucian carp than Ovopel-treated fish. These results may arise from the fact that hormonal treatments cause over-ripening of mature oocytes, in addition to facilitating the final maturation of immature oocytes, thereby negatively affecting the quality of a part of the produced embryos. From a practical point of view, the administration of dopamine antagonists, particularly MET, could be a reliable method for inducing Caspian kutum, as this approach appears to achieve similar induction success as hormonal treatments but produces higher-quality offspring at a much lower cost. Future research should validate promising dopamine antagonist protocols (especially MET-focused) across different broodstock sources (wild vs. captive-bred), environments (ponds vs. tanks), and seasons.

Previous studies have not investigated the effectiveness of dopamine antagonists, as well as Ovopel, in inducing spermiation in Caspian kutum. In a recent study, Akbari Nargesi et al. (2024) investigated the effects of sGnRH α + DOM (Ovaprim) at doses of 0.2 and 0.4 mL kg⁻¹ on sperm quality, seminal plasma metabolites, and the fertilization ability of spermatozoa in Caspian kutum. This study concluded that sGnRH α + DOM at a dose of 0.2 mL kg⁻¹ can be a practical hormonal strategy for the induction of Caspian kutum male spawners. It has been well established that dopamine antagonists play an indirect role in the spermiation process and sperm hydration (Dufour et al., 2010). It was hypothesized that using a dopamine antagonist alone (without combination with a hormonal agent) may increase sperm production and improve the quality of the sperm produced in Caspian kutum. According to the results obtained, both dopamine antagonists, namely, DOM and MET, positively affect sperm volume, sperm quantity, and total sperm produced, which in all cases were comparable to the results obtained in

Ovulin and Ovopel-treated groups. These results indicate that dopamine antagonists could be promising agents for inducing spermiation in Caspian kutum. In line with present results, Cejko and Kucharczyk (2015) also suggested that injection of 20 mg of MET alone was as effective on sperm volume and sperm quantity as the stimulation of male crucian carp using a mGnRH α + MET (Ovopel). In the current study, an increase in osmotic pressure was observed in fish treated with DOM and MET, similar to the findings reported in crucian carp following MET induction (Cejko & Kucharczyk, 2015). Previous studies suggested that hormone-induced alterations in ion transport, hydration, and protein secretion could cause the rise in seminal plasma osmolality following hormonal treatment in fish (Alavi & Cosson, 2006; Dietrich et al., 2019). These changes are important for the maturation, protection, and storage of spermatozoa before either natural or artificial spawning. Additionally, it has been proven that low osmolality can indicate urine contamination or incomplete maturation (Cejko et al., 2015, 2018). Consequently, an increase in the osmotic pressure of Caspian kutum seminal plasma in DOM and MET-treated fish could indicate the positive effect of the inducing agent on the last phase of sperm maturation. Taken together, the findings of this study suggest that using dopamine antagonists can effectively stimulate the final sperm maturation in Caspian kutum. This approach has the potential to improve the controlled reproduction process of this species in hatchery centers.

Ovulin and Ovopel consistently demonstrate strong positive correlations across multiple sperm quality parameters, indicating a direct relationship between sperm production and quality after hormonal treatments. In addition, MET exhibits several similarities with Ovulin and Ovopel regarding the relationship between sperm production and quality. However, DOM shows fewer significant relationships, suggesting it has a limited effect on sperm quality parameters compared to MET. Accordingly, MET may be a more appropriate agent for inducing spermiation in Caspian kutum. Although for the sustainable development of an effective dopamine antagonist as an induction agent, it is essential to optimize its dose and explore more approaches, particularly the assessment of sex steroids and stress responses, together with sperm quality parameters.

5 | CONCLUSION

Our results indicate that dopamine antagonists (DOM and MET) can successfully induce ovulation and spermiation in Caspian kutum spawners under controlled conditions. In many cases, both DOM- and MET-treated fish demonstrated results comparable to those of hormonal treatments, highlighting their potential use as an inducing agent in the controlled reproduction process of this species. It is noteworthy that the injection of DOM and MET alone resulted in fewer deformed larvae compared to commercial hormonal treatments. Therefore, the injection of dopamine antagonists is recommended as a practical strategy for inducing Caspian kutum in hatchery centers to optimize the controlled reproduction process. In future studies, it could be interesting to optimize dopamine antagonist doses and examine their impact on sex steroids and the well-being of Caspian kutum and other fish species.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. **PDF Compressor Free Version**

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